
PHYSIOLOGY AND ECOLOGY TO INFORM CLIMATE ADAPTATION STRATEGIES FOR DESERT AMPHIBIANS

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Abstract.—Many amphibian populations in desert environments are likely at risk of decline or extirpation due to more extreme weather driven by climate change. Most desert species are explosive breeders, taking advantage of rainfall large enough to potentially support reproduction. Hence, management strategies for amphibians in general may not apply to anurans in temperate and subtropical deserts. Sustaining populations of desert amphibians is complex in that we are managing species assemblages that are relatively vulnerable to climate change, while planning for an environment that will change in ways that are not clear. However, we can improve the success of proactive management by integrating physiology with ecology within the context of a changing climate. Explicit consideration of physiology and ecology can target efficient habitat management actions such as identifying where to add shading or to extend hydroperiod. This approach can also improve outcomes when re-establishing native fauna by identifying life stages robust to release. Further we can improve our management of invasive species by explicit consideration of physiological constraints on dispersal capability of the invasive species to help plan where to fragment habitat connectivity to block invasions. To effectively plan for desert amphibians and climate change, science, management and policy makers must openly communicate about what we know, what information we lack, and the limitations of our knowledge. By explicitly including physiology in our management decisions we can refine our approach and more efficiently apply limited resources of time and money.

Key Words.—climate change; collaboration; desert ecology; ecological interactions; habitat enhancement; head-starting; landscape planning; vulnerability assessment

INTRODUCTION

Climate change threatens the persistence of desert amphibians with environmental change that is likely to outpace evolutionary change for at least some physiological tolerances (Lapola et al. 2009; Cayan et al. 2010; Stahlschmidt et al. 2011; Intergovernmental Panel on Climate Change [IPCC] 2014a,b). Consequently, organisms in these temperate and subtropical environments, such as the desert southwestern USA, may be forced to adapt, move, or face extinction. Unfortunately, weather conditions are much more variable than in the past (Cayan et al. 2010; Coumou and Rahmstorf 2012), and we do not have good estimates of the adaptive potential for most desert amphibian species. Humans can help buy time for desert species to adapt by providing limiting resources and improving habitat quality. Management strategies for dealing with climate change are referred to by agencies as Climate Adaptation Strategies (Mawdsley et al. 2009). By designing these strategies using physiology and ecology to target management actions to particular seasons or developmental stages, we can optimize efficient application of resources to mitigate climate change and other stressors. Work of this scale requires communication and the integration of cross-disciplinary expertise with management practices based

in science, including physiology, natural and life history, ecology, and evolution.

Climate change is causing already hot deserts to be more extreme, which is expected to cause physiological harm rather than benefitting most species (IPCC 2014b). Desert amphibians are especially vulnerable to climate change because the projected increased variability in the desert climate will cause drying faster than in most other systems (Seager 2007; Lapola et al. 2009; IPCC 2014a) and because of the complex ways these species interact with their environment. In addition, desert systems tend to have a relatively large number of endemic species with relatively small ranges (Brito et al. 2014) that tend to have populations vulnerable to declines caused by stochastic factors (e.g., genetic, demographic, environmental, and natural catastrophes; Frankham et al. 2004). Further, species found in already hot environments may have a lower tolerance to further warming than species from other locations (Duarte et al. 2012; IPCC 2014b), suggesting desert amphibians could be more vulnerable than non-desert species to climate change.

Globally, desert climates are changing faster than other non-polar terrestrial ecosystems (IPCC 2014b). All temperate and subtropical deserts (i.e., North American, South American, African, Asian, and Australian) are expected to become an average of 2–5° C (4–9° F)

hotter over the next century (based on RCP4.5 emissions scenarios for moderate to rapid economic growth; IPCC 2013). Additionally, many desert areas are likely to experience declines in humidity and declines in precipitation of up to 20% based on high emission scenarios (although areas projected to have increased precipitation include most Asian deserts, the Peruvian coast, parts of the Arabian Peninsula, and parts of India; Kunkel et al. 2013; IPCC 2013; IPCC 2014a). Within the southwestern deserts of the U.S., extremely hot days (maximum > 35° C) are projected to increase from 15–40 d currently to 40–160 d per year over the next century (Kunkel et al. 2013), and the decrease in water availability, including declines in soil moisture seen over the 20th Century, are expected to continue (Komuscu et al. 1998; Seager et al. 2007). Whereas spatiotemporal variability in desert weather patterns tends to be naturally high, punctuated by periods of extreme heat and aridity (Comrie and Broyles 2002; Augustine 2010), climate change is expected to exacerbate the amplitude and frequency of these severe weather patterns (Weiss and Overpeck 2005; Stahlschmidt et al. 2011; Petrie et al. 2014).

Changing climate and weather patterns are creating conditions that may exceed physiological constraints of the organisms, affecting their ecological relationships (Lapola et al. 2009; Cayan et al. 2010; Stahlschmidt et al. 2011; IPCC 2014a, b). Organisms consist of groups of differentiated cells driven by chemical reactions, and anything that influences chemical reactions (e.g., temperature and water availability) will influence physiological functions such as survival, reproduction, growth, and development (Amarasekare and Coutinho 2013). Understanding the physiology of a species and patterns in demographics and ecology can thus provide a mechanistic explanation of changes in population and community structure, abundances and distributions, and a prediction of how the species may be influenced by increased climate variability (Angilletta 2009; Kearney and Porter 2009). In general, organisms are thought to have relatively narrow physiological tolerances compared to the variability of the environment because of maintenance costs (Poertner and Farrell 2008). There is concern that desert environments are changing faster than organisms can adapt leading to species dealing with conditions outside of their tolerances (Lapola et al. 2009; Stahlschmidt et al. 2011; IPCC 2014b).

Many amphibians, including those in deserts, are relatively susceptible to dehydration and require surface water for reproduction (Duellman and Trueb 1986; Rome et al. 1992), meaning they are sensitive to changing water availability. Further, desert species that use isolated ephemeral waters for breeding, which often lack thermal refuges because they are shallow, are likely to be sensitive to changing water availability and temperature. The net results of these environmental chang-

es and cascading ecological consequences may lead to differential physiological and behavioral responses between species, affecting interactions (e.g., Martinez 2012; Tylianakis et al. 2008; Dell et al. 2014). These changes in interactions may then affect desert amphibian population persistence.

