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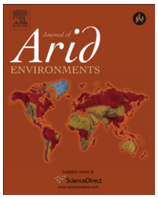

Arid environments: Opportunities for studying co-evolutionary patterns of scorpion venoms in predator–prey systems

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ABSTRACT

We review the literature on the geographic and taxonomic diversity of species of lizards and scorpions that are involved in predator–prey interactions. Somewhat surprisingly, lizards are often the predators in these interactions. Consequently, our goals were to evaluate whether lizard predators had evolved morphological or physiological resistance to scorpion venom or whether the rely on behavioral evasions, and also to document co-evolutionary patterns. Diverse lizards prey on scorpions, but most studies are surprisingly anecdotal. Whether lizard predators tolerate scorpion venom is largely unexplored. Our review highlights opportunities for studies of the evolution of tolerance to scorpion venom by lizards and of the ecology and evolution of lizard–scorpion interactions in arid zones. Progress will be facilitated by collaborations between experts in ecology and toxicology, and by incorporating molecular approaches such as proteomics and transcriptomics. Much is to be learned about scorpion venoms and their effects on predators, with potential benefits to humans.

1. Introduction

Predator–prey interactions occur in all habitats, but are particularly conspicuous in deserts and extreme arid ecosystems. Such interactions affect the fitness of both predator and prey; and not surprisingly, predator–prey interactions are often marked by co-evolutionary adjustments (Barlow et al., 2009; Gibbs and Rossiter, 2008; Richards et al., 2012).

Some predators (scorpions, some spiders and vipers) have evolved venoms that increase their predation success, at least on some species. Venoms are cocktails of complex mixtures of proteins and peptides, and typically stun, kill, or even help digest prey. The evolution of venom increases selection on prey species to evolve counter-predation mechanisms. Some prey have evolved increased sensory abilities to detect approaching predators (venomous or not), alter behavior to reduce their exposure to predators, or have even evolved the ability to detoxify the predator's venom. For example, some garter snakes can eat and detoxify tetrodotoxins sequestered in the skin of some salamanders (Feldman et al., 2010; Geffeney et al., 2002), and some grounds squirrels and opossums are largely immune to rattlesnake venom (Biardi et al., 2006; Jansa and Voss, 2011).

All scorpions are predators and are especially diverse and abundant in deserts (Polis, 1990) where they are important components of food webs. Scorpions are often considered classic examples of venomous predators, and indeed the dynamics of scorpions as predators has been studied extensively (Brownell and Polis, 2001; Polis, 1990). However, most research on scorpions focuses on properties of their venoms, which are used extensively in basic and biomedical research (Abdel-Rahman et al., 2010; Aroui et al., 2009; Jiménez-Vargas et al., 2012; Pereanez and Vargas, 2009).

Far less appreciated is the fact that scorpions, despite their venoms, are themselves prey of many species. Scorpions are desirable prey because of their large body size, rich nutrient content, high densities, wide distribution, and predictable surface behavior (Williams, 1987). It has been proposed that venom is more significant in prey capture than in predator deterrence (Polis, 1990). In any

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case, all previous information leads to an obvious set of biological questions. For example, why don't these venoms, which clearly promote foraging success by scorpions, also provide protection against predators of scorpions? Does predation on scorpions take place at times, or under circumstances, when or where scorpions are unable to defend themselves effectively? Have scorpion predators evolved chemical defenses against scorpion venoms?

Lizards are important components of deserts, and almost all are predators, especially of arthropods (Pianka, 1973). Diverse lizards are known to prey on scorpions (Table 1), and a few appear to be

Table 1
Studies that examine the role of lizards as predator (P) or prey (PR) of scorpions or if they do coexist (CO) in different geographic zones. Indicated are lizard species and the family, and whether the lizard shows some type of defenses, either morphological—mechanical (M), physiological (PH), behavioral (BE), or no defense has been reported (N). Nocturnal species are indicated in bold, and the literature citation is also indicated.

