VOLUME 91, NO. 2 *THE QUARTERLY REVIEW OF BIOLOGY* JUNE 2016

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RESILIENCE TO DROUGHTS IN MAMMALS: A CONCEPTUAL FRAMEWORK FOR ESTIMATING VULNERABILITY OF A SINGLE SPECIES

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KEYWORDS
allostasis, homeostasis, metabolism, osmoregulation, preadaptation, thermoregulation

The Quarterly Review of Biology, June 2016, Vol. 91, No. 2

0033-5770/2016/9102-0002$15.00

ABSTRACT

The frequency and severity of droughts in certain areas is increasing as a consequence of climate change. The associated environmental challenges, including high temperatures, low food, and water availability, have affected, and will affect, many populations. Our aims are to review the behavioral, physiological, and morphological adaptations of mammals to arid environments, and to aid researchers and nature conservationists about which traits they should study to assess whether or not their study species will be able to cope with droughts. We provide a suite of traits that should be considered when making predictions about species resilience to drought. We define and differentiate between general adaptations, specialized adaptations, and exaptations, and argue that specialized adaptations are of little interest in establishing how nondesert specialists will cope with droughts. Attention should be placed on general adaptations of semidesert species and assess whether these exist as exaptations in nondesert species. We conclude that phenotypic flexibility is the most important general adaptation that may promote species resilience. Thus, to assess whether a species will be able to cope with increasing aridity, it is important to establish the degree of flexibility of traits identified in semidesert species that confer a fitness advantage under drying conditions.

Introduction

ANTHROPOGENIC-induced environmental change, including habitat loss (Galbraith et al. 2002), fragmentation (Fahrig 2003), and climate change (Etterson and Shaw 2001; Alley et al. 2003), is accelerating at a rate unprecedented in Earth's history (Etterson and Shaw 2001; Alley et al. 2003). In fact, the rate of vertebrate species climatic niche evolution is considerably slower than the current predicted rates of anthropogenic environmental change (Quintero and Wiens 2013). The accelerated rates of human-induced environmental change could thus be driving a sixth mass extinction event, requiring conservation efforts to be focused on reducing the rate of extinctions (Pimm 2009; Black et al. 2011; Harley 2011). However, we are currently unable to predict which species will be threatened by extinction under increased environmental change and which species will survive (Moritz and Agudo 2013).

Many studies have assessed the probability and potential of species to adapt to rapid environmental change via evolutionary adaptation (e.g., evolutionary rescue; Gonzalez et al. 2013; Box 1). However, evolutionary adaptation is generally a slow process, occurring over generations (Hoffmann and Sgrò 2011), and may occur too slowly for species to respond to rapid environmental and climate change. Under such circumstances, species may become extinct, change their distribution range, or show an active response to change through adaptive (Breed et al. 2011; Box 1) or exaptive (Ghalambor et al. 2007; Box 1) phenotypic plasticity. Interestingly, a number of local declines and extinctions due to environmental change have been associated with changes in species interactions (Cahill et al. 2013; Ockendon et al. 2014). However, an individual's ability to cope with its prevailing environment is also dependent on its behavior, physiology, and morphology. These responses to abiotic factors then likely also influence species interactions, for example, through changes in activity patterns, ultimately further impacting extinction risk.

One of the main consequences of global climate change is an increase in the frequency and intensity of droughts (IPCC 2007; Dai 2011). Regions where droughts have become, and are projected to become, longer and more frequent include the Mediterranean, central Europe, central North America, and southern Africa (IPCC 2007). Although the latest IPCC report (2013) mentions a lower confidence for the increased incidence of droughts since the 1950s, it is still predicted that droughts are likely to increase in some areas in the future. Droughts are a normal part of climate variation, which means that, independent of global climate change, natural populations have and will continue to face this problem repeatedly. For example, in the last 500 years, BOX 1

Definition of terms

Term	Definition
Adaptive phenotypic plasticity	Alteration of some aspect of the phenotype in response to prevailing environmental conditions, which increases an individual's chance of survival and reproduction (maximizes fitness; Charmantier et al. 2008; Ozgul et al. 2009, 2010; Piersma and van Gils 2010) and that may facilitate population persistence and potentially evolutionary adaptation (Hoffmann and Sgrò 2011). Traits that specifically evolved in response to historical selection pressures and have current utility in the same context (phenotypic adaptation).
Aridity index	$I_m = \frac{(100S - 60D)}{\mathrm{PE_t}}$; where I_m = index of moisture availability; S = total moisture surplus (mm) from all months with a water surplus; D = total of all monthly deficiencies (mm); and PE = annual potential evapotranspiration (mm; Meigs 1953). Both S and D are represented by the difference between monthly precipitation and monthly potential evapotranspiration (Nash and Engineering Group Working Party 2012). Deserts have an aridity index below 0.2, semideserts between 0.2 and 0.5.
Behavioral evader	Animals able to escape environmental extremes using primarily behavioral and physiological adaptations (Willmer et al. 2000).
Developmental plasticity	Nonreversible phenotypic plasticity occurring during ontogeny (Piersma and Lindström 1997).
Drought	Current precipitation falls significantly below the long-term mean of a defined area (Dai 2011). Is defined on a temporal scale and can occur in any environment.
Drought-affected areas	Areas that are neither deserts nor semideserts, but experience unpredicted droughts, which might occur more often and become more intense in the future due to climate change (Li et al. 2009). In the future, increasingly more areas might become drought prone due to climate change.
Environmental stressor	Any stimulus that could affect an individual negatively if it cannot respond to it via a specific stress response, which itself is costly (e.g., Charmandari et al. 2005). Typically uncontrollable for the individual, but can be predictable (e.g., seasonal changes in food) or unpredictable (e.g., a storm; Wingfield 2013).

continued

BOX 1
Continued

Term	Definition
Evolutionary adaptation	Change in the relative gene frequencies of alleles (and associated phenotypic changes) within a population over multiple generations, with a corresponding increase in species fitness over time (Pianka 2011; Rezende and Diniz-Filho 2012).
Exaptation	Formerly called preexisting adaptations or preadaptations. Traits that evolved in response to historical selection pressures, which have current utility but in a different context (i.e., different environment or selection pressures; Gould and Lewontin 1979).
Exaptive phenotypic plasticity	Alteration of traits in response to prevailing environmental conditions, which specifically evolved in response to historical selection pressures and have current utility in a different context (exaptation), increasing an individual's chance of survival and reproduction (increasing fitness) in novel environments (Ghalambor et al. 2007).
Interannual rainfall variability	Expressed as a percentage of the mean deviation of precipitation from the average over the average precipitation (Nash and Engineering Group Working Party 2012).
Phenotypic flexibility	Reversible phenotypic plasticity (Piersma and Lindström 1997).
Physiological endurer	Animals that tolerate environmental extremes using physiological and morphological adaptations (Willmer et al. 2000).
Predictable environment	Resources spatially and/or temporally heterogeneous; selection pressures imposed on populations over multiple generations are seasonal/cyclical (e.g., Negus et al. 1986; Ylönen and Ronkainen 1994); species show evolutionary adaptation and phenotypic plasticity in response to change (Ledón-Rettig et al. 2008; Rymer et al. 2013).
Resilience	The ability of a species (populations or individuals) to persist following a disturbance or disturbances (Hughes et al. 2007; Tanentzap et al. 2013; Hodgson et al. 2015).
Unpredictable environment	Resources spatially and/or temporally heterogeneous with random, rare, or sporadic environmental changes (Valladares et al. 2002); rapid environment pressure imposed on individuals; and species show phenotypic flexibility in response to change (Piersma and Drent 2003; Rymer et al. 2013).
Vulnerability	The predisposition or susceptibility of a species (population or individual) to be negatively affected by a disturbance (Smit et al. 2000; Williams et al. 2008; Oppenheimer et al. 2014).

megadroughts (extreme drought events persisting for several years) have occurred in North America, China, and West Africa (Dai 2011).

Droughts are characterized by periods of unusually low water availability due to reduced precipitation and/or increased evaporation due to increased temperatures (Dai 2011). Droughts create water shortages, leading to reduced plant primary productivity (McNaughton et al. 1983) and thus an associated food reduction for animals, ultimately leading to an increased risk of individual death and population extinction (Miller et al. 2005; Seager et al. 2007). Animals exposed to such environmental conditions may respond through changes in behavior, physiology, and/or morphology that facilitate survival and/or reproduction. If individual differences in survival/reproductive probabilities are due to genetic differences, genetic selection within the population will result in evolutionary adaptation (Rezende and Diniz-Filho 2012). Under drought conditions, reproduction is often terminated or forfeited, and dry seasons are typically the nonbreeding season (Pinter 1994; Schradin and Pillay 2005; Sperry and Weatherhead 2008). Droughts represent periods of low resource availability that individuals must survive in order to reach a season when reproduction again becomes possible. For this reason, our focus rests with survival and not on reproductive success.

Individuals can cope with droughts using a variety of morphological, physiological, and behavioral traits, and to predict the extent to which species are resilient to droughts requires some measure of these traits. Here, we review these traits to provide researchers and nature conservationists with a guide to which phenotypic traits should be studied in order to assess whether or not a species of interest may be able to cope with droughts. We describe three different ways species can cope with droughts, namely through evolutionary adaptation (future change), adaptive phenotypic plasticity (current change), and exaptations (including exaptive phenotypic plasticity, current change). We focus specifically on adaptive phenotypic plasticity (as per Ghalambor et al. 2007) here, although we recognize that phenotypic plasticity is not necessarily always adaptive, as the environment can also induce changes that decrease fitness, for example, due to constraints or morphological changes indicating significant costs. Another example is evolutionary traps, whereby a fitness increasing ("good") choice changes into a fitness decreasing ("poor") one as previously reliable environmental cues become unreliable, leading to an evolutionary mismatch and thereby trapping the individual into continuing use of the poorer option (Robertson et al. 2013), which could be particularly common in predictable environments (Box 1). Within this context, we argue that whether a trait is specialized and fixed or flexible is important for determining the resilience (the ability to persist following a disturbance or disturbances; Hughes et al. 2007; Tanentzap et al. 2013; Hodgson et al. 2015) or vulnerability (predisposition or susceptibility to be negatively affected by a disturbance; Smit et al. 2000; Williams et al. 2008; Oppenheimer et al. 2014) of a species (or population) to droughts (Box 1). Species with fixed adaptations to droughts are generally well adapted to arid environments, although in species with flexible adaptations and exaptations, the degree of flexibility determines resilience and will likely facilitate adaptive evolution in novel environments (Ghalambor et al. 2007). Resilience to droughts requires individuals to be able to cope with three environmental stressors: water shortage, food shortage, and fluctuating (often very high) temperatures. We define the term "environmental stressor" as any stimulus that could affect an individual negatively if it cannot respond to it via a specific stress response, which itself is costly to some extent. A stress response can be an increase in energy mobilization (i.e., increased blood glucocorticoid levels to mobilize energy; Charmandari et al. 2005), but also comprise other physiological responses (for example, decrease of blood glucocorticoid levels, if the stressor is reduced energy availability and the individual has to reduce energy mobilization).

