

Ecological Function of Venom in *Varanus*, with a Compilation of Dietary Records from the Literature

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Abstract - Until recently, venom in reptiles was thought to be present in two lineages: Serpentes and Heloderma. Research has now shown that venom evolved only once in reptiles, in a venom clade known as Toxicofera. This has resulted in venoms being discovered in many more species within this clade, including monitor lizards, genus *Varanus*. To date, very little work has been published on the ecological function of venom in monitor lizards. More generally, venom can fulfill four functions: defence, prey capture, aiding digestion, and maintaining oral hygiene through antimicrobial effects. Although more than one function may be served by the venom of any given species, in most cases one of these is more important than others, i.e., the primary function. Previous evidence for prey capture as the primary function of venoms has often used data on wild prey to assist interpretation, and as a result, a compilation of wild monitor lizard diets is presented. Subsequently, speculations on the primary function of *Varanus* venoms are made and discussed. Although many data are needed to support or refute many of the points discussed, I suggest that an enhancement of digestive function may be an important element of the venom, possibly the primary function in at least some species. The suggestions are made with the aim of encouraging future work to empirically test the hypotheses which derive from the ideas herein. Only in this way can we hope to further our knowledge on the ecology of venom in reptiles.

Until recently, the prevailing view was that reptile venoms were restricted to two clades of extant squamates: Serpentes and *Heloderma* (Minton and Minton, 1969; Pough et al., 2004). Effects of the toxins from *Varanus* have usually been ascribed to bacterial infections caused by a virulent oral bacterial flora (Gillespie et al., 2002), but recent systematic and toxinological analyses have discovered the presence of venom glands and venom in *Varanus* (Vidal and Hedges, 2005; Fry et al., 2006). It should be borne in mind that only few *Varanus* species have been examined in this way (*V. acanthurus*, *V. mitchelli*, *V. panoptes rubidus*, and *V. varius*), but *V. griseus*, *V. komodensis* and *V. scalaris* bites on humans have also shown signs consistent with envenomation (Sopiev et al., 1987; Ballard and Antonio, 2001; Fry et al., 2006; Fry and Scheib, 2007). However, the early evolution of toxins relative to the origin of the genus and the widespread presence of venom in the clade containing it suggest that toxins are likely a ubiquitous

character in monitor lizards.

This research has led to the naming of a clade including all anguimorph lizards, iguanian lizards, snakes, and the most recent common ancestor of these three clades (Vidal and Hedges, 2005). This clade has been called Toxicofera, and basal toxicoferan toxins include AVIT, B-type natriuretic peptide (BNP), Cysteine-rich Secretory Protein (CRISP), Cobra Venom Factor (CVF), Kallikrein, Nerve Growth Factor (NGF), Crostamine, Cystatin, and Vespryn (Fry et al., 2006; Fry and Scheib, 2007). The latter three toxins appear to be secondarily lost in varanids, but to the other six toxins listed above can be added Phospholipase A₂ (type III; PLA₂) (a basal anguimorph toxin) to give the currently known composition of varanid venoms. It is possible that additional toxins unique to *Varanus* or species within the genus are yet to be discovered, as only a few species have been examined. Likewise, variation in venom composition between species is likely to occur, but has

thus far been poorly documented.

What research has so far been published is still in its preliminary stages, and has focussed on the pharmacology, toxicology, toxinology, molecular evolution, and systematic implications of varanid venom, but its natural history has for the most part been ignored. The only other paper of which I am aware that discusses the ecology of *Varanus* venom is an abstract from a presentation at the 6th World Congress of Herpetology (Fry, 2008). This highlights that, at least in *V. komodoensis*, venom may be important in subduing prey as neither bite force nor pathogenic bacteria were found to be effective in prey capture. It also demonstrated that significant quantities of venom may be produced at least in some species, and so that these may be ecologically relevant. In this paper I offer speculations on the ecological function of venom in monitor lizards, in the hope that future work may empirically test these ideas and further our knowledge of the ecology of reptile venoms.

