1 **Eagle's responses to a venomous mammal – do chemical cues in the venom of slow lorises repel**

2 **avian predators?**

3

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

5

6 [a] Oxford Brookes University, Oxford, OX3 0BP, UK

7 [b] Center for Zoo Animal Welfare, Detroit Zoological Society, 8450 W. 10 Mile Road, Royal Oak, MI 48067

8 USA

9 [c] Division Zoology, Research Center for Biology, Lembaga Ilmu Pengetahuan Indonesia (LIPI), Gd.

10 Widyasatwaloka, Jakarta-Bogor, Indonesia.

11

12 Corresponding Author:

13 Vincent Nijman

14 Nocturnal Primate Research Group, Oxford Brookes University

15 School of Social Sciences and Law, Headington Campus, Gipsy Lane

16 Oxford, OX3 0BP, UK

17 E: vnijman@brookes.ac.uk

18

19 Short running page heading: eagles and slow loris venom

20

21 **Abstract**

22 Raptors are confirmed predators of Asian slow lorises (*Nycticebus* spp.) the only primates with a toxic

23 bite. A possible function of slow loris venom is to protect against predators. Slow lorises release volatile

24 chemicals when disturbed or threatened, thus potentially communicating venomous status toward

25 predators. Crested Serpent-eagles *Spilornis cheela* and Changeable Hawk-eagles *Nisaetus cirrhatus* are

26 known to predate on venomous snakes and small mammals, and are potential predators of slow lorises.

27 We tested the anti-predator potential of slow loris venom by presenting pieces of chicken combined with

28 swabs of Greater Slow Loris *Nycticebus coucang* venom to 10 Changeable Hawk-eagles and 5 Crested

29 Serpent-eagles. The eagles showed few behavioural responses in reaction to slow loris venom,

30 examining swabs with venom or control scents equally. Both eagle species did show higher rates of face-

31 rubbing behaviour following consumption of foods paired with venom compared to control scents. Our

32 data suggest that slow loris venom does not function to repel avian predators, but may have an anti-

33 predator defence function. We also show that while Crested Serpent-eagles and Changeable Hawk-

34 eagles are not repelled by the smell of slow lorises, contact with their venom causes discomfort, thus

35 potentially limiting the palatability of slow lorises to eagles.

36

37 Keywords: *Nisaetus cirrhatus*, *Spilornis cheela,* Indonesia, venomous mammal; chemosensory behaviour;

38   predator-prey interactions

39

40

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).

3

63   that potentially warn off predators (Caro 2013), but they also exhibit a suite of characters, including visual

64   (serpentine locomotion and dorsal striping) and auditory components (snake-like vocalizations), which are

65   postulated to mimic cobras *Naja* spp. (Nekaris *et al.* 2013).

66   In Asia, species such as Short-toed Snake-eagle *Circaetus gallicus*, serpent-eagles *Spilornis* spp.

67   as well as in certain areas White-bellied Sea-eagle *Haliaetus leucogaster* specialise on predating on

68   venomous (sea) snakes (Wells 1999; Ferguson-Lees and Christie 2001). Short-toed Snake-eagle is

69   largely allopatric with slow lorises, overlapping only in northeastern India, Myanmar and eastern Java, but

70   serpent-eagles and White-bellied Sea-eagles occur largely sympatrically with slow lorises throughout

71   Southeast Asia. Understanding the relationship of the life histories of these predators and their prey is

72   especially important when a potential prey species is undergoing negative anthropogenic pressures

73   (Beron *et al.* 2011; Cavalli *et al.* 2013). Here we experimentally test the hypothesis that slow loris brachial

74   gland exudate repels avian predators, specifically Changeable Hawk-eagle and Crested Serpent-eagle

75   *Spilornis cheela*.

