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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.