Function of Venoms

Toxins are taxonomically widespread in animals, and reptile venoms consist of a cocktail of different toxins, and so the venom as a whole may not be, and probably is not in most cases, restricted to one use (Russell, 1983; Kardong, 1996). Four main functions, which are not mutually exclusive, have previously been attributed to reptile venoms: a defensive mechanism (Russell and Bogert, 1981; Greene, 1997, p. 110), as an aid to digestion of prey (Thomas and Pough, 1979; Rodriguez-Robles and Thomas, 1992; McCue, 2005), to assist in the maintenance of oral hygiene via an antimicrobial effect (e.g. Stiles et al., 1991; Blaylock, 2000; Sachidananda et al., 2007; Ciscotto et al., 2009), or to assist in prey capture by killing or immobilizing prey. This last function is by far the most commonly implicated in a variety of animals including such divergent taxa as cnidarians and even mammals (Tomasi, 1978; Martin, 1981), as well as reptiles. Although more than one of these hypotheses may hold true for a given species, in most cases it is likely that one of them will be more important than the others, serving a primary function although other benefits may also be afforded by the venoms.

In squamate taxa, as currently known, only spitting cobras and *Heloderma* are specialised for the functional use of venom for defensive purposes. *Heloderma* largely prey on eggs, a diet known to lead to reduction of venom apparatus in other reptiles (Heatwole, 1999), and these lizards have certain components of their venom

seemingly highly tailored for a defensive role (Beck, 2005). Although spitting cobras are specialised for defensive use of venom, they also use venom for prey capture, so in this case both defence and prey capture are likely to be important functions. Therefore, as currently understood, defence is an infrequent primary function of venom in reptiles. Associations suggestive of the use of venom for prey capture are common, and include an ontogenetic shift in both venom characteristics and diet (Andrade and Abe, 1999; Mackessy et al., 2003), substantial differences in venom amongst closely related species with different diets (Sanz et al., 2006), regression of the venom apparatus and a vast reduction in venom toxicity for ovophagous species that are part of highly toxic clades (Heatwole, 1999), and geographic variation in venom that may be explained by variation in diets (Glenn et al., 1983; Daltry et al., 1996, 1997).

The toxicity of any given venom can vary greatly between 'prey species' (Mebs, 2001), which may be a result of a predator-prey arms race. For instance, prey will be under strong selection pressure to evolve resistance to a predator's venom, potentially rendering them less susceptible to the effects of these toxins over time. Conversely, if a predator preys largely on insects, the toxins contained in its venom may be specific to insects and so have little effect on other prey types. This close relationship between the predator's venom and its effect on prey further supports the importance of venom for prey capture. Because of this, the following section will comment on the diets of monitor lizards to enable better evaluation of the function of venom within this lineage.

Diet of Varanid Species

The diet of monitor lizards is reported for many species, and as a group they have a variety of trophic modes, such as carnivory, insectivory, herbivory and frugivory. Gaalema (2007) assessed the prey choice for a collection of captive *Varanus*, including *V. komodoensis*, *V. rudicollis*, and *V. griseus*, by assigning preference scores using a method formulated by Ciccone et al. (2005). He found the strongest preference was for mice in all three species, but the two other prey items tested demonstrated variable preference scores between the species. *V. komodoensis* preferred avian prey (chicks) to fish, and *V. griseus* showed a preference for eggs over fish, but neither of these latter two preferences appear particularly strong. Two individuals of *V. rudicollis* selected fish over crickets, and this seems a relatively

strong preference, but a third specimen had a slightly higher preference for crickets, but this seemed low. A survey of the diets of *Varanus* species taken mainly from the primary literature is presented in Table 1. As can be seen, many of the smaller species prey largely on insects whereas larger species select more mammalian and reptile prey items. Note that 'small' and 'large' are used somewhat subjectively here, in that no absolute size is given as a cut-off between these categories, however, they serve as a guide relative to the range of sizes in the genus (e.g. *V. prasinus* is small, *V. salvator* is large). While exceptions to this do exist, the data compiled here from a number of dietary studies in natural settings suggest a greater importance of vertebrate prey in larger species as compared with smaller species. Importance is a difficult term to define, as Losos and Greene (1988) found that while mammals may comprise a relatively small proportion of the number of prey in some species, they are still important in terms of the proportion of dietary energy they provide. An attempt has been made here to evaluate importance for use in Table 1, but these limitations should be borne in mind. In addition, aquatic prey items are common components in the diet only in those species exhibiting more aquatic habits, as may be expected.

