

The predator defence system of an African king cricket (Orthoptera: Anostostomatidae): does it help to stink?

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We examined the putative defence system of a king cricket, *Onosandrus* sp., in particular the efficacy of the noxious faeces against two types of predator: a lizard, the skink *Mabuya striata* (an active, diurnal forager), and the toad *Bufo gutturalis* (a nocturnal, ambush predator). Contrary to our predictions, the faeces did not act as a deterrent to either predator. Tongue-flick trials with cotton scent applicators indicated that the skinks showed a heightened predatory response to king cricket faeces over king cricket integument, field cricket integument and an odourless control. We suggest that 'primary' defence mechanisms, such as nocturnal behaviour, cryptic colouration and immobility, are more effective than 'secondary' defence mechanisms, such as stridulation, kicking and defecation. Given that the noxious faeces already have a demonstrated role in inter- and intrasexual communication, we suggest that the assumed defensive role of the faeces is minor or an epiphenomenon.

Key words: Anostostomatidae, king cricket, defence behaviour, tongue-flicks, predatory behaviour.

INTRODUCTION

It is a truism that, while a day without food or without sex may have a short-term influence on fitness, nothing reduces fitness as totally and effectively as being killed and eaten by a predator (Lima & Dill 1989). Predation pressure, therefore, is one of the most important selective forces resulting in the evolution of crypsis, aposematism, escape behaviour, armour and chemical defence (Lima & Dill 1989). Many organisms have evolved early or relatively long-range detection of predators. Acoustic signals (Moiseff *et al.* 1978), vibrations (Spieler 2003), visual signs (Spieler 2003) and especially chemical cues can indicate the presence of a predator and can be detected by a wide range of taxa, e.g. amphibians, Rohr & Madison (2001); amphibian tadpoles, Laurila *et al.* (1997); reptiles, López & Martín (2001) and orthopterans, Brettschneider & Bateman (2005). Crypsis is one of the most widespread anti-predator tactics in many taxa (e.g. amphibians, Laurila *et al.* 1997; Petranka & Hayes 1998; reptiles, López & Martín 2001; orthopterans, Hatle & Faragher 1998). Alternatively, prey organisms may also respond to potential predation with escape, or retreat behaviour (Moiseff *et al.* 1978; López & Martín 2001), or by forming aggregations, presumably to reduce individual risk of predation (Hatle & Salazar 2001;

Spieler 2003). Perhaps the ultimate defence system is to become unpalatable or even poisonous to potential predators (e.g. amphibian tadpoles, Laurila *et al.* 1997; orthopterans, Hatle & Salazar 2001).

The effectiveness of the several defence mechanisms strongly depends on the predator, however, and on its hunting strategy. It follows, therefore, that only a few prey species rely on only one defence method, and combinations of several defence mechanisms are common (e.g. Hatle & Salazar 2001). Chemically defended organisms, for instance, are usually also aposematically coloured, or part of the same general adaptation, e.g. crypsis and flash colouration (Hatle & Salazar 2001; De Cock & Matthysen 2003).

Most members of the Anostostomatidae (Orthoptera: Stenopelmatoidea), the weta and king crickets, are very large insects (female giant weta *Deinacrida heteracantha* from New Zealand can weigh up to 41 g (McIntyre 2001)), and are usually flightless and relatively slow-moving, making them potentially highly vulnerable to predation. The defence behaviour of anostostomatids in general has been little studied, and in African species not at all. In the best known African king cricket, *Libanasidus vittatus*, commonly known as the 'Parktown Prawn' (Toms 1985), only anecdotal observations of apparent defence behaviour have

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been published, namely: kicking, jumping, biting, stridulation, defecation and feigning death (Bateman & Toms 1998).

Some investigations, however, have been carried out on Australian king crickets (Monteith & Field 2001) and New Zealand weta (Field & Glasgow 2001). Field & Glasgow (2001) distinguished between primary and secondary defence mechanisms. Primary defence mechanisms decrease the probability that an interaction will occur between a prey animal and a potential predator, and function regardless of whether a predator is present or not. For anostomatids, the main primary mechanisms are nocturnal activity, and taking refuge in logs or underground chambers during the day. This behaviour would be enhanced by their cryptic colouration.

