

Review

Tolerance mechanisms in North American deserts: Biological and societal approaches to climate change

Z.R. Stahlschmidt^{a,*}, D.F. DeNardo^a, J.N. Holland^b, B.P. Kotler^c, M. Kruse-Peeples^d

^a School of Life Sciences, Arizona State University, Life Sciences C-wing, Tempe, AZ 85287, USA

^b Department of Ecology and Evolution, Rice University, Houston, TX 77005, USA

^c Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion 84990, Israel

^d School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA

ARTICLE INFO

Article history:

Received 20 September 2010

Received in revised form

22 November 2010

Accepted 16 March 2011

Available online 6 April 2011

Keywords:

Adaptation

Adaptive plasticity

Energy

Global warming

Precipitation

Temperature

ABSTRACT

The deserts of North America and elsewhere may serve as 'ecological petri dishes' that can be used to study the general effects of global climate change (GCC) as these regions are expected to become warmer and drier at faster rates than other terrestrial regions. We highlight the biological and societal responses to such shifts in environmental parameters predicted to vary with GCC, and we introduce the term *tolerance mechanism* (TM) to inclusively describe the means by which organisms of natural systems or human society cope with such environmental challenges. We review the historical relationships between biological TMs and water availability, temperature, and energy resources, as well as describe societal TMs. We create a simplified conceptual model to predict the effectiveness of TMs in the context of GCC and conclude that, although currently functional, some desert TMs (e.g., biological adaptations by long-lived taxa) may be outpaced by GCC. We finish with suggested future TM-related research.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Arid environments have been utilized by organisms and human societies for millennia, despite their inherently uncertain availability of resources. This uncertainty is largely attributable to the high variability and unpredictability of desert systems (Ward et al., 2000; Ward, 2009). For example, precipitation in North America's deserts exhibits both high frequency (i.e., monthly or seasonally) and low frequency (i.e., inter-annual or inter-decadal) temporal variation (Bullock, 2003; Comrie and Broyles, 2002), the latter of which has increased over the past 50–70 years (Anderson et al., 2010; Arriaga-Ramirez and Cavazos, 2010). With the looming effects of global climate change (GCC), deserts of North America are predicted to become drier and warmer at faster rates relative to most other regions (IPCC, 2007; Seager et al., 2007; but see Wentz et al., 2007). Thus, this geographic region may serve as an 'ecological petri dish' for considering the impacts of GCC on biological systems and human societies.

Correlates between ecological resilience (i.e., the ability of an ecosystem to resist damage and recover quickly from disturbance) and social resilience (i.e., the ability of groups or communities to cope with external stresses and disturbances) exist (Adger, 2000). Yet, the specific means by which both organisms of biological systems and human societies cope with environmental challenges in hot deserts (e.g., extreme temperatures and highly uncertain rainfall) have not been characterized in a synthetic manner. Henceforth, we refer to such processes as tolerance mechanisms (Table 1). Tolerance mechanisms (TMs) often subsume familiar biological phenomena (e.g., adaptation and adaptive phenotypic plasticity) and socio-anthropological processes (e.g., diversification and inter-social interactions). Notably, societal TMs often have biological TM analogs (Table 1) that allow for biological-societal comparison, and TMs are not restricted to organisms and societies of arid zones. Thus, TMs can broadly describe processes between- and within-disciplines.

Three variables that are often of particular importance for socio-ecological systems of North American deserts include precipitation, temperature, and energy resources (e.g., food availability). We examine the role of specific TMs in meeting the challenges associated with these three variables across a diverse set of biological systems and, specifically, use case studies from empirical research.

* Corresponding author. School of Life Sciences, Graduate Program, Tempe, AZ 85287-4601 Tel.: +1 480 390 7958.

E-mail address: zs@asu.edu (Z.R. Stahlschmidt).

Table 1
Definitions and examples of biological and societal tolerance mechanisms (TMs).

<i>Biological</i>	
Adaptation	The process, which takes place under natural selection, whereby an organism becomes better suited to its environment Example: having a low surface area-to-volume ratio to reduce water loss
Adaptive phenotypic plasticity	Phenotypic plasticity that confers a fitness advantage Example: increasing heart rate to meet the increased metabolic needs of foraging
<i>Societal</i>	
Diversification (a.k.a., “bet-hedging” in biological systems)	A risk averse management technique wherein societies invest their resources among several ventures Example: investing resources into the pursuit of multiple energy sources (e.g., wind power, solar power, and fossil fuels)
Inter- and intra-social interactions (a.k.a., inter- or intra-specific interactions in biological systems)	Interactions such as trade, communication, community gatherings, conflict and warfare between individuals of the same group or members of different cultural groups Example: trade for fish and grain between coastal and inland cultural groups during periods of subsistence shortfalls
Movement (a.k.a., “migration” in biological systems)	Physical movement from one area to another, sometimes over long distances or in large groups Example: mass movement to an area with more favorable climatic conditions
Specialization (a.k.a., the same term in biological systems)	A risk-seeking strategy wherein societies heavily invest their resources into one or few ventures to potentially maximize return Example: investing extensive resources (e.g., land, irrigation, and labor) into mono-agriculture
Storage (a.k.a., the same term in biological systems)	The retention of resources for the purpose of future utilization Example: storing surplus food resources for seasonal and inter-annual shortfalls

We discuss specific TMs of human societies, and compare them with biological TMs. Last, we consider the effectiveness of these particular TMs in the context of GCC and suggest future directions of research and policy.