Stressors are typically uncontrollable for the individual. For example, the individual cannot control rainfall during a given period. Stressors can occur predictably (e.g., seasonal changes in food) or unpredictably (e.g., a storm; Wingfield 2013).

We then highlight some approaches to categorize behavioral, physiological, and morphological traits of mammals for existence in deserts and semideserts and introduce our own categorization system, the adaptive triquetra, which categorizes traits facilitating coping with aridity instead of categorizing the species themselves. The adaptive triquetra system considers the primary driving stressor, the body system mounting the adaptive response (behavior, physiology, and/or morphology), and the extent to which this trait is flexible. We suggest that the selection pressures operating in deserts (defined below) drive the evolution of specialized, nonplastic adaptations, whereas those in semideserts (defined below) promote phenotypic flexibility. We also stress that traits that could potentially facilitate future coping (which would be classified as exaptations) must not be ignored. We focus our explanation of the adaptive triquetra on mammals, which are one of the best studied taxa for desert adaptations. Although adaptations in other taxa, such as insects and birds, might be quite different, we believe that our general conclusions would apply to them as well. Finally, we conclude that the degree of flexibility of traits that exist as exaptations in nondesert species will determine how well they can cope with droughts, and comparing their degree of flexibility with those of species from semideserts will enable us to predict their resilience.

Evolutionary Adaptation, Adaptive Phenotypic Plasticity, and Exaptations

Evolutionary adaptation involves genetic changes over generations (Rezende and Diniz-Filho 2012). Over time, species may show genetic changes, leading to changes in morphology (e.g., peppered moths *Biston betularia*; Saccheri et al. 2008), physiology (e.g., red abalone *Haliotis rufescens*; de Wit and Palumbi 2013), and behavior (e.g., bird song; Podos et al. 2004). The degree of adaptive phenotypic plasticity also represents an evolutionary adaptation. These adaptations confer a fitness advantage and evolved in response to particular past selection pressures (Baum and Larson 1991; Coddington 1994). Evolutionary adaptation represents how species responded to previous environmental change, and raises the question of whether, and the degree to which, species can respond to prevailing environmental change via genetic change. Although it is becoming increasingly recognized that evolutionary adaptation can be quite rapid (Hoffmann and Sgrò 2011), the evolutionary response to a changing environment can be constrained by a lack of genetic variation or genetic correlations (i.e., genetic constraints; Chevin 2013), the rate at which individuals within a population reproduce (Lewontin 1970), and the rate and predictability at which the strength and direction of selection changes (due to environmental change) over time (Lande and Shannon 1996; Gomulkiewicz and Houle 2009; Chevin 2013; Michel et al. 2014).

Species might not be adapted to prevailing specific environmental pressures, but may still show some degree of resilience to change due to exaptations, also called preexisting adaptations or preadaptations (e.g., Pekár et al. 2013). In contrast to evolutionary adaptations, exaptations are traits that evolved in response to specific past selection pressures, and provide a fitness advantage in the prevailing environment under different selection pressures, meaning that the past and current environments are different for at least some specific aspects (Gould and Lewontin 1979). In other words, these traits provide a function in their current role, but were not selected for this purpose (Gould and Vrba 1982). For example, Hoffman (2014) proposed that euryhalinity (i.e., salinity tolerance) in the green toad *Bufo viridis* evolved to facilitate migration across the variable habitats of Eurasia and the North African Mediterranean coastal regions. These toads now occupy arid and semiarid regions, suggesting that euryhalinity is an exaptation important for drought resistance (Hoffman 2014). Euryhalinity in these toads did not evolve in response to direct selection pressure from an arid or semienvironment (i.e., evolved in response to past selection pressure), but it does have current utility (i.e., provides a use in the existing context). The usefulness of the term exaptation has frequently been criticized because exemplary traits are often not clearly distinguishable from adaptations (Larson et al. 2013). The distinction between adaptation and exaptation is particularly important to consider when assessing whether an individual could survive in a future environment not experienced previously, as is predicted under accelerated environmental change (Sih et al. 2011). Existing phenotypic plasticity is likely to be of importance in the prevailing environment, even if it has evolved under different selection pressures in a different environment (i.e., exaptive phenotypic plasticity; Box 1). Therefore, a population might be able to respond to increased severity of droughts, not because it previously experienced droughts and is adapted to droughts, but because it experienced different environmental conditions that imposed similar selection pressures (e.g., food shortage). This population could thus possess beneficial exaptations in response to droughts.

Adaptive phenotypic plasticity is an evolved trait, enabling a comparatively rapid response by individuals to cope with environmental change. Phenotypic traits are altered adaptively in response to prevailing environmental conditions, which increases individual fitness (Charmantier et al. 2008; Ozgul et al. 2009, 2010; Piersma and van Gils 2010). Adaptive phenotypic plasticity may determine an individual's survival and reproduction in the short term, which may facilitate population persistence and evolutionary adaptation in the long term (West-Eberhard 1989; Hoffmann and Sgrò 2011). This could be especially important for juveniles and subadults that might be more vulnerable to stressful conditions than adults (e.g., Rivers et al. 2012). Importantly, adaptive phenotypic plasticity itself is the product of evolution (Baldwin 1896). Phenotypic plasticity can be divided into developmental plasticity and phenotypic flexibility (Piersma and van Gils 2010; Box 1). For developmental plasticity (Nettle and Bateson 2015), the environment during early ontogeny determines which one of two or more developmental pathways is adopted, leading to alternative adult phenotypes that cannot change to any of the other phenotypes (Ledón-Rettig et al. 2008). The resulting phenotype is often robust, being able to cope with environmental changes. For developmental plasticity to be adaptive, the population must have experienced particular environments in the past and, as a result, the developmental input to produce particular phenotypes under particular sets of conditions experiences positive selection (Nettle and Bateson 2015). In other words, individuals experience a particular environment during early development that is predictive of the environmental conditions they are likely to experience in later life. In the case of phenotypic flexibility, the trait can change back and forth (i.e., it is reversible), such as changes of the osmoregulatory hormone arginine vasopressin (AVP), whose levels increase when the organism has to save water, but later decrease again. Importantly, individuals may have both developmentally plastic traits and also phenotypically flexible traits.

One specific case of developmental plasticity is epigenetic variation (Piersma and van Gils 2010; Champagne 2013). Epigenetic mechanisms can also be influenced by hormones, which can link organizational effects of hormones to differences in behavior (Champagne and Rissman 2011). Importantly, epigenetic inheritance can occur via at least four different pathways, including cellular epigenetic inheritance (information transmitted via the gametes), developmental inheritance (information transmitted via maternal effects), behavioral inheritance (information transmitted via niche construction), and symbiotic inheritance (Jablonka and Lamb 2005, 2007; Piersma and van Gils 2010). Several recent reviews have focused on the links between epigenetics and phenotypic plasticity (e.g., Reik 2007; Champagne and Rissman 2011; Champagne 2013; Bale 2015; Dochtermann et al. 2015). However, the majority of studies on phenotypic plasticity provide little or no information on the underlying genetic and epigenetic mechanisms. Therefore, in the context of this review, we consider plasticity in general, rather than in relation to the absolute underlying mechanisms, by determining how variable the trait can be under varying environmental conditions.

Phenotypic plasticity has been hypothesized to be costly because of the need for the development and continued maintenance of neural structures (Dukas 1999), and sensory and/or response pathways involved in facilitating the flexible response (DeWitt et al. 1998; Mery and Burns 2010). However, estimating the actual costs of plasticity is difficult, and these costs might be more easily detected under certain conditions. For example, costs of plasticity are said to be greater in stressful conditions, and if plasticity utilizes resources that become scarce in response to the stress, these costs would be easier to detect (Steiner and Van Buskirk 2008). Van Buskirk and Steiner (2009) argue that the costs of plasticity are actually relatively weak and there might be a compromise or tradeoff between the fitness benefits and costs of greater phenotypic plasticity. One of the main costs of plasticity might be the time needed to mount an appropriate plastic response. Because plasticity seems to have surprisingly low costs, it has been argued recently that relaxed and variable selection intensities are more important constraints for the evolution of plasticity than are its costs (Murren et al. 2015).

Phenotypic plasticity, enabling a coping response to droughts, can either be evolutionary adaptations (adaptive phenotypic plasticity) or exaptations (exaptive phenotypic plasticity). For example, all mammals have the hormone AVP, which is important in osmoregulation, but not all mammals have experienced droughts as a selection pressure modifying the AVP system. Therefore, an increase of AVP plasma levels to reduce water loss during droughts might be higher in desert species, representing an adaptation to previous droughts, but would also occur—although maybe at a lower level—in species from nondesert environments when exposed to droughts, as an exaptation that evolved to save water under different environmental conditions, such as during winter or during periods when food has a lower water content due to seasonal changes. In sum, phenotypic plasticity can have very low flexibility (being fixed) or high flexibility, and represent adaptations or exaptations to droughts.

THREE PRIMARY STRESSORS OF ARID ENVIRONMENTS

Identifying the limits of phenotypic plasticity is foundational for assessing the degree to which individuals can respond to rapid environmental change. To evaluate which adaptations and exaptations could promote species persistence to increased periodicity and/or intensity of droughts, we will focus on species that currently inhabit areas characterized by periods of dryness (i.e., semideserts and deserts) with low annual precipitation and high aridity index (Box 1).

Deserts and semideserts are characterized by three principal environmental stressors, namely low water availability, low food availability, and extremes in temperature. The definition of "drought" is a relative one, taken to mean that current precipitation falls significantly below the long-term mean of a defined area (Dai 2011). In this context, drought is defined on a temporal scale and can occur in any environment. In contrast, naturally dry areas, such as deserts, experience permanent water shortage, and semideserts experience seasons with water shortage. An aridity index, used in conjunction with total rainfall, enables us to categorize habitats based on water availability (e.g., deserts versus semideserts; Nash and Engineering Group Working Party 2012). Hyperarid areas, such as the northeastern parts of the Negev Desert in Israel (Boroda et al. 2014), experience more than 12 months without rainfall, have less than 25mm rainfall/annum, and an average aridity index below 0.05, whereas arid areas, such as the Namib Desert in southwestern Africa (Viles and Goudie 2013), receive less than 100mm of rainfall per year, which is often very unreliable, and have an aridity index below 0.2 (Nash and Engineering Group Working Party 2012). In our review, we group both arid categories into "deserts," as the selection pressures in both habitat types will drive the establishment of specialized adaptations (see below). Semideserts, such as the Hardeveld of the Succulent Karoo in South Africa (Acocks 1988) and the Victoria River district in Australia (Webb et al. 2014), generally receive between 100 and 200mm of rainfall per year on average, have a moderate aridity index of between 0.2 and 0.5, and a 25–50% interannual rainfall variability (for definition see Box 1; Nash and Engineering Group Working Party 2012). We define "drought-affected areas" as those that are neither deserts nor semideserts, but experience unpredictable droughts, which might occur more often and become more intense in the future due to climate change (Box 1).