Secondary defence mechanisms operate when a prey animal detects a predator, or when under attack from a predator. These would include those behaviours posited by Bateman & Toms (1998) as defence, and the various behaviour patterns reviewed by Field & Glasgow (2001) and Monteith & Field (2001). These behaviours include kicking, mandible gaping, stridulation, jumping, biting, and back-flipping in New Zealand species (Field & Glasgow 2001) and escape jumping (nymphs of *Transaevum* jump into water to be borne away from predators), stridulation, and back-flipping to bite and to flash yellow and white abdominal tergites in Australian species (Monteith & Field 2001).

The weta of New Zealand evolved under a different intensity of predation pressure to the king crickets of Australia and Africa. Before the introduction of exotic predators, only birds and a limited range of bats and reptiles predated upon weta. Australian and African species, however, have evolved in the face of a wider range of bird, mammal, amphibian and reptile predators. Unlike the weta, the king crickets of these two continents produce liquid, foul-smelling faeces which they can eject forcefully. The smell is very strong and persistent to a human observer (Bateman & Toms 1998; Monteith & Field 2001).

The aim of this study was to examine how king crickets defend themselves in staged predator encounters. We assumed that a king cricket would use the noxious faeces as a defence and predicted that the faeces would deter both ambush and actively foraging predators. We further predicted that the experimental application of the noxious faeces to a species that did not produce a chemical defence would improve survival of that species in predator encounters.

METHODS

Study species

We used *Onosandrus* sp. from Ngome Forest, KwaZulu-Natal, either collected at night, when active, or dug from their shallow burrows during the day. We kept them communally in large (70 × 120 × 70 cm) containers with a deep layer of soil and leaf litter, where they were supplied with commercial fish food, snails, lettuce and water *ad libitum*. We used field crickets (*Gryllus bimaculatus*) from colonies maintained in the Department of Zoology at the University of Pretoria as a control in the feeding trials, as there is no evidence that they produce a chemical defence.

Predator species

We used two predator species: an actively foraging diurnal lizard; the striped skink (*Mabuya striata punctatissima*) ($n = 10$), and a nocturnal ambush predator; the guttural toad (*Bufo gutturalis*) ($n = 8$). We caught the skinks on the Pretoria University campus and kept them individually in terrariums (30 × 15 × 15 cm) under a natural light regime with heating mats, sand, leaf litter, a stone for basking, and water provided *ad libitum*. The toads came from a suburban garden in Pretoria and were kept singly in tubs (55 cm diameter) with a platform of stone and earth, and water deep enough to submerge completely. Before the experimental trials, we fed the predators every second day on wild-caught grasshoppers, *Grylloides sigillatus* nymphs and mealworm larvae (*Tenebrio molitor*). All predators were released at the site of capture after the experiments.

Tongue-flick trials

We tested the response of skinks to chemical stimuli from:

- a) Field cricket integument;
- b) *Onosandrus* integument;
- c) *Onosandrus* faeces;
- d) Odourless control (deionised water).

We followed the protocol of Cooper (2000) in preparing stimuli. We dampened cotton swabs with deionized water and, for the integument stimuli, rubbed the swab over the cuticle of either a field cricket or an *Onosandrus*. We collected faeces by grasping an *Onosandrus* between finger and thumb and holding it in a glass tube. Most *Onosandrus* reacted to this by kicking and defecating into the tube. We first added a drop of deionised water to the faeces to aid uptake by the cotton, and dipped the swab once, for two seconds

in the faeces. We tested the skinks with each stimulus once in random order, with at least one hour between tests by removing the lid of the each terrarium and slowly advancing the cotton swab on the end of a 15 cm wooden stick to 1–2 cm anterior to the focal skink's snout. Following Cooper (2000) with some modifications, we recorded the latency to tongue-flick and if the skink tongue-flicked within 60 seconds, we recorded the number of tongue-flicks in the 60 seconds following the first tongue-flick. If the skink bit the cotton applicator, we recorded the total number of bites.