Lizard species	Family	Zone	Role	Defense	Author	Journal
Amphibolurus isolepis	Agamidae	Australia, W	P	N	Pianka, 1971; in Polis et al., 1981	J. Arid Environ.
Uromastyx aegyptia	Agamidae	Saudi Arabia	CO	BE	Al-Saleh and Al-Johany, 1995	Arab Gulf Sci. Res.
Uromastyx aegyptia	Agamidae	Saudi Arabia	CO	BE	Al-Johany and Al-Saleh, 2000	Pakistan J. Zool.
Diploglossus lessonae	Anguidae	America, Brazil	P	N	Vitt, 1985	Papeis Avulsos de Zoologia
Gerrhonotus kingi	Anguinidae	USA, SW	P	N	Beheler and King, 1979, in Polis et al., 1981	J. Arid Environ.
Gerrhonotus multicarinatus	Anguinidae	USA, New Mexico	P	N	Beheler and King, 1979, in Polis et al., 1981	J. Arid Environ.
Cordylus cataphactus	Cordylidae	Africa, S	P	M	Mouton et al., 2000	Afr. Zool.
Chondrodactylus angulifer	Gekkonidae	Africa, Khalahari	P	N	Pianka and Huey, 1978	Copeia
Coleonix variegatus	Gekkonidae	USA, SW	P	N	Parker and Pianka, 1974, in Polis et al., 1981	J. Arid Environ.
Colopus wahlbergi	Gekkonidae	Africa, Khalahari	P	N	Pianka and Huey, 1978	Copeia
Diplodactylus ciliaris	Gekkonidae	Australia, W	P	N	Pianka and Pianka, 1976, in Polis et al., 1981	J. Arid Environ.
Eublepharis macularius	Gekkonidae	Asia, Iran	P	N	Anderson, 1963, in Polis et al., 1981	J. Arid Environ.
Gehyra variegata	Gekkonidae	Australia, W	P	N	Pianka and Pianka, 1976, in Polis et al., 1981	J. Arid Environ.
Nephrurus laevissimus	Gekkonidae	Australia, W	P	N	Pianka and Pianka, 1976, in Polis et al., 1981	J. Arid Environ.
Nephrurus levis	Gekkonidae	Australia, W	P	N	Pianka and Pianka, 1976, in Polis et al., 1981	J. Arid Environ.
Oedura ocellata	Gekkonidae	Australia	P	N	Bustard, 1971, in Polis et al., 1981	J. Arid Environ.
Pachydactylus bibroni	Gekkonidae	Africa	P	N	Pianka and Huey, 1978	Copeia
Pachydactylus capensis	Gekkonidae	Africa, Khalahari	P	N	Pianka and Huey, 1978	Copeia
Ptyodactylus guttatus	Gekkonidae	Africa, Israel	P	BE/PH	Zlotkin et al., 1978	J. Nat. Hist.
Ptyodactylus puiseuxi	Gekkonidae	Africa, Israel	P	BE	Zlotkin et al., 2003	J. Nat. Hist.
Phrynosoma sp	Iguanidae	USA, Utha	P	N	Fauntin, 1946, in Polis et al., 1981	J. Arid Environ.
Plica plica	Iguanidae	America,Venezuela	P	N	Beebe, 1944, in Polis et al., 1981	J. Arid Environ.
Sceloporus graciosus	Iguanidae	USA, Utha	P	N	Knowlton et al., 1965, in Polis et al., 1981	J. Arid Environ.
Sceloporus occidentalis	Iguanidae	USA, California	P	N	Johnson, 1965, in Polis et al., 1981	J. Arid Environ.
Sceloporus sp	Iguanidae	USA, Utha	P	N	Fauntin, 1946, in Polis et al., 1981	J. Arid Environ.
Uta stansburiana	Iguanidae	USA, Utha	P	N	Knowlton et al., 1965, in Polis et al., 1981	J. Arid Environ.
Cnemidophorus gularis	Lacertidae	USA, Texas	P	BE	O'Connell and Formanowicz, 1998	J. Herpetol.
Eremias lineo-ocellata	Lacertidae	Africa, Khalahari	P	N	Pianka et al., 1979	Ohio State Univ. Press
Eremias lugubris	Lacertidae	Africa, Khalahari	P	N	Pianka et al., 1979	Ohio State Univ. Press