Natural resource managers need a suite of flexible climate adaptation strategies to improve the resiliency and persistence of amphibian populations inhabiting increasingly extreme desert environments. These strategies should be built on insights from physiology and ecological relationships to be successful. Here, I outline ways to use knowledge of physiological mechanisms to inform management actions. First, I draw from our current understanding of amphibian physiology and the desert environment to provide a mechanistic understanding of how climate change will affect individuals. Then I demonstrate how individual physiology can influence ecological relationships to affect populations and species interactions. Next, I recommend climate adaptation strategies informed by physiology and ecology for desert amphibians that incorporate evaluation and ranking of species vulnerability and proactive management actions such as habitat improvements. Last, I propose large-scale coordination and iterative communication to best plan and implement physiology- and ecology-informed conservation.

PATTERNS OF AMPHIBIAN TOLERANCE AND SENSITIVITY

General patterns.—Amphibian tolerance to changing climatic conditions is controlled by a combination of evolutionary history, demographics of the species, and behavior. A number of desert amphibian species are endemics with small ranges. Species with small ranges tend to be adapted to narrow ecological niches; consequently, they tend to have narrower thermal tolerances than species with larger ranges (Slatyer et al. 2013), putting them on average at a higher extinction risk from climate change and other chance events (Pimm et al. 1988; Purvis et al. 2000; Payne and Finnegan 2007; Slatyer et al. 2013). Demographic attributes such as late maturity, fewer eggs, or slower growth also tend to make individuals and populations more vulnerable to stressors like climate change than individuals with early maturity, faster growth, and larger clutch sizes (McKinney 1997; Purvis et al. 2000). So, for example, we would expect species such as the Relict Leopard Frog (*Lithobates onca*), a ranid that lays several hundred eggs, takes several months to develop, and has a small range (Bradford et al. 2005), to be highly vulnerable to stressors including climate change. Conversely, we would expect species such as the Red-spotted Toad (*Anaxyrus punctatus*), a bufonid that lays an average of 1,500 eggs (Tevis

1966), can metamorphose in eight days, and is found throughout much of the desert and desert grasslands in North America (Sullivan 2005), to be much more resilient to stressors like climate change.

Additionally, desert amphibians behaviorally mediate their exposure to water availability and temperature. Many adult desert amphibians are fossorial for most of the year (Shoemaker et al. 1992), while others take advantage of habitat such as springs that provide thermal and hydric refuge (Scott and Jennings 1985). Those species that rely on springs are likely to be more at risk as land use and climatic changes reduce hydric inputs to, and therefore outputs from, springs (Unmack and Minckley 2008). Additionally, relatively shallow ephemeral waters do not provide a great deal of thermal refuge for larval amphibians. Species that use these sites for embryonic and larval development may be at risk if thermal tolerances are exceeded or if hydroperiod is shorter than the species-specific minimum required time to metamorphosis.

Temperature.—Amphibians are ectotherms; their body temperature generally tracks environmental temperatures. Consequently, extreme ambient temperatures can have severe consequences for individuals lacking adequate physiological or behavioral adaptations to these conditions (Bentley 1966; Warburg 1967; Hutchinson and Dupre 1992; Hillman et al. 2009). Because increases in temperature increase biological activity, ectotherms in warmer temperatures can grow faster and may reach reproductive maturity at smaller sizes (Bradford 1990; Atkinson et al. 2001; Sheridan and Bickford 2011); and smaller size at metamorphosis has been associated with lower lifetime fitness (Ficetola and De Bernardi 2006; Cabrera-Guzman et al. 2013), suggesting that increased natal temperature has the potential to slow population growth. Response to temperature increases is not a linear relationship; when temperatures are too high, growth and development can be compromised (Polasik et al. 2016). Increased temperature can also increase productivity, potentially increasing food resources leading to faster growth. These interactions may be important in desert systems where temperatures already are extremely hot, for example in the southwestern U.S., exceeding 47° C (117° F) and recorded as high as 53° C (128° F; Arizona State Climate Office, National Weather Service; <https://azclimate.asu.edu/weather/>). Consequently, more study into the interactions between temperature, resource availability, physiological tolerances, and lifetime fitness will be essential for teasing apart how they interact to affect desert amphibians.

Variation in temperature sensitivity can also influence the outcome of ecological relationships. Amphibians show interspecific and intraspecific variation in thermal sensitivity, which can influence competitive and

predatory relationships and alter community composition (Tylianakis et al. 2008; Dell et al. 2014). Some species found in deserts can tolerate extreme heat, such as the Green Toad (*Anaxyrus debilis*; about 40° C); other species have lower thermal limits, such as the Northern Leopard Frog (*Lithobates pipiens*; about 36° C) found in parts of the Chihuahuan Desert (Brattstrom 1968). There is also variation between populations (Ralin and Rogers 1972); for example, Pacific Treefrogs (*Pseudacris regilla*) from Dry Lake, California were more tolerant of hot temperatures (37° C) than an El Toro, California, population (36° C; Brattstrom 1968, data from Fig. 3.g, showing data ranges not overlapping). These differences in sensitivity are important for predicting species and populations that are more likely to tolerate increased temperatures with climate change and may become more successful in consumptive or competitive interactions.

Stage specific vulnerability to temperature occurs in desert amphibians. First, the vulnerability of eggs and larvae is large because they require an aquatic environment, which can be influenced by increasing temperature and evaporation. Additionally, lower thermal tolerances than other stages are documented in young embryos (< Gosner stage 9; Gosner 1960; Zweifel 1977) and tadpoles going through metamorphosis (Gosner stages 42 through 44; Sherman 1980; Floyd 1983). Young embryos of most organisms tend to lack heat shock proteins that provide protection from heat and other stressors, leading to higher thermal sensitivity and greater vulnerability to temperature very early in development (Feder et al. 1999). Additionally, large and rapid physiological change occurs later in development as anuran tadpoles start to metamorphose, a period in development that also shows thermal sensitivity (Sherman 1980; Floyd 1983). Tadpoles going through metamorphosis cease feeding and depend on resources stored in their tail to meet energetic requirements as mouthparts atrophy at stage 41, and feeding does not begin again until stage 45 (Gosner 1960). During this time, high temperatures cue the production of heat shock proteins that are energetically expensive and may reduce the ability of the individual to accomplish other physiological tasks (Krebs and Loeschcke 1994; Somero 2002; Fitzgerald-Dehoog et al. 2012) suggesting that the process of metamorphosis may be compromised by the energetic requirements for the production of heat shock proteins. However, this relationship should be explored further, because no work on this topic has been done on desert anurans. Even so, the knowledge that late tadpole stages are particularly vulnerable to stressors can help those involved in head-starting programs to identify vulnerable stages to temperature and other stressors, and better gauge the timing of release of young into the environment.