Cardboard tile trials

We followed the protocol of Whiting & Cooper (2003), with minor modifications, in preparing cardboard squares (2×2 cm; hereafter tiles) treated with: 1) deionised water; 2) crushed *G. bimaculatus*; 3) crushed *Onosandrus*; and 4) *Onosandrus* faeces. In all cases we ensured that no body parts or faecal material were visible on the tiles. We then air-dried the tiles and placed each one, sequentially and in a randomized order, in each skink's cage with 24 hours between each tile trial. We placed the tile on the smooth stone in each cage that the skink used for basking. Once the skink had returned to the basking stone, we recorded its latency to tongue-flick, the number of tongue-flicks and number of bites at the tile in a 60 s period after the first tongue-flick. In this way, we obtained a measure of the skinks' response to chemical cues and controlled for the potential disturbance of approaching them with the cotton applicators. We terminated the trial if the skink did not tongue-flick within 2 min.

Predation trials

After a starvation period of three days, we offered each skink, in random order and on subsequent days, either an adult *Onosandrus* (20–25 mm body length), a similarly sized field cricket nymph or a field cricket nymph that was painted with fresh *Onosandrus* faeces. We recorded the behaviour of both prey and predator continuously for the first five minutes and at five-minute intervals for the following hour. We used the same protocol in the trials with the eight toads (mouth width range: 21.2–31.4 mm) as predator. We stopped the trials after one hour or when the predator killed the prey.

RESULTS

Tongue-flick trials

In contrast to our expectations, the skinks tongue-flicked significantly sooner (Kruskal-Wallis, $H_{(3,40)} = 9.6$, $P < 0.05$) at the *Onosandrus* faeces than any of the other treatments, and more often (Kruskal-Wallis, $H_{(3,40)} = 19.5$, $P < 0.01$) at the *Onosandrus* faeces than any of the treatments except the *Onosandrus* integument (Fig. 1). The only bites we observed were at the cotton applicators treated with *Onosandrus* faeces.

Cardboard tile trials

Latency to tongue-flick at the different treatment tiles did not reach significance, but showed much the same trend as in the tongue-flick trials (Kruskal-Wallis, $H_{(3,40)} = 3.1$, $P = 0.41$). However, the skinks tongue-flicked significantly more often at the *Onosandrus* faeces-treated tiles than at the other tiles (Kruskal-Wallis, $H_{(3,40)} = 19.2$, $P < 0.001$). Again, the only bites recorded were at the *Onosan-*

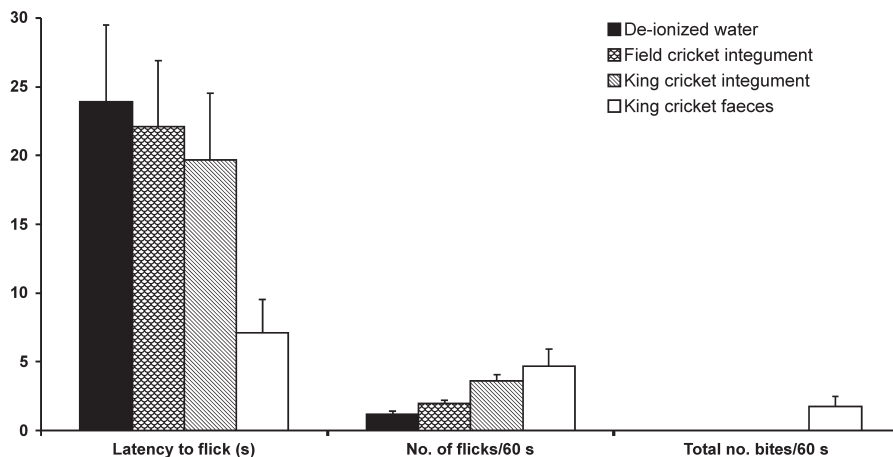


Fig. 1. Latency to tongue-flick, numbers of tongue-flicks and numbers of bites by skinks (*Mabuya striata*) at the cotton applicators.

