Eagle's responses to a venomous mammal – do chemical cues in the venom of slow lorises repel avian predators?

Grace Fuller[a, b], Vincent Nijman[a], Wirdateti[c], K.A.I. Nekaris[a]

[a] Oxford Brookes University, Oxford, OX3 0BP, UK
[b] Center for Zoo Animal Welfare, Detroit Zoological Society, 8450 W. 10 Mile Road, Royal Oak, MI 48067 USA
[c] Division Zoology, Research Center for Biology, Lembaga Ilmu Pengetahuan Indonesia (LIPI), Gd. Widyasatwaloka, Jakarta-Bogor, Indonesia.

Corresponding Author:
Vincent Nijman
Nocturnal Primate Research Group, Oxford Brookes University
School of Social Sciences and Law, Headington Campus, Gipsy Lane
Oxford, OX3 0BP, UK
E: vnijman@brookes.ac.uk

Short running page heading: eagles and slow loris venom

Abstract

Raptors are confirmed predators of Asian slow lorises (*Nycticebus* spp.) the only primates with a toxic bite. A possible function of slow loris venom is to protect against predators. Slow lorises release volatile chemicals when disturbed or threatened, thus potentially communicating venomous status toward predators. Crested Serpent-eagles *Spilornis cheela* and Changeable Hawk-eagles *Nisaetus cirrhatus* are known to predate on venomous snakes and small mammals, and are potential predators of slow lorises. We tested the anti-predator potential of slow loris venom by presenting pieces of chicken combined with swabs of Greater Slow Loris *Nycticebus coucang* venom to 10 Changeable Hawk-eagles and 5 Crested Serpent-eagles. The eagles showed few behavioural responses in reaction to slow loris venom, examining swabs with venom or control scents equally. Both eagle species did show higher rates of face-rubbing behaviour following consumption of foods paired with venom compared to control scents. Our data suggest that slow loris venom does not function to repel avian predators, but may have an anti-predator defence function. We also show that while Crested Serpent-eagles and Changeable Hawk-eagles are not repelled by the smell of slow lorises, contact with their venom causes discomfort, thus potentially limiting the palatability of slow lorises to eagles.

Keywords: *Nisaetus cirrhatus*, *Spilornis cheela,* Indonesia, venomous mammal; chemosensory behaviour; predator-prey interactions

Introduction

Raptors, including Changeable Hawk-eagles *Nisaetus cirrhatus*, are one of the few confirmed predators of Asian slow lorises *Nycticebus* spp. (Hart 2007; Kenyon *et al*. 2014; Moore *et al*. 2014). Characterised by a cautious locomotion and inability to leap, slow lorises are unique in that they are one of the few mammals, and the only primate, that produce venom (Ligabue-Braun *et al*. 2012; Starcevic *et al*. 2015)[1]. While the nocturnal slow lorises have a mass of between 300 g and 2.1 kg, swabs of their venom led to avoidant responses in ~22 kg binturongs *Arctictis binturong* and ~64 kg sun bears *Helarctos malayanus* (Alterman, 1995). Their bite also has been show to seriously endanger an 80 kg human (Madani and Nekaris 2014). One hypothesis for the evolution of venom in slow lorises is that venom aids in defence against predators (Rode-Margono and Nekaris 2015). Slow lorises have a pungent smell, especially when agitated. When slow lorises are disturbed, brachial gland exudate (the source of slow loris venom) is mixed with saliva, and volatile chemicals are released; these chemicals have been proposed to serve a communicative function aimed toward predators, conspecifics, or both (Alterman 1995; Hagey *et al*. 2007). Therefore, even without delivering a venomous bite, odours arising from slow loris venom may be a form of chemical defence or even olfactory aposematism (Eisner and Grant 1981).

Defensive displays often combine visual, auditory, and, in some taxa, olfactory elements either to strengthen the message or target different predator species (Caro 2005; Mariano-Jelicich *et al.* 2011; Rowe and Halpin 2013). Direct effects of odours on predators (such as respiratory burn or irritation) may also explain the evolutionary puzzle of how conspicuous warning colouration and other features presumably deleterious to individual survival become fixed in populations of prey species (Gohli and Hogstedt 2009). In this context, slow loris venom may serve as an olfactory warning signal that is part of a multimodal aposematic-signalling complex. Not only do slow lorises have striking contrasting facial masks

---

[1] There is a debate in the toxin literature what comprises a venomous animal and what comprises a poisonous animal (Casewell *et al.* 2013), and whether the slow loris is indeed either of these (Ligabue-Braun *et al.* 2012). We here take the view that a venomous animal is one that is able to inject venom actively and that a poisonous animal is one that causes chemical disruption when it is consumed. Slow lorises are venomous, i.e. they can inject a substance comprised of saliva and brachial gland oil, with grooves in the powerful front teeth acting as accelerators pushing the venom upwards, allowing slow lorises to kill rodents, various arthropods, other slow lorises, or humans (Alterman 1995; Madani and Nekaris 2014; Grow *et al.* 2015).

that potentially warn off predators (Caro 2013), but they also exhibit a suite of characters, including visual (serpentine locomotion and dorsal striping) and auditory components (snake-like vocalizations), which are postulated to mimic cobras *Naja* spp. (Nekaris *et al.* 2013).

In Asia, species such as Short-toed Snake-eagle *Circaetus gallicus*, serpent-eagles *Spilornis* spp. as well as in certain areas White-bellied Sea-eagle *Haliaetus leucogaster* specialise on predating on venomous (sea) snakes (Wells 1999; Ferguson-Lees and Christie 2001). Short-toed Snake-eagle is largely allopatric with slow lorises, overlapping only in northeastern India, Myanmar and eastern Java, but serpent-eagles and White-bellied Sea-eagles occur largely sympatrically with slow lorises throughout Southeast Asia. Understanding the relationship of the life histories of these predators and their prey is especially important when a potential prey species is undergoing negative anthropogenic pressures (Beron *et al.* 2011; Cavalli *et al.* 2013). Here we experimentally test the hypothesis that slow loris brachial gland exudate repels avian predators, specifically Changeable Hawk-eagle and Crested Serpent-eagle *Spilornis cheela*.

Changeable Hawk-eagles prey on a wide range of animals, including small vipers and small mammals, including slow lorises (Nijman 2004; Hart 2007, Naoroji 2007, Fam and Nijman 2011). Crested Serpent-eagles eat a range of animals, including small mammals (Ferguson-Lees and Christie 2001; Naoroji 2007) and especially snakes. Naoroji (2007) observed that Crested Serpent-eagles mainly take non-venomous snakes, and that attacks on venomous snakes were rare and could result in the eagle's death. Rare though it may be, observations have been made of Crested Serpent-eagles feeding on venomous snakes such as Russell's Viper *Vipera russelli*, Malayan Ground Pit Viper *Calloselasma rhodostoma,* Dog-faced Water Snake *Cerberus rynchops*, Elegant Bronzeback *Dendrelaphis formosus* and cobras *Naja* spp. (Sody 1989; Wells 1999; Naoroji 2007). To the best of our knowledge there are no records of Crested Serpent-eagles preying on slow lorises. Changeable Hawk-eagles have feathered legs whereas Crested Serpent-eagles' legs are thick-skinned, thus providing protection against unwilling (and venomous) prey (Fig. 1). Both Changeable Hawk-eagles and Crested Serpent-eagles largely use a sit-and-wait hunting strategy during the day. While slow lorises are largely nocturnal, data from activity-loggers attached to wild slow lorises show that they are active (and move) for 10-15% of daylight hours (K.A.I. Nekaris, unpubl. data) thus increasing the likelihood they are detected by diurnal raptors.

Working with animals in a rescue centre in West Java, Indonesia, we collected samples of brachial gland exudate, saliva, and cage scents from wild-caught captive Greater Slow Lorises *N. coucang* and systematically presented these olfactory cues to Changeable Hawk-eagles and Crested Serpent-eagles. Birds of prey (Accipitridae) have high visual acuity (Jones *et al*. 2007), including in the ultraviolet spectrum (Cuthill *et al*. 2000), and generally have an acute sense of hearing (Rice 1982; Klump *et al*. 1986). While birds of prey have a relatively small olfactory bulb (Cobb 1968), suggesting that smell does not play an important role in locating prey, given its pungency, they almost certainly are physically able to detect slow loris' scent, especially when encountered at close range.

We predicted that if slow loris venom repels avian predators, eagles would differentiate between neutral scents, slow loris scent and venom, in that order. This should express itself in differences in approach latency times, in proportion of time spent in proximity, in the willingness to consume food associated with these scents, and in behavioural signs of aversion when confronted with venom.

Methods

Study animals and sample collection

The subjects for this study were five Crested Serpent-eagles and ten Changeable Hawk-eagles housed at Cikananga Wildlife Rescue Centre (Pusat Penyelamatan Satwa Cikananga) in West Java, Indonesia. All eagles had been rescued from the illegal wildlife trade, and the subjects were healthy. Crested Serpent-eagles and Changeable Hawk-eagles occur in Java but the wildlife traders on Java have strong links with suppliers on the island of Sumatra making both Java and Sumatra a likely origin of the eagles. The eagles were housed in identical, contiguous outdoor cages containing a concrete floor with a water bowl and two elevated wooden perches. The eagles were fed a single meal every other day consisting of 175 g of chicken, guinea pig, or other raw meat. We performed all testing on non-feeding days.

Cikananga Wildlife Rescue Centre houses > 60 Greater Slow Lorises also rescued from the illegal wildlife trade; the most likely origin of all these is Sumatra (the species occurs also in the Thai-Malay Peninsula). We opportunistically collected samples of venom from slow lorises during manual captures for de-worming or other medical procedures. We collected brachial gland exudate samples by rubbing a cotton swab over the brachial exudate, which pooled on the surface of the skin in slow lorises during the capture procedure. Swabs were immediately frozen. Finally, we collected saliva samples voluntarily using Salimetric's Children's Swabs (Salimetrics LLC, State College PA, USA). We flavoured the swabs by lightly rubbing a film of banana on the swab, and the slow lorises readily chewed on these swabs when they were presented through the cage bars. Individual saliva samples were pooled and frozen prior to use. We also collected swabs of slow loris scent by running cotton swabs over perching and cage floors in areas obviously soiled by urine and/or faeces. All procedures were approved by the Animal Welfare Sub-Committee of the University Research Ethics Committee of Oxford Brookes University.

Experimental procedure

We experimentally exposed the eagles to three olfactory conditions and measured their behaviour. Theoretically predators could learn to associate any odour as a cue of toxicity (Eisner and Grant 1981), so we felt it was important to test slow loris odour (cage swabs) in addition to testing the venom directly. We tested two slow loris odours (slow loris brachial gland exudate on its own or incubated in saliva- hereafter venom; slow loris cage swabs – hereafter slow loris scent) against a control (blank swabs or ones with a neutral lavender odour – hereafter neutral scent). We incubated brachial gland exudate samples in 200 μl of pooled slow loris saliva for 15 minutes at room temperature prior to use (Alterman 1995). We tested each eagle with a combination of these conditions in a within-subjects repeated measures experimental design. We randomized the order treatments and conducted only a single test per eagle, and each eagle received exactly the same set of treatments. Individual eagles were tested multiple times, with at least 2 days between successive trials (mean of 5.2 days and 6.2 days between trials for Changeable Hawk-eagle and Crested Serpent-eagle, respectively).

The willingness of predators to approach and/or consume potential prey items may depend on their internal motivational state. For this reason, experimenters have tested the repellent properties of spider (Machado *et al*. 2005) and snake secretions (Weldon and McNease 1991) by applying test substances to a typically palatable prey item. We modified this approach by presenting the olfactory test swabs in conjunction with a palatable food item (chicken). We taped the swab to a thin shaft of bamboo measuring approximately 12 cm in length and 0.5 cm in diameter and affixed a small piece of chicken (about 50 g) to the bamboo by spearing it on the end.

The experiment began when the bamboo test device was placed in the eagle's cage. We then recorded the latency to approach the test device, whether or not the chicken was consumed, and the behaviour of the eagle over a 20-min period. During behavioural observations, we recorded the eagle's activity at 1-min intervals using scan sampling in addition to all-occurrences (Altmann 1974) of behaviours directed toward the testing device, olfactory behaviours, and abnormal behaviours (Table 1).

Data analysis

We analysed data for Crested Serpent-eagles and Changeable Hawk-eagles separately. We compared latencies to approach the test object, percentage of time spent performing behaviours (or behaviour rates when appropriate) using a general linear model for repeated measures. We compared binary outcomes (food consumed or not; facial-rubbing or not) between neutral scent and slow loris scent and venom pooled with Fisher Exact probability tests. A General Linear Model, with repeated measures MANOVA, was used to test for differences in behavioural responses based on odour treatment. Given that we had a strong prediction (slow loris venom repels avian predators), and a specific direction (most strong response towards venom, less strong response towards slow loris scent, and the least strong response to neutral scents) we used one-tailed tests. We conducted all analyses in SPSS v. 21 (IBM Corporation, USA) and accept significance when $P \leq 0.05$.

Results

We found little evidence that slow loris venom repelled avian predators. Both Crested Serpent-eagles and Changeable Hawk-eagles were generally quick to approach the test object and recover the chicken attached, but there was considerable variation between individuals. We found no difference between Crested Serpent-eagles and Changeable Hawk-eagles in the ratio of eagles that approached the test objects versus the ones that did not (20/5 vs 31/19, Fisher's Exact probability test P=0.09) or between the ratio of individuals that consumed the food attached to the test object versus those that did not (17/7 vs 28/22 Fisher's Exact probability test P=0.17). Neither for Crested Serpent-eagles (Kruskal Wallis, H=3.801, *P*=0.15) nor Changeable Hawk-eagles (H=2.594, *P*=0.273) did latency times differ between the three test conditions, and only in Changeable Hawk-eagles was there a trend in the predicted direction (Table 2). Crested Serpent-eagles spent more time in close contact with the test objects than Changeable Hawk-eagles (24.5% vs 9.75% of time for the neutral scent, 27% vs 15% for the slow loris scent, and 14.5% vs 10% for venom) but for neither species did this reach statistical significance (Kruskal Wallis, H=0.483, *P*=0.786 and H=0.810, *P*=0.667 for Crested Serpent-eagle and Changeable Hawk-eagle respectively). The proportion of chicken eaten in the different test conditions was not consistent with our prediction: Crested Serpent-eagles ate 70% of the chicken in the neutral test condition, 60% when slow loris scent is added and 70% when the venom is added. The same pattern is present for Changeable Hawk-eagles, i.e. neutral 55%, loris scent 60% and venom 55%.

Individual differences in eagles' responses to the test conditions varied greatly between individuals, and the GLM did not show any significant differences in behaviour based on odour treatment (repeated measures MANOVA: Crested Serpent-eagle, Wilks' lambda = 0.15, $F_{20,\ 40.749}$ = 1.572, *P* = 0.109; Changeable Hawk-eagle, Wilks' lambda = 0.463, $F_{20,\ 107.082}$ = 1.399, *P* = 0.139). Because the overall model was non-significant, here we are not reporting statistical differences for individual behaviours. However, some possible trends are worth noting.

For Crested Serpent-eagles there were differences in the latency time for approaching the test object between the three test conditions, but they were not statistically significant and it was not in the predicted direction. Likewise, there were differences in the latency time for approaching the test object for the Changeable Hawk-eagles, and while this was in the predicted direction, it did not reach statistical significance. There were also no apparent differences in rates of grabbing, dropping, or moving test objects as a function of odour type.

The eagles as a group performed few or no abnormal behaviours. We did observe the eagles rubbing their faces along the perches, a behaviour that was quickly executed and appeared to be associated with discomfort, as if the birds were scratching an itch. Changeable Hawk-eagles rubbed their face 67% of the time (4/6) after having been in contact with slow loris scent, 64% (7/11) after contact with venom, but only 21% of the time (3/14) following contact with the neutral test item. Crested Serpent-eagle always rubbed their face having been in contact with the venom (7/7) but only did so 67% (2/3) of the time following contact with slow loris scent and 60% of the time (6/10) with the neutral scent. The difference between the neutral scent and those with slow loris scent or venom differed significantly (Fisher Exact Probability test, *P*=0.019 for Changeable Hawk-eagles and *P*=0.01 for Crested Serpent-eagle).

Discussion

For an avian predator, preying on venomous animals is potentially dangerous. In experimental settings slow lorises venom injected in mice (Alterman 1995) or applied to arachnids (Grow *et al*. 2015) is fatal. Several medically evaluated cases of anaphylaxis in humans following a slow loris bite have been reported (reviewed in Madani and Nekaris 2014), and slow loris venom also severely injures or even results in the death of other slow lorises (Nekaris *et al*. 2013). There is no reason to assume that slow lorises cannot be dangerous to eagles wanting to prey on them. Slow lorises do not use nests and instead perch in branch tangles, which could be relatively accessible for eagles. If the eagle surprises the slow lorises at their diurnal sleep sites the slow loris may not have enough time to prepare its venom thus reducing the risk to the eagles. If the slow loris is awake, however, the eagles must take great care not to be bitten. While we know eagles do predate on slow lorises, albeit rarely reported, it is unclear if the eagles consume the entire animal or discard certain, less palatable or potentially harmful parts.

Both Changeable Hawk-eagles and Crested Serpent-eagles wiped their faces and beaks along horizontal perches in an almost violent fashion after consuming food presented with loris venom. Beak-wiping behaviour is associated with unpalatable prey in other birds; for example, Red-winged Blackbirds *Agelius phoeniceus* wiped their beaks along perches significantly more after feeding on bees than mealworms (Evans and Waldbauer 1982), and European Starling *Sturnus vulgaris* showed aversive behaviour (head shaking and beak wiping) towards mealworms coated with a quinine sulphate solution (Skelhorn and Rowe 2006). Facial rubbing can also be a sign of respiratory distress in raptors, which will rub against a substrate to relieve pressure in the infraorbital sinus (Orosz and Lichtenberger 2011). This behaviour indicates that eagles showed some discomfort after exposure to slow loris venom. It is often necessary for predators to learn to avoid noxious prey (Gohli and Hogstedt 2009); it is possible that the eagles we tested were naïve to slow loris venom and would have shown more dramatic avoidant responses to it in additional trials.

The sensory and behavioural ecology of the eagles we tested may also account for the lack of dramatic reactions to venom presentation in our experiments. Both raptor species tested here are diurnal predators with morning activity peaks (Nijman 2004; Sano 2012), and their still-hunting mode of capturing prey may preclude regular enough contact with slow lorises. Although emerging data show a previously unrecognized role for olfaction in the behaviour of some avian species active in low light, most birds are visually-oriented (Martin 2012), and the diurnal eagles in this study are likely no exception. If slow loris venom is part of a multimodal signalling complex mimicking cobras (Nekaris *et al.* 2013), then it is possible that isolating the olfactory component of this warning display resulted in a stimulus that was too weak to repel these visually-oriented raptors fully. Previous tests of the repellent properties of brachial gland exudate alone have shown positive results in a variety of carnivore species, for which olfaction likely plays a larger role in predatory behaviour (Alterman 1995). Thus, perhaps we would have observed a more robust response if we had presented the venom to the raptors in conjunction with a visual and/or auditory model of a slow loris. Alternatively, eagles with different hunting modes, such as the highly specialised Black Eagle *Ictinaetus malayanus* that glide through the trees searching for bird nests thus bringing them in contact with slow lorises in their sleeping sites, may show stronger responses to slow loris venom.

It is also possible that the eagles in our study are simply adapted to process and consume the venomous slow loris. In addition to venomous snakes, Crested Serpent-eagles are known to consume venomous Marine Toads *Bufo marinus*, scorpions, and strongly odorous Asian House Shrews *Suncus murinus* (Sody 1989; Sano 2012), suggesting that perhaps they are not generally repelled by chemical defences in prey species. It is likely that aerial predators are not the primary targets for slow loris chemical defences. Although a Reticulated Python *Python reticulatus* and monitor lizards *Varanus* spp. are known to have killed slow lorises (Wiens and Zitzmann 1999; Kenyon *et al.* 2014), responses of reptilian predators to slow loris venom have not been evaluated. Given that other mammals are known to anoint themselves with snake scent to avoid snake predation (Clucas *et al*. 2008), snakes could be a likely target for this defence mechanism and further studies should examine their response to slow loris venom.

It is not clear if slow lorises show strong fear-based responses to predator presence. Wiens and Zitzmann (1999) and Nekaris *et al*. (2007) noted that wild slow and slender lorises were unperturbed by palm civets, small cats and large owls moving in close proximity to them. Another intriguing possibility is that the volatile chemicals released in slow loris venom serve as an intraspecific alarm signal (Hagey *et al*. 2007). For example, Giant Mesquite Bugs *Thasus neocalifornicus* produce defensive secretions in response to predator threat, and exposing aggregations of mesquite bugs to their own secretions causes individuals to disperse (Prudic *et al.* 2008). A similar response has been observed in Lamellose Ormer *Haliotis tuberculata* in response to starfish predation (Bancala 2009). An olfactory-based alarm system could serve as a vital warning function while simultaneously being more cryptic to at least visually orientated predators such as eagles.

Our study represents one of the first attempts to test the function of the venom of slow lorises experimentally. We presented eagles with swabs of slow loris venom and scent and compared their behavioural reaction to these scents relative to controls. The eagles were not slower to approach test objects containing venom, did not spent less time examining brachial gland exudate scented objects, but did show higher rates of a facial rubbing after contact with loris venom. Although far from definitive, our results suggest that repelling raptors in not a primary function of slow loris venom. These results add to an already complicated picture of the role played by predator avoidance in the evolution of the unique behavioural and morphological traits of these enigmatic nocturnal primates (Nekaris *et al.* 2007).

Acknowledgements

We thank the authorities Kementerian Riset and Teknologi (RISTEK, Permit 109/SIP/FRP/SM/V/2014), Balai Konservasi Sumber Daya Alam Bandung (BKSDA Bandung), Research Center for Biology, Indonesian Institute of Sciences (LIPI) and Konservasi Sumber Daya Alam Garut (KSDA Garut) for their support in this project. The authors thank the staff at Cikananaga Wildlife Rescue Center, including W. Eggen, Ono, and I. Iryantoro, who provided the photographs. The authors also wish to thank N. Grow, A. Palu, A. Zango and T. Blanthorn for assisting with data collection. Swabs were kindly donated by Salimetrics. The Leverhulme Trust (RPG-084), People’s Trust for Endangered Species, the Primate

Society of Great Britain, Augsburg Zoo, Columbus Zoo, Cleveland Metroparks Zoo and the Cleveland Zoological Society funded this project.

References

Alterman, L. (1995). Toxins and toothcombs: potential allospecific chemical defenses in *Nycticebus* and *Perodicticus*. In ' Creatures of the Dark ' (Eds L. Alterman, G. Doyle and M. K. Izard.) pp. 413-424. (Springer: US.)

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* **48**, 227-265.

Bancala, F. (2009). Function of mucus secretion by lamellose ormer, *Haliotis tuberculata lamellosa*, in response to starfish predation. *Animal Behaviour* **78(5)**, 1189-1194.

Beron, M.P., Garcia, G.O., Luppi, T., and Favero, M. (2011). Age-related prey selectivity and foraging efficiency of Olrog's Gulls (atlanticus) feeding on crabs in their non-breeding grounds. *Emu* **111(2)**, 172-178.

Caro, T. (2005). 'Antipredator defenses in birds and mammals.' (University of Chicago Press: Chicago.)

Caro, T. (2013). The colours of extant mammals. *Seminars in Cell & Developmental Biology* **24**, 542-552.

Casewell, N.R., Wüster, W., Vonk, F.J., Harrison, R.A., and Fry, B.G. (2013). Complex cocktails: the evolutionary novelty of venoms. *Trends in Ecology & Evolution* **28**, 219-229.

Cavalli, M., Baladron, A.V., Isacch, J.P., Martinez, G., and Bo, M.S. (2013). Prey selection and food habits of breeding Burrowing Owls (*Athene cunicularia*) in natural and modified habitats of Argentine pampas. *Emu* **114(2)**, 184-188.

Clucas, B., Rowe, M.P., Owings, D.H., and Arrowood, P.C. (2008). Snake scent application in ground squirrels, *Spermophilus* spp.: a novel form of antipredator behaviour? *Animal Behaviour* **75(1)**, 299-307.

Cobb, S. (1968). The size of the olfactory bulb in 108 species of birds. *The Auk* **85**, 55-61.

Cuthill, I.C., Partridge, J.C., Bennett, A.T., Church, S.C., Hart, N.S., and Hunt, S. (2000). Ultraviolet vision in birds. *Advances in the Study of Behavior* **29**, 159-214

Eisner, T. and Grant, R.P. (1981). Toxicity, odor aversion, and olfactory aposematism. *Science* **213(4506)**, 476-476.

Evans, D.L. and Waldbauer, G.P. (1982). Behavior of adult and naive birds when presented with a bumblebee and its mimic. *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology* **59(3)**, 247-259.

Fam, S.D. and Nijman, V. (2011). *Spizaetus* hawk-eagles as predators of arboreal colobines. *Primates* **52**(2),105-110.

Ferguson-Lees, J., and Christie, D.A. (2001). 'Raptors of the world.' (Christopher Helm: London.)

Gohli, J., and Hogstedt, G. (2009). Explaining the evolution of warning coloration: secreted secondary defence chemicals may facilitate the evolution of visual aposematic signals. *Plos One* ***4*****(6)**, e5779.

Grow, N.B., Wirdateti, and Nekaris, K.A.I. (2015). Does toxic defence in *Nycticebus* spp. relate to ectoparasites? The lethal effects of slow loris venom on arthropods. *Toxicon* ***95***, 1-5.

Hagey, L.R., Fry, B.G., Fitch-Snyder, H. (2007). Talking defensively: A dual use for the brachial gland exudate of slow and pygmy lorises. In 'Primate Anti-Predator Strategies.' (Eds S. Gursky and K.A.I. Nekaris) pp. 251-270. (Springer: New York.)

Hart, D. (2007). Predation on primates: a biogeographical analysis. In 'Primate Anti-Predator Strategies′ (Eds S. Gursky and K.A.I. Nekaris) pp. 27-59. (Springer: New York.)

Jones, M.P., Pierce, K.E., Ward, D. (2007). Avian vision: a review of form and function with special consideration to birds of prey. *Journal of Exotic Pet Medicine* **16(2)**, 69-87.

Kenyon, M., Streicher, U., Loung, H., Tran, T., Tran, M., Vo, B., and Cronin, A. (2014). Survival of reintroduced pygmy slow loris *Nycticebus pygmaeus* in South Vietnam. *Endangered Species Research* **25**, 185-195.

Klump, G.M., Kretzschmar, E., and Curio, E. (1986). The hearing of an avian predator and its avian prey. *Behavioral Ecology and Sociobiology* **18(5)**, 317-323.

Ligabue-Braun, R., Verli, H., and Carlini, C.R. (2012). Venomous mammals: a review. *Toxicon* **59(7)**, 680-695.

Machado, G., Carrera, P.C., Pomini, A.M., and Marsaioli, A.J. (2005). Chemical defense in harvestmen (Arachnida, Opiliones): do benzoquinone secretions deter invertebrate and vertebrate predators? *Journal of Chemical Ecology* **31(11)**, 2519-2539.

Madani, G., and Nekaris, K.A.I. (2014). Anaphylactic shock following the bite of a wild Kayan slow loris (*Nycticebus kayan*): implications for slow loris conservation. *Journal of Venomous Animals and Toxins including Tropical Diseases* **20(1)**, 43.

Mariano-Jelicich, R., Rodriguez, M.P.S., Copello, S., Seco Pon, J.P., Beron, M.P., Mauco, L., Ghys, M.I., and Favero, M. (2011). The diet of the South American tern: the Argentine anchovy as key prey in the non-breeding season. *Emu* **111(4)**, 292-296.

Martin, G.R. (2012). Through birds' eyes: insights into avian sensory ecology. *Journal of Ornithology* **153**, 23-48.

Moore, R.S., Wihermanto, and Nekaris, K.A.I. (2014). Compassionate conservation, rehabilitation and translocation of Indonesian slow lorises. *Endangered Species Research* **26**, 93-102.

Naoroji, R. (2007). 'Birds of prey on the Indian subcontinent.' (Om Books International: New Delhi.)

Nekaris, K.A.I., Moore, R.S., Rode, E.J., and Fry, B.G. (2013). Mad, bad and dangerous to know: the biochemistry, ecology and evolution of slow loris venom. *Journal of Venomous Animals and Toxins including Tropical Diseases* **19**, 21.

Nekaris, K.A.I., Pimley, E.R., and Ablard, K.M. (2007). Predator defense by slender lorises and pottos. In 'Primate Anti-Predator Strategies' (Eds S. Gursky and K.A.I. Nekaris.) pp. 220-238. (Springer: New York.)

Nijman, V. (2004). Habitat segregation in two congeneric hawk-eagles (*Spizaetus bartelsi* and *S. cirrhatus*) in Java, Indonesia. *Journal of Tropical Ecology* **20**, 105-111.

Orosz, S.E., and Lichtenberger, M. (2011). Avian respiratory distress: etiology, diagnosis, and treatment. *Veterinary Clinics of North America: Exotic Animal Practice* **14(2)**, 241-255.

Prudic, K.L., Noge, K., and Becerra, J.X. (2008). Adults and nymphs do not smell the same: the different defensive compounds of the giant mesquite bug (*Thasus neocalifornicus*: Coreidae). *Journal of Chemical Ecology* **34(6)**, 734-741.

Rice, W.R. (1982). Acoustical location of prey by the marsh hawk: adaptation to concealed prey. *The Auk* **99(3)**, 403-413.

Rode-Margono, J.E., and Nekaris, K.A.I. (2015). Cabinet of curiosities: venom systems and their ecological function in mammals, with a focus on primates. *Toxins* **7(7)**, 2639-2658.

Rowe, C., and Halpin, C. (2013). Why are warning displays multimodal? *Behavioral Ecology and Sociobiology* **67(9)**, 1425-1439.

Sano, K. (2012). Crested serpent eagle Kanmuri-Washi (Jpn) *Spilornis cheela*. *Bird Research News* **9(2)**, 4-5.

Skelhorn, J., and Rowe, C. (2006). Predator avoidance learning of prey with secreted or stored defences and the evolution of insect defences. *Animal Behaviour* **72**, 827-834.

Sody, H.J.V. (1989). Diet of Javanese birds. In 'Henri Jacob Victor Sody (1892-1959), his life and work.' (Ed J.H. Becking.) pp. 164-221 (Brill: Leiden.)

Starcevic, A., Moura-da-Silva, A.M., Cullum, J., Hranueli, D., and Long, P.F. (2015). Combinations of long peptide sequence blocks can be used to describe toxin diversification in venomous animals *Toxicon* **95**, 84-92.

Weldon, P.J., and McNease, L. (1991). Does the American alligator discriminate between venomous and nonvenomous snake prey. *Herpetologica* **47(4)**, 403-406.

Wells, D.R. (1999). 'The birds of the Thai–Malay Peninsula. Vol I, Non- passerines.' (Academic Press: London.)

Wiens, F., and Zitzmann, A. (1999). Predation on a wild slow loris (*Nycticebus coucang*) by a reticulated python (*Python reticulatus*). *Folia Primatologica **70***, 362-364.

Table 1. Ethogram for responses of Changeable Hawk-eagles *Nisaetus cirrhatus* and Crested Serpent-eagles *Spilornis cheela* to food items treated with control or Greater Slow Loris *Nycticebus coucang* scents.

Behaviour	**Operational Definition**
*Scan Behaviours (also scored all-occurrences of behaviours marked *)*	
Feed	Ingesting a food item *(note test item or diet item)*
Tactile-investigation*	Manipulation of the test item with claws, beak, or another body part.
Perch-rubbing*	Rubbing the sides of the face along branches or substrates in the enclosure.
Approach	Moving directly toward the area containing the test item.
Retreat	Moving directly away from the area containing the test item.
Movement (neutral)	Locomotion not directed toward the test item or lateral to it.
Abnormal behaviour*	Eagle is pacing (retracing the same path more than two times), feather plucking, or performing another repetitive behaviour without an apparent function.
Other/Maintenance	The eagle is performing an undefined behaviour, including rest or self-maintenance behaviours.
Not Visible	The eagle or its behaviour cannot be seen.
Proximity to test item	
Contact	Eagle is physically touching the test item.
Near	Eagle is close enough to reach the test item if it chooses.
Distant	Eagle is too far away from the test item to reach it.
Additional all-occurrence behaviours	
Grab Test Item	Eagle grasps the test item with the beak or claws.
Move Test Item	The eagle transports the test item at least one meter.
Vocalise	Eagle is producing sounds.

Table 2. Responses of five Crested Serpent-eagles *Spilornis cheela* and ten Changeable Hawk-eagles *Nisaetus cirrhatus* towards chicken pieces in combination with neutral scents (blank and lavender), Greater Slow Loris *Nycticebus coucang* scent, or its venom (brachial gland exudate on its own or incubated in saliva). Medians and interquartile ranges are presented for Latency (time in seconds between start of trial and first contact with sample)

	Trials	**Contact with sample**	**Latency in s (range)**	**Face-rubbing following contact**	**Eaten**
Crested Serpent-eagle					
-neutral scent	10	10	80 (21-216)	6	7
-slow loris scent	5	3	1 (1-2)	2	3
-venom	10	7	57 (3-124))	7	7
Changeable Hawk-eagle					
-neutral scent	20	14	117 (49-266)	3	11
-slow loris scent	10	6	147 (59-290)	4	6
-venom	20	11	230 (108-332)	7	11

Figure 1. The species used in this study, photographed by I. Iryantoro at Cikananga Wildlife Centre, West Java (clockwise): Greater Slow Loris *Nycticebus coucang,* Crested Serpent-eagle *Spilornis cheela*, Changeable Hawk-eagle *Nisaetus cirrhatus*,