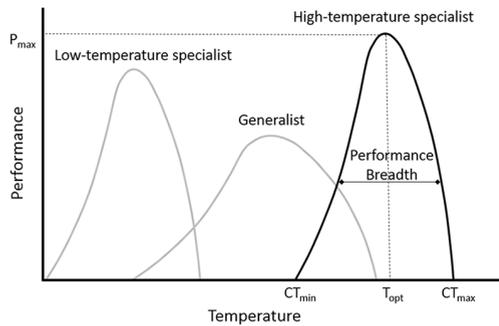


FIGURE 1. Model species performance curves for high-temperature specialists (dark curve), and for low-temperature specialists and generalists (light curves). Indicated for the high-temperature specialist are its maximum performance (P_{\max}), which occurs at the optimal temperature (T_{opt}), and its performance breadth, which is the range of temperatures over which the animal performs well. The critical thermal minimum (CT_{\min}) and the critical thermal maximum (CT_{\max}) are temperatures beyond which performance is nil (modified from Tattersall et al. 2012).

Temperature has a large and often non-linear effect on physiological processes, and can influence amphibian fitness, behavior, and population persistence and demographics (Berven et al. 1979; Angilletta 2009; Hillman et al. 2009). Biological functions related to temperature are generally asymmetrically hump-shaped, with performance and efficiency of the function increasing as temperature rises until some maximum is reached, after which performance drops, often steeply (Fig. 1; Rome et al. 1992; Angilletta 2009; Tattersall et al. 2012). Some processes are greatly influenced by temperature whereas others are only weakly influenced (Rome et al. 1992). These misalignments in biological processes are caused by (1) denaturing of proteins including hormones and enzymes at different rates (Teipel and Koshland 1971); (2) speeding of reactions that drive metabolism increasing oxygen demand, at times to levels greater than what respiration can supply (Portner and Knust 2007; Rummer et al. 2014); and (3) nonparallel changes in the transport of ions across biological membranes (Somero 2002). Negative effects of temperature can occur at less than the thermal maximum for a process, leading to reduced competitive ability in the field (Rome et al. 1992). These are complex processes and interactions, but provide key insights into predicting the potential success or failure of population persistence.

These physiological responses to high temperatures can be reduced in part by access to microclimatic refuges (Feder 1982; Scheffers et al. 2014), and acclimation and evolution (Navas et al. 2008; Niehaus et al. 2012). Desert amphibians tend to be nocturnal and fossorial for most of the year, so most adults may never reach their upper thermal critical limits in the field. However, some desert tadpoles are in environments, such as ephemeral pools, that can surpass those thermal limits (Rome et al.

1992). For example, some of these populations experience ambient temperatures of up to 34° to 39° C, which is near the limit of their laboratory thermal tolerances (Zweifel 1968; Brown 1969), putting populations at risk of declines.

Water limitation.—Water is vital for all life processes, and limitation can impair biological function and reduce reproductive opportunities for amphibians. Amphibians have a variety of physiological and behavioral adaptations making them fairly tolerant to desiccation relative to other vertebrates (Hillman et al. 2009). In general, size of the individual and the degree to which it is terrestrial correlates with resistance to desiccation more so than skin texture or habitat type (Thorson 1955; Warburg 1965; Young et al. 2005). All stages of development have at least some vulnerability to water limitation. Most embryos and tadpoles are aquatic and depend on surface water for development; consequently, declining hydroperiods can have a large impact on successful metamorphosis. Metamorphs may be affected by longer periods between precipitation events, increasing their risk of desiccation mortality (Carey and Alexander 2003; Polasik et al. 2016). Adults may be more affected by declining soil moisture (Cayan et al. 2010; Seneviratne et al. 2010), potentially leading to the creation and use of deeper burrows during most of the year. As a result, amphibians are considered to be sensitive to declines in water availability as a result of climate change.

In general, amphibians can withstand losing 20–50% of their body mass in water, with toads (Bufonidae), spadefoots (Scaphiropodidae), and the Tiger Salamander (*Ambystoma tigrinum*) tolerating > 35% (Alvarado 1972; Shoemaker et al. 1992). Terrestrial species are generally better adapted to water loss than aquatic species (Thorson 1955; Warburg 1965; Young et al. 2005), and some terrestrial species rapidly absorb water from moist substrates (Pinder et al. 1992; Shoemaker et al. 1992; Hillman et al. 2009). Amphibians also use their bladder to hold water, storing up to 50% of their body mass in some species (Shoemaker et al. 1992; Hillman et al. 2009), and some cocoon forming species can store more than 130% of their body weight (Tracy et al. 2007). Amphibians then reabsorb water from dilute urine (Shoemaker et al. 1992; Hillman et al. 2009). Amphibians also tolerate water limitation by avoiding harsh conditions and seeking shelter during the day and aestivating and/or forming cocoons during dry periods to conserve water and other resources (Lee and Mercer 1967; Tracy et al. 2007).

Despite these adaptations, dehydration can occur when water loss exceeds storage and the tolerance of an amphibian. During dehydration, amphibians first increase activity to find shelter but then slow when

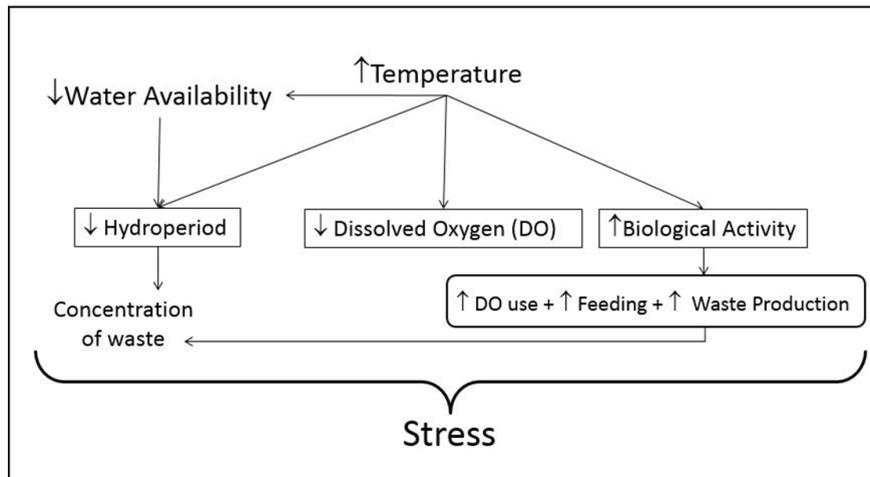


FIGURE 2. Increasing environmental temperatures and declining rainfall can create stress (e.g., increased competition, decreased immune function) for larval amphibians through a variety of paths including physical changes in abiotic conditions and speeding up biological reactions.

physiological damage leads to locomotor dysfunction and organ failure (Heatwole et al. 1971; Heatwole and Newby 1972; Putnam and Hillman 1977; Moore and Gatten 1989). Dehydration increases the concentration of solutes in the body, which can impair organ function (Alvarado 1972; Shoemaker et al. 1992). The heart is especially affected as blood concentrates and is harder to move; when this happens, the cardiovascular system may not support aerobic respiration (Hillman 1987).