2. Biological tolerance mechanisms (TMs)

2.1. Water availability

2.1.1. Role of water in desert TMs

As the “universal solvent” and a foundational resource for nearly all biological processes, water is of general importance to organisms. Minimally, animals require water to transport nutrients (including oxygen), remove metabolic waste products, and regulate body temperature. Likewise, plants use water for nutrient transportation, as well as for structural integrity (e.g., turgor pressure) and photosynthesis. Given the inherent scarcity of standing water and its variable inputs (e.g., 2–70 cm annual precipitation) (Bender, 1982; Bullock, 2003), deserts of North America have long presented challenging environments for organisms.

2.1.2. Case study: water-limited reproduction in the *senita* cactus

Common among desert plants, including many species of Cactaceae and in particular columnar cacti, is a hermaphroditic breeding system (i.e., flowers contain male and female sex functions) in which plants allocate and partition resources between flower production and seed/fruit production. This often includes

excess flower production at the expense of reduced seed/fruit production. This strategy can increase the male fitness function of plants through high flower (and hence pollen) production. Yet, excess flower production also results in resource-limited fruit set, in which not all flowers initiate fruit development due to limited resources available for seed/fruit maturation. As an example, consider the reproductive biology of *senita* cacti (*Pachycereus/Lophocereus schottii*) in the Sonoran Desert of North America, including northwestern Mexico and southwestern U.S.A. Upon reaching reproductive maturity, the seasonal flower phenology of *senita* cacti can entail 10–500 flowers per plant in a given night and 1000–5000 flowers per plant over their spring/summer flowering season; moreover, as a polycarpic plant, the phenology of flowering in *senita* cacti can vary from 2–5 months per year among years of periodic seasonal flowering (Holland and Fleming, 1999, 2002). For *senita* cacti, water availability through precipitation is a key resource contributing to resource allocation between excess flower production and seed/fruit production (Holland, 2002; Holland and Fleming, 2002; Holland et al., 2004). Intra- and inter-annual variation in precipitation characteristic of the aridity of desert environments (Davidowitz, 2002) can be important in shaping the aforementioned variation in the daily, seasonal, and annual phenology in flower and fruit production of *senita* cacti.

Indeed, such flower and fruit production is not constant, but rather variable among years. Both the timing of the onset of flowering and the magnitude of flower (and fruit) production among individual flowering seasons appear to be coupled with patterns in precipitation. For the six years of low precipitation inputs following the heavy rainfall event of a 1994 hurricane, the onset of flowering by *senita* became increasingly delayed and the magnitude of flower (and fruit) production declined (Holland and Fleming, 2002). Such observational results are consistent with experimental results in which both flower and fruit production increased with a water treatment compared with unwatered, control plants (Holland, 2002). In this way, *senita* appears to have a reproductive strategy that entails some degree of plasticity to tolerate periods of low precipitation (or take advantage of times of high rainfall) by adjusting their intra- and inter-annual timing and magnitude of seasonal flower production and fruit set. Despite such apparent plasticity and tolerance of *senita* to the inherent intra-annual, inter-annual, and decadal variation in rainfall of deserts, whether or not plants are able to adjust to the long-term shifts in precipitation with GCC remains a critical issue in need of study. Further, shifts in precipitation and temperature with GCC may disrupt the phenological synchrony between cactus flowering and the emergence and population dynamics of their obligate pollinating moth if both species do not adjust the phenology of their life history events in accord with one another.

While it is well-recognized that, in polycarpic plants with seasonal reproduction among years, the key life history stage in most demographic models is the bottom right-hand corner, that is the size/age class of reproduction which determines life-time reproductive output. Yet, this is not to dismiss seed and seedling mortality of such reproductive output, which can also be critical to the dynamics of desert plants confronted with GCC. Causes of such mortality of seeds and seedlings due to a host of factors (e.g., post-dispersal predation, herbivory, nurse plants, and rainfall) can reduce the recruitment and establishment of plants, including many species cacti such as *senita*.

2.2. Temperature

2.2.1. Temperature-related TMs of desert organisms

Organisms require temperature-sensitive proteins to perform many of their basic tasks, including processing nutrients and intra-

cellular transport. Temperature also affects water balance and respiration, two critical variables for survival. Clearly, desert plants and animals must maintain their temperature within an acceptable range to survive. Air temperatures are highly variable within the deserts of North America, with extremes reaching 50 °C in summer and <0 °C in winter (Balling et al., 1998). Coping with either of these temperature extremes is challenging, but being able to cope with both extremes over the course of a year can be a formidable challenge to organisms. Temperature regulation is often achieved via evaporative cooling, which comes with a hydric price tag. Because water is often limiting, animals often take advantage of temperature-buffering refugia or reduce their activity during hot periods to navigate a trade-off between temperature regulation and water balance (Ricklefs and Hainsworth, 1968).

2.2.2. Case study: interdependent TMs of the Gila monster address thermal challenges

TMs evolve in response to specific environmental conditions and are often limited by existing behavior and morphology (e.g., exaptations). The Gila monster (*Heloderma suspectum*) is an iconic resident of the Sonoran Desert that provides an exceptional example of the interdependence of behavioral and physiological TMs and the environmental specificity in which they are effective. Like many desert animals, Gila monsters use behavioral TMs to reduce their exposure to thermal extremes. During the cooler spring months, Gila monsters are predominantly diurnal and surface active ~20–25% of the time (Davis and DeNardo, 2010). However, during the hot, dry summer months, Gila monsters

become nocturnal and limit surface activity to 10–15% (Davis and DeNardo, 2010). Gila monsters also use behavioral TMs while inactive, in that they seasonally alter the types of refugia they select based on the thermal conditions of the refugia (D.F. DeNardo, unpublished data).