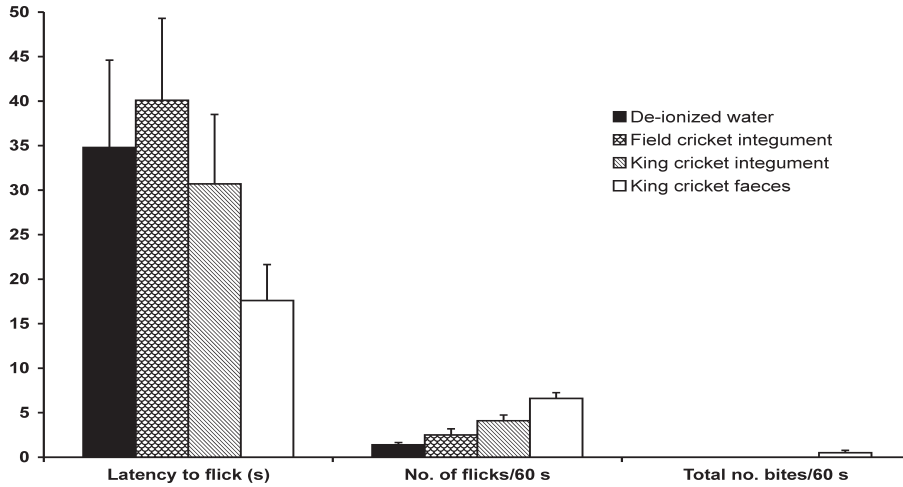


Fig. 2. Latency to tongue-flick, numbers of tongue-flicks and numbers of bites by the skinks (*Mabuya striata*) at the cardboard tiles.

drus faeces (we recorded as 'bites' when the skink orientated its snout directly down on the tile and opened its mouth even only slightly. 'Bites' during these trials, therefore, are slightly different to bites directed at the treated cotton applicators) (Fig. 2).

Predation trials

All toads ate all types of prey (Table 1), and in all but one case the toads attacked and swallowed the *Onosandrus* within 10 seconds. When seized by a toad, in most cases the *Onosandrus* did not have time to react before it was swallowed. In only one case did the toad drop the prey after the *Onosandrus* kicked the toad in the face with its hind legs when held in the toad's jaws. The *Onosandrus*, when grabbed from above, raised its hind legs above its back so that they came in contact with the toad's face. The toad made a second successful attack immediately. When under attack *Onosandrus* was not seen to defecate. We could see no difference between the feeding behaviour of toads provided with *Onosandrus* and field crickets. All the faeces-painted field crickets were eaten, and we could see no difference in behaviour or reaction by the toads having eaten

these crickets. The toads all approached the *Onosandrus* and field crickets when we placed them in their terrariums, and even if the prey were otherwise motionless, slight movement of the antennae elicited an attack.

All skinks eventually killed and ate all the types of prey, with the exception of two *Onosandrus* that managed to avoid detection by skinks for the full hour of the trial (Table 1). In most cases, the immediate response of the *Onosandrus* upon introduction into the skink cage was to remain motionless, or immediately to move under the leaf litter. This was how the two *Onosandrus* survived. All the skinks tongue-flicked several times before attacking. When the skinks attacked the *Onosandrus*, they all orientated themselves to grab the prey from above. On three occasions, the *Onosandrus* defecated, but did not make contact with the predator due to its orientation. When seized the *Onosandrus* raised their hind legs above their back and sometimes kicked out with their tibia. On four occasions, the *Onosandrus* kicked so vigorously (none made contact with the skink) that the predator released the prey, but immediately grabbed it again. On one occasion, this was repeated three

Table 1. Proportion of prey types eaten by each predator.

Predator	n	Prey type		
		King cricket	Field cricket	Field cricket painted with king cricket faeces
Toads (<i>Bufo gutturalis</i>)	8	8/8	8/8	8/8
Skinks (<i>Mabuya striata</i>)	10	8/10	10/10	10/10

times and it took 48 min for the skink to subdue the *Onosandrus*.

The field crickets were more active than the *Onosandrus*, and although some were motionless at first, eventually all moved and drew the attention of the skinks. The skinks all tongue-flicked before attacking, but it was not possible to gain accurate counts for comparison due to rapid movement of the skinks when attacking. We could observe no repellent effect caused by painting faeces on the field crickets.