Ambient moisture is also related to amphibian reproduction and growth. The vulnerability of eggs and larvae laid in aquatic environments is greater than that of adults because, in part, they are tied to open water, whereas terrestrial adults are generally not. Rainfall in mesic areas is positively correlated with the number of eggs laid, the likelihood of metamorphosis, and the number of metamorphs produced (Toft 1980; Pechmann et al. 1989; Hillman et al. 2009; Pails 2012), but this relationship has not been studied for desert amphibians. Increased water availability lengthens the time available for the terrestrial forms to forage (Rohr and Palmer 2013; Polasik et al. 2016), and foraging time is related to growth. A lack of moisture can decrease activity, such as foraging, potentially leading to starvation and mortality of metamorphs and adults (Carey and Alexander 2003). Because amphibian growth is greater in wet years in arid environments (Tinsley and Tocque 1995), and because size in amphibians can be correlated with fitness (Ficetola and De Bernardi 2006; Cabrera-Guzman et al. 2013), wetter years in deserts are likely important for individual fitness and population persistence. Captive-release and head-starting programs can use this in long-term planning to target years with predicted greater rainfall to more efficiently apply conservation strategies at times with the greatest chance of success.

ECOLOGICAL RESPONSES OF AMPHIBIANS TO CLIMATE CHANGE

An organism’s physiological responses to climate change may alter how it relates to the biotic and abiotic environment. It follows that species- and population-specific tolerances and their evolutionary history, combined with species interactions and changes in the physical environment, will cause stress and have complex ecological consequences (Relyea 2002; Dell et al. 2014). For example, drought is facilitating the success of invasive crayfish (*Orconectes* spp.) to the detriment of native species, and projected climate change is likely to make this worse through changing competitive relationships and food webs (Martinez 2012). To increase the likelihood for success of climate adaptation strategies, managers will need to consider these ecological interactions. Below are examples of these interactions between climate change and amphibian ecology, linking physiological mechanisms to ecological relationships and landscape-scale patterns.

Thermo-ecophysiology.—Increased temperatures can cause hypoxic conditions for aquatic organisms (Fig. 2). High temperatures increase kinetic energy in water, weakening the attractive forces between water molecules and oxygen and leading to declines in dissolved oxygen (Tromans 1998). Some larval amphibians can gulp air to compensate for low dissolved oxygen (Hoff et al. 1999). However, organisms generally have difficulty supplying their cells with enough oxygen for aerobic cellular respiration at high temperatures (Portner and Knust 2007; Rummer et al. 2014). Concurrently, there is a greater demand for oxygen because of

accelerated biochemical activity (Fig. 2). This can lead to physiological stress.

Increased biological activity requires more food consumption, resulting in more waste production (Fig. 2). Because high temperatures increase evaporation, water volume declines. When waste products and number of individual animals concentrate, habitat quality declines, competition increases, and stress escalates (Fig. 2; Woodward and Mitchell 1991; Griffis-Kyle et al. 2014). Because temperature and size at metamorphosis are inversely related (Voss 1993; Gillooly et al. 2002), those individuals who achieve metamorphosis are likely to be smaller, and smaller size is associated with lowered lifetime fitness (Ficetola and De Bernardi 2006; Cabrera-Guzman et al. 2013). Additionally, intense competition, such as found in desert pools, also delays metamorphosis (Newman 1987, 1998). In sum, increased temperature resulting from climate change is likely to increase competition and stress, slow development, reduce size at metamorphosis, and result in fewer metamorphs (Fig. 2).

Stress can have strong negative indirect consequences for animals including amphibians. Stress and the physiological mechanisms for coping with stress are energetically costly; thus, energy is directed away from performing normal processes and can reduce lifetime fitness (Newman 1998; Kishida et al. 2014). For example, as stress decreases immune function and increases susceptibility to diseases such as *Ranavirus* and *Batrachochytrium dendrobatidis*, populations may decline or become extirpated (Raffel et al. 2013). The indirect effects of climate that exacerbate the effects of stress and disease on amphibian populations in some cases may be greater than the direct effects of climate on physiological function (Li et al. 2013; Raffel et al. 2013).

Hydro-ecophysiology.—Many amphibians rely on water (e.g., ephemeral isolated waters, streams, and springs) for reproduction, which make them vulnerable to climate change. Many desert amphibians reproduce at surface waters that are often small, ephemeral, and widely spaced. Hydroperiods within these ephemeral waters will decline as temperatures increase, rainfall becomes less frequent, and consumption by wildlife increases (see Goetting 2015), leading to more stress for developing amphibians (Fig. 2; IPCC 2014b). These heavier downpours will likely increase erosion and transport of sediment into surface waters (IPCC 2014a), reducing water volume by displacement. Many of these ephemeral basins, such as rock pools and depressional wetlands, hold a constrained volume of water, so excess rain runs off and is not available for amphibian reproduction. The sedimentation and scouring of streambeds are likely to also influence species that use streams, but the

outcomes are not well understood. Species dependent on more permanent waters, like springs, are also at risk. As urban populations increase and aquifers are mined for anthropogenic uses, springs are drying (Unmack and Minckley 2008; Minckley et al. 2013). Hence, with fewer, larger rainfall events, more droughts, declining hydroperiods, and increased anthropogenic demands on water resources, reproductive opportunities for desert amphibians will generally decrease and the conditions for larval development are likely to become more stressful.