Eremias namaquensis	Lacertidae	Africa, Khalahari	P	N	Pianka et al., 1979	Ohio State Univ. Press
Iberolacerta horvathi	Lacertidae	Europe, Slovenia	P	N	Zagar et al., 2011	Herpetol. Notes
Ichnotropis squamulosa	Lacertidae	Africa, Khalahari	P	N	Pianka et al., 1979	Ohio State Univ. Press
Lacerta horvathi	Lacertidae	Europe, Italy	P	N	Richard and Lapini, 1993	Atti. Mus. Civ. Star. Nat. Trieste
Lacerta sp	Lacertidae	Europe, Africa	P	N	Pianka et al., 1979	Ohio State Univ. Press
Meroles suborbitalis	Lacertidae	Africa, Khalahari	P	N	Pianka et al., 1979	Ohio State Univ. Press
Nucras intertexta	Lacertidae	Africa, Khalahari	P	N	Branch, 1988	Book
Nucras intertexta	Lacertidae	Africa, Khalahari	P	N	Pianka et al., 1979	Ohio State Univ. Press
Nucras tessellata	Lacertidae	Africa, Khalahari	P	N	Pianka et al., 1979	Ohio State Univ. Press
Nucrass tessellata	Lacertidae	Africa, Khalahari	P	N	van der Meer et al., 2010	Copeia
Podarcis atrata	Lacertidae	Europe, Spain	P/PR	PH?	Castilla et al., 2008	J. Nat. Hist.
Podarcis atrata	Lacertidae	Europe, Spain	P/PR	PH?	Castilla and Herrel, 2009	J. Arid Environ.
Phrynocephalus mystaceus	Phrynosomatidae	Asia	P	N	Mishagina, 1993	Bul. Mosk. Obs. Isp. Pri. Ot. Biol.
Phrynosoma platyrhinos	Phrynosomatidae	USA, Arizona	PR	N	Turner and Rorabaugh, 1998	Herp. Rev.
Anolis porcatus	Polychrotidae	America, Cuba	P	N	de Armas et al., 1999	Cocuyo
Lialis burtonis	Pygopodidae	Australia	P	N	Wall and Shine, 2007	Biol. J. Linn. Soc.
Lialis burtonis	Pygopodidae	Australia	P	N	Philipp, 1980	Western Aust. Nat.
Ctenotus grandis	Scincidae	Australia, W	P	N	Pianka, 1969, in Polis et al., 1981	J. Arid Environ.
Ctenotus leonhardii	Scincidae	Australia, W	P	N	Pianka, 1969, in Polis et al., 1981	J. Arid Environ.
Ctenotus quattuordecimlineatus	Scincidae	Australia, W	P	N	Pianka, 1969, in Polis et al., 1981	J. Arid Environ.
Ameiva ameiva	Teiidae	America,Venezuela	P	N	Beebe, 1945, in Polis et al., 1981	J. Arid Environ.
Cnemidophorus sacki	Teiidae	USA, Texas	P	N	Milstead, 1958, in Polis et al., 1981	J. Arid Environ.
Cnemidophorus sp	Teiidae	USA, Utha	P	N	Fauntin, 1946, in Polis et al., 1981	J. Arid Environ.
Cnemidophorus tessellatus	Teiidae	USA, SW	P	N	Milstead, 1958, in Polis et al., 1981	J. Arid Environ.
Cnemidophorus tigris	Teiidae	USA, SW	P	N	Milstead, 1958, in Polis et al., 1981	J. Arid Environ.
Varanus caudolineatus	Varanidae	Australia	P	N	Thompson and King, 1995	Western Aust. Nat.
Varanus gouldii	Varanidae	Australia, S	P	N	King and Green, 1979, in Polis et al., 1981	J. Arid Environ.
Varanus gouldii	Varanidae	Australia	P	N	Koch, 1970	Western Aust. Nat.
Varanus indicus group	Varanidae	Australia	P	N	Philipp et al., 2007	Mertensiella
Varanus sp	Varanidae	Africa, N	P	N	Cisse, 1972	Bull. Inst. Fran. AF Scien. Nat.
Klauberina riversiana	Xantusiidae	USA, California	P	N	Brattstrom, 1952, in Polis et al., 1981	J. Arid Environ.
Xantusia henshawi	Xantusiidae	USA, California	P	N	Brattstrom, 1952, in Polis et al., 1981	J. Arid Environ.