DISCUSSION

Our prediction that the foul smelling faeces would be an efficient defence against predators was not supported. Not only did both the skinks and the toads eat *Onosandrus*, but also field crickets painted with *Onosandrus* faeces. Faeces squirting (observed in 30% of the trials) did not deter skinks and was not utilized against the toads. Tongue-flicking by lizards for prey chemical discrimination is widespread in active foragers such as *Mabuya striata* (Cooper 2000). Tongue-flick rate and biting rate are higher for prey items than for an odourless control in, for example, the generalist predator lacertid *Podarcis lilfordi* (Cooper & Pérez-Mellado 2002). That the skinks in our experiments tongue-flicked sooner and more often, and only bit at the *Onosandrus* faeces stimuli suggests that they identified it as a prey cue. *Onosandrus* integument also provoked a higher tongue-flick rate than field cricket integument, suggesting an ability to differentiate the two, and suggests a preference for *Onosandrus*, compared to field cricket, prey.

The behaviour of the *Onosandrus* when attacked by the skinks was similar to that recorded for New Zealand tree weta (*Hemideina crassidens*) attacked by geckos (*Hoplodactylus pacificus*) and South Island robins (*Petroica australis australis*) (Field & Glasgow 2001) – hind legs raised above the back, and kicking. This defence behaviour was not generally successful against the birds, but none of the geckos was successful in subduing the weta (Field & Glasgow 2001). As in our trials, movement was important in eliciting attack. Anuran predators are primarily motion orientated (Hatle & Salazar 2001; Robins & Rogers 2004), though Taylor (2001), found a minor role of the auditory sense. Therefore, a primary defence of slow movement or immobility combined with crypsis is probably the best strategy against such a predator (e.g. Hatle & Faragher 1998), although the toads in our experiments were extremely predatory and were able to detect slight movement. By contrast, the skinks

sense prey not only by motion but also by scent (Cooper & Vitt 1986; Cooper & Habegger 2001), reducing the efficiency of this primary defence.

Our predation trials indicated that the presumed secondary defence of king crickets (e.g. kicking and defecating) during a direct attack was less efficient than expected. Attack by toads was so swift that secondary defences could not be used, and they proved useless against skinks. Field crickets painted with *Onosandrus* faeces also fell prey to both predators. King crickets are primarily nocturnal and spend the day in burrows except on overcast or rainy days (P.W.B., pers. obs.). According to McDonald & Hanrahan (1993), *Libanasidus vittatus* (Anostomatidae) return to their burrows several times a night when foraging, possibly reducing exposure to predation. When *Onosandrus* are dug from burrows, they stridulate and vigorously defend themselves by orienting themselves to kick and squirt faeces towards the source of disturbance and leap from the burrow only when completely exposed (pers. obs.).

That the skinks seemed to be attracted by the scent of the *Onosandrus* faeces is the opposite to our prediction, and to that seen in investigations with other chemically defended orthopterans (Whitman 1982). This raises the question of the primary function of the chemical component. In the king cricket *Libanasidus vittatus*, Bateman & Toms (1998) showed a major role for the scent of the faeces in attracting potential mates. The scent also has a role in deflecting cannibalism and male-male competition (Bateman & Toms 1998; Bateman 2000). If the apparent defence function of the faeces were a minor epiphenomenon of the communication role of the chemical component in the faeces, this would not explain why the faeces are ejected forcefully when the cricket is disturbed. More research is needed.

Even though the results might lead to a clear suggestion of major and subordinate functions of the chemical component of the faeces, the results of this study demonstrate the ineffectiveness of this defence mechanism against two predators only. The faeces might have a repellent effect to other predators, particular small mammals. Interestingly the evolutionary appearance of a putative chemical defence in anostomatids seems to be linked to the presence of diverse mammalian predators (Monteith & Field 2001). Investigations with wingless and chemically defended orthopterans from North America showed a strong repellent effect of the secretion against grasshopper mice (*Onychomys torridus*) (Whitman 1982). Mainly

nocturnal predators threaten king crickets; the chemical component is, therefore, likely to have evolved in response to nocturnal hunters such as insectivores, small carnivores, bats, nocturnal birds and amphibians. The skink *Mabuya striata* is strictly diurnal, although there are nocturnal lizards.

In conclusion, although *Onosandrus* do forcefully eject their foul-smelling faeces when disturbed (e.g. when disturbed in burrows), this and other apparent secondary defence behaviour such as kicking with their spiny legs, was not a sufficient deterrent against the two predators used in our trials, and the faeces even induced a heightened feeding response from skinks. Primary defence mechanisms (i.e. remaining motionless) were more efficient, but still failed in the presence of toads.

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