Hydroperiod determines the success of aquatic larvae completing metamorphosis (Wilbur 1987; Rowe and Dunson 1995). Many desert amphibians are adapted to short hydroperiods; some species can transition from embryo through metamorphosis in just over one week (Newman 1989), whereas others may take several months or longer (e.g., Crawford et al. 2005; Rorabaugh 2005; Sredl 2005). Though amphibian development typically accelerates with temperature (Zuo et al. 2012), there are physiological limits to its speed. Desiccation of the natal pool before tadpoles metamorphose can kill the entire cohort, a common occurrence for desert amphibians (Newman 1987; Tinsley and Tocque 1995), and increased drought frequency can extend the time between successful cohorts. As the number of years without reproductive output increases, extinction risk also increases (Salice 2012). Long life spans mitigate loss of reproductive opportunities, but few desert amphibians worldwide are known to be older than 10 y (Tinsley and Tocque 1995; Kuzmin and Ischenko 1997; Sullivan and Fernandez 1999), suggesting that adult life spans may become insufficient to ensure reproduction and species survival if drought increases as expected (Salice 2012).

Large-scale patterns.—Globally, some amphibians have altered their phenological (seasonal) cycle in response to climate change (Ficetola and Maiorano 2016). Because different species use different cues for breeding, some populations now breed earlier in the year and others show no or non-intuitive change (Feehan et al. 2009; Li et al. 2013; While and Uller 2014). Warmer winters can lead to earlier breeding, but can also result in lowered fecundity; unfortunately, this pattern has only been assessed in anurans hibernating in cold climates (Benard 2015). Changes in the timing of reproduction can desynchronize the dynamics of a population from resource availability (Stenseth et al. 2002; Nosaka et al. 2015). For example, an uncoupling between the timing of reproduction and food resources can alter behavioral tradeoffs that affect interspecific relationships, potentially altering population growth rates (Yang and Rudolf 2010; Orizaola et al. 2013).

In desert systems, precipitation is strong driver of the evolution of amphibian breeding strategies as it is

considered a limiting resource. Precipitation in the deserts of the southwestern U.S. is projected to decline, but there is uncertainty in this due to the complex interaction of sea surface temperatures in the tropical region of the Pacific Ocean (IPCC 2014b). Many desert regions, in addition to North America, are also projected to have lower rainfall, including those in Patagonia, Africa, northern Saudi Arabia, and the southern reaches of both the Turkistan desert and the Australian deserts (IPCC 2014c). By contrast, most Asian deserts, the southern Saudi Arabian peninsula, parts of the Great Indian Desert, and the Atacama Desert in South America are projected to receive more rain (IPCC 2014c). In the southwestern U.S., under high emissions scenarios and multi-model averaging, most of the declines are projected to occur in the spring and the summer (Kunkel et al. 2013) when most, but not all, desert amphibians breed (Sullivan 1989). Species have evolved to take advantage of currently existing seasonal pulses of moisture, so the consequences of changing rainfall patterns will depend on the breeding strategy of the population (Sullivan 1989).

Range distributions of some amphibian species are shifting in response to climate change (Kearney et al. 2008; Lawler et al. 2010; Li et al. 2013). However, the drivers and constraints of range shifts are complex and can be counterintuitive (Early and Sax 2011). Range shifts and population dynamics may be more strongly related to moisture gradients or water availability than to temperature gradients (Wright et al. 2013; Ficetola and Maiorano 2016) and different stages may be limited by different physiological constraints (Kearney and Porter 2009). For example, spadefoots in western North America have likely expanded their ranges further into deserts to take advantage of breeding opportunities at earthen livestock tanks, demonstrating their relatively quick responses to changes in water availability (Farrar and Hey 2005; Morey 2005a, b). Range shifts can also be constrained by geography (Early and Sax 2011), such as at the northern boundary of the Sonoran Desert of Arizona, where an abrupt rise of 1,000 m in elevation may obstruct latitudinal range shifts. An understanding on the constraints both within species and by topography can help managers plan for range shifts and identify areas where assisted movements may allow species to get to appropriate habitat that might otherwise not be available.

MANAGEMENT AND CLIMATE ADAPTATION

Given the physiological, behavioral, and distributional shifts that climate change may cause, conservation of desert amphibians will require an integration of disciplines to provide and apply information for management. Uncertainty is high; we are faced with man-

aging species in novel and fluid conditions. Paradigms may need to change; for example, currently common species may be more at risk from climate change than species designated as threatened or endangered (Dubois et al. 2011; Rosset and Oertli 2011), which means managers may need to change the way they prioritize conservation efforts. By identifying species at risk, we can use efficient strategies to help mitigate these changing conditions for desert amphibians (Heller and Zavaleta 2009; Mawdsley et al. 2009).

Planning restoration and habitat improvements that increase the resilience of a habitat to change, and linking science, management, and policy are critical for addressing climate change (Mawdsley et al. 2009; Scarlett 2010; Groves et al. 2012). Historically, managers focused on maintaining or restoring past conditions and treated climate as a hypothetical threat (Poiani et al. 2011). Now, natural resource managers must manage for both current and future environments and their species assemblages (Kujala et al. 2013). To accomplish these new goals management must identify strategies to maintain or promote habitat resiliency, the ability of the system to recover from disturbance (Curtin and Parker 2014). These strategies should include activities that identify vulnerable species (Foden et al. 2013), determine habitat improvements (Mawdsley et al. 2009; Shoo et al. 2011) that support physiological function in populations of interest, apply techniques to re-establish fauna informed by physiology and ecology (Polasik et al. 2016), and use landscape level coordination between scientists, managers, and policy makers (Loyola et al. 2013).

Assessing vulnerability.—Desert amphibians, as a group, are likely to be threatened with climate change in part because they are dependent on highly vulnerable aquatic habitats and may be at the edges of their thermal and hydric tolerances already (Cayan et al. 2010; IPCC 2014a, b). Quantification of this vulnerability is a necessary step in planning climate adaptation strategies (Foden et al. 2013) and integration of physiological sensitivity into this process can refine the assessments of species. Some species may benefit from climate change, but many will not, so it is necessary to evaluate population and species vulnerability to this risk. There are a variety of methods for evaluating vulnerability, including qualitative modeling, species distribution modeling using climate envelopes, and physiological modeling. These techniques use or assume information on the physiology of species and their current ranges to project the effects of a changing environment.