Possible Functions of *Varanus* Venoms

To return to the four previously mentioned functions of reptile venoms, although they are not mutually exclusive, as a means to explain the primary function of the venom the defensive hypothesis seems least likely, despite its obvious utility in the closely related *Heloderma*. The unusual situation in this genus is thought to be primarily the result of the relatively poor escape capabilities of gila monsters and beaded lizards (Beck, 2005), a situation which does not hold true for monitors. The presence of kallikrein in the venom (known to be a key cause of pain in other lizard venoms) may provide some weak support for a defensive role. Alternatively, these may serve other roles (e.g. as an aid to immobilize prey), or may simply be inherited from an evolutionary ancestor, but now unimportant in *Varanus*, albeit this is unlikely due to the energetic costs of producing venom (McCue, 2006). Therefore, assuming this suggestion is correct, the function of *Varanus* venom is likely to be related to the processing of prey in some way – either acting in the procurement of prey and/or assisting the digestive process. Note that the possibility of a role in oral health is not discussed further, and this is due to

a lack of any studies of any antimicrobial properties of *Varanus* venom. However, this seems unlikely as a diverse oral flora has been documented from *Varanus* (Gillespie et al., 2002).

For venom to serve the primary function of dispatching prey, it must clearly bestow an advantage over not using venom, particularly as it is metabolically expensive to produce (McCue, 2006). Two key aspects of the ecology of the lizard are important in the evaluation of this hypothesis – diet and foraging tactics. For those monitors preying chiefly on groups such as insects, other invertebrates and eggs, it is difficult to see the advantage that using venom to subdue prey would give because, for example, eggs do not need subdued and the massive size difference between even the smaller monitors and their invertebrate prey allows them to be quickly and efficiently overpowered in at least most circumstances. The same is likely true for those that prey on relatively small reptiles, such as other lizards, but those monitors that do prey on potentially dangerous prey, such as many mammals or venomous species could conceivably gain an advantage from the venom. The powerful jaws of *Varanus*, however, allow the crushing of prey items small enough to be taken, often resulting in a quick death and so minimal risk of injury. One exception worth mentioning in this regard is *V. komodoensis*, which regularly preys on large mammals (with greater body size than the lizard). Prey falling into this category may well pose a risk to the predator, so could venom serve the primary role of assisting safe capture of prey in *V. komodoensis*? The foraging tactics of this large monitor make it unlikely. When hunting for large mammals, the Komodo monitor employs ambush tactics by lying in wait for passing prey before attacking and typically taking one large bite which causes extensive bleeding and severs tendons, both of which act to cripple the prey with minimal risk to the lizard (Auffenberg, 1981; King et al., 2002). With these massive injuries caused by the teeth and jaw musculature, which often lead reasonably quickly to incapacitation of the prey, it again becomes difficult to see an advantage here in producing venom for prey capture. Although virulent bacteria is transferred to prey during the bite, this is likely incidental and not a deliberate tactic by the monitor, and the quantity of blood lost from the injuries inflicted is likely enough to disable the prey even without these bacteria. However, this last point is difficult to test adequately using experimental methods, and so no data are available to confirm this suspicion. Nevertheless, Fry (2008) did propose a role of venom in prey capture, and although he did not examine

other possible functions of the venom, this deserves further study in *V. komodoensis*.

While any analysis of the toxins in *Varanus* venom could potentially be complicated by bacterial toxins (in the manner of more traditional schools of thought), toxinological analysis would reveal the nature of the toxins, which are very different between toxicofers and bacteria (cf. Arni and Ward, 1996; Snijder and Dijkstra, 2000). The author predicts that, at least in terms of any possible role in prey capture, bacterial infection will eventually prove to be of limited importance due to the effect on prey species noted from the venom (Fry et al., 2006) and the effects of massive blood loss from bites, but further work is needed to confirm this suspicion.