In addition to behavioral TMs, Gila monsters also use physiological TMs. Gila monsters, unlike most lizards, use their urinary bladder as an internal water reservoir (Davis and DeNardo, 2007). Such reliable “availability” of water makes water balance less of an immediate concern, enabling Gila monsters to use evaporative cooling as a physiological TM that allows for active foraging at ambient temperatures above their thermal optimum (approximately 29 °C, Bogert and Del Campo, 1956). Gila monsters are restricted to the Sonoran Desert, where they can exploit late-summer precipitation (i.e., annual monsoon) (Fig. 1). In laboratory conditions, Gila monsters deprived of food and water take approximately 80 days to reach a biologically relevant dehydration state if they begin the deprivation with a full bladder (Davis and DeNardo, 2007). However, the same level of dehydration is reached after only 33 d of deprivation if the Gila monster begins with an empty urinary bladder (Davis and DeNardo, 2007). The 80 d time frame to reach dehydration provided by the urinary bladder provides the necessary buffer to enable Gila monsters to survive the hot dry summer prior to the onset of the monsoon rains. Nevertheless, such a buffer would be insufficient for Gila monsters to survive the longer dry period typical of the adjacent Mojave Desert that does not experience a summer monsoon. A similar outcome would result in the Sonoran Desert if GCC significantly extended

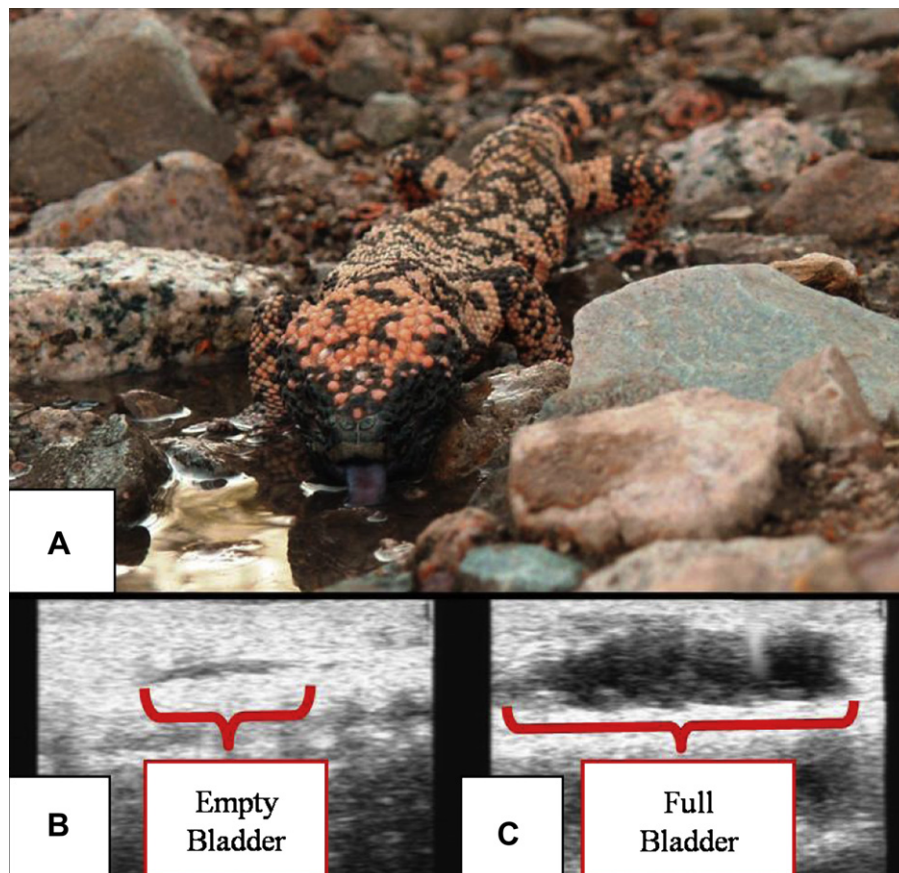


Fig. 1. Gila monsters (*Heloderma suspectum*) in the Sonoran Desert exhibit behavioral and physiological plasticity by becoming nocturnal during the hot, dry summers and by storing water from rare rainfall events in their urinary bladders. (A) Photo depicts a Gila monster binge-drinking from a rain puddle following a prolonged period of dehydration. Below the image are ultrasonograms that show (B) an empty and (C) a full Gila monster urinary bladder (dark areas demarcated by brackets). When full, the urinary bladder can hold up to 75 ml (20% of body mass). Photograph and ultrasonograms by J.R. Davis.

the drought period through shifts in the timing of either spring or monsoonal rains even for a single season. Furthermore, juvenile live stages are even more sensitive than adults to water restriction (Moeller and DeNardo, unpublished data); thus, recruitment and long-term population persistence may be very sensitive to detrimental shifts in rainfall patterns.

2.3. Energy resources

2.3.1. Energetic challenges of desert animals

Energy is a prerequisite for all life because it is instrumental to maintenance, growth, and reproduction. Desert plants use ATP as a source of chemical energy to transport glucose, build structural vasculature, and synthesize disperser-attracting fruit. Similarly, desert animals require energy to pump blood, promote skeletal growth, and invest in reproduction. However, deserts present energy-related challenges to animals since most of their chemical energy is tied up in vegetation that is often sparse or difficult to acquire due to mechanical or chemical defenses. Additionally, energy expenditure for most desert animals is related to environmental temperature. Therefore, animals in hot deserts find energy difficult to acquire and easy to lose.