Deserts and semideserts are characterized by low food availability. Under these conditions, vegetation is typically sparse and patchily distributed across the landscape (Zhang et al. 2005). Consequently, food availability and quality is spatially and temporally variable and the availability of food resources might be unpredictable. For example, some areas might experience seasonal periods of dryness, which are relatively predictable (predictable environment; Box 1), while other areas might experience unpredictable, extreme climatic events leading to droughts (unpredictable environment; Box 1). Animals inhabiting these environments have to cope both with periods of low water availability and simultaneously low food availability (Willmer et al. 2000). One important consideration is that plants in deserts are also adapted to low water availability (Chaves et al. 2003), whereas plants in areas experiencing increased frequencies of droughts due to climate change may not be adapted to cope with dry conditions over long periods (Vicente-Serrano et al. 2013). As a result, food and water availability in drought-affected areas may have an even greater influence on animal populations than those in naturally dry areas.

Ambient temperature (T_a) is the third factor influencing species in naturally dry and in drought-affected areas. These habitats are often characterized by extreme daily fluctuations in T_a that can range from very cold at night to very hot during the day, a consequence of reduced absorption of heat by vegetation (Sarma et al. 2001), leading to greater reflection of solar radiation by the ground during the day (i.e., increased albedo; Charney et al. 1977), and rapid loss of heat at night (Sarma et al. 2001). Animals living in naturally dry environments have evolved under selective pressures of fluctuating temperature and tend to show specific behavioral, physiological, and/or morphological adaptations to these environmental extremes. For example, several large desert artiodactyls (Table 1), such as camels *Camelus dromedarius* (Elkhawad 1992; Ouajd and Kamel 2009) and Arabian oryx *Oryx leucoryx* (Hetem et al. 2012), utilize the carotid rete, a network of interlacing arterioles in the venous sinus, for selective brain cooling (Hetem et al. 2012). Venous blood cooled through the nasal countercurrent exchange mechanism (Ouajd and Kamel 2009) drains into the venous sinus, cooling the arterial blood moving to the brain (Mitchell et al. 1987).

To identify flexible traits that could confer a fitness advantage under conditions of increasing aridity, it is useful to study species that inhabit deserts or semideserts. Categorizing species living in these dry environments can help us to: identify key adaptations that have arisen in response to aridity; establish a comparative database of traits that can be used to compare with other species for which we lack information; and recognize traits in nondesert-adapted species that could promote responses to increasing aridity and droughts.

CATEGORIZING SPECIES FROM DESERTS AND SEMIDESERTS AS ENDURERS OR EVADERS

Willmer et al. (2000) classified desert animals into two main groups—physiological endurers, such as the Arabian oryx, which are able to tolerate environmental extremes using physiological and morphological adaptations (Table 1) and behavioral evaders, such as Merriam's kangaroo rat

TABLE 1

Characteristic desert adaptations of physiological endurers and behavioral evaders

Behavior	Physiology	Morphology	Principal examples and references
Mechanisms for coping with water restriction			**Physiological endurers** [1] Camel *Camelus dromedarius* [a] Schmidt-Nielsen et al. 1956 [b] Macfarlane et al. 1963 [c] Schmidt-Nielsen et al. 1967 [d] Siebert and Macfarlane 1971 [e] Maloiy 1972 [f] Siebert and Macfarlane 1975 [g] Emmanuel et al. 1976 [h] Young 1976 [i] Finberg et al. 1978 [j] Schmidt-Nielsen et al. 1981a [k] Yagil 1985 [l] Gihad et al. 1989 [m] Wilson 1989 [n] Elkhawad 1992 [o] Ben Goumi et al. 1993 [p] Faye 1997 [q] Selim et al. 1999 [r] Dereje and Udén 2005 [s] Ouajd and Kamel 2009 [2] Arabian oryx *Oryx leucoryx* [a] Hetem et al. 2010 [b] Stewart 1963 [c] Spalton 1999 [d] Williams et al. 2001 [e] Ostrowski et al. 2002 [f] Ostrowski et al. 2003 [g] Ostrowski et al. 2006 [h] Gilad et al. 2008 **Behavioral evaders** [3] Golden spiny mouse *Acomys russatus* [a] Shkolnik and Borut 1969 [b] Castel and Abraham 1972 [c] Haim and Borut 1981 [d] Rubal et al. 1992 [e] Haim and Izhaki 1993 [f] Kam and Degen 1993 [g] Merkt and Taylor 1994 [h] Haim and Rozenfeld 1995 [i] Mendelssohn and Yom-Tov 1999 [j] Ron and Haim 2001 [k] Shanas and Haim 2004 [l] Ehrhardt et al. 2005 [m] Gutman et al. 2006
• Can go for extended periods without drinking [1l,o], [2b,e,f], shows water independence [4c], or may survive on water gained through food [2d,e,f,g,h], [3f,k], [4j] • Reduced food intake [1o]	• Constant [1a,b, but see 1o] or decreased [1f,s] plasma volume • Increased plasma Na [1b,d,f,i,o,s], protein [1f,s], [2e], sugar [1s], cholesterol [1s], and urea [2g, but see 1g,k] concentration • Increased plasma arginine vasopressin [1o], [3b,k], aldosterone [1i], and renin [1i,o] secretion • Decreased insulin secretion [3k] • Maintenance [2g] or increased plasma osmolality [2e], [3k] • Increased urine concentration [1o,s], [2g], [3a,c,j,k], [4a,e,j] • Reduced urine production [1f,o,s] and volume [1a,b,i], [2g], [3k] • Low glomerular filtration rate [1f,s] • Increased urine Na excretion [1o] • High tolerance to salt [1e], [3k] • Excretion of relatively dry feces [1a,b,f,i], [2g], [4b,j] • Reduction in metabolic rate [1c], [2d,h], [3a,c,d,e,f,g,j,m], [4j] • Reduction in evaporative water loss [1a,b,i], [2d,g], [4c,j] • Production of metabolic water [2d], [4c] • Low water turnover [1a,b,i] • Increased urine creatinine concentration [2g] and decreased creatinine clearance [1s] • Decreased respiration rate [1c,k,m,s], [2g] • Reduction of digestive secretions [1s]	• Nasal countercurrent exchange system [1j,s], [4d,j] • Well-developed nasal glands [1s] • Nostrils can close completely [1s] • Kidney with long loops of Henle and well-developed medulla [1s] • Increased tubular reabsorption of the kidney [1s], [2g] • Thin erythrocyte with increased surface area: volume ratio [1s]	
Mechanisms for coping with food restriction			
• Specialist feeder [1r,s], [4i] or favors specific food type [2c,d], [3i] • Feeds on water-rich invertebrates [3i] or green matter [1s], [2g], or digs up water-rich underground plant storage organs [2c] • Stores/caches food [2b] • Exploits newly emergent food material [2g] • Migratory behavior [1f,l,s), [2b] or shifting home range to areas with ephemeral high food abundance [2h], [4h]	• Maintenance [3f,m] or minimal loss of body mass [1a,f,s], [2g] for physiological endurers, but tolerance to loss of body mass [3j,k] for behavioral evaders • Mobilization of hepatic lipids [1s] and fatty acids [2g] to fuel metabolism • Decreased leptin production [2g], [3m] • Good aptitude for recycling nitrogen [1g] • Enters torpor [3l,m]	• Reduction in organ size/volume [2g] • Strong digestive efficiency [1q,s], [2g] • Storage of fat/lipids [1r], [3m]	

continued

TABLE 1
Continued

Behavior	Physiology	Morphology	Principal examples and references
Mechanisms for coping with extreme temperatures			^{4}Merriam's kangaroo rat *Dipodomys merriami* ^{a} Schmidt-Nielsen et al. 1948 ^{b} Schmidt-Nielsen and Schmidt-Nielsen 1951 ^{c} Schmidt-Nielsen and Schmidt-Nielsen 1952 ^{d} Jackson and Schmidt-Nielsen 1964 ^{e} Carpenter 1966 ^{f} Soholt 1974 ^{g} Schmidt-Nielsen et al. 1970 ^{h} Brown and Munger 1985 ^{i} Mares 1993 ^{j} Nagy 1994
• Utilizes burrows/nests [4f,j], cover [3h], or retreats to shade when available [1s], [2d,g] • Utilizes substrate surface for conductance of body heat [2b,d] • Primary activity: crepuscular or nocturnal [2b,d,g] • Decreased activity [2g] • Bipedal locomotion [2b] • Minimizes exposure to sun by altering body posture [1p,s] • Does not pant [1c,s]	• Adaptive heterothermy [1o], [2a,f] • Adaptive hyperthermia [1c] • Storage of body heat during the day and dissipation at night [1c] • Higher stable hematocrit [1p], [2e] • Increased erythrocyte circulation efficiency [1s], erythrocyte volume flexibility [1s], and enhanced erythrocyte life span [1s] • Low cardiac rate and low blood pressure [1s] • Selective brain cooling [1n,s] • Enters torpor [3l,m]	• Subdivision of nasal sinus [1j], [4d,g] • Limited subcutaneous fat deposition [1h,s] • Short coarse pelage [2b] • Light-colored pelage for reflecting solar radiation and reducing heat uptake [2b] • Maintenance of nonshivering thermogenesis [3e] • Dark pigmented skin [3h]	

Superscript numbers designate species (endurers: ^{1}*Camelus dromedarius,* ^{2}*Oryx leucoryx*; evaders: ^{3}*Acomys russatus,* ^{4}*Dipodomys merriami*) and letters designate associated references, which appear in Appendix 1.

Dipodomys merriami, which are able to escape environmental extremes behaviorally (Table 1). Later, Ward (2009) recognized that endurers are typically large-bodied animals while evaders are typically small-bodied animals.