Selecting a method for assessing vulnerability is a function of the type, quantity, and quality of available data. Qualitative modeling of vulnerability can deal with large uncertainties in data by transforming a va-

riety of data sources and types into a qualitative ranking (Dawson et al. 2011; Davison et al. 2012; Foden et al. 2013). Unfortunately, data of better quality and resolution are not given more weight than lower quality data and physiology may or may not be explicitly included. Niche envelope modeling (also called climate envelope or species distribution modeling; Pineda and Lobo 2009; Garcia et al. 2014), calculates future ranges based on current climate conditions, where the species is found, and on projections of future climate. This method can handle presence-only data (Phillips et al. 2006); thus, data from a variety of study designs and monitoring programs can be used. However, this method does not include the influence of ecological interactions or directly address physiological tolerances of species, and data from range edges can confound results (Shoo et al. 2006). Physiological modeling of vulnerability evaluates how changes in abiotic conditions match the physiological responses of species, which can be used to calculate extinction risk and can be used to parameterize other approaches (Kearney and Porter 2009; Bartelt et al. 2010; Milanovich et al. 2010; Sinervo et al. 2010). This is a powerful method; however, it requires detailed information and does not address ecological interactions that may strongly influence the range of a species. Managers can use qualitative methods for evaluating large numbers of species, and those most at risk may require more detailed exploration using climate envelope and physiological tolerance modeling to better inform management decisions.

Incorporation of physiology into species vulnerability analyses produces more realistic projections of changes in geographic ranges and extinctions than in models without these mechanistic relationships (Morin and Thuiller 2009; Elith et al. 2010). Explicitly including physiological tolerances into at least some types of vulnerability assessments can improve assessment accuracy (Morin and Thuiller 2009). As we proceed in our planning for future conditions, vulnerability assessments can help us prioritize species for management or potentially for facilitated dispersal and enhance our chances of successful outcomes.

Enhance habitat features.—At small spatial scales, habitat features can be enhanced in ways that target specific life-history stages and work with the physiology of an animal. For desert amphibians that are fossorial for much of the year, habitat enhancement should focus on breeding sites where they do not have the same thermal or hydrologic refuge as they do underground. Managers can promote reproduction through habitat enhancement or creation by paying attention to life histories and specific physiological needs of species. In wetlands that are shallow and likely to get extremely hot, shade can be added or the basin deepened to provide more thermal

refuge for young and to increase the dissolved oxygen concentration in the water, which may alleviate stress (Fig. 2).

Physiology dictates rate of development, which dictates the time spent in the aquatic system. Catastrophic loss of amphibian cohorts occurs when a pool dries before tadpoles can metamorphose (Newman 1987; Tinsley and Tocque 1995), and this will happen more frequently with fewer precipitation events and increased evaporation (Kunkel et al. 2013). Consequently, increasing hydroperiod is the most direct way to enhance breeding habitat (Shoo et al. 2011) through increased water capacity (especially water depth), increased runoff capture and retention, decreased sedimentation, or water additions. There are already a number of efforts to increase water capacity and persistence for game species by removing sediment and debris, excavation, building up basin sides, sealing cracks and leaks, and using shade to decrease sun exposure and evaporation (Arizona Game and Fish Department 2014). When hydroperiod is still too short, water can be added to a pool from nearby sources (e.g., windmill and well) or delivered from off-site via pipe, truck, or helicopter (Shoo et al. 2011); however, trucking or flying in water is expensive. Managers can target water additions based on developmental requirements, ensuring hydroperiods that last through metamorphosis.

Those managing natural resources have been constructing and improving water sites in the desert southwestern U.S. to provide water for livestock and game species since the 1940s (Arizona Game and Fish Department 2014). The goal is to increase the number of water sites to increase the accessibility of water in the desert environment, as it is assumed water is a limiting resource for wildlife. Amphibians breed at constructed water sites such as earthen cattle tanks and anthropogenic catchments (Griffis-Kyle et al. 2011; Harings and Boeing 2014; Griffis-Kyle et al. 2014). This can be a successful strategy as shown by range expansions in some of the desert spadefoots in response to the addition of water sites (Farrar and Hey 2005; Morey 2005a, b).

However, modification of natural water sites or construction of new water sites can have unintended biotic (invasive species) and abiotic (water quality) consequences detrimental to amphibians and other wildlife. For example, increasing the density of water sites can increase connectivity and facilitate invasions by unwanted species (McIntyre et al. 2016). Invasions of exotics in desert wetlands can lead to sedimentation and fouling of water (Edwards et al. 2010), declines in species diversity (Holmquist et al. 2011), and declines in populations of native species through competition and predation (Rosen et al. 1994; Rosen and Schwalbe 1995; Luja and Rodriguez-Estrella 2010). Additionally, constructed water sites, and modification of natural water

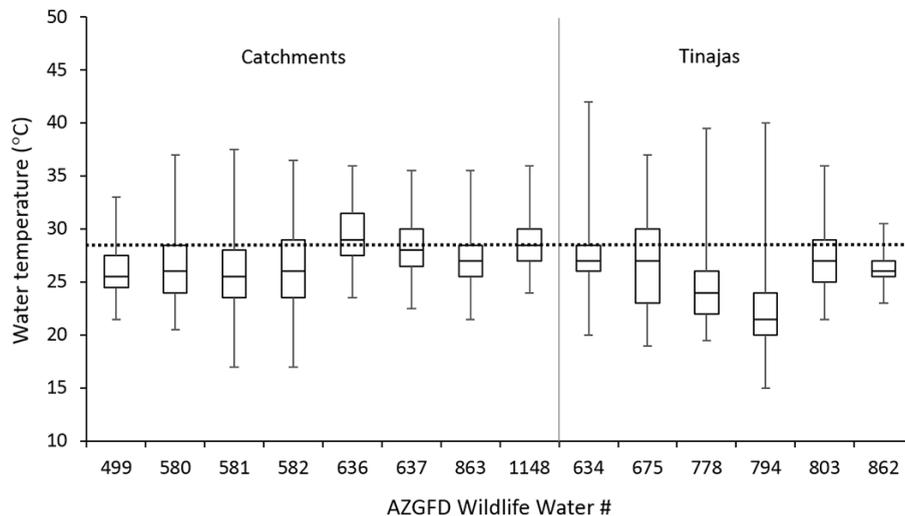


FIGURE 3. Summary of hourly surface water temperature readings from individual desert wildlife water features (x-axis represents individual water features identified by Arizona Game and Fish Department [AZGFD]) located on the Barry M. Goldwater Range - East, United States Air Force, southwestern Arizona, USA, August to October 2012. Data were collected by the author using I-buttons (Maxim Integrated, San Jose, California, USA) and are represented by the median, second, and third quartiles (box), and maximum and minimum (vertical bars). The dotted horizontal line at 28° C indicates the upper thermal limit for *Batrachochytrium dendrobatidis* (Stevenson et al. 2013), the fungal disease that has decimated amphibian populations worldwide.