2.3.2. Case study: adaptively plastic foraging in desert vertebrates

Foraging decision-making is a noteworthy example of adaptive behavioral plasticity since acquiring energy is the focus of much of an organism's activities. When an animal leaves the shelter of its refuge (e.g., burrow and nest), it may succeed in finding food. The energy obtained can be used for maintenance and reproduction. At the same time, such foragers necessarily expose themselves to increased risk of predation, which may affect survivorship. Thus, there are two corollaries to adaptively plastic foraging: (1) it should be under strong natural selection because foraging traits are variable and affect fitness parameters (i.e., fecundity and survival), and (2) foragers face a fundamental trade-off between food and safety whereby they cannot obtain the former without sacrificing some of the latter.

In arid regions, animals face additional trade-offs, including those between energy intake versus water balance and exposure to extreme temperatures. Relative to ambient conditions, refugia are often characterized by more amenable hydric and thermal environments which reduce occupants' evaporative water loss. Thus, leaving the refuge to forage should give rise to increased costs from water loss. In this way, food and water may be complementary resources for animals in deserts. Indeed, for Australian raven (Kotler et al., 1998), ibex (Hochman and Kotler, 2006), springbok (J.S. Brown, unpublished data), goats (Shrader et al., 2008) and even crested larks (Kotler and Brown, 1999), water is complementary to food, and immediate access to water decreases foraging costs and increases foraging efficiency. While giving-up densities (GUD, the final amount food left behind in a resource patch following exploitation; a measure of foraging efficiency) for crested larks decrease just 7% in the presence of water, for these other foragers GUDs may fall by half (Fig. 2) (Brown, 1988).

3. Societal TMs

3.1. Adaptive responsiveness of desert societies

Although humans may be under limited natural selection, human societies have more potential for behavioral responses to the environmental stresses of arid living relative to other organisms, particularly over the short term and at the individual and societal levels. Humans can more easily cope with or tolerate the stresses associated with uncertain water, high temperatures, and

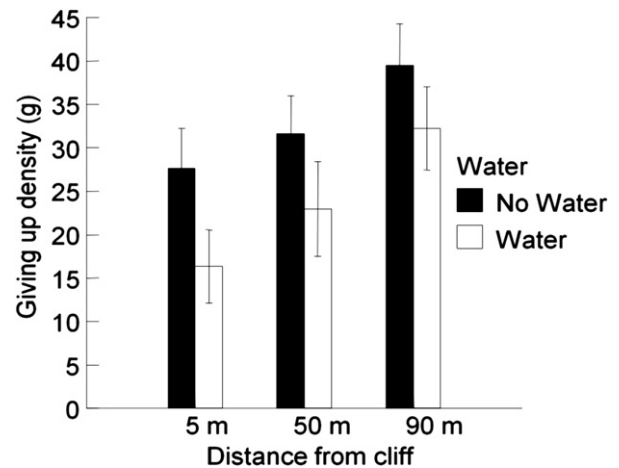


Fig. 2. The effect of water and distance from the cliff refuge on patch exploitation as expressed as giving up densities (i.e., the final amount food left behind in a resource patch following exploitation; a measure of foraging efficiency) for Nubian ibex (*Capra ibex nubiana*) in the Negev Desert (after Hochman and Kotler, 2006). As in the systems of other desert foragers, the availability of water and food interact to affect decision-making as ibex become more efficient foragers when water is limited.

securing energy through changes in what can be broadly classified as behavioral TMs. Human behavioral responses are also extremely flexible because humans are able to learn from the past and plan for the future (Redman, 2001). Behavioral responses allow for additional tolerances that are not exclusively reliant on evolutionary adaptations. Such adjustments in behavioral strategies include decisions about population migration, diversifying resource procurement, specialization of a procurement strategy to maximize energy return, and/or increasing investment in the storage of resources (Table 1). However it should be noted that the use of behavioral TMs has as much or more to do with individual or societal perceptions of problems than a situation which necessitates a response (O'Connor et al., 1999).

3.2. Case study: decision-making in agricultural societies

Agricultural societies are particularly vulnerable to the variability and unpredictability of arid landscapes. Thus, societies of the past and present have employed many TMs to alleviate the stresses associated with arid-land farming (Table 1). The specific TMs employed depend upon the environmental, agricultural, and social contexts; thus, a portfolio of TMs is often used. For example, contemporary small scale agriculturalists in the arid regions of Africa commonly alternate field locations, diversify the types of crops grown, and use economic strategies such as wage economies (Graef and Haigis, 2001; Roncoli et al., 2001). In addition to diversification strategies, small-scale agriculturalists in the prehistoric southwest USA frequently engaged in extensive food sharing networks or storage to reduce the risks associated with arid uncertainty (Halstead and O'Shea, 1989). Other agricultural societies with the labor capacity, complexity, and the appropriate environmental conditions cope with uncertain agricultural production through specialization by constructing irrigation systems that reduce risk by increasing the predictability of water resources (Mabry, 1996). Large-scale industrial agriculture is currently in a phase of coping with GCC knowing that these methods of maximizing output are a significant contributor to greenhouse gas emissions. Not only does industrialized agriculture need to focus on the types of TMs summarized here, but it also needs to address its role in anthropogenic GCC (Wreford et al.,

2010). Understanding the specific social and ecological contexts is necessary to determine the TMs relied upon by societies which depend on agriculture for their energy needs.

