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Does toxic defence in *Nycticebus spp.* relate to ectoparasites? The lethal effects of slow loris venom on arthropods

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ABSTRACT

The venom produced by slow lorises (*Nycticebus* spp.) is toxic both intra- and inter-specifically. In this study we assessed the ecoparasite repellent properties of their venom. We tested venom from two Indonesian slow loris species: *Nycticebus javanicus* and *Nycticebus coucang*. Arthropods directly exposed to brachial gland secretions mixed with saliva from both species were immediately impaired or exhibited reduced activity (76%), and often died as a result (61%). We found no significant difference in the result of 60-min trials between *N. coucang* and *N. javanicus* [$X^2(1, n = 140) = 2.110$, $p = 0.3482$]. We found evidence that the degree of lethality of the venom varies according to the arthropod taxa to which it is exposed. While most maggots (84%) were initially impaired from the venom after 10 min, maggots died after a 1 h trial 42% of the time. In contrast, at the end of 1 h trial, spiders died 78% of the time. For all arthropods, the average time to death from exposure was less than 25 min ($M = 24.40$, SD = 22.60). Ectoparasites including ticks, members of the arachnid order, are known to transmit pathogens to hosts and may be an intended target of the toxic secretions. Our results suggest that one function of slow loris venom is to repel parasites that affect their fitness, and that their topical anointing behaviour may be an adaptive response to ectoparasites.

1. Introduction

Few mammals are known to produce toxic secretions (Ligabue-Braun et al., 2012). The functions of mammal venom vary but include suppressing prey, anti-predator defence and intraspecific competition (Ligabue-Braun et al., 2012). Slow lorises (*Nycticebus* spp.) are unusual Southeast Asian primates; they are cryptic, nocturnal, and produce a toxic compound, which they administer topically or through their bite. Slow lorises are the only primates known to produce venom, and they do this by combining saliva with oil from a brachial gland in their mouth (Alterman, 1995), and licking their fur or biting the intended victim. Here we explore the adaptive significance of venom amongst Indonesian slow lorises in regard to its effects on invertebrates.

Nekaris et al. (2013) suggested that slow loris venom might function to repel or defend against predators, conspecifics, prey or ectoparasites in four competing, although not mutually exclusive, hypotheses. Little evidence exists to suggest that loris venom is used against prey, given that venom is not used to paralyze prey (Alterman, 1995) and the fact that lorises rapidly consume prey. Previous studies suggest that loris venom may serve as a defense against conspecifics, where bite wounds are a major cause of morbidity and mortality in captivity (Sutherland-Smith and Stalis, 2001). Further, predators may be the target of loris venom, where predators may be less likely to select prey that produces toxic compounds (Alterman, 1995; Nekaris et al., 2013). In support of this hypothesis, a female *Nycticebus javanicus* was witnessed anointing her offspring in venom (Nekaris et al., 2013), which could render a vulnerable infant unpalatable to potential predators.

In terms of the latter hypothesis, chemical toxicity is one feature that renders vertebrates as unsuitable hosts for ectoparasites (Weldon, 2010). Ectoparasites are important selective forces that negatively affect the fitness of their hosts (Weldon and Carroll, 2006), and they are common in the tropical Southeast Asian countries that slow lorises inhabit (Anastos, 1950). Ectoparasites are not commonly observed on both wild and captive slow lorises,

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and of the more than 300 wild lorises observed, representing all species, only two instances of infestation by ectoparasites have been observed (Nekaris et al., 2013; Streicher, 2004). It has been proposed that this is due to the chemicals produced by their saliva, brachial grand secretions, or a combination of the two.

We explored whether the secretions produced by slow lorises are lethal to ectoparasites by examining the physiological responses of arthropods to slow loris venom. We predicted that: a) arthropods will die more rapidly after direct exposure to slow loris secretions and b) arthropods will avoid moving to test areas that have been applied with slow loris secretions.

2. Materials and methods

2.1. Study site

We tested the repellent effects of venom produced by adult wild Javan slow lorises (*N. javanicus*) in an agroforest study site in the district of Garut, West Java, Indonesia (S7°6′6 & E 107°46′5) and adult wild-born greater slow lorises (*Nycticebus coucang*), recently confiscated from the illegal wildlife trade in Sumatra, at Cikananga Wildlife Centre, Sukabumi District, West Java (S7°00′23.9 & E 108°33′3.9).

2.2. Sample collection and preparation

The research conducted complies with the relevant laws of Indonesia and the institutional guidelines of the authors' institutions. Between July 2013 and January 2014, we collected brachial gland exudate (BGE) and saliva samples from Javan slow lorises using Sterilin swab kits ($n = 49$). In March 2014, we collected saliva and BGE samples from greater slow lorises using cotton swabs stored in sterile glass vials and Salimetrics oral swabs that we centrifuged ($n = 42$). The swab was wiped across one or both brachial glands. We froze all samples until usage.

Following methods employed by Alterman (1995), we diluted and extracted frozen BGE swabs with a 2 ml solvent of 6% formic acid, which solvates hydrophilic compounds, or alternatively with 2 ml of 1:1 50% methanol and 50% methylene chloride, which is lipid soluble. Solvents were first tested on two of each species of experimental subject to determine their effects (not included in analysis), and as a result the methanol:methylene chloride solvent was only used on maggots, as the solvent alone impaired other types of arthropods. After a 30-min incubation at room temperature, we mixed 100 μl aliquots of saliva with the extracted solutions and incubated for an additional 15 min. Alternatively, we added saliva on swabs to the venom solution, incubated for 15 min, and mixed with a pipette afterward. In experiments using only saliva, we applied saliva directly with no solvent. The sample storage type and sex of the sampled individual(s) were recorded for all solutions used in the experiment.

We collected multiple types of insects for use in the experiments, including spiders (Arachnida), maggots (Diptera larvae), ants (Hymenoptera), fleas (Siphonaptera), and caterpillars (Lepidoptera larvae) controlled for length: 2 cm for maggots; 1–1.5 cm for spiders, and 2 cm for caterpillars. We attempted to sample tick abundance in the study area using a combination of methods, including the drag-flag method for adult hard ticks (Carroll and Schmidtmann, 1992) and dry ice traps for soft ticks, given that ticks are drawn to CO_2 emissions to locate hosts (Sonenshine, 2013). When no adult ticks were found in two weeks of surveys, arboreal spiders (Suborder Araneomorphae, Family Theridiidae) collected from 7 m height at 1100 m a.s.l. were used as an analogy of the effects on ticks.

2.3. Experimental procedure

2.3.1. Direct tests of parasite response to secretions

A solution of brachial gland secretions, saliva, and solvent was topically applied to subjects in glass petri dishes. A control of the same size and species was treated only with the solvent. In the case of tests using saliva only, water was used as a control. The following amounts were applied with a micropipette to the abdomen of each arthropod, avoiding the head: 100 μl for <1 cm in length; 200 μl for 1.5 cm; 300 μl for 2 cm. We conducted all tests on forward locomoting individuals. We recorded responses at 0-, 10-, 30-, and 60-min intervals: no effect (subject continues locomoting with no response), reduced activity (locomotor activity slows), impaired (motor impairment), death, and time until death.

2.3.2. Repellency tests

Next, "choice" experiments (Dautel, 2004; Dautel et al., 1999) tested whether secretions actually repel parasites. In choice tests, a petri dish was divided into two zones, one for the chemically treated zone (200 μl dropped directly on the dish) and one for the experimental subject. At the beginning of the experiment, the subject was initially placed in the non-annointed zone. The subject's immediate response within 15 s of the beginning of the trial was recorded: locomoting toward treatment (e.g. through the venom pipetted into the petri dish) and locomoting away from the treatment (e.g. turns away from treatment). Subject activity (no reaction, reduced activity, impairment, death) was then recorded at the end of a 1-h trial. In choice experiments involving fleas, both treated and untreated tufts of loris fur were placed in the treatment zone; the "chosen" tuft was the one that the flea was located on the most frequently.

2.4. Data analysis

Statistical analyses were performed in JMP 11 (SAS Institute Inc., 2014) and Excel 14.2.0 (Microsoft Corp., 2011). In the analyses we combined the "impaired" and "reduced activity" behavioural categories into one category for simplification purposes.

3. Results

3.1. Direct application tests

We tested 121 subjects (Arachnida: $n = 53$; Siphonaptera: $n = 8$; Diptera: $n = 35$; Hymenoptera: $n = 13$; Lepidoptera: $n = 12$) in 93 venom application trials with 28 control trials. The average time to death for trials that resulted in death was 24.40 min ($n = 50$; SD = 22.60).

Tests using saliva or brachial oil only on fleas ($n = 3$), maggots ($n = 3$), and spiders ($n = 10$) did not have a significantly different outcome ($\alpha = 0.05$) than the control [$(X^2(1, n = 16) = 1.27, p = 0.53$]. These tests were stopped to preserve the limited samples, and a

Table 1
Proportion of arthropods that exhibit no effect, impairment, or death at the end of 10-and 60- min single experimental trials.

Result of trials						
Type	Death		Impaired		No effect	
	10 min	60 min	10 min	60 min	10 min	60 min
Ant (n = 10)	0.90	0.90	0	0	0.10	0.10
Caterpillar (n = 10)	0.00	0.00	0.10	0.00	0.90	0.10
Maggot (n = 19)	0.00	0.42	0.84	0.26	0.16	0.32
Spider (n = 40)	0.18	0.78	0.63	0.08	0.20	0.15

combination of brachial oil and saliva was used for the remaining tests ($n = 73$).

Arthropods directly exposed to slow loris brachial gland secretions mixed with saliva from both species were immediately impaired (76%), and died as a result 61% of the time; treated arthropods had a significantly different response than those exposed to the solvent alone [$X^2(1,n = 113) = 22.59$ $p < 0.0001$]. The immediate results of the application are not included in the analysis, as the response to having a foreign substance applied is a confounding factor. We found no significant difference in time to death between spiders and maggots [$t(40) = 1.37$, $p = 0.177$]. While most maggots (84%) were initially impaired from the venom after 10 min, only 42% of maggots died after a 1-h trial (Table 1; Fig. 1). In contrast, 63% of spiders were impaired or and 18% had died after only 10 min after direct application of a venom treatment (Table 1), and at the end of 1 h, 78% of spiders died (Table 1).

We found no significant difference in the result of 60-min trials between *Nycticebus coucang* and *Nycticebus javanicus* [$X^2(\mathrm{df} = 1,n = 93) = 2.11$, $p = 0.35$; Table 1]. For spiders, there was a slight difference in time until death between *N. javanicus* and *N. coucang* (Kruskal Wallis: $Z = -1.974$, p- $= 0.048$), where subjects applied with venom of *N. javanicus* took a mean of 39.18 min to die compared to 23.38 min for *N. coucang*. We found no significant difference between the 60-min effects of male and female venom [$X^2(1, n = 93) = 7.45$, $p = 0.11$) or in time to death for male, female, and combination male/female venom (ANOVA: $F(2,47) = 3.06$, $p = 0.06$).

3.2. Repellancy tests

A total of 17 choice experiments were conducted with fleas ($n = 2$), maggots ($n = 10$), and spiders ($n = 3$). No consistent results were found to suggest that any experimental subjects avoided the venom treated areas. Half of the maggots (50%) and all of the spiders (100%) moved through the treated area of BGE mixed with saliva secretions, even if this resulted in impairment.

4. Discussion

We show here that the venom of slow lorises is toxic and often lethal to a variety of insect species. Consistent with previous findings (Alterman, 1995), we confirm that this is only the case when brachial grand secretion is combined with saliva. The degree of lethality of the venom is taxon-specific and varies according to the type of arthropod to which it is exposed. Venom was more lethal for spiders and ants than for maggots and caterpillars, suggesting its use as a deterrent against some ectoparasites.

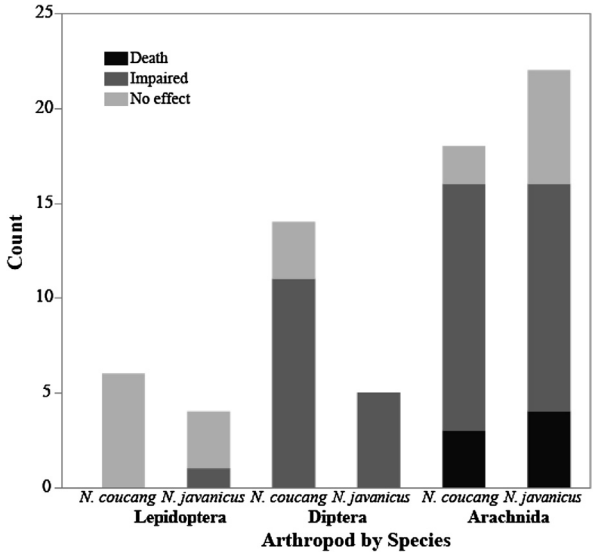

Fig. 1. Bar chart indicating the proportion of results (lethality, motor impairment, or no effect) from the 1 h trial of treated arthropods (Lepidoptera $n = 10$, Arachnida $n = 45$, Diptera $n = 23$).

Chemical toxicity is one feature that renders vertebrates unsuitable as hosts for ectoparasites (Weldon, 2010). Alterman (1995) found that there are two different types of toxic compounds in slow loris venom by using two different kinds of solvents in venom experiments, one aqueous soluble and one lipid soluble; the toxins can thus be delivered through either the circulatory system or more rapidly into adipose tissue. Thus, it is possible that one kind of toxin is more effective against predators (bite delivery) while the other is more effective against ectoparasites (topical delivery).

Slow lorises spend up to 10% of their active time autogrooming (Rode et al. in Press) and can lick most body parts with the tongue, especially licking their arms to rub on their head and face (Schulze and Meier, 1995). The brachial gland secretions of slow lorises, when combined with their saliva and manually or orally applied to their fur, would be a feasible means of reducing ectoparasite load. One reason why ectoparasite load may be a strong selective pressure on slow lorises is their social organization. Slow lorises sleep solitarily (Wiens and Zitzmann, 2003), and thus less opportunities for social grooming arise than more social grouping pattern, potentially raising the risk of parasites. While social living may increase the costs of parasitism and introduce more opportunities for cross-infection, behavioural adaptations like grooming can reduce the chances of becoming infected.

Other vertebrates are known to use toxic compounds with pesticide qualities. Numerous bird species take advantage of the repellent chemical properties of ants (Weldon and Carroll, 2006), and New Guinean pitohuis absorb chemicals from their melyrid beetle prey as a potential predator and parasite defense system (Dumbacher et al., 2004). Other primates, including *Cebus*, *Aotus*, and *Ateles*, anoint themselves with insects and plants to ward off ectoparasites, especially ticks (Alfaro et al., 2012; Falótico et al., 2007; Laska et al., 2007). Tri-monthly manual examination of all slow loris individuals from this study did not reveal any detectable ectoparasites, despite domestic animals in the agroforest environment being heavily infected (Albers et al., 2013).

The fact that slow loris venom has a more pronounced effect on spiders than other types of arthropods is notable, as ticks are arachnids and a likely recipient of anointed slow loris venom. It is unlikely that topically applied secretions would be repellent to other types of ectoparasites, such as mosquitos, that do not spend a protracted time on hosts (Weldon et al., 2011). In ectoparasites, the venom may be sensed by olfactory means. While ectoparasites themselves may not represent a significant impact on the fitness of a host animal, parasites - especially ticks - may carry pathogens that serve as a more potent threat.

Ticks are a likely threat for Indonesian slow lorises. Sumatra is home to 22 known species of ticks, while Java is home to 18 different species (Anastos, 1950). Specifically, *Nycticebus coucang* is reportedly a known host for *Haemaphysalis koningsbergeri* (Anastos, 1950). Although ticks are usually exclusively found at terrestrial and understory levels, ticks have been sampled in the forest canopy, possibly transported from arboreal primate hosts (Loaiza et al., 2014). The lorises in this study would have been susceptible to attracting ticks. The wild Javan slow lorises frequently move on the ground due to habitat disturbance (Rode et al. in Press). The greater slow lorises were kept in captivity near many other vertebrate species, and during their time in trade would have been more susceptible to high stress and low immunity

(Streicher, 2004). Lack of ectoparasites on both populations provides support that another factor, venom, may contribute to low ectoparasite load.

Ticks are commonly recognized carriers of pathogens for humans and animals (Dautel et al., 1999; Sonenshine and Mather, 1994). Tick-borne pathogens are common in Southeast Asia, although there is a lack of knowledge on the extent of these pathogens in both humans and non-humans (Petney et al., 2007). It is feasible that in areas where ticks are common, defences against this threat may have evolved. In particular, ticks may be more vulnerable to substances applied topically because they attach to the host for a prolonged period of time (Carroll et al., 2005).

Slow loris brachial gland secretions may act as an allergen, as indicated by a study that found a protein isolated from the BGE not combined with saliva of *N. coucang* is very similar to a domestic cat allergen (Krane et al., 2003). Hagey et al. (Hagey et al., 2007) found that BGE of *Nycticebus pygmaeus contains* a complex mixture of 212 volatile and semi-volatile compounds, and found variation in the compounds between species. Further, Alterman (1995) found that the brachial gland secretions of Sumatran slow lorises, mixed with saliva, were toxic to some test animals (laboratory mice), but not all. It is possible that variability in toxicity of secretions exists between individuals, depending on level of perceived threat, as well as species, diet, health status, and age. In this study we only tested adult individuals and found no sex differences in lethality. Dietary variation may contribute to variation in venom production both within and between species. The diet of *Nycticebus* varies between species; different *Nycticebus* species consume various degrees of animal prey, fruits, and exudates. For example, *N. pygmaeus* primarily feeds on exudates, fruits, and arthropods, in that order (Starr and Nekaris, 2013). As a result, a potential confounding variable is individual variation in venom toxicity, as well as individual variation in parasite susceptibility. For example, one study explored the genetic effects of lemur parasite loads and found that individuals with one MHC allele positively associated with infection by a specific type of parasite (Schwensow et al., 2010). Certain individuals may be more prone to infection; thus, the genetics, age, and sex of individuals may affect the way both parasites and predators react to the secretions. These sources of variation may explain, in part, the differences between individual samples when applied to arthropods.

This research contributes to our understanding of the selective pressures involved in the production of toxic compounds in primates; results suggest there are anti-parasitic effects of the venom, which may be in conjunction with other potential targets of the venom, such as predators or conspecifics (Nekaris et al., 2013). Detailed studies of the biochemistry of Indonesian slow lorises are on-going and may yield further support that slow loris venom contains anti-parasitic properties, and how those properties develop.

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Ethical statement

The authors assert that the research presented in this manuscript is original, accurate, and objectively presented. All chemical substances were handled with proper safety protocols, and toxins obtained from *Nycticebus* individuals were collected using humane and institutionally-approved guidelines. The Leverhulme Trust (RPG-084), Primate Society of Great Britain, Augsburg Zoo, Columbus Zoo, Cleveland Zoo and the Cleveland Zoo Society funded the work in this submitted manuscript.

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