sites, can change abiotic conditions such as temperature and ionic concentrations from what is found at natural sites like tinajas, which are erosional pools in bedrock found across the Sonoran Desert (Griffis-Kyle et al. 2014; Heard et al. 2014). Strong rains clear accumulated debris from the basin and restart succession. By contrast, anthropogenic catchments in this region have been established to maximize water capture and minimize evaporation (Arizona Game and Fish Department 2014). Consequently, these sites accumulate organic matter (i.e., plant and animal debris) that decomposes and produces ammonia, and this has been documented in areas without livestock influence (Environmental Protection Agency 2013; Griffis-Kyle et al. 2014; Edyth Hermosillo, unpubl. report). Ammonia interferes with aquatic organism physiological processes: it inhibits osmoregulation and circulation in amphibian larvae by damaging gills, disrupting uptake of dissolved oxygen, and hindering brain, liver, and kidney function (Russo 1985; Lang et al. 1987; Camargo and Alonso 2006). More constructed catchments will be added in response to climate change, leading to more water sites with large concentrations of ammonia ions, creating a larger problem than we currently have with water quality. Very little work has been done on this relationship and further study is needed to understand ammonia dynamics and desert amphibian responses. It is important that we understand how changing the placement of wetlands, as well as the abiotic conditions, affect physiological function and influence amphibian populations.

Climate change and our interactions with this change are effectively transforming the environment and magnifying the effects of other stressors on populations and communities (Tylianakis et al. 2008; Raffel et al. 2006). For example, disease, and in particular the chytrid fungus, *Batrachochytrium dendrobatidis*, is a huge issue for amphibians and has caused catastrophic declines in populations globally (Li et al. 2013). Sampling of several desert water sites in the Sonoran Desert revealed *B. dendrobatidis* in four out of five artificial catchments but not in the one tinaja sampled (Edyth Hermosillo, unpubl. report). The catchments are constructed in response to water limitation and are used as a way to mitigate environmental extremes in the desert and climate change. This fungus has an upper thermal tolerance of 26–28° C (Stevenson et al. 2013). The temperature of desert waters can exceed 30° C in artificial catchments and tinajas (Fig. 3), above the lethal limit of the fungus. Interestingly, artificial catchments store water in large, often underground storage tanks (Arizona Game and Fish Department 2014) where temperatures are buffered by the soil. This suggests catchments with cooler, underground tanks might provide a physiological refuge for the fungus in an otherwise inhospitable environment. Additionally, differences in environmental conditions (Raffel et al. 2006; Savage et al. 2015), like underground storage tanks can provide, may have large impacts on infection intensity; however, no work to date has examined this issue. We need to understand the relationship between our management of water sources and how that

can change the environment and either enhance or restrict disease persistence so that we can better support desert wildlife with water as its availability declines, without putting populations at risk of disease.

Consideration of the physiology of native species, invasive species, and pathogens are all critically important in planning habitat modifications. The goal is to promote the conservation of native species. For example, understanding the hydro-ecophysiology of Bibron's Toadlet (*Pseudophryne bibronii*), the relationship between breeding site water potential and reproductive success, has allowed researchers and managers to increase reproductive activity by increasing the humidity on breeding grounds (Mitchell 2001). Polasik et al. (2016) demonstrated that even under conditions where water was not thought to be limiting in pens where metamorphs were conditioned to the outside environment before release (automatic water systems were used), Wyoming Toad (*Anaxyrus baxteri*) metamorphs still clustered around water systems as the temperature rose. Their work suggests that our assumptions about limiting resources may underestimate the conditions optimal for physiological function, and that detailed physiological tolerance information would be important for improving habitat. Further, to promote native species, invasive species and pathogens should be controlled; understanding the physiological requirements of all species involved may be essential for this. For example, invasive species like the American Bullfrog (*Lithobates catesbeianus*) and crayfish often need long hydroperiods, so ensuring that habitat modifications or additions dry up occasionally can help guard against invasion (Rosen and Schwalbe 1995). An understanding of physiology can thus provide us with guidance on how to modify habitat to better support desirable species or exclude undesirable species.

Re-establishing fauna.—Re-establishing fauna, including both in-situ and ex-situ strategies such as moving, reintroducing, or introducing individuals, can reverse amphibian population declines and extirpations (Griffiths and Pavajeau 2008; Germano and Bishop 2009; Sprankle 2008; Vignieri 2014). The success rate has generally been low, but is improving (Dodd and Seigel 1991; Griffiths and Pavajeau 2008; Germano and Bishop 2009) and explicit consideration of physiological and ecological constraints will improve the success of these programs. For example, understanding the timing and development of energetically expensive heat shock proteins can help identify life-history stages that are less tolerant of stress, such as young embryos and tadpoles going through metamorphosis. Once amphibians get through metamorphosis and begin to feed on invertebrates, they become more difficult to feed in captivity, so consequently efforts have focused on releasing tadpoles or very young metamorphs (Michael Sredl,

pers. comm.). Unfortunately, these developmental stages may be more vulnerable to temperature and other stresses. There is little work on the interaction between temperature, development, and heat-shock proteins in amphibians, and none in the context of head-starting or reintroducing amphibian populations; this work has the potential to improve the success of re-establishing fauna.

The success of the Wyoming Toad reintroduction program will be improved by including physiology (Polasik et al. 2016). These authors found that warm shallow waters decreased time to metamorphosis, a possible benefit in some circumstances, and suggested that reducing water temperature may increase size at metamorphosis, with the latter result possibly increasing lifetime fitness. After metamorphosis, vegetation cover, likely related either directly or indirectly to microclimate and in particular humidity, improved juvenile toad survival (Polasik et al. 2016). Lessons from Polasik et al. (2016) include that alterations in the thermal profile of the aquatic environment can increase tadpole fitness via effects on development and size (Atkinson 1994). If the critical issue is to facilitate getting tadpoles out of predator filled habitat, warmer conditions may be appropriate; if the goal is to maximize lifetime fitness and aquatic predators are not as much a problem, cooler temperatures may be more important. Further, forb cover may help the success of Wyoming Toads head-starting programs that release individuals first into outdoor enclosures to acclimate them to the environment and improve survival, potentially because of microclimate temperature or a microhabitat-based increase in the food resources (Polasik et al. 2016). An understanding of anuran metamorph physiology and ecology linked with abiotic conditions would help managers increase the survival of soft-release metamorphs through modification of enclosure conditions.