Finally, therefore, how probable is the hypothesis that the primary function of venom in monitor lizards is to enhance digestion of prey? Given that *Varanus* often consume large meals in relation to their body size, it is likely that an increase in the speed and/or efficiency of digestion would be selected for, particularly where prey items have a relatively rounded cross section, such as vertebrates (a common component of wild monitor diets [see table 1]). Further support may be found in the composition of the venom. Fry et al. (2006) found that PLA₂ has evolved in the anguimorph clade subsequent to the evolution of the basal toxicofers toxins. Venom phospholipases can act as potent neurotoxins, but also function in the breakdown of molecules in a way that assists digestion of prey items (Condrea and de Vries, 1965; Harris, 1997), and this latter action, if shown to be the case for *Varanus* venom, renders it highly plausible that it is well suited to the enhancement of prey digestion. Coupled with the problems discussed above for other explanations, I suggest that the primary function of venom in monitor lizards is to increase the speed and/or efficiency of digestion. Future research should aim to test this hypothesis experimentally by comparing digestion of prey items with or without the influence of *Varanus* venom.

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Appendix

Table 1. Published diets of monitor lizards. Items are listed in descending order of importance as far as can be ascertained.

<i>Varanus sp.</i>	Dietary Items	Reference
<i>acanthurus</i>	Insects, reptiles, other invertebrates, plant material	King, 2008
<i>albigularis</i>	Other invertebrates, insects, reptiles, amphibians, birds, bird eggs, mammals	Branch, 1991; Bennett, 1998
<i>baritji</i>	Other invertebrates (mainly theraphosid spiders)	King, 2004
<i>beccarii</i>	Other invertebrates (mainly crabs), reptiles, amphibians	de Lisle, 1996; Bennett, 1998
<i>bengalensis</i>	Insects, other invertebrates, reptile eggs, mammals, reptiles, bird eggs, amphibians, fish, birds	Auffenberg, 1994; Bennett, 1998; Pianka, 2004a; Liu, 2007
<i>brevicauda</i>	Insects, other invertebrates, reptiles, reptile eggs	Pianka, 1970a, 1994; King and Pianka, 2007
<i>caerulivirens</i>	Other invertebrates, insects, amphibians	Ziegler, Böhme and Philipp, 2004; Philipp, Ziegler and Böhme, 2007
<i>caudolineatus</i>	Insects, reptiles, other invertebrates, plant material	Pianka, 1969
<i>cerambonensis</i>	Other invertebrates, insects, reptiles, reptile eggs	Philipp, Ziegler and Böhme, 2004a; Philipp, Ziegler and Böhme, 2007
<i>doreanus</i>	Reptiles, reptile eggs (mainly turtle eggs), insects	Bennett, 1998; Philipp, Ziegler and Böhme, 2007

Table 1. *Continued*

<i>Varanus sp.</i>	Dietary Items	Reference
<i>eremius</i>	Reptiles, insects, other invertebrates, mammals, seeds	Pianka, 1968, 2004b, 2007
<i>exanthematicus</i>	Insects, mammals, birds, reptiles, bird eggs, other invertebrates, amphibians	Yeboah, 1993; de Lisle, 1996; Bennett, 1998
<i>finschi</i>	Reptiles, insects, birds, other invertebrates	Philipp, Ziegler and Böhme, 2004b; Philipp, Ziegler and Böhme, 2007
<i>flavescens</i>	Amphibians, reptile eggs, insects, other invertebrates, mammals, birds, bird eggs	Bennett, 1998
<i>flavirufus</i>	Mammals, reptiles, reptile eggs, insects, fish, other invertebrates, birds, bird eggs, amphibians	Bennett, 1998
<i>giganteus</i>	Reptiles, mammals, insects, other invertebrates, reptile eggs, birds	Pianka, 1994; Bennett, 1998; Macdonald, 2007
<i>gilleni</i>	Reptiles, insects, other invertebrates, bird eggs, mammals	Pianka, 1969, 1982; de Lisle, 1996; Horn, 2004
<i>glauerti</i>	Insects, other invertebrates, reptiles, reptile eggs	de Lisle, 1996; Sweet, 1999
<i>glebopalma</i>	Reptiles, other invertebrates, insects, amphibians	de Lisle, 1996; Bennett, 1998; Sweet, 1999
<i>gouldii</i>	Insects (mainly caterpillars or beetles), reptile eggs, other invertebrates, reptiles, amphibians, mammals, fish, birds, birds eggs	Pianka, 1970b; Shine, 1986; Thompson, 2004
<i>griseus</i>	Mammals, birds, reptiles, eggs, amphibians, insects, other invertebrates	Stanner and Mendelsohn, 1987; Bennett, 1998
<i>indicus</i>	Other invertebrates (mainly crabs), insects, reptile eggs, fish, reptiles, birds, bird eggs, mammals	de Lisle, 1996; Philipp, Ziegler and Böhme, 2007
<i>jobiensis</i>	Insects, amphibians, other invertebrates, reptile eggs	Philipp, Ziegler and Böhme, 2004c; Philipp, Ziegler and Böhme, 2007
<i>keithhornei</i>	Insects	Irwin, 1994; Bennett, 1998
<i>kingorum</i>	Insects	Bennett, 1998
<i>komodoensis</i>	Mammals (mainly large species such as boar and deer), eggs, birds, reptiles, insects	Burden, 1928; Auffenberg, 1981; King et al., 2002