4. Global climate change and TMs

4.1. Biological TMs

The potential impact of climate change on ecosystems is a source of concern for biologists, sociologists, and policy makers alike. In particular, researchers predict that the deserts of North America will become warmer and drier at a relatively fast rate (IPCC, 2007; Seager et al., 2007). Also, the variability of precipitation in this region has recently increased and this trend is expected to continue (Hughes and Diaz, 2008). Recent evidence demonstrates that much of the hydrological and temperature-related climate trends of the western United States are human-induced (Barnett et al., 2008). As a possible result of these and other related factors (e.g., shifts in the seasonal timing of reproduction), the deserts of North America have experienced several vegetation die-offs related to prolonged drought (Breshears et al., 2005; Miriti et al., 2007). Given these troubling signs, we discuss the effectiveness of TMs of desert organisms to respond to GCC.

As the products of natural selection, biological adaptations operate on an evolutionary timescale. In some species from non-arid regions, genetic responses to the effects of GCC can evolve quickly. For example, the genetically controlled photoperiodic response of the pitcher-plant mosquito (*Wyeomyia smithii*) from eastern North America has shifted as growing seasons have become longer due to GCC in as few as five years (Bradshaw and Holzapfel, 2001). Also, organisms can evolve increased phenotypic plasticity, and such selection for plasticity coincides with GCC. For example, GCC has selected for longer reproductive seasons in the red squirrel (*Tamiasciurus hudsonicus*) of northern North America due to increasingly prolonged growing seasons of food sources (Reale et al., 2003). However, other adaptations evolve at a much slower rate. For example, bird feathers were initially selected for display and thermoregulation millions of years before they became adapted for flight (Cowen, 1991). Thus, adaptations are often long-term solutions even with amenable bauplane. Given the potential for such inherent rigidity, organismal success in the context of GCC often heavily relies on adaptive phenotypic plasticity.

The extent to which organisms and ecosystems function through periods of disturbance, which can be human-induced and/or natural (e.g., Brown et al., 1997), can be described in terms of fundamental niches, current available micro-climates, and predicted available micro-climates in 100 years. We propose a simplified conceptual model incorporating these parameters as they relate to temperature and water availability (Fig. 3) because temperature and water availability: (1) are universally important factors to organism fitness, (2) are significantly changing due to GCC at a relatively fast rate in the deserts of North America (e.g., IPCC, 2007; Seager et al., 2007), and (3) have effects on organisms that are inter-related (e.g., increased body temperature generally leads to increased evaporative water loss in ectothermic animals). Using this framework, it is unlikely that all desert organisms will adapt to the predicted 2–5 °C increase in mean annual temperature on a century level timescale (Fig. 3: species II). Long-lived species (e.g., columnar cacti and Gila monsters) may be at a particular disadvantage because they have slower reproductive life histories and longer generation times, which will likely inhibit rapid evolution and adaptation in response to GCC. However, these large species may have an advantage over smaller-bodied counterparts because organisms with relatively large biomass are less adversely affected by periods of prolonged drought (McKechnie and Wolf,

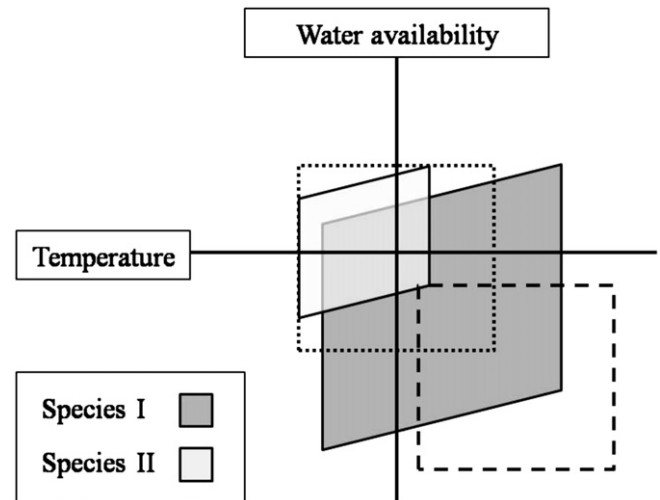


Fig. 3. Conceptual diagram for organismal fundamental niches (N_f , shaded boxes), current available micro-climates (dotted box), and predicted available micro-climates in 100 years (MC_{100} , dashed box) as a function of temperature (°C) and water availability (e.g., precipitation or soil water potential). Organisms will not be suited for their environment in 100 years if their N_f fails to overlap with MC_{100} (e.g., Species II). Species I may have a more successful suite of TMs (e.g., a greater buffering capacity due to larger body size or a higher rate of adaptation) than Species II.

2010). Therefore, even small-bodied desert organisms with high rates of adaptation (e.g., *Drosophila* species) may succumb to severe environmental stress related to GCC (Fig. 3).

Clearly, organisms with large fundamental niches, potentially due to high rates of adaptation and highly plastic TMs, will likely better cope with rapid GCC (Fig. 3). For example, reproductive bet-hedging in desert plants allows seeds the option to forego germination in years when environmental conditions are stressful. However, seed viability has a shelf-life, and evidence demonstrates that perennial plants in the desert may not outlive prolonged periods of drought (Miriti et al., 2007). On the other hand, desert animals often use behavioral plasticity to better cope with adverse environmental conditions. For example, if a woodrat's nest is too warm in the Sonoran Desert, it may dig a deeper one that is more thermally buffered by the ground. Yet, behavioral plasticity may not completely offset the effects of global warming in other vertebrate systems (Schwanz and Janzen, 2008; Sinervo et al., 2010). In sum, GCC may seriously challenge and, with time, could overwhelm the TMs used by many desert plants and animals.