scorpion specialists (e.g., *Pygopus nigriceps*; Pianka, in Polis et al., 1981). Scorpions also prey on diurnal and nocturnal lizards, snakes and turtles (Castilla 1995; Turner and Rorabaugh, 1998).

Cross predation, where both lizard and scorpion can act as predator or prey, depending on circumstances has also been reported (Castilla et al., 2008, 2009; Polis, 1990). Castilla and coworkers have described a number of instances of predation by *Buthus occitanus* on *Podarcis atrata*, a lizard endemic to the volcanic Columbretes Archipelago (Mediterranean, Castellón, Spain), a set of very small (0.5–13 ha) islands characterized by an extreme aridity and a scarcity of insects (Castilla et al., 2009). Thus, both lizards and scorpions are often abundant in the same desert habitats, and they can and do kill and eat each other.

In particular, lizards may constitute important parts of the diet of scorpions in xeric areas where insect prey are scarce. Figures 1 and 2 in Castilla et al. (2009) illustrate, respectively, *B. occitanus* predating on juveniles of *P. atrata* under natural or captive conditions, and adult male *P. atrata* predating on *B. occitanus* when offered in the field under captive conditions. Cross predation has the potential to be an important factor in determining the structure of both lizard and scorpion populations. Surprisingly, no review exists of venom-mediated interactions between these predators. Accordingly, we decided to survey the literature and evaluate the geographic and taxonomic diversity of species of scorpions and lizards that are involved in predator–prey interactions. We also wished to evaluate evidence of morphological or physiological resistance of lizards to scorpion venom as well as the abilities of lizards predators to evade scorpion stings.

2. Results and Discussion

We found 61 studies where 57 lizard species interact with at least 9 different species of scorpions in deserts on five continents (Table 1). In most interactions, the lizard is the predator: only two studies report scorpions (*B. occitanus* and *Hadrurus arizonensis*) preying on lizards (Castilla, 1995; Turner and Rorabaugh, 1998). Phylogenetically and geographically diverse diurnal lizards prey on scorpions: 14 different families including Agamidae (2 species), Anguidae (1 species), Anguinidae (2 species), Cordylidae (1 species), Gekkonidae (13 species), Iguanidae (6 species), Lacertidae (11 species), Phrynosomatidae (2 species), Polychrotidae (1 specie), Scincidae (4 species), Teiidae (5 species), Varanidae (4 species), Xantusiidae (2 species) (Table 1). No phylogenetic or geographic trend is obvious, though the available data are obviously scarce.

Most studies are descriptive, merely reporting the prey and predator species. In some cases the scorpion species consumed was not been identified. One study has experimentally examined behavioral responses of lizards to scorpions from different geographic areas (Castilla et al., 2008). Others suggest behavioral coexistence between the lizard *Uromastyx aegyptia* and the scorpion *Androctonus crasicauda* in Saudi Arabia (Al-Johany and Al-Saleh, 2000; Al-Saleh and Al-Johany, 1995).

Despite the importance of scorpion venoms in biomedical research, we found only a single study that examined lizard tolerance to venom: the gecko *Ptyodactylus guttatus* tolerates an amazing dose of 1 mg crude dry venom of the poisonous yellow scorpion *Leiurus quinquestriatus* per 1 g of body mass (Zlotkin et al., 2003), whereas its LD50 (sc) for mice is 0.25–0.35 μg/g (http://members.tripod.com/~c_kianwee/rpotent.htm). However, a gecko of the same genus and body mass (*Ptyodactylus puiseuxi*) died in few hours after the injection of a similar venom dose (Zlotkin et al., 2003). Thus, closely related lizards of the same genus but different species appear to differ in tolerance to scorpion venom, but this result needs to be replicated.

Most desert lizards are diurnal predators, although some desert lizards are nocturnal (Cogălniceanu et al., 2014; Pianka and Huey, 1978). Scorpions are strictly nocturnal (Polis, 1990). What is surprising is that most of the lizards that are known to prey on scorpions are themselves diurnal (Table 1). Many scorpion species spend most of the time in crevices and burrows (presumably to decrease risk of predation), and some are only active 20 percent of the time available for foraging at night (Polis, 1990). So how do diurnal lizards find scorpions? The answer is currently unknown. The diurnal Kahalari lacertid *Nucras tessellata* regularly eats scorpions (Pianka et al., 1979), and it seemingly searches scorpion burrows during the late morning, when scorpions are underground and perhaps unable to defend themselves effectively. Other lizards may use chemical cues to detect scorpions and then dig them up. Some lizards (*P. atrata*) are very efficient capturing scorpions (Castilla and Herrel, 2009). Thus, despite the widespread occurrence of lizard predation on scorpions (Table 1), the natural history of these interactions remains largely unknown.