Table 1. *Continued*

<i>Varanus sp.</i>	Dietary Items	Reference
<i>mabitang</i>	Fruit, leaves, seeds, insects, other invertebrates	Gaulke, 2004; Gaulke et al., 2007
<i>melinus</i>	Insects, amphibians, bird eggs	Ziegler and Böhme, 2004
<i>mertensi</i>	Other invertebrates (mainly crustaceans), insects, fish, amphibians, reptile eggs, mammals, reptiles, birds, fruit	Mayes, 2006
<i>mitchelli</i>	Insects, fish, other invertebrates, reptile eggs, amphibians, reptiles, mammals, birds	Shine, 1986
<i>niloticus</i>	Other invertebrates (mainly gastropods and crustaceans), insects, reptiles, fish, mammals, bird eggs, amphibians	Yeboah, 1993; Bennett, 1998; Luiselli et al., 1999; Lenz, 2004
<i>olivaceus</i>	Fruit, other invertebrates (primarily molluscs), insects, birds, bird eggs	Auffenberg, 1988; Bennett, 1998
<i>ornatus</i>	Other invertebrates (mainly crabs), reptiles	Böhme and Ziegler, 2004
<i>panoptes</i>	Insects (mainly crickets), amphibians, other invertebrates, reptiles, reptile eggs, mammals, fish, birds	Shine, 1986; Shannon, 2008
<i>pilbarensis</i>	Insects, other invertebrates, reptiles	de Lisle, 1996
<i>prasinus</i>	Insects, other invertebrates, mammals	Greene, 1986
<i>primordius</i>	Reptiles, reptile eggs, insects	Bennett, 1998; Husband and Christian, 2004
<i>rosenbergi</i>	Mammals, insects, reptiles, other invertebrates, amphibians, birds	Bennett, 1998; King and Green, 1999
<i>rudicollis</i>	Insects, other invertebrates, amphibians	Bennett, 1998
<i>salvadorii</i>	Birds, bird eggs, mammals	de Lisle, 1996; Bennett, 1998
<i>salvator</i>	Mammals, insects, other invertebrates, reptiles, birds, amphibians, fish, birds eggs, reptile eggs	Gaulke, 1991; Bennett, 1998; Shine et al., 1998; Gaulke and Horn, 2004; de Lisle, 2007
<i>scalaris</i>	Insects, other invertebrates, reptiles, birds	de Lisle, 1996; Bennett, 1998; Sweet, 2007
<i>semiremex</i>	Other invertebrates (mainly crustaceans), fish, frogs, insects, reptiles, mammals	Jackson, 2005
<i>spenceri</i>	Mammals, reptiles, insects	Bennett, 1998; Jackson and Lemm, 2009

Table 1. *Continued*

<i>Varanus sp.</i>	Dietary Items	Reference
<i>spinulosus</i>	Insect, other invertebrates, birds	Böhme and Ziegler, 2007; Dwyer, 2008
<i>storri</i>	Insects, reptiles, other invertebrates	Bennett, 1998
<i>timorensis</i>	Reptiles, insects, other invertebrates	Bennett, 1998
<i>tristis</i>	Reptiles, insects (mainly grasshoppers), reptile eggs, birds, bird eggs, other invertebrates, leaves	Bennett, 1998; Pianka, 1971, 1982, 1994; Sweet, 2007
<i>varius</i>	Mammals, insects, other invertebrates, birds, reptiles, bird eggs, reptile eggs	Bennett, 1998; Guarino, 2001
<i>yemenensis</i>	Insects, other invertebrates	Bennett, 1998