The endurer-evader concept is useful for categorizing desert specialists primarily in relation to one characteristic of arid environments, namely extremes in environmental temperature (T_a). However, this concept is a simplistic approach, based on the assumption that it is easier for small animals to find refuge in the shade than it is for large animals, while in fact we know that large animals will use any little shade they can find in their environment to avoid high T_a (Williams et al. 2001; Ostrowski et al. 2006; Ouajd and Kamel 2009). Although this concept, to a degree, considers the ability of animals to be behaviorally flexible (e.g., seeking shade), it generally assumes that animals have limited flexibility in their behavioral and morphological responses and neglects the important aspect of exaptive phenotypic plasticity, which we consider to be a key mechanism to cope with change, including droughts. As such, the endurer-evader categorization provides an initial framework from which to further identify important traits to be studied in nondesert-adapted species for coping with heat, food, and water restriction as a consequence of droughts.

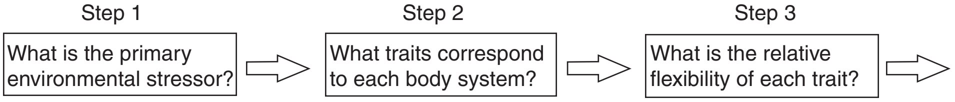
A Novel Classification: The Adaptive Triquetra

Given the simplicity of the endurer-evader concept, we developed a three-tier system, the adaptive triquetra, that categorizes adaptations to aridity instead of categorizing species (Box 2). Having a species categorization is not helpful for generalizing adaptations across species, and importantly overlooks the underlying general adaptive responses to drought. We stress that providing this framework is only the first step. The framework we develop here must be validated in the future by data from a variety

BOX 2

Using the adaptive triquetra system

The adaptive triquetra considers a three-step approach that can be used for either: directly assessing resilience in species for which good biological information already exists; and/or for identifying areas where more research may be required. For example, if someone is interested in a particular species, they might have good knowledge of its life history, but little knowledge about its environment, and could therefore focus on establishing which environmental stressor is more important before understanding how the species could respond. Similarly, someone might have good knowledge about the physiology of a species, but little about its behavior. Focus could be placed on how that species responds behaviorally to particular environmental stressors.



Step 1: What is the Primary Environmental Stressor? (Water, Food, Temperature)
Consider the environment in which the species of interest occurs, and what the primary stressor would be, taking microhabitat use into account (Tables 2a, b, and c). This is important because not all habitats will experience the same intensity of change and some environments will buffer some stressors better than others. For example, temperature extremes might be more critical in subtropical areas experiencing droughts than in temperate or polar climate zones. For a diurnal burrowing rodent, such as Brants's whistling rat *Parotomys brantsii* (Jackson et al. 2004), extreme temperatures may not represent a problem due to the buffering effects of burrows.

Step 2: What Traits Correspond to Each Body System? (Behavioral, Physiological, Morphological)
This step considers the presence of, and number of traits, corresponding to each system (Tables 2a, b, and c). The greater the number of traits allowing for coping with the stressors, the more likely it is that the species might be able to cope with rapid environmental changes. However, this will also heavily depend on the flexibility of the traits (Step 3).

Step 3: What is the Relative Flexibility of Each Trait? (Fixed, Developmentally Plastic, Flexible)
The ability of a species to persist under increasing likelihood of droughts is dependent on how individuals are able to respond with the traits they possess. An individual has a greater likelihood of responding to unpredictable events if it has greater flexibility (Tables 2a, b, and c). The interaction between two traits can also change the potential for resilience. For example, the interaction between a fixed morphological trait and a flexible behavioral trait is important for African striped mice *Rhabdomys pumilio* in the Succulent Karoo of South Africa. Striped mice have dark skin (Schradin and Pillay 2005), which facilitates thermoregulation through basking (Schradin et al. 2007), allowing mice to conserve energy in the early morning when temperatures are lower.

of different species and different research programs to determine its accuracy, and then modified as appropriate. Our comprehensive review of adaptations to droughts of specialist and nonspecialist species provides the foundational information needed for such future research programs on the effects of droughts on individual survival and population and species persistence.

The term "triquetra" is derived from the Latin *tri-* "three" and *quetrus* "cornered," emphasizing the three-tiered nature of this classification system, as well as the interconnectedness of its parts. Our adaptive triquetra considers: which stressor is addressed (water restriction, food restriction, or extremes in T_a); which body system mounts an appropriate adaptive response (behavior, physiology, or morphology); and the nature of the trait (fixed versus flexible). Although these stressors are often interlinked (e.g., plants are dependent on water and, therefore, food is likely to be restricted if water is restricted), we argue that each stressor should first be examined independently, because some species might have adaptations or exaptations that facilitate better coping with one stressor compared to another. This is especially important for designing effective management strategies to support populations at risk. For example, during a severe drought period (1981–1984) in southern Africa, mortality of herbivores was quite high, but in some areas, such as the northeastern Tuli region of Botswana, mixed grazers-browsers (e.g., impala *Aepyceros melampus*) were little affected compared to grazers (e.g., blue wildebeest *Connochaetes taurinus* and zebra *Equus burchelli*), whereas in other areas, such as the central Kruger National Park in South Africa, the same grazers (blue wildebeest and zebra) were unaffected (Walker et al. 1987). Walker et al. (1987) suggest that mortality in Klaserie Reserve in South Africa (adjacent to the Kruger National Park) was heightened by close spacing of permanent water sources. Heavy grazing occurred around these areas, eliminating reserve stands. Instead, dropping fences and widely spacing water sources would have allowed animals to move between areas, accessing forage and promoting survival. Therefore, supplemental feeding in Klaserie could have been highly beneficial to promote species survival.

WHICH STRESSOR IS ADDRESSED?

The first step of the adaptive triquetra model is to identify which of the three primary stressors has driven the evolution of the particular adaptation in question (Box 2). First, low water availability leads to the need for improved osmoregulation, resulting in adaptations that reduce water loss or increase water intake (Table 2a). Second, since food availability is a direct consequence of water restriction, there is a need for improved energy storage mechanisms, resulting in adaptations that minimize energy loss or maximize energy gain (Table 2b). These include both intrinsic adaptations, such as storage of body fat (e.g., Mongolian gerbils *Meriones unguiculatus*; Zhang and Wang 2007), and extrinsic adaptations, such as food caching (e.g., kangaroo rats *Dipodomys* spp.; Randall 1993). Third, high T_a leads to the need for improved thermoregulatory ability, resulting in adaptations that decrease the risk of overheating or increase the ability to tolerate heat (Table 2c).

These three stressors are not fully independent of each other. For example, in mammals, the need for improved thermoregulation is directly related to the need to save water because the ability to reduce water loss in mammals is constrained by the need for evaporative cooling to reduce overheating (Taylor 1970). Furthermore, water can be obtained from food directly (e.g., consumption of succulents by viscacha rats *Octomys mimax*; Bozinovic and Contreras 1990) and/or indirectly (e.g., use of metabolic water by the desert pocket mouse *Chaetodipus penicillatus*; Grubbs 1980). However, most animals cannot obtain sufficient water from their food to survive without access to freestanding water or condensed water. For species that are dependent on freestanding water, the primary stressor will be water availability, whereas for water-independent species, the primary stressor will be food availability.

TABLE 2A

The adaptive triquetra system for the environmental stressor water restriction

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
Behavior	Flexible	Consumes water-rich food resources or green matter	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin and Pillay 2005b		
			• Black-tailed tree rat *Thallomys nigricauda*	Frean et al. 1998		
			• Springbok *Antidorcas marsupialis*	Nagy 1994		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Stewart 1963		
			• Banner-tailed kangaroo rat *Dipodomys spectabilis*	Schmidt-Nielsen and Schmidt-Nielsen 1952		
		Reduces food intake	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin et al. 2010		
			• Kirk's dik-dik *Madoqua kirkii*	Maloiy 1973		
			• Namaqua rock rat *Aethomys namaquensis*	Buffenstein 1985		
			Desert			
			• Camel *Camelus dromedarius*	Ben Goumi et al. 1993		
			• Jackrabbit *Lepus californicus*	Reese and Haines 1978		
		Alters home range or changes distribution to increase access to water/take advantage of new water sources	**Semidesert**			
			• African buffalo *Syncerus caffer*	Funston et al. 1994		
			• Mehely's horseshoe bat *Rhinolophus mehelyi*	Salsamendi et al. 2012		
			Desert			
			• Desert mule deer *Odocoileus hemionus crooki*	Rautenstrauch and Krausman 1989		
			• Hairy-footed gerbil *Gerbillurus paeba*	Christian 1980		
		Drinks sea water or tolerates high salt content in food	**Semidesert**			
			• Mongolian gerbil *Meriones unguiculatus*	Winkelmann and Getz 1962		
			• Tammar wallaby *Macropus eugenii*	Purohit 1971		
			Desert			
			• Desert bighorn sheep *Ovis canadensis nelsoni*	Turner 1979		
			• Fawn hopping mouse *Notomys cervinus*	MacMillen and Lee 1969		
	Fixed	Can go for extended periods without drinking, but is not independent of water	**Semidesert**			
			• Eland *Tragelaphus oryx*	King et al. 1975		
			• European free-tailed bat *Tadarida teniotis*	Rainho 2007		
			Desert			
			• Camel *Camelus dromedarius*	Schmidt-Nielsen et al. 1956		
			• Eastern Patagonian laucha *Eligmodontia typus*	Mares 1977a		
Physiology	Flexible	Increases arginine vasopressin secretion and/or replenishes AVP store	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schoepf and Schradin 2014		
			• Degu *Octodon degus*	Bozinovic et al. 2003		
			• Ethiopian Somali goat *Capra aegagrus hircus*	Mengistu et al. 2007		