From a broader ecological perspective, species interactions affect multiple levels of biological organization (i.e., organism to ecosystem) and depend on when and where foragers can profit. Familiar mechanisms that mediate interspecific interactions include resource partitioning and habitat selection, storage effect, seasonal variation of foraging efficiencies, spatial variance in resource abundances, and temporal variation in resource abundances (e.g., Kotler and Brown, 1999). Thus, adaptations and the plasticity of adaptations are fundamental to species interactions. GCC is expected to increase the inter-annual variation in precipitation and resource pulses that drives mechanisms involving the storage effect and the sizes of the resource pulses. Those species with adaptations favored by such variability will also be favored.

4.2. Societal TMs

Because TMs for human societies do not rely on the necessarily slow moving process of adaptation, the behavioral TMs utilized by human societies are likely much more effective at absorbing the

shock of GCC because they can be enacted much more quickly. Additionally, the arsenal of societal TMs is much more diverse, and there is greater potential for specialization based on context. The human ability to learn from the past, plan for the future, and determine causes of conditions make humans flexible in their means of responding to environmental stresses (Richerson and Boyd, 1999; Redman, 2001).

However, as organizations and their institutions become more connected and inflexible, behavioral TMs may no longer be sufficient to handle stresses associated with GCC. These types of systems, particularly highly bureaucratic, interconnected and complex systems of today, are grounded within a “rigidity trap” (Holling et al., 2002). The more rigid a system, the more severe are potential societal collapses or transformations (Hegmon et al., 2008). In many ways, such societal rigidity is comparable to phylogenetic constraints (i.e., components of the phylogenetic history of a lineage that prevents evolution in that lineage) in biological systems. Thus, complex human societies may be more or less adaptable to GCC than biological systems. Our conceptual model regarding the efficacy of biological TMs in response to GCC (Fig. 3) could be modified and applied to societal systems because societal and biological systems reflect both adaptive traits (Table 1) and inherent constraints.

5. Future directions

Tackling GCC problems should be rooted in science and facilitated with policy and education. Mathematical modeling has provided considerable insight into the large-scale effects of climate change. However, finer-scale investigations into empirical systems (i.e., organismal, population-, and community-level) are necessary to flesh out species- and system-specific conceptual models of biological responses to GCC (e.g., Fig. 3), and are thus far few. Questions in dire need of attention include, but are not limited to: (1) *Do organisms have the propensity to genetically adapt to the adverse effects of GCC in desert systems?* Short-lived species in other systems exhibit some ability to adapt (Bradshaw and Holzapfel, 2001; Reale et al., 2003), but further investigation is necessary to assess GCC's impact in arid systems, particularly in long-lived taxa. (2) *How much “wobble room” is there between the demands currently placed on TMs and the maximal buffering capacity of the TMs?* For example, common TMs presently used by organisms (e.g., the ability of molecular chaperones to repair damaged proteins) may be operating at or near their maximum capacity. (3) *To what extent can the plasticity of behavioral TMs buffer organisms from the negative impacts of anticipated environmental changes?* Recent evidence suggests that some populations in arid environments will be drastically affected by the thermal effects of GCC despite extensive behavioral plasticity (McKechnie and Wolf, 2010). (4) *To what extent will anticipated changes in air temperatures alter the thermal and hydric properties of critical microhabitats?* Although useful on a large scale, mathematical models rarely take into consideration the environments in which organisms actually live (e.g., refugia; available micro-climates in Fig. 3). (5) *Which species represent keystone species, what is their scope of influence, and how susceptible are these organisms to anticipated climate change?* In the scope of GCC, understanding the interaction between abiotic (e.g., temperature and precipitation) and biotic (e.g., inter-specific interactions) ecological factors should be combined with fundamentals of organismal biology (e.g., thermal tolerance).

Human societies have a long history of dealing with changes in climate and overcoming stresses associated with desert living (Barker and Gilbertson, 2000; Doyel and Dean, 2006; deMenocal, 2001). The history and archaeology of these cases will prove to be useful in evaluating the effectiveness of TMs for conditions in the present and future (Fisher et al., 2009; McIntosh et al., 2000). While

this predicted global future includes changes at unprecedented scales, the lessons of the past can provide useful roadmaps for the future. Along these lines, several questions that should be addressed include: (1) *How can the successes, failures, and trade-offs made by past societies in coping with the challenges of environmental change be considered in future policy considerations?* Current interdisciplinary research endeavors are attempting to integrate the successes and failures of past and present human societies to clarify future management decisions. For example, one such project, Integrated History and Future of People on Earth, is developing credible options for the future through the compilation and comparison of historical case studies (Costanza et al., 2007). (2) *How diverse, flexible, adaptive, and contextual will policy decisions be in planning and coping for GCC?* The type and configuration of employed TMs is dependent upon the social and environmental context and must remain flexible to avoid the so-called rigidity trap (Holling et al., 2002). Policy therefore must take into account these lessons and realize a “one size fits all” approach is inappropriate. In addition, maintaining a diversity of response options is important to minimize vulnerability to environmental change because loss of potential response options makes systems more susceptible and unable to absorb change (Fazey et al., 2010). (3) *What trade-offs are we as a society willing to make, and what aspects are we unwilling to abandon as we are faced with the challenges of GCC?* We as a human society must prioritize our goals and consider which future trajectory is worth undertaking. We must also develop a clearer understanding of how human societies perceive the problems associated with GCC, and how they are willing to meet these challenges. This will require an increased engagement between environmental scientists, policy makers, and the public which will require a reevaluation of how scientists communicate with the stakeholders (e.g., Groffman et al., 2010).