Landscape planning.—Landscape-scale planning can improve the likelihood that management actions successfully mitigate at least some aspects of climate change. Planning at a large spatial scale facilitates accomplishing multiple goals including: (1) identifying and constructing corridors between populations to accommodate range shifts (Hannah et al. 2002; Mawdsley et al. 2009; Beier and Brost 2010; Vos et al. 2010; Feeley and Rehm 2014), (2) management of invasive species (Comrie and Broyles 2002) and coordinating tradeoffs between the management of natives and exotics (Drake et al., in press), and (3) increasing management efficiency by decreasing duplication of effort and resources (Vos et al. 2010; Loyola et al. 2013).

Management of connectivity between habitats and planning for climatic changes is inherently landscaped-based and can be addressed with both coarse- and fine-scaled filters. Course-scale filters include evaluating

connectivity as related to the diversity of abiotic conditions such as structure and types of substrates (geodiversity; Beier et al. 2015; Lawler et al. 2015). The idea is that if a diversity of types of abiotic conditions are conserved, there is a better chance of conserving at least some species because conditions have been safeguarded that support a diversity of physiological tolerances. Fine-scaled filters for managing connectivity are focused on life history, ecology, and physiology that can help inform corridor planning. Unfortunately, biologists creating corridors lack detailed information on species, and we have a limited ability to design optimal corridors to address connectivity for multiple species (Noss and Daly 2006; Shafer 2014). Even when assessing a single species, such as the Chiricahua Leopard Frog (*Lithobates chiricahuensis*), habitat alone is not adequate for understanding dispersal between breeding sites (Jarchow et al. 2016). Physiology-based mechanistic information on species environmental tolerances and how they respond to abiotic and biotic conditions can help in this planning, for example, in identifying suitable habitat with appropriate microclimate and aquatic resources available at appropriate times. Additionally, by identifying physiologically and ecologically critical abiotic conditions, scientists and managers may also identify appropriate areas for facilitated dispersal to increase the chances of success for the amphibians.

Increasing connectivity is not always the goal in landscape planning; strategies for managing invasive species and pathogens may require ensuring fragmentation of the network of aquatic breeding sites to isolate native populations from pathways of invasion (McIntyre et al. 2016; Drake et al., in press). An understanding of the physiology and life history of the invasive species or pathogen, and knowledge of source populations, can provide guidance in identifying constriction points in habitat networks, allowing managers to target areas where fragmenting the system can reduce connectivity and hence the probability of invasion (Cromie et al. 2012). For example, proactive control of the American Bullfrog, a species that often decimates native amphibian populations (Rosen et al. 1994; Rosen and Schwalbe 1995; Luja and Rodriguez-Estrella 2010) should receive considerable attention (Drake et al., in press).

Landscape-scale planning facilitates efficient application of resources and time by prioritizing areas of greatest need and synchronizing actions to take advantage of resources (Loyola et al. 2013; Vos et al. 2010). As increasingly variable weather patterns make it difficult to administer limited assets to manage for the new dynamics of our natural resources (Pressey et al. 2007; Beier and Brost 2010), finding efficiencies and synergies will be required, and coordination and iterative communication between scientists and managers as well as federal, state, and private land holders will be essential

(Shafer 2014). As climate change and land-use change alter the playing field for conservation, a mechanistic understanding of appropriate habitat for different life-history stages will improve our ability to craft connectivity for at-risk species.

CONCLUSIONS

As climate change alters the stage upon which species live and interact, managers will be well served by understanding the physiological basis for responses of organisms to their environment, and scientists will conduct more conservation relevant research by listening to the concerns of managers. By enhancing iterative communication and integrating physiology with ecology and management, we can improve the efficiency and success of conservation efforts. Thermal and hydric tolerances in desert amphibian species are especially important for management planning as temperature is increasing, water availability is decreasing, and extreme weather events is becoming more common. We can use knowledge of these tolerances to determine length of hydroperiods (e.g., planning for water additions), the need for temperature reductions for vulnerable life-history stages, or the need to increase dissolved oxygen (e.g., adding shade). Additionally, understanding of physiology can help us identify appropriate developmental stages for re-establishment efforts, so as to focus on using stages that are more resistant to stressors such as temperature than more vulnerable stages. Also, we must consider that habitat modification can change the abiotic and biotic conditions in the environment, potentially changing physical or chemical conditions of the habitat to outside the tolerances of amphibians. Habitat alteration can also modify conditions in such a way as to support unwanted invasive species or pathogens, or to alter managed assemblages in unwanted ways, so detailed consideration of their physiology and ecology should also be included during planning.

Physiology can also be integrated into larger scale planning. For example, explicitly integrating physiological and ecological mechanisms into vulnerability assessments can help refine our ability to identify populations or species at risk in addition to better predicting potential habitat for range expansions. Examining these larger scale patterns of appropriate habitat or environmental conditions, based on analyses including physiology and ecology can assist in creating corridors. This level of planning can also allow us to identify constriction zones where small management actions can be taken to exclude unwanted species and pathogens.

A mechanistic understanding of the physiology and ecology of species can facilitate the creation of practical and efficient climate adaptation strategies, and improve our ability to project population trends and plan policy

(Hofmann and Todgham 2010), but the application of effective strategies will require the integration of cross-disciplinary expertise. This cross-disciplinary network includes physiologists that understand how environmental factors and stress affect the functions and processes within individuals, and help detail the mechanistic responses of amphibians to their changing environment. This network also includes the geneticists who investigate the adaptive potential and genetic health, identifying populations at risk from environmental change. Wildlife biologists and ecologists then integrate the information on physiology, genetics, and ecology (e.g., thermo- and hydro-ecophysiology) to investigate how the environment and other species influence population and community dynamics. The outputs from the wildlife biologists are then integrated with large scale patterns by landscape ecologists to understand and identify corridors to improve the resilience of populations and species to environmental change. The information from all these disciplines is then used by natural resource managers, trained in biology, to better plan management strategies. All this work is used by scientifically literate policy makers that can take the scientifically based evidence and ethically meld it with societal constraints. Platforms and programs to bring these groups together are essential to better address climate threats and plan adaptation strategies to these changing conditions. Communication among scientific disciplines and between scientists, managers, and policy makers is inherently disjunct. However, if the managers, scientists, and policy makers establish and maintain mechanisms for iterative communication, to both strengthen the science and communicate the limitations of that science, the applicability and usability of the information will be increased and management and policy better informed (Dilling and Lemos 2010).

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