76   Changeable Hawk-eagles prey on a wide range of animals, including small vipers and small

77   mammals, including slow lorises (Nijman 2004; Hart 2007, Naoroji 2007, Fam and Nijman 2011). Crested

78   Serpent-eagles eat a range of animals, including small mammals (Ferguson-Lees and Christie 2001;

79   Naoroji 2007) and especially snakes. Naoroji (2007) observed that Crested Serpent-eagles mainly take

80   non-venomous snakes, and that attacks on venomous snakes were rare and could result in the eagle's

81   death. Rare though it may be, observations have been made of Crested Serpent-eagles feeding on

82   venomous snakes such as Russell's Viper *Vipera russelli*, Malayan Ground Pit Viper *Calloselasma*

83   *rhodostoma,* Dog-faced Water Snake *Cerberus rynchops*, Elegant Bronzeback *Dendrelaphis formosus*

84   and cobras *Naja* spp. (Sody 1989; Wells 1999; Naoroji 2007). To the best of our knowledge there are no

85   records of Crested Serpent-eagles preying on slow lorises. Changeable Hawk-eagles have feathered legs

86   whereas Crested Serpent-eagles' legs are thick-skinned, thus providing protection against unwilling (and

87   venomous) prey (Fig. 1). Both Changeable Hawk-eagles and Crested Serpent-eagles largely use a sit-

88   and-wait hunting strategy during the day. While slow lorises are largely nocturnal, data from activity-

89   loggers attached to wild slow lorises show that they are active (and move) for 10-15% of daylight hours

90   (K.A.I. Nekaris, unpubl. data) thus increasing the likelihood they are detected by diurnal raptors.

91   Working with animals in a rescue centre in West Java, Indonesia, we collected samples of

92   brachial gland exudate, saliva, and cage scents from wild-caught captive Greater Slow Lorises *N.*

93   *coucang* and systematically presented these olfactory cues to Changeable Hawk-eagles and Crested

94   Serpent-eagles. Birds of prey (Accipitridae) have high visual acuity (Jones *et al.* 2007), including in the

95   ultraviolet spectrum (Cuthill *et al.* 2000), and generally have an acute sense of hearing (Rice 1982; Klump

96   *et al.* 1986). While birds of prey have a relatively small olfactory bulb (Cobb 1968), suggesting that smell

97   does not play an important role in locating prey, given its pungency, they almost certainly are physically

98   able to detect slow loris' scent, especially when encountered at close range.

99   We predicted that if slow loris venom repels avian predators, eagles would differentiate between

100   neutral scents, slow loris scent and venom, in that order. This should express itself in differences in

101   approach latency times, in proportion of time spent in proximity, in the willingness to consume food

102   associated with these scents, and in behavioural signs of aversion when confronted with venom.

103

104   **Methods**

105

106   *Study animals and sample collection*

107   The subjects for this study were five Crested Serpent-eagles and ten Changeable Hawk-eagles housed at

108   Cikananga Wildlife Rescue Centre (Pusat Penyelamatan Satwa Cikananga) in West Java, Indonesia. All

109   eagles had been rescued from the illegal wildlife trade, and the subjects were healthy. Crested Serpent-

110   eagles and Changeable Hawk-eagles occur in Java but the wildlife traders on Java have strong links with

111   suppliers on the island of Sumatra making both Java and Sumatra a likely origin of the eagles. The

112   eagles were housed in identical, contiguous outdoor cages containing a concrete floor with a water bowl

113   and two elevated wooden perches. The eagles were fed a single meal every other day consisting of 175 g

114   of chicken, guinea pig, or other raw meat. We performed all testing on non-feeding days.

115   Cikananga Wildlife Rescue Centre houses > 60 Greater Slow Lorises also rescued from the

116   illegal wildlife trade; the most likely origin of all these is Sumatra (the species occurs also in the Thai-

117   Malay Peninsula). We opportunistically collected samples of venom from slow lorises during manual

118   captures for de-worming or other medical procedures. We collected brachial gland exudate samples by

119   rubbing a cotton swab over the brachial exudate, which pooled on the surface of the skin in slow lorises

120   during the capture procedure. Swabs were immediately frozen. Finally, we collected saliva samples

121   voluntarily using Salimetric's Children's Swabs (Salimetrics LLC, State College PA, USA). We flavoured

122   the swabs by lightly rubbing a film of banana on the swab, and the slow lorises readily chewed on these

123   swabs when they were presented through the cage bars. Individual saliva samples were pooled and

124   frozen prior to use. We also collected swabs of slow loris scent by running cotton swabs over perching

125   and cage floors in areas obviously soiled by urine and/or faeces. All procedures were approved by the

126   Animal Welfare Sub-Committee of the University Research Ethics Committee of Oxford Brookes

127   University.

128

129   *Experimental procedure*

130   We experimentally exposed the eagles to three olfactory conditions and measured their behaviour.

131   Theoretically predators could learn to associate any odour as a cue of toxicity (Eisner and Grant 1981),

132   so we felt it was important to test slow loris odour (cage swabs) in addition to testing the venom directly.

133   We tested two slow loris odours (slow loris brachial gland exudate on its own or incubated in saliva-

134   hereafter venom; slow loris cage swabs – hereafter slow loris scent) against a control (blank swabs or

135   ones with a neutral lavender odour – hereafter neutral scent). We incubated brachial gland exudate

136   samples in 200 μl of pooled slow loris saliva for 15 minutes at room temperature prior to use (Alterman

137   1995). We tested each eagle with a combination of these conditions in a within-subjects repeated

138   measures experimental design. We randomized the order treatments and conducted only a single test per

139   eagle, and each eagle received exactly the same set of treatments. Individual eagles were tested multiple

140   times, with at least 2 days between successive trials (mean of 5.2 days and 6.2 days between trials for

141   Changeable Hawk-eagle and Crested Serpent-eagle, respectively).

142   The willingness of predators to approach and/or consume potential prey items may depend on

143   their internal motivational state. For this reason, experimenters have tested the repellent properties of

144   spider (Machado *et al*. 2005) and snake secretions (Weldon and McNease 1991) by applying test

145   substances to a typically palatable prey item. We modified this approach by presenting the olfactory test

146   swabs in conjunction with a palatable food item (chicken). We taped the swab to a thin shaft of bamboo

147   measuring approximately 12 cm in length and 0.5 cm in diameter and affixed a small piece of chicken

148   (about 50 g) to the bamboo by spearing it on the end.

149   The experiment began when the bamboo test device was placed in the eagle's cage. We then

150   recorded the latency to approach the test device, whether or not the chicken was consumed, and the

151   behaviour of the eagle over a 20-min period. During behavioural observations, we recorded the eagle's

152   activity at 1-min intervals using scan sampling in addition to all-occurrences (Altmann 1974) of behaviours

153   directed toward the testing device, olfactory behaviours, and abnormal behaviours (Table 1).

154

155   *Data analysis*

156   We analysed data for Crested Serpent-eagles and Changeable Hawk-eagles separately. We compared

157   latencies to approach the test object, percentage of time spent performing behaviours (or behaviour rates

158   when appropriate) using a general linear model for repeated measures. We compared binary outcomes

159   (food consumed or not; facial-rubbing or not) between neutral scent and slow loris scent and venom

160   pooled with Fisher Exact probability tests. A General Linear Model, with repeated measures MANOVA,

161   was used to test for differences in behavioural responses based on odour treatment. Given that we had a

162   strong prediction (slow loris venom repels avian predators), and a specific direction (most strong

163   response towards venom, less strong response towards slow loris scent, and the least strong response to

164   neutral scents) we used one-tailed tests. We conducted all analyses in SPSS v. 21 (IBM Corporation,

165   USA) and accept significance when $P \leq 0.05$.

166

167   **Results**

168   We found little evidence that slow loris venom repelled avian predators. Both Crested Serpent-eagles and

169   Changeable Hawk-eagles were generally quick to approach the test object and recover the chicken

170   attached, but there was considerable variation between individuals. We found no difference between

171   Crested Serpent-eagles and Changeable Hawk-eagles in the ratio of eagles that approached the test

172   objects versus the ones that did not (20/5 vs 31/19, Fisher's Exact probability test P=0.09) or between the

173   ratio of individuals that consumed the food attached to the test object versus those that did not (17/7 vs

174   28/22 Fisher's Exact probability test P=0.17). Neither for Crested Serpent-eagles (Kruskal Wallis,

175   H=3.801, *P*=0.15) nor Changeable Hawk-eagles (H=2.594, *P*=0.273) did latency times differ between the

176   three test conditions, and only in Changeable Hawk-eagles was there a trend in the predicted direction

177   (Table 2). Crested Serpent-eagles spent more time in close contact with the test objects than Changeable

178   Hawk-eagles (24.5% vs 9.75% of time for the neutral scent, 27% vs 15% for the slow loris scent, and

179   14.5% vs 10% for venom) but for neither species did this reach statistical significance (Kruskal Wallis,

180   H=0.483, *P*=0.786 and H=0.810, *P*=0.667 for Crested Serpent-eagle and Changeable Hawk-eagle

181   respectively). The proportion of chicken eaten in the different test conditions was not consistent with our

182   prediction: Crested Serpent-eagles ate 70% of the chicken in the neutral test condition, 60% when slow

183   loris scent is added and 70% when the venom is added. The same pattern is present for Changeable

184   Hawk-eagles, i.e. neutral 55%, loris scent 60% and venom 55%.

185   Individual differences in eagles' responses to the test conditions varied greatly between

186   individuals, and the GLM did not show any significant differences in behaviour based on odour treatment

187   (repeated measures MANOVA: Crested Serpent-eagle, Wilks' lambda = 0.15, $F_{20,\ 40.749}$ = 1.572, *P* =

188   0.109; Changeable Hawk-eagle, Wilks' lambda = 0.463, $F_{20,\ 107.082}$ = 1.399, *P* = 0.139). Because the

189   overall model was non-significant, here we are not reporting statistical differences for individual

190   behaviours. However, some possible trends are worth noting.

191   For Crested Serpent-eagles there were differences in the latency time for approaching the test

192   object between the three test conditions, but they were not statistically significant and it was not in the

193   predicted direction. Likewise, there were differences in the latency time for approaching the test object for

194   the Changeable Hawk-eagles, and while this was in the predicted direction, it did not reach statistical

195   significance. There were also no apparent differences in rates of grabbing, dropping, or moving test

196   objects as a function of odour type.

197   The eagles as a group performed few or no abnormal behaviours. We did observe the eagles

198   rubbing their faces along the perches, a behaviour that was quickly executed and appeared to be

199   associated with discomfort, as if the birds were scratching an itch. Changeable Hawk-eagles rubbed their

200   face 67% of the time (4/6) after having been in contact with slow loris scent, 64% (7/11) after contact with

201   venom, but only 21% of the time (3/14) following contact with the neutral test item. Crested Serpent-eagle

202   always rubbed their face having been in contact with the venom (7/7) but only did so 67% (2/3) of the time

203   following contact with slow loris scent and 60% of the time (6/10) with the neutral scent. The difference

204   between the neutral scent and those with slow loris scent or venom differed significantly (Fisher Exact

205   Probability test, *P*=0.019 for Changeable Hawk-eagles and *P*=0.01 for Crested Serpent-eagle).

206

207   **Discussion**

208   For an avian predator, preying on venomous animals is potentially dangerous. In experimental settings

209   slow lorises venom injected in mice (Alterman 1995) or applied to arachnids (Grow *et al*. 2015) is fatal.

210   Several medically evaluated cases of anaphylaxis in humans following a slow loris bite have been

211   reported (reviewed in Madani and Nekaris 2014), and slow loris venom also severely injures or even

212   results in the death of other slow lorises (Nekaris *et al*. 2013). There is no reason to assume that slow

213   lorises cannot be dangerous to eagles wanting to prey on them. Slow lorises do not use nests and

214   instead perch in branch tangles, which could be relatively accessible for eagles. If the eagle surprises the

215   slow lorises at their diurnal sleep sites the slow loris may not have enough time to prepare its venom thus

216   reducing the risk to the eagles. If the slow loris is awake, however, the eagles must take great care not to

217   be bitten. While we know eagles do predate on slow lorises, albeit rarely reported, it is unclear if the

218   eagles consume the entire animal or discard certain, less palatable or potentially harmful parts.

219   Both Changeable Hawk-eagles and Crested Serpent-eagles wiped their faces and beaks along

220   horizontal perches in an almost violent fashion after consuming food presented with loris venom. Beak-

221   wiping behaviour is associated with unpalatable prey in other birds; for example, Red-winged Blackbirds

222   *Agelius phoeniceus* wiped their beaks along perches significantly more after feeding on bees than

223   mealworms (Evans and Waldbauer 1982), and European Starling *Sturnus vulgaris* showed aversive

224   behaviour (head shaking and beak wiping) towards mealworms coated with a quinine sulphate solution

225   (Skelhorn and Rowe 2006). Facial rubbing can also be a sign of respiratory distress in raptors, which will

226   rub against a substrate to relieve pressure in the infraorbital sinus (Orosz and Lichtenberger 2011). This

227   behaviour indicates that eagles showed some discomfort after exposure to slow loris venom. It is often

228   necessary for predators to learn to avoid noxious prey (Gohli and Hogstedt 2009); it is possible that the

229   eagles we tested were naïve to slow loris venom and would have shown more dramatic avoidant

230   responses to it in additional trials.

231   The sensory and behavioural ecology of the eagles we tested may also account for the lack of

232   dramatic reactions to venom presentation in our experiments. Both raptor species tested here are diurnal

233   predators with morning activity peaks (Nijman 2004; Sano 2012), and their still-hunting mode of capturing

234   prey may preclude regular enough contact with slow lorises. Although emerging data show a previously

235   unrecognized role for olfaction in the behaviour of some avian species active in low light, most birds are

236   visually-oriented (Martin 2012), and the diurnal eagles in this study are likely no exception. If slow loris

237   venom is part of a multimodal signalling complex mimicking cobras (Nekaris *et al.* 2013), then it is

238   possible that isolating the olfactory component of this warning display resulted in a stimulus that was too

239   weak to repel these visually-oriented raptors fully. Previous tests of the repellent properties of brachial

240   gland exudate alone have shown positive results in a variety of carnivore species, for which olfaction

241   likely plays a larger role in predatory behaviour (Alterman 1995). Thus, perhaps we would have observed

242   a more robust response if we had presented the venom to the raptors in conjunction with a visual and/or

243   auditory model of a slow loris. Alternatively, eagles with different hunting modes, such as the highly

244   specialised Black Eagle *Ictinaetus malayanus* that glide through the trees searching for bird nests thus

245   bringing them in contact with slow lorises in their sleeping sites, may show stronger responses to slow

246   loris venom.

247   It is also possible that the eagles in our study are simply adapted to process and consume the

248   venomous slow loris. In addition to venomous snakes, Crested Serpent-eagles are known to consume

249   venomous Marine Toads *Bufo marinus*, scorpions, and strongly odorous Asian House Shrews *Suncus*

250   *murinus* (Sody 1989; Sano 2012), suggesting that perhaps they are not generally repelled by chemical

251   defences in prey species. It is likely that aerial predators are not the primary targets for slow loris

252   chemical defences. Although a Reticulated Python *Python reticulatus* and monitor lizards *Varanus* spp.

253   are known to have killed slow lorises (Wiens and Zitzmann 1999; Kenyon *et al.* 2014), responses of

254   reptilian predators to slow loris venom have not been evaluated. Given that other mammals are known to

255   anoint themselves with snake scent to avoid snake predation (Clucas *et al*. 2008), snakes could be a

256   likely target for this defence mechanism and further studies should examine their response to slow loris

257   venom.

258   It is not clear if slow lorises show strong fear-based responses to predator presence. Wiens and

259   Zitzmann (1999) and Nekaris *et al*. (2007) noted that wild slow and slender lorises were unperturbed by

260   palm civets, small cats and large owls moving in close proximity to them. Another intriguing possibility is

261   that the volatile chemicals released in slow loris venom serve as an intraspecific alarm signal (Hagey *et*

262   *al*. 2007). For example, Giant Mesquite Bugs *Thasus neocalifornicus* produce defensive secretions in

263   response to predator threat, and exposing aggregations of mesquite bugs to their own secretions causes

264   individuals to disperse (Prudic *et al.* 2008). A similar response has been observed in Lamellose Ormer

265   *Haliotis tuberculata* in response to starfish predation (Bancala 2009). An olfactory-based alarm system

266   could serve as a vital warning function while simultaneously being more cryptic to at least visually

267   orientated predators such as eagles.

268   Our study represents one of the first attempts to test the function of the venom of slow lorises

269   experimentally. We presented eagles with swabs of slow loris venom and scent and compared their

270   behavioural reaction to these scents relative to controls. The eagles were not slower to approach test

271   objects containing venom, did not spent less time examining brachial gland exudate scented objects, but

272   did show higher rates of a facial rubbing after contact with loris venom. Although far from definitive, our

273   results suggest that repelling raptors in not a primary function of slow loris venom. These results add to

274   an already complicated picture of the role played by predator avoidance in the evolution of the unique

275   behavioural and morphological traits of these enigmatic nocturnal primates (Nekaris *et al.* 2007).

276

277   **Acknowledgements**

287

288 **References**

289 Alterman, L. (1995). Toxins and toothcombs: potential allospecific chemical defenses in *Nycticebus* and

290   *Perodicticus*. In ' Creatures of the Dark ' (Eds L. Alterman, G. Doyle and M. K. Izard.) pp. 413-424.

291   (Springer: US.)

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

293 Bancala, F. (2009). Function of mucus secretion by lamellose ormer, *Haliotis tuberculata lamellosa*, in

294   response to starfish predation. *Animal Behaviour* **78(5)**, 1189-1194.

295 Beron, M.P., Garcia, G.O., Luppi, T., and Favero, M. (2011). Age-related prey selectivity and foraging

296   efficiency of Olrog's Gulls (atlanticus) feeding on crabs in their non-breeding grounds. *Emu* **111(2)**,

297   172-178.

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

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

300 Casewell, N.R., Wüster, W., Vonk, F.J., Harrison, R.A., and Fry, B.G. (2013). Complex cocktails: the

301   evolutionary novelty of venoms. *Trends in Ecology & Evolution* **28**, 219-229.

302 Cavalli, M., Baladron, A.V., Isacch, J.P., Martinez, G., and Bo, M.S. (2013). Prey selection and food

303   habits of breeding Burrowing Owls (*Athene cunicularia*) in natural and modified habitats of Argentine

304   pampas. *Emu* **114(2)**, 184-188.

305 Clucas, B., Rowe, M.P., Owings, D.H., and Arrowood, P.C. (2008). Snake scent application in ground

306   squirrels, *Spermophilus* spp.: a novel form of antipredator behaviour? *Animal Behaviour* **75(1)**, 299-

307   307.

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

309 Cuthill, I.C., Partridge, J.C., Bennett, A.T., Church, S.C., Hart, N.S., and Hunt, S. (2000). Ultraviolet vision

310   in birds. *Advances in the Study of Behavior* **29**, 159-214

311 Eisner, T. and Grant, R.P. (1981). Toxicity, odor aversion, and olfactory aposematism. *Science*

312   **213(4506)**, 476-476.

313 Evans, D.L. and Waldbauer, G.P. (1982). Behavior of adult and naive birds when presented with a

314   bumblebee and its mimic. *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology* **59(3)**, 247-

315   259.

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

317 **52**(2),105-110.

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

319 Gohli, J., and Hogstedt, G. (2009). Explaining the evolution of warning coloration: secreted secondary

320 defence chemicals may facilitate the evolution of visual aposematic signals. *Plos One* ***4*(6)**, e5779.

321 Grow, N.B., Wirdateti, and Nekaris, K.A.I. (2015). Does toxic defence in *Nycticebus* spp. relate to

322 ectoparasites? The lethal effects of slow loris venom on arthropods. *Toxicon* **95**, 1-5.

323 Hagey, L.R., Fry, B.G., Fitch-Snyder, H. (2007). Talking defensively: A dual use for the brachial gland

324 exudate of slow and pygmy lorises. In 'Primate Anti-Predator Strategies.' (Eds S. Gursky and K.A.I.

325 Nekaris) pp. 251-270. (Springer: New York.)

326 Hart, D. (2007). Predation on primates: a biogeographical analysis. In 'Primate Anti-Predator Strategies*'*

327 (Eds S. Gursky and K.A.I. Nekaris) pp. 27-59. (Springer: New York.)

328 Jones, M.P., Pierce, K.E., Ward, D. (2007). Avian vision: a review of form and function with special

329 consideration to birds of prey. *Journal of Exotic Pet Medicine* **16(2)**, 69-87.

330 Kenyon, M., Streicher, U., Loung, H., Tran, T., Tran, M., Vo, B., and Cronin, A. (2014). Survival of

331 reintroduced pygmy slow loris *Nycticebus pygmaeus* in South Vietnam. *Endangered Species*

332 *Research* **25**, 185-195.

333 Klump, G.M., Kretzschmar, E., and Curio, E. (1986). The hearing of an avian predator and its avian prey.

334 *Behavioral Ecology and Sociobiology* **18(5)**, 317-323.

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

336 695.

337 Machado, G., Carrera, P.C., Pomini, A.M., and Marsaioli, A.J. (2005). Chemical defense in harvestmen

338 (Arachnida, Opiliones): do benzoquinone secretions deter invertebrate and vertebrate predators?

339 *Journal of Chemical Ecology* **31(11)**, 2519-2539.

340 Madani, G., and Nekaris, K.A.I. (2014). Anaphylactic shock following the bite of a wild Kayan slow loris

341 (*Nycticebus kayan*): implications for slow loris conservation. *Journal of Venomous Animals and Toxins*

342 *including Tropical Diseases* **20(1)**, 43.

343   Mariano-Jelicich, R., Rodriguez, M.P.S., Copello, S., Seco Pon, J.P., Beron, M.P., Mauco, L., Ghys, M.I.,

344   and Favero, M. (2011). The diet of the South American tern: the Argentine anchovy as key prey in the

345   non-breeding season. *Emu* **111(4)**, 292-296.

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

347   23-48.

348   Moore, R.S., Wihermanto, and Nekaris, K.A.I. (2014). Compassionate conservation, rehabilitation and

349   translocation of Indonesian slow lorises. *Endangered Species Research* **26**, 93-102.

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

351   Nekaris, K.A.I., Moore, R.S., Rode, E.J., and Fry, B.G. (2013). Mad, bad and dangerous to know: the

352   biochemistry, ecology and evolution of slow loris venom. *Journal of Venomous Animals and Toxins*

353   *including Tropical Diseases* **19**, 21.

354   Nekaris, K.A.I., Pimley, E.R., and Ablard, K.M. (2007). Predator defense by slender lorises and pottos. In

355   'Primate Anti-Predator Strategies' (Eds S. Gursky and K.A.I. Nekaris.) pp. 220-238. (Springer: New

356   York.)

357   Nijman, V. (2004). Habitat segregation in two congeneric hawk-eagles (*Spizaetus bartelsi* and *S.*

358   *cirrhatus*) in Java, Indonesia. *Journal of Tropical Ecology* **20**, 105-111.

359   Orosz, S.E., and Lichtenberger, M. (2011). Avian respiratory distress: etiology, diagnosis, and treatment.

360   *Veterinary Clinics of North America: Exotic Animal Practice* **14(2)**, 241-255.

361   Prudic, K.L., Noge, K., and Becerra, J.X. (2008). Adults and nymphs do not smell the same: the different

362   defensive compounds of the giant mesquite bug (*Thasus neocalifornicus*: Coreidae). *Journal of*

363   *Chemical Ecology* **34(6)**, 734-741.

364   Rice, W.R. (1982). Acoustical location of prey by the marsh hawk: adaptation to concealed prey. *The Auk*

365   **99(3)**, 403-413.

366   Rode-Margono, J.E., and Nekaris, K.A.I. (2015). Cabinet of curiosities: venom systems and their

367   ecological function in mammals, with a focus on primates. *Toxins* **7(7)**, 2639-2658.

368   Rowe, C., and Halpin, C. (2013). Why are