Acknowledgements

We thank other members of the ‘Adaptive Traits’ working group at the *Dynamic Deserts: Resource Uncertainty in Arid Environments* conference for their input, including Gary Nabhan, Larry Venable, Glenn Walsberg, and Doug Craig. We also appreciate comments on the manuscript by Brad Butterfield, Elizabeth Hagen, Kevin McCluney, and two anonymous reviewers. We are also grateful for the generous funding of the *Dynamic Deserts* conference by our sponsors at Arizona State University, including the Research and Training Initiatives office through the School of Life Sciences, Decision Center for a Desert City, and the Global Institute of Sustainability, as well as the Central Arizona Project for Long-term Ecological Research.

References

- Adger, W.N., 2000. Social and ecological resilience: are they related? *Progress in Human Geography* 24, 347–364.
- Anderson, B.T., Wang, J.Y., Salvucci, G., Gopal, S., Islam, S., 2010. Observed trends in summertime precipitation over the Southwestern United States. *Journal of Climate* 23, 1937–1944.
- Arriaga-Ramirez, S., Cavazos, T., 2010. Regional trends of daily precipitation indices in northwest Mexico and southwest United States. *Journal of Geophysical Research – Atmospheres* 115, D14111–D14120.
- Balling, R.C., Klopatek, J.M., Hildebrandt, M.L., Moritz, C.K., Watts, C.J., 1998. Impacts of land degradation on historical temperature records from the Sonoran Desert. *Climatic Change* 40, 669–681.
- Barker, G., Gilbertson, D., 2000. *The Archaeology of Drylands: Living at the Margin*. Routledge, London.
- Barnett, T.P., Pierce, D.W., Hidalgo, H.G., Bonfils, C., Santer, B.D., Das, T., Bala, G., Wood, A.W., Nozawa, T., Mirin, A.A., Cayan, D.R., Dettlinger, M.D., 2008. Human-induced changes in the hydrology of the western United States. *Science* 319, 1080–1083.
- Bender, G.L., 1982. *Reference Handbook on the Deserts of North America*. Greenwood Press, Westport, CT.