continued

TABLE 2A
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
			Desert			
			• Camel *Camelus dromedarius*	Ben Goumi et al. 1993		
			• Golden spiny mouse *Acomys russatus*	Castel and Abraham 1972		
		Increased plasma aldosterone and/or renin secretion, often in response to rehydration	**Semidesert**			
			• Awassi sheep *Ovis aries*	Jaber et al. 2004		
			• Common spiny mouse *Acomys cahirinus*	Bukovetzky et al. 2012		
			Desert			
			• Black Bedouin goat *Capra aegagrus hircus*	Wittenberg et al. 1986		
			• Tarabul's gerbil *Gerbillus tarabuli*	Saadi and Lebaili 2012		
		Decreased thyroxine secretion	**Semidesert**			
			• Awassi sheep *Ovis aries*	Jaber et al. 2011		
			• Cactus mouse *Peromyscus eremicus*	Hulbert et al. 1985		
			Desert			
			• Marwari sheep *Ovis aries*	Kataria and Kataria 2006		
			• Merriam's kangaroo rat *Dipodomys merriami*	Yousef and Johnson 1975		
		Increased urine concentration	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Buffenstein 1984		
			• Bush karoo rat *Otomys unisulcatus*	Jackson et al. 2004		
			• Kirk's dik-dik *Madoqua kirkii*	Hoppe 1977		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Merriam's kangaroo rat *Dipodomys merriami*	Nagy 1994		
		Reduced urine production and volume	**Semidesert**			
			• Bushy-tailed hairy-footed gerbil *Gerbillus vallinus*	Downs and Perrin 1990		
			• Dorcas gazelle *Gazella dorcas*	Ghobrial 1970		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Spinifex hopping mouse *Notomys alexis*	MacMillen and Lee 1969		
		Excretion of relatively dry feces	**Semidesert**			
			• Kirk's dik-dik *Madoqua kirkii*	Maloiy 1973		
			• Springhare *Pedetes capensis*	Peinke and Brown 1999		
			Desert			
			• Agile kangaroo rat *Dipodomys agilis*	Schmidt-Nielsen and Schmidt-Nielsen 1952		
			• Desert bighorn sheep *Ovis canadensis nelsoni*	Turner 1970		
		Decreased respiration rate	**Semidesert**			
			• Eland *Tragelaphus oryx*	Taylor 1969		
			• Rock hyrax *Procavia capensis*	Rübsamen and Kettembeil 1980		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Spinifex hopping mouse *Notomys alexis*	Withers et al. 1979		

continued

TABLE 2A
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Utilization of metabolic water to reduce overall water loss	**Semidesert**			
			• Mongolian gerbil *Meriones unguiculatus*	Winkelmann and Getz 1962		
			• Siorhi goat *Capra aegagrus hircus*	Misra and Singh 2002		
			Desert			
			• Desert pocket mouse *Chaetodipus penicillatus*	Grubbs 1980		
			• Rüppell's fox *Vulpes rueppelli*	Williams et al. 2002		
		Increased tubular reabsorption of water from the kidney or the bladder	**Semidesert**			
			• Degu *Octodon degus*	Bozinovic et al. 2003		
			• Kirk's dik-dik *Madoqua kirkii*	Maloiy et al. 1988		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Agile kangaroo rat *Dipodomys agilis*	Howell and Gersh 1935		
		Maintenance or higher hematocrit	**Semidesert**			
			• Awassi sheep *Ovis aries*	Laden et al. 1987		
			• Springhare *Pedetes capensis*	Peinke and Brown 1999		
			Desert			
			• Pronghorn *Antilocapra americana*	McKean and Walker 1974		
			• Spinifex hopping mouse *Notomys alexis*	Heimeier and Donald 2006		
		Mobilization of hepatic lipids and fatty acids to fuel metabolism * And/or in response to food availability	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Fourie and Haim 1980		
			• Least gerbil *Gerbillus pusillus*	Buffenstein 1984		
			• Awassi sheep *Ovis aries*	Jaber et al. 2011		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Hairy-footed gerbil *Gerbillurus paeba*	Buffenstein 1985		
		Enters torpor (or hibernation) * And/or in response to temperature extremes and food restriction. Information on this topic is limited and equivocal (Geiser 2010) Information on large mammals is lacking in the literature	**Semidesert**			
			• Grey mouse lemur *Microcebus murinus*	Schmid and Speakman 2009		
			• Cactus mouse *Peromyscus eremicus*	MacMillen 1965		
			Desert			
			• Pinyon mouse *Peromyscus truei*	Bradford 1974		
			• Stripe-faced dunnart *Sminthopsis macroura*	Song and Geiser 1997		
	Fixed	Shows water independence	**Semidesert**			
			• Drylands vesper mouse *Calomys musculinus*	Mares 1977b		
			• Springbok *Antidorcas marsupialis*	Nagy and Knight 1994		
			Desert			
			• Desert leopard *Panthera pardus*	Bothma and Riche 1984		
			• Peruvian desert mouse *Phyllotis gerbillus*	Koford 1968		

continued

TABLE 2A
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Maintenance or tolerance of decreased plasma volume	**Semidesert**			
			• German mutton merino sheep *Ovis aries*	Degen 1977		
			• Springhare *Pedetes capensis*	Peinke and Brown 1999		
			Desert			
			• Camel *Camelus dromedarius*	Siebert and Macfarlane 1975		
			• White-tailed antelope squirrel *Ammospermophilus leucurus*	Hartman and Morton 1973		
		Maintenance or increased plasma osmolality (sodium, protein, sugar, cholesterol, and/or urea)	**Semidesert**			
			• Degu *Octodon degus*	Bozinovic et al. 2003		
			• Tammar wallaby *Macropus eugenii*	Kinnear et al. 1968		
			Desert			
			• Barmer goat *Capra aegagrus hircus*	Khan et al. 1978		
			• Desert wood rat *Neotoma lepida*	MacMillen and Lee 1967		
		Tolerates increased urinary urea concentration	**Semidesert**			
			• Kirk's dik-dik *Madoqua kirkii*	Maloiy 1973		
			• Namib brush-tailed gerbil *Gerbillurus setzeri*	Buffenstein et al. 1985		
			Desert			
			• Camel *Camelus dromedarius*	Emmanuel et al. 1976		
			• Kowari *Dasyuroides byrnei*	Haines et al. 1974		
		Production of allantoin precipitate in place of urea * Lack of evidence in larger mammals	**Semidesert**			
			• Bushveld gerbil *Gerbilliscus leucogaster*	Buffenstein et al. 1985		
			• Cape gerbil *Gerbilliscus afra*	Buffenstein et al. 1985		
			Desert			
			• Dune hairy-footed gerbil *Gerbillurus tytonis*	Downs and Perrin 1991		
			• Gerbil mouse *Malacothrix typica*	Buffenstein et al. 1985		
		Low glomerular filtration rate	**Semidesert**			
			• Kirk's dik-dik *Madoqua kirkii*	Rugangazi and Maloiy 1988		
			• Least gerbil *Gerbillus pusillus*	Buffenstein 1984		
			Desert			
			• Black Bedouin goat *Capra aegagrus hircus*	Wittenberg et al. 1986		
			• Merriam's kangaroo rat *Dipodomys merriami*	Schmidt-Nielsen and Schmidt-Nielsen 1952		
		Reduced metabolic rate	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Haim and Fourie 1980a		
			• Damara ground squirrel *Xerus princeps*	Haim et al. 1986		
			• Kirk's dik-dik *Madoqua kirkii*	Hoppe 1977		
			Desert			
			• Euro *Macropus robustus erubescens*	Dawson et al. 1975		
			• Viscacha rat *Octomys mimax*	Bozinovic and Contreras 1990		

continued

TABLE 2A
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Reduction in evaporative water loss	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Christian 1978		
			• Kirk's dik-dik *Madoqua kirkii*	Maloiy 1973		
			• Panamint kangaroo rat *Dipodomys panamintinus*	Hinds and MacMillen 1985		
			Desert			
			• Desert kangaroo rat *Dipodomys deserti*	Hinds and MacMillen 1985		
			• Gemsbok *Oryx gazella*	Taylor 1969		
		Low water turnover	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Scantlebury et al. 2006		
			• Shaw's jird *Meriones shawi*	de Rouffignac and Morel 1965		
			• Tammar wallaby *Macropus eugenii*	Kinnear et al. 1968		
			Desert			
			• Namib desert golden mole *Eremitalpa granti namibensis*	Fielden et al. 1990		
			• Red kangaroo *Macropus rufus*	Dawson et al. 1975		
		Good aptitude for recycling (urea) nitrogen	**Semidesert**			
			• Rock hyrax *Procavia capensis*	Hume et al. 1980		
			• Tammar wallaby *Macropus eugenii*	Kennedy and Hume 1978		
			Desert			
			• Black Bedouin goat *Capra aegagrus hircus*	Silanikove et al. 1980		
			• Fat sand rat *Psammomys obesus*	Kaißling et al. 1975		
		Tolerates some level of dehydration	**Semidesert**			
			• Desert sheep *Ovis aries*	El-Hadi 1986		
			• Springhare *Pedetes capensis*	Peinke and Brown 1999		
			Desert			
			• Burro *Equus asinus*	Yousef et al. 1970		
			• Peruvian desert mouse *Phyllotis gerbillus*	Koford 1968		
Morphology	Flexible	Storage of water in the stomach/ rumen/ pharyngeal pouch * Lack of evidence in smaller mammals	**Semidesert**			
			• African elephant *Loxodonta africana*	Leggett 2004		
			Desert			
			• Camel *Camelus dromedarius*	Elkhawad 1992		
	Fixed	Nasal countercurrent exchange system * Also provides a benefit against high temperatures	**Semidesert**			
			• Kirk's dik-dik *Madoqua kirkii*	Kamau et al. 1984		
			• Little red kaluta *Dasykaluta rosamondae*	Withers and Cooper 2009		
			Desert			
			• Camel *Camelus dromedarius*	Elkhawad 1992		
			• Greater bilby *Macrotis lagotis*	Hulbert and Dawson 1974		

continued

TABLE 2A

Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Kidney with well-developed medulla and long loops of Henle	**Semidesert**			
			- Salt flat mouse *Salinomys delicatus*	Diaz and Ojeda 1999		
			- Tammar wallaby *Macropus eugenii*	Kinnear et al. 1968		
			Desert			
			- Camel *Camelus dromedarius*	Ouajd and Kamel 2009		
			- Darwin's leaf-eared mouse *Phyllotis darwini darwini*	Vermeulen and Nel 1988		
		Elongated renal papilla * Large desert mammals do not show this characteristic (Mbassa 1988)	**Semidesert**			
			- Black-tailed tree rat *Thallomys nigricauda*	Frean et al. 1998		
			- Salt flat mouse *Salinomys delicatus*	Diaz and Ojeda 1999		
			Desert			
			- Egyptian gerbil *Gerbillus gerbillus*	Khalil and Tawfic 1963		
			- Plains viscacha rat *Tympanoctomys barrerae*	Diaz and Ojeda 1999		

Systems providing an appropriate adaptive response (behavior, physiology, or morphology); flexibility of traits (flexible or fixed). Fixed traits also include traits that show developmental plasticity during ontogeny. Researchers should identify the relative plasticity of fixed traits in particular environments (i.e., the reaction norm). A list of traits that could confer a fitness advantage under increasing likelihood of droughts, in relation to the three parts of the triquetra. We have included examples of a large- and small-bodied semidesert and desert species for each trait. The final two columns can be used by researchers and nature conservationists to categorize their study species, to identify areas where information is lacking, and to reach conclusions about the relative status of their species. The selected references appear in Appendix 1.

TABLE 2B

The adaptive triquetra system for the environmental stressor food restriction.

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
Behavior	Flexible	Stores/caches food/scatter hoards	**Semidesert**			
			- Black-backed jackal *Canis mesomelas*	Nel 1984		
			- Giant kangaroo rat *Dipodomys ingens*	Shaw 1934		
			Desert			
			- Desert kit fox *Vulpes macrotis arsipus*	Cypher 2003		
			- Wagner's gerbil *Gerbillus dasyurus dasyurus*	Hatough-Bouran 1990		
		Exploits newly emergent food material	**Semidesert**			
			- African striped mouse *Rhabdomys pumilio*	Schradin and Pillay 2006		
			- Vicuña *Vicugna vicugna*	Donadio et al. 2012		
			Desert			
			- Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			- Piute ground squirrel *Spermophilus mollis*	Rickart 1986		

continued

TABLE 2B
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Migratory behavior or shifting home range (mobility) to areas with higher food abundance	**Semidesert**			
			• African buffalo *Syncerus caffer*	Funston et al. 1994		
			• African striped mouse *Rhabdomys pumilio*	Schradin and Pillay 2006		
			• Round-eared sengi *Macroscelides proboscideus*	Schubert et al. 2009		
			Desert			
			• Banner-tailed kangaroo rat *Dipodomys spectabilis*	Brown and Munger 1985		
			• Desert mule deer *Odocoileus hemionus crooki*	Albert and Krausman 1993		
		Coprophagy	**Semidesert**			
			• Feral horse *Equus caballus*	Krysl et al. 1984		
			• Southern mountain cavy *Microcavia australis*	Sassi et al. 2010		
			Desert			
			• African elephant *Loxodonta africana*	Leggett 2004		
			• Noki *Petromus typicus*	Rathbun and Rathbun 2005		
		Generalist feeder	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Curtis and Perrin 1979		
			• Ash-grey mouse *Pseudomys albocinereus*	Murray et al. 1999		
			• Tammar wallaby *Macropus eugenii*	Kinnear et al. 1968		
			Desert			
			• Camel *Camelus dromedarius*	Dereje and Udén 2005		
			• Grey leaf-eared mouse *Graomys griseoflavus*	Giannoni et al. 2001		
		Dietary flexibility	**Semidesert**			
			• Drylands vesper mouse *Calomys musculinus*	Giannoni et al. 2005		
			• Springbok *Antidorcas marsupialis*	Nagy and Knight 1994		
			Desert			
			• Brush-tailed mulgara *Dasycercus blythi*	Chen et al. 1998		
			• Sand gazelle *Gazella marica*	Schulz et al. 2013		
	Fixed	Specialist feeder	**Semidesert**			
			• Black-tailed tree rat *Thallomys nigricauda*	Frean et al. 1998		
			• Springbok *Antidorcas marsupialis*	Nagy 1994		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Spalton 1999		
			• Fat sand rat *Psammomys obesus*	Daly and Daly 1973		
Physiology	Flexible	Mobilization of hepatic lipids and fatty acids to fuel metabolism * And/or in response to water availability	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Fourie and Haim 1980		
			• Least gerbil *Gerbillus pusillus*	Buffenstein 1984		
			• Awassi sheep *Ovis aries*	Jaber et al. 2011		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Hairy-footed gerbil *Gerbillurus paeba*	Buffenstein 1985		

continued

TABLE 2B
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Enters torpor (or hibernation) * And/or in response to water restriction and temperature extremes. Information on large mammals is lacking in the literature	**Semidesert**			
			• Grey mouse lemur *Microcebus murinus*	Schmid 2001; Schmid and Speakman 2009		
			• North African elephant shrew *Elephantulus rozeti*	Lovegrove et al. 2001		
			Desert			
			• Round-tailed ground squirrel *Spermophilus tereticaudus*	Hudson 1964		
			• Stripe-faced dunnart *Sminthopsis macroura*	Song and Geiser 1997		
		Reduced leptin secretion in response to starvation, to reduce mobilization of fatty acid reserves	**Semidesert**			
			• Awassi sheep *Ovis aries*	Jaber et al. 2011		
			• Common spiny mouse *Acomys cahirinus*	Bukovetzky et al. 2012		
			• **Desert**			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Golden spiny mouse *Acomys russatus*	Gutman et al. 2008		
		Ecological leptin hypothesis * This dissociation between leptin and fattening is lacking in the literature	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin et al. 2014		
			• Mongolian gerbil *Meriones unguiculatus*	Zhang and Wang 2007		
			• **Desert**			
			• Golden spiny mouse *Acomys russatus*	Gutman et al. 2006		
	Fixed	Maintenance, tolerance, or minimal loss of body mass	**Semidesert**			
			• Least gerbil *Gerbillus pusillus*	Buffenstein 1984		
			• Springbok *Antidorcas marsupialis*	Nagy 1994		
			Desert			
			• Camel *Camelus dromedarius*	Siebert and Macfarlane 1975		
			• Sandy inland mouse *Pseudomys hermannsburgensis*	MacMillen and Lee 1967		
Morphology	Flexible	Flexibility in length/mass of portions of the gut/intestine/and mass of other vital organs (e.g., liver, kidneys, cecum)	**Semidesert**			
			• Burro *Equus asinus*	Sneddon et al. 2006		
			• Southern mountain cavy *Microcavia australis*	Sassi et al. 2007		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Darwin's leaf-eared mouse *Phyllotis darwini rupestris*	Naya et al. 2005		
		Storage of fat/lipids (i.e., fattening)	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin and Pillay 2005a		
			• Awassi sheep *Ovis aries*	Khachadurian et al. 1966		
			• Fat-tailed dunnart *Sminthopsis crassicaudata*	Morton 1978		
			Desert			
			• Camel *Camelus dromedarius*	Elkhawad 1992		
			• Golden spiny mouse *Acomys russatus*	Gutman et al. 2006		

continued

TABLE 2B
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
	Fixed	Strong digestive efficiency	**Semidesert**			
			• Degu *Octodon degus*	Veloso and Bozinovic 1993		
			• Kirk's dik-dik *Madoqua kirkii*	Hoppe 1977		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Great Basin pocket mouse *Perognathus parvus*	Schreiber 1979		

Systems providing an appropriate adaptive response (behavior, physiology, or morphology); flexibility of traits (flexible or fixed). Fixed traits also include traits that show developmental plasticity during ontogeny. Researchers should identify the relative plasticity of fixed traits in particular environments (i.e., the reaction norm). A list of traits that could confer a fitness advantage under increasing likelihood of droughts, in relation to the three parts of the triquetra. We have included examples of a large- and small-bodied semidesert and desert species for each trait. The final two columns can be used by researchers and nature conservationists to categorize their study species, to identify areas where information is lacking, and to reach conclusions about the relative status of their species. The selected references appear in Appendix 1.

WHICH BODY SYSTEM MOUNTS AN APPROPRIATE ADAPTIVE RESPONSE?

The second step of the adaptive triquetra model is to identify which body systems have changed in response to the environmental challenges associated with increasing droughts (Box 2). We expect that all species may use multiple adaptive strategies at the behavioral, physiological, and morphological levels to adapt to, and cope with, the prevailing environment. First, animals may use specific behaviors to avoid harsh environmental conditions. Animals can reduce water stress by choosing to consume water-rich food, by reducing their food intake (thereby minimizing water required for digestion), and/or by reducing respiration to minimize evaporative water loss (Table 2a). Animals can reduce food stress by consuming newly emergent food (e.g., plant/insect), by altering the diet to include a wider variety of food types (opportunistic feeders), or by storing or caching food (Table 2b). To avoid temperature extremes, animals can employ a range of behavioral strategies to minimize overheating, such as utilizing burrows/cover/shade that buffer temperature extremes and also minimize water loss, or altering body posture to minimize exposure to the sun (Tables 2a, b, and c). Altering activity levels by shifting to nocturnal activity is another strategy minimizing exposure to lethal diurnal temperatures, as well as minimizing water loss (Tables 2a and c).

Second, physiological traits of osmoregulation, metabolism, and thermoregulation enable individuals to offset the limited resources of water and food, and to respond to thermal stress (Tables 2a, b, and c). We need to differentiate between physiological mechanisms of the three processes and the physiological markers indicating deviation from the optimal physiological state, which could suggest that the individual is struggling to maintain homeostasis. For example, decreased thyroxine levels could indicate a mechanism to save metabolic energy (Yousef and Johnson 1975), while reduced blood glucose levels might not be an adaptation, but rather a physiological marker of deviation (stress) from the optimal physiological state (McCue 2010).

Recently, the term allostasis has been used to describe the physiological mechanisms that maintain stability (homeostasis of blood glucose, pH, and O_2 levels) through change of the osmoregulatory, metabolic, and/or thermoregulatory system (McEwen and Wingfield 2003). Importantly, allostasis depends on the energy availability in the environment, which decreases during droughts, leading to allostasis overload type 1 (energy expenditure to cope with environmental stressors is greater than energy intake; McEwen and

TABLE 2C

The adaptive triquetra system for the environmental stressor extremes in environmental temperature (T_a)

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
Behavior	Flexible	Utilizes burrows/nests, cover, or retreats to shade when available	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin 2005		
			• Giant kangaroo rat *Dipodomys ingens*	Randall 1997		
			• Southern hairy-nosed wombat *Lasiorhinus latifrons*	Walker et al. 2007		
			Desert			
			• Euro *Macropus robustus erubescens*	Dawson and Brown 1970		
			• Sundevall's jird *Meriones crassus crassus*	Lewis et al. 1965		
		Utilizes substrate surface for conductance of body heat * Information is lacking for large semidesert species	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin 2006		
			• Cape ground squirrel *Xerus inauris*	Marsh et al. 1978		
			• Suricate *Suricata suricatta*	Hinton and Dunn 1967		
			Desert			
			• Desert mule deer *Odocoileus hemionus crooki*	Cain et al. 2006		
			• White-tailed antelope squirrel *Ammospermophilus leucurus*	Chappell and Bartholomew 1981a		
		Uses body parts to facilitate shading	**Semidesert**			
			• Cape ground squirrel *Xerus inauris*	Bennett et al. 1984		
			• Springbok *Antidorcas marsupialis*	Fuller et al. 2005		
			Desert			
			• Camel *Camelus dromedarius*	Ouajd and Kamel 2009		
			• White-tailed antelope squirrel *Ammospermophilus leucurus*	Chappell and Bartholomew 1981b		
		Activity variable or polyphasic	**Semidesert**			
			• Mongolian gerbil *Meriones unguiculatus*	Lewis et al. 1965		
			• Black wildebeest *Connochaetes gnou*	Maloney et al. 2005		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Stewart 1963		
			• Lybian jird *Meriones libycus*	Aulagnier et al. 2008		
		Primary activity—crepuscular	**Semidesert**			
			• African wild dog *Lycaon pictus*	Woodroffe 2011		
			• Bush karoo rat *Otomys unisulcatus*	Vermeulen and Nel 1988		
			Desert			
			• King jird *Meriones rex*	Alagaili et al. 2013		
			• Red kangaroo *Macropus rufus*	Dawson et al. 1975		

continued

TABLE 2C
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Decreased activity	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schumann et al. 2005		
			• Degu *Octodon degus*	Lagos et al. 1995		
			• Feral pig *Sus scrofa*	Dexter 2003		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Ostrowski et al. 2006		
			• Greater bilby *Macrotis lagotis*	Hulbert and Dawson 1974		
		Social huddling at night to minimize heat loss	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Scantlebury et al. 2006		
			• Brants's whistling rat *Parotomys brantsii*	du Plessis et al. 1992		
			• Vervet monkey *Chlorocebus pygerythrus*	Lubbe 2013		
			Desert			
			• Collared peccary *Pecari tajacu*	Zervanos and Hadley 1973		
			• Spinifex hopping mouse *Notomys alexis*	Withers et al. 1979		
		Bask to increase solar absorption	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin et al. 2007		
			• Eland *Tragelaphus oryx*	Hetem et al. 2011		
			• Fat-tailed dunnart *Sminthopsis crassicaudata*	Warneke et al. 2008		
			Desert			
			• Collared peccary *Pecari tajacu*	Zervanos and Hadley 1973		
			• Fat-tailed antechinus *Pseudantechinus macdonnellensis*	Geiser and Pavey 2007		
		Social flexibility or group flexibility	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Schradin et al. 2012		
			• Hamadryas baboon *Papio hamadryas hamadryas*	Schreier and Swedell 2012		
			• Round-eared sengi *Macroscelides proboscideus*	Schubert et al. 2009		
			Desert			
			• Great gerbil *Rhombomys opimus*	Randall et al. 2005		
			• Pronghorn *Antilocapra americana*	Deblinger and Alldredge 1989		
	Fixed	Primary activity—nocturnal	**Semidesert**			
			• Greater Egyptian jerboa *Jaculus orientalis*	El Ouezzani et al. 2001		
			• Tammar wallaby *Macropus eugenii*	Kinnear et al. 1968		
			Desert			
			• Desert bighorn sheep *Ovis canadensis nelsoni*	Hansen 1982		
			• Yellow-rumped leaf-eared mouse *Phyllotis xanthopygus rupestris*	Tirado et al. 2008		

continued

TABLE 2C
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Primary activity—diurnal	**Semidesert** • African striped mouse *Rhabdomys pumilio* • Black wildebeest *Connochaetes gnou* • Brants's whistling rat *Parotomys brantsii* **Desert** • Fat sand rat *Psammomys obesus* • Nubian ibex *Capra nubiana*	Haim and Fairall 1986 Mitchell et al. 2002 Jackson et al. 2004 Ilan and Yom-Tov 1990 Hochman and Kotler 2006		
		Does not pant except in the final stages of heat stress * Reflects a reflex to thermal extremes (i.e., may not have adaptive significance for all species; Woodroffe 2011)	**Semidesert** • African buffalo *Syncerus caffer* • Lesser long-nosed bat *Leptonycteris yerbabuenae* **Desert** • Camel *Camelus dromedarius* • Greater bilby *Macrotis lagotis*	Taylor 1970a Carpenter and Graham 1967 Ouajd and Kamel 2009 Hulbert and Dawson 1974		
Physiology	Flexible	Pants to reduce temperature	**Semidesert** • Kirk's dik-dik *Madoqua kirkii* • Rock hyrax *Procavia capensis* **Desert** • Arabian oryx *Oryx leucoryx* • Fennec fox *Vulpes zerda*	Maloiy 1973 Rübsamen and Kettembeil 1980 Ostrowski et al. 2003 Noll-Banholzer 1979		
		Adaptive hypo- or hyperthermia	**Semidesert** • Grant's gazelle *Nanger granti* • Greater Egyptian jerboa *Jaculus orientalis* **Desert** • Camel *Camelus dromedarius* • Jackrabbit *Lepus californicus*	Taylor 1970b El Hilali and Veillat 1975 Grigg et al. 2009 Shoemaker et al. 1976		
		Wide thermoneutral zone	**Semidesert** • Littledale's whistling rat *Parotomys littledalei* • Tammar wallaby *Macropus eugenii* **Desert** • Allenby's gerbil *Gerbillus allenbyi* • Camel *Camelus dromedarius*	Jackson et al. 2004 Kinnear et al. 1968 Haim 1984 Schmidt-Nielsen et al. 1967		
		Maintenance of nonshivering thermogenesis * Information in large mammals is lacking	**Semidesert** • African lesser bushbaby *Galago moholi* • African striped mouse *Rhabdomys pumilio* • Damara ground squirrel *Xerus princeps* **Desert** • Golden spiny mouse *Acomys russatus* • Palestine mole rat *Spalax ehrenbergi* (chromosomal form $2n = 60$)	Nowack et al. 2013 Haim and Fourie 1980b Haim et al. 1986 Kronfeld-Schor et al. 2000 Haim et al. 1984		

continued

TABLE 2C
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Enters torpor (or hibernation) * And/or in response to food/water restriction. Information on large mammals is lacking in the literature	**Semidesert**			
			• Grey mouse lemur *Microcebus murinus*	Schmid 2001; Schmid and Speakman 2009		
			• North African elephant shrew *Elephantulus rozeti*	Lovegrove et al. 2001		
			Desert			
			• Round-tailed ground squirrel *Spermophilus tereticaudus*	Hudson 1964		
			• Stripe-faced dunnart *Sminthopsis macroura*	Song and Geiser 1997		
	Fixed	Storage of body heat during the day and dissipation at night * The terms “adaptive heterothermy” and “heterothermy” are also used	**Semidesert**			
			• Grant’s gazelle *Nanger granti*	Taylor 1970a		
			• Little red kaluta *Dasykaluta rosamondae*	Withers and Cooper 2009		
			Desert			
			• Sand gazelle *Gazella marica*	Ostrowski and Williams 2006		
			• Harris’s antelope squirrel *Ammospermophilus harrisii*	Osborn 1991		
		Increased erythrocyte circulation efficiency; erythrocyte volume flexibility and enhanced erythrocyte life span * Information is lacking in small mammals and semidesert species	**Semidesert**			
			• Guanaco *Lama guanicoe*	Cornelius and Kaneko 1962		
			Desert			
			• Camel *Camelus dromedarius*	Oyewale et al. 2011		
			• Desert bighorn sheep *Ovis canadensis nelsoni*	Turner 1979		
		Selective brain cooling * The incidence is lacking in the literature, and is debated in large mammals	**Semidesert**			
			• Beisa oryx *Oryx beisa*	Fuller et al. 2004		
			• Springbok *Antidorcas marsupialis*	Mitchell et al. 1997		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Hetem et al. 2012		
			• Camel *Camelus dromedarius*	Elkhawad 1992		
		Narrow but high thermoneutral zone * Information in large mammals is lacking	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Haim and Fourie 1980a		
			• Cape short-eared gerbil *Desmodillus auricularis*	Downs and Perrin 1994		
			• Palmer’s chipmunk *Tamias palmeri*	Lowrey and Longshore 2005		
			Desert			
			• Naked-footed gerbil *Gerbillus nanus*	Haim 1984		
			• Spiny mouse *Acomys spinosissimus*	Perrin and Downs 1994		

continued

TABLE 2C
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		High thermal conductance	**Semidesert**			
			• African striped mouse *Rhabdomys pumilio*	Haim and Fairall 1986		
			• Awassi sheep *Ovis aries*	Degen and Shkolnik 1978		
			• Western barred bandicoot *Perameles bougainville bougainville*	Larcombe and Withers 2006		
			Desert			
			• Collared peccary *Pecari tajacu*	Zervanos and Hadley 1973		
			• Desert kit fox *Vulpes macrotis arsipus*	Golightly and Ohmart 1983		
Morphology	Flexible	Limited subcutaneous fat deposition or localized storage	**Semidesert**			
			• Boer goat *Capra aegagrus hircus*	Casey and van Niekerk 1988		
			• Fat-tailed dunnart *Sminthopsis crassicaudata*	Morton 1978		
			Desert			
			• Camel *Camelus dromedarius*	Young 1976		
			• Soda Spring Valley kangaroo mouse *Microdipodops pallidus*	Bartholomew and MacMillen 1961		
	Fixed	Bipedal locomotion (or tendency)	**Semidesert**			
			• Great jerboa *Allactaga major*	Schmidt-Nielsen and Schmidt-Nielsen 1952		
			• Tammar wallaby *Macropus eugenii*	Baudinette et al. 1992		
			Desert			
			• Dusky hopping mouse *Notomys fuscus*	Schmidt-Nielsen and Schmidt-Nielsen 1952		
			• Red kangaroo *Macropus rufus*	Dawson and Taylor 1973		
		Short coarse pelage	**Semidesert**			
			• African buffalo *Syncerus caffer*	Marai and Haeeb 2010		
			• Gulf coast kangaroo rat *Dipodomys compactus*	Baumgardner 1991		
			Desert			
			• Arabian oryx *Oryx leucoryx*	Stewart 1963		
			• Round-tailed ground squirrel *Spermophilus tereticaudus*	Walsberg 1988		
		Light colored pelage for reflecting solar radiation and reducing heat uptake	**Semidesert**			
			• Panamint kangaroo rat *Dipodomys panamintinus*	Intress and Best 1990		
			• Springbok *Antidorcas marsupialis*	Mitchell et al. 1997		
			Desert			
			• Desert bighorn sheep *Ovis canadensis nelsoni*	McCutchen 1981		
			• Eastern Patagonian laucha *Eligmodontia typus*	Giannoni et al. 2001		

continued

TABLE 2C
Continued

System	Nature of the trait	Trait	Example species	Selected references	Present in my study species?	Degree of plasticity or flexibility?
		Dark pigmented skin	**Semidesert**			
			• African buffalo *Syncerus caffer*	Marai and Haeeb 2010		
			• African striped mouse *Rhabdomys pumilio*	Timm and Kermott 1982		
			• Damara ground squirrel *Xerus princeps*	Waterman and Herron 2004		
			Desert			
			• Addax *Addax nasomaculatus*	Portas et al. 2003		
			• Golden spiny mouse *Acomys russatus*	Haim and Rozenfeld 1995		
		Presence of a carotid rete * Information is lacking for small mammals	**Semidesert**			
			• Kirk's dik-dik *Madoqua kirkii*	Kamau et al. 1984		
			• Springbok *Antidorcas marsupialis*	Mitchell et al. 2002		
			Desert			
			• Camel *Camelus dromedarius*	Elkhawad 1992		
			• Pronghorn *Antilocapra americana*	Mitchell et al. 2009		
		Nasal countercurrent exchange system * This concurrently provides a benefit against water loss	**Semidesert**			
			• Giraffe *Giraffa camelopardalis*	Langman et al. 1979		
			• Little red kaluta *Dasykaluta rosamondae*	Withers and Cooper 2009		
			Desert			
			• Camel *Camelus dromedarius*	Schmidt-Nielsen et al. 1981b		
			• Merriam's kangaroo rat *Dipodomys merriami*	Jackson and Schmidt-Nielsen 1964		

Systems providing an appropriate adaptive response (behavior, physiology, or morphology); flexibility of traits (flexible or fixed). Fixed traits also include traits that show developmental plasticity during ontogeny. Researchers should identify the relative plasticity of fixed traits in particular environments (i.e., the reaction norm). A list of traits that could confer a fitness advantage under increasing likelihood of droughts, in relation to the three parts of the triquetra. We have included examples of a large- and small-bodied semidesert and desert species for each trait. The final two columns can be used by researchers and nature conservationists to categorize their study species, to identify areas where information is lacking, and to reach conclusions about the relative status of their species. The selected references appear in Appendix 1.

Wingfield 2003). Whether this leads to permanent damage and pathology, and finally death, can be modeled using the reactive scope model, which takes into account the short- and long-term effects of physiological mediators of allostasis (Romero et al. 2009; Romero 2012).

Osmoregulation is regulated by the secretion of several hormones, especially AVP, aldosterone, and renin (Finberg et al. 1978; Ben Goumi et al. 1993), which regulate water reabsorption in the kidneys and water excretion via urine. Several physiological markers can indicate a deviation from osmotic homeostasis, such as decreased plasma volume (Siebert and Macfarlane 1975; Ouajd and Kamel 2009) or increased concentration of proteins and sugars (Ouajd and Kamel 2009). Metabolism is regulated by corticosterone and thyroxine, mobilizing hepatic lipids and fatty acids in response to food restriction (Ostrowski et al. 2006; Ouajd and Kamel 2009). Thermoregulation is maintained by corticosterone, dexamethasone, and prednisolone, as well as sodium, and their influence on the sympathetic nervous system (Maickel et al. 1967). Thermoregulatory enhancements are indicated by increased erythrocyte circulation efficiency and changes in erythrocyte volume flexibility (Ouajd and Kamel 2009), which would facilitate oxygen circulation in the body.

Third, morphological structures, both internal and external, can help an animal to cope with water and food shortage, as well as high T_a (Tables 2a, b, and c). Kidney morphology, in particular long loops of Henle, increases water reabsorption and minimizes water loss by increasing urine concentration (Ouajd and Kamel 2009). Organ size and volume can be altered in response to food restriction to minimize the energetic costs of maintaining those organs (Ostrowski et al. 2006). Body size itself can have a profound effect on resilience to climate, and can change both plastically or due to evolutionary adaptation (Brown and Brown 1998). In mammals, paleontologists have observed dwarfing (reduction in body size) during the Paleocene-Eocene boundary, a period of global warming (Gingerich 2006), and dwarfing might also occur in extant mammals in response to increasing T_a. Similarly, pelage color and pattern, and skin color can assist in thermoregulation, minimizing solar absorption and increasing solar radiation (Stewart 1963; Haim and Rozenfeld 1995).

HOW FLEXIBLE IS THE TRAIT?

The final stage of the adaptive triquetra model is to establish the flexibility of the trait under increasing drought conditions (Box 2). Specialized adaptations evolve in response to strong selection pressures imposed by particular habitats. These adaptations are likely to be species-specific because different species adopt different strategies, as well as a combination of strategies, for survival and reproduction under challenging environmental conditions. Furthermore, these adaptations are relatively fixed, with limited flexibility. Specialized adaptations, such as the carotid rete utilized in brain cooling, enables individuals of some species to cope with increasing heat load (Mitchell et al. 2002). In sum, specialized adaptations are of little interest in establishing how a nondesert-adapted species would respond to the increasing frequency of droughts, because such species will not have specialized adaptations.

Traits that show adaptive developmental plasticity can vary between individuals due to environmental factors. However, although developmentally plastic traits are flexible during early life stages, they are generally fixed by adulthood (Piersma and van Gils 2010). Adaptive developmental plasticity is thus an important determinant of resilience to drought. Essentially, every fixed trait can be categorized according to the nature and degree of its developmental plasticity, also known as a reaction norm (Cassidy et al. 2014). This reaction norm can be narrow, with a slope close to zero (totally fixed trait), or it can be broad. Here, we include traits that show adaptive developmental plasticity as fixed traits, because they are not flexible in adults (Tables 2a, b, and c). As a consequence, to determine the resilience to droughts by a species, the level of adaptive developmental plasticity of every fixed trait should be estimated. Broad adaptive developmental plasticity indicates a greater likelihood that a generation exposed to droughts during early development (or to environmental stimuli predicting droughts) will develop traits enabling resilience to droughts.

General adaptations evolve in response to fluctuating and dynamic selection pressures in multiple habitats and are likely to be common among most (if not all) mammals. For example, all mammals secrete AVP from the pituitary to regulate water reabsorption in the kidneys (Acher 1993). Many general adaptations are likely to be phenotypically flexible. Exaptations must also be considered here because their utilization in the current context is flexible, even if the trait evolved as a specialized adaptation in another context. Recent evidence from the available vertebrate literature suggests that most phenotypic responses to climate change and increased droughts would be due to the flexibility of traits (Canale and Henry 2010). Therefore, we suggest that identifying flexible traits representing general adaptations and exaptations of nondesert-adapted species is vital for determining whether a species has the potential to persist under increasing drought conditions (Tables 2a, b, and c).

Using the Adaptive Triquetra to Estimate Species Resilience or Vulnerability to Drought

We have attempted to summarize all known traits of the adaptive triquetra that mammals could use to cope with droughts (Tables 2a, b, and c). These can be used by ecologists and nature conservationists to assess the resilience or vulnerability of one or several species to drought. These tables reflect the variety of traits and species possessing these traits. Currently, in most cases, more research on a specific species would be required by ecologists/nature conservationists to accurately estimate the resilience to drought by a particular species. The tables enable a comparison to be made between different traits, as well as between different large- and/or small-bodied species. They provide a step-by-step approach that could help in making decisions on conservation action, especially of which species to focus on, and which of the three stressors is relevant. For example, for species A it might be most important to offer water at artificial water points during droughts, although for species B food shortage could be more important, so supplemental food should be the priority.

We have planned Tables 2a, b, and c in such a manner that they can be directly applied. In the second to last column, one can mark whether or not a specific trait is present in a species. In the last column, the flexibility of that trait for that species can be estimated. These two columns provide the first overview for a specific species and will give some indication of how resilient or vulnerable it could be. Nonetheless, we realize that, in nearly all cases, filling in these tables will generate more questions than answer the critical question of how resilient a species is to droughts. Thus, one conclusion is that to assess drought resilience of a species, a detailed understanding of the biology and evolutionary history of the species is the requisite first step prior to large-scale decision-making processes.

One important aspect not covered by this process is the environment. By definition, drought occurs when the current precipitation falls significantly below the long-term mean of a defined area, leading to water shortage (Dai 2011). Thus, droughts can differ dramatically in intensity and duration, and a population that can cope well with, for example, a 30% reduction of precipitation over a few months, might not survive a 60% reduction in precipitation over a longer period. In addition, a population's habitat may provide suitable microclimatic refugia that could facilitate persistence, but not the habitat of another population of the same species. However, it is important to understand the complexity of the species first, and then focus on the environment and habitat later, as the biology of an animal will determine its vulnerability, while the modulating role of the environment may promote or hinder resilience.

Concluding Remarks: The Importance of Flexibility

Phenotypic flexibility, rather than future evolutionary adaptation, will most likely facilitate adaptive responses to climate change and increased droughts in the short term (Canale and Henry 2010), which in the long term might lead to evolutionary adaptation (Lind et al. 2015; Scheiner et al. 2015). Identifying those traits that promote persistence in a period of change, as well as understanding the degree of their flexibility, is crucial for assessing whether or not a species will persist under increased frequency and/or periodicity of droughts. In addition to flexibility, resilience might also arise because of exaptation. The concept of exaptation has been criticized as not being useful to understand how species are successful in their current environment (Larson et al. 2013). Yet, the concept might be useful for understanding whether and how species will be able to cope with rapid global change because exaptations could provide important benefits for species not currently accustomed to drought conditions.

Phenotypic flexibility operates at the individual rather than at the population level (Rymer et al. 2013), so the ability of species to cope with change will depend largely on the flexibility of its individuals. In addition, individuals that persist and reproduce transmit genes for trait flexibility to their offspring, and flexibility can be a strong driver of phenotypic evolution (Piersma and van Gils 2010; Standen et al. 2014). Thus, in the mid to long term, these traits, as well as the ability to be flexible, could become fixed through evolutionary adaptation, becoming general or specialized adaptations. However, because phenotypic flexibility can be costly, it is important to study to what degree those traits that are phenotypically flexible in order to establish the limits of this plasticity in promoting persistence.

To understand which traits could promote species persistence to increased periodicity of droughts and increased aridification, we should focus on those species currently inhabiting semideserts because they are likely to possess a suite of existing traits that could be advantageous during droughts and that could be present in species from nondesert environments, in contrast to specialized traits of desert species. Comparative assessment of these species will facilitate identification of traits that could provide fitness advantages for other species encountering increasingly drier conditions. Furthermore, although a species may have a suite of existing phenotypic adaptations or exaptations to droughts, the interaction with other species in its environment, its habitat requirements, amount of available habitat, and human persecution/exploitation will all influence its persistence. Future empirical studies and conservation programs will test the usefulness and applicability of the adaptive triquetra and possibly modify it, enabling us to better predict which populations are vulnerable to drought-related extinction.

ACKNOWLEDGMENTS

The suggestions provided by the editor and two anonymous reviewers greatly improved the manuscript. We are grateful for support by the University of the Witwatersrand (Neville Pillay), James Cook University (Tasmin L. Rymer), the Université de Strasbourg's Institute for Advanced Study (Carsten Schradin), and the CNRS (Carsten Schradin).

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Associate Editor: Andrew Sih
Handling Editor: John J. Wiens

APPENDIX 1

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