Most of the lizards listed in Table 1 do not have obvious mechanical defenses against scorpions. *Cordylus cataphactus* (Mouton et al., 2000) from South Africa is the exception, as its body is covered by extreme hard spines. Whether this evolved as a defense against scorpions is unknown but unlikely. Two studies document that lizards use behavioral mechanisms (e.g., handling) to avoid being stung (O'Connell and Formanowicz, 1998; Zlotkin et al., 2003). We suspect this is common, but it has neither been observed for *P. atrata* (Castilla and Herrel, 2009) nor described for other lizard species. However, in the case of *P. atrata*, some adult individuals have shown to tolerate *B. occitanus* venom (Castilla et al., 2008).

The nine scorpion species that are prey of lizards belong to four families including Buthidae (*Centruroides anchurellus*, *Centruroides vittatus*, *Leiurus quiquestriatus*, *Androctonus crasicauda*, *B. occitanus*), Oplurinae (*Urodacus hoplurus*), Vaejovidae (*Vajeovis* sp) and Diplocentridae (*Diplocentrus* sp) (Table 1). We suspect that many more scorpion species are eaten by lizards, if only because scorpions found in lizard stomachs are often not identified to species (Table 1). The scorpion species that prey on lizards belong to the families Bhutidae (*B. occitanus*) and Luridae (*Hadrurus arizonensis*).

The diversities of lizard and of scorpions in deserts on different continents offer many opportunities to explore intra and interspecific variability of venoms that may covary with scorpion sympatry and allopatry. Moreover, studies should examine whether some lizards have evolved resistance to neutoroxic venoms of scorpion. Large numbers of lizard and of scorpion species interact in many desert zones (Table 1), and many more potentially interact in deserts. For example, in Qatar, a small (11,571 km^2) country of extreme aridity (annual mean temperature of 27 °C and 75 mm rainfall/year), there are at least 21 lizard species (Cogălniceanu et al., 2014; MOE, 2004) and at least four scorpion species (personal observations). Many of these probably live in sympatry and may interact in some way. They offer great opportunities for future co-evolutionary studies.

Scorpion toxins are promising templates for pharmaceutical applications (Heinen and Veiga, 2011). Indeed, most scorpion venoms have medical, pharmaceutical or insecticidal applications and few of them are ecologically or evolutionary oriented (Abdel-Rahman et al., 2009; Badhe et al., 2006; Borges et al., 2006; Newton et al., 2007; Smith et al., 2013). Scorpion venoms are chemically diverse (Ma et al., 2012) and have different effects on different kinds of prey (Chugunov et al., 2013). Research on venoms has been continuously enhanced by advances in technology, and the last decade has witnessed the development of proteomics and transcriptomics approaches that reveal the complexity of various animal venoms (Calvete, 2011).

Toxin diversity may result from directional selection as well as from reciprocal co-evolutinoary processes between prey and hunter (arms-race). An increasing number of “omics” studies (genomics, proteomics, transcriptomics) strongly support the idea that venom variation reflects local adaptation for feeding on different prey. Because the proteome is responsive to natural selection and allows studies of adaptations (Gibbs and Mackessy, 2009; Gibbs et al., 2009), proteomics tools will particularly help advance our knowledge in this field.

We recommend that future studies should explore intra and interspecific variability of venoms, and whether venom properties covary with scorpion sympatry and allopatry. Further, if some lizards are shown to be resistant to scorpion venom, it will be interesting to determine whether that resistance evolved as an adaptive response to feeding on venomous prey.

We consider it quite urgent to conduct such studies before many desert species disappear. The biodiversity of deserts is highly vulnerable because of global warming and intense human activities. In the Gulf region and particularly in Qatar, human development, constructions and roads have been growing exponentially in recent years (Richer, 2009). Coastal areas are undergoing vast habitat loss from development (Yasseen and Al Thani, 2007). Similarly, large inland terrestrial areas are lost to development or being actively degraded, even those in protected areas (Sillitoe et al., 2010). Because of continuous habitat destruction in Qatar and many other deserts, lizards and other species populations are suffering substantial reductions. This is why we must speed the process of acquiring scorpion venom samples and ecological and evolutionary data of interacting species before is too late.

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