- Bogert, C.M., Del Campo, R.M., 1956. The Gila monster and its allies. *Bulletin of the American Museum of Natural History* 109, 1–238.
- Bradshaw, W.E., Holzapfel, C.M., 2001. Genetic shift in photoperiodic response correlated with global warming. *Proceedings of The National Academy of Sciences of The United States of America* 98, 14509–14511.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of The National Academy of Sciences of The United States of America* 102, 15144–15148.
- Brown, J.S., 1988. Patch use as an indicator of habitat preference, predations risk, and competition. *Behavioral Ecology and Sociobiology* 22, 37–47.
- Brown, J.H., Valone, T.J., Curtin, C.G., 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of The National Academy of Sciences of The United States of America* 94, 9729–9733.
- Bullock, S.H., 2003. Seasonality, spatial coherence and history of precipitation in a desert region of the Baja California peninsula. *Journal of Arid Environments* 53, 169–182.
- Comrie, A.C., Broyles, B., 2002. Variability and spatial modeling of fine-scale precipitation data for the Sonoran Desert of south-west Arizona. *Journal of Arid Environments* 50, 573–592.
- Costanza, R., Graumlich, L., Steffen, W., Crumley, C., Dearing, J., Hibbard, K., Leemans, R., Redman, C., Schimel, D., 2007. Sustainability or to collapse: what can we learn from integrating the history of humans and the rest of nature? *Ambio* 36, 522–527.
- Cowen, R., 1991. In: *History of Life*, fourth ed. Wiley-Blackwell, Malden, MA.
- Davidowitz, G., 2002. Does precipitation variability increase from mesic to xeric biomes? *Global Ecology and Biogeography* 11, 143–154.
- Davis, J.R., DeNardo, D.F., 2007. The urinary bladder as a physiological reservoir that moderates dehydration in a large desert lizard, the Gila monster *Heloderma suspectum*. *Journal of Experimental Biology* 210, 1472–1480.
- Davis, J.R., DeNardo, D.F., 2010. Seasonal patterns of body condition, hydration state, and activity of Gila monsters (*Heloderma suspectum*) at a Sonoran Desert site. *Journal of Herpetology* 44, 83–93.
- Doyel, D.E., Dean, J.S., 2006. *Environmental Change and Human Adaptation in The Ancient American Southwest*. The University of Utah Press, Salt Lake City, UT.
- Fisher, C., Hill, J.B., Feinman, G.M., 2009. *The Archaeology of Environmental Change: Socionatural Legacies of Degradation and Resilience*. University of Arizona Press, Tucson, AZ.
- Fazey, I., Gamarra, J.G.P., Fischer, J., Reed, M.S., Stringer, L.C., Christie, M., 2010. Adaptation strategies for reducing vulnerability to future environmental change. *Frontiers in Ecology and the Environment* 8, 414–422.
- Graef, F., Haigis, J., 2001. Spatial and temporal rainfall variability in the Sahel and its effects on farmers' management strategies. *Journal of Arid Environments* 48, 221–231.
- Groffman, P.M., Stvlnski, C., Nisbet, M.C., Duarte, C.M., Jordans, R., Burgin, A., Previtali, M.A., Coloso, J., 2010. Restarting the conversation: challenges at the interface between ecology and society. *Frontiers in Ecology and The Environment* 8, 284–291.
- Halstead, P., O'Shea, J., 1989. *Bad Year Economics: Cultural Responses to Risk and Uncertainty*. Cambridge University Press, Cambridge, UK.
- Hegmon, M., Peebles, M.A., Kinzig, A.P., Kulow, S., Meegan, C.M., Nelson, M.C., 2008. Social transformation and its human costs in the prehispanic US Southwest. *American Anthropologist* 110, 313–324.
- Hochman, V., Kotler, B.P., 2006. Effects of food quality, diet preference and water on patch use by Nubian ibex. *Oikos* 112, 547–554.
- Holland, J.N., 2002. Benefits and costs of mutualism: demographic consequences in a pollinating seed-consumer interaction. *Proceedings of the Royal Society of London Series B – Biological Sciences* 269, 1405–1412.
- Holland, J.N., Bronstein, J.L., DeAngelis, D.L., 2004. Testing hypotheses for excess flower production and low fruit-to-flower ratios in a pollinating seed-consuming mutualism. *Oikos* 105, 633–640.
- Holland, J.N., Fleming, T.H., 1999. Mutualistic interactions between *Upiga virescens* (Pyralidae), a pollinating seed-consumer, and *Lophocereus schottii* (Cactaceae). *Ecology* 80, 2074–2084.
- Holland, J.N., Fleming, T.H., 2002. Co-pollinators and specialization in the pollinating seed-consumer mutualism between senita cacti and senita moths. *Oecologia* 133, 534–540.
- Holling, C.S., Gunderson, L.H., Peterson, G.D., 2002. Sustainability and panarchies. In: Gunderson, L.H., Holling, C.S. (Eds.), *Panarchy: Understanding Transformations in Human and Natural Systems*. Island Press, Washington, DC, pp. 63–102.
- Hughes, M.K., Diaz, H.F., 2008. Climate variability and change in the drylands of Western North America. *Global and Planetary Change* 64, 111–118.
- IPCC, 2007. *Climate change 2007: the physical science basis*. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Kotler, B.P., Brown, J.S., 1999. Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. *Journal of Mammalogy* 80, 361–374.
- Kotler, B.P., Dickman, C.R., Brown, J.S., 1998. The effects of water on patch use by two Simpson Desert granivores (*Corvus coronoides* and *Pseudomys hermannsburgensis*). *Australian Journal of Ecology* 23, 574–578.
- Mabry, J.B., 1996. *Canals and Communities: Small Scale Irrigation Systems*. University of Arizona Press, Tucson, AZ.
- McIntosh, R.J., Tainter, J.A., McIntosh, S.K., 2000. *The Way The Wind Blows: Climate, History, and Human Action*. Columbia University Press, New York.
- McKechnie, A.E., Wolf, B.O., 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters* 6, 253–256.
- deMenocal, P.B., 2001. Cultural responses to climate change during the Late Holocene. *Science* 292, 667–673.
- Miriti, M.N., Rodriguez-Buritica, S., Wright, S.J., Howe, H.F., 2007. Episodic death across species of desert shrubs. *Ecology* 88, 32–36.
- O'Connor, R.E., Bord, R.J., Fisher, A., 1999. Risk perceptions, general environmental beliefs, and willingness to address climate change. *Risk Analysis* 19, 461–471.
- Reale, D., McAdam, A.G., Boutin, S., Berteaux, D., 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London Series B – Biological Sciences* 270, 591–596.
- Redman, C., 2001. *Human Impact on Ancient Environments*. University of Arizona Press, Tucson, AZ.
- Richerson, P.J., Boyd, R., 1999. Complex societies – the evolutionary origins of a crude superorganism. *Human Nature – An Interdisciplinary Biosocial Perspective* 10, 253–289.
- Ricklefs, R.E., Hainsworth, F.R., 1968. Temperature dependent behavior of cactus wren. *Ecology* 49, 227–233.
- Roncoli, C., Ingram, K., Kirshen, P., 2001. The costs and risks of coping with drought: livelihood impacts and farmers' responses in Burkina Faso. *Climate Research* 19, 119–132.
- Schwanz, L.E., Janzen, F.J., 2008. Climate change and temperature-dependent sex determination: can individual plasticity in nesting phenology prevent extreme sex ratios? *Physiological and Biochemical Zoology* 81, 826–834.
- Seager, R., Ting, M.F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.P., Harnik, N., Leetmaa, A., Lau, N.C., Li, C.H., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181–1184.
- Shrader, A.M., Kotler, B.P., Brown, J.S., Kerley, G.I.H., 2008. Providing water for goats in arid landscapes: effects on feeding effort with regard to time period, herd size and secondary compounds. *Oikos* 117, 466–472.
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M.L., Meza-Lazaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I., Sepulveda, P.V., Rocha, C.F.D., Ibaguengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites Jr., J.W., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899.
- Ward, D., 2009. *The Biology of Deserts*. Oxford University Press, Oxford, UK.
- Ward, D., Saltz, D., Olsvig-Whittaker, L., 2000. Distinguishing signal from noise: long-term studies of vegetation in Makhtesh Ramon erosion cirque, Negev Desert, Israel. *Plant Ecology* 150, 27–36.
- Wentz, F.J., Ricciardulli, L., Hilburn, K., Mears, C., 2007. How much more rain will global warming bring? *Science* 317, 233–235.
- Wreford, A., Moran, D., Adger, N., 2010. *Climate Change and Agriculture: Impacts, Adaptation and Mitigation*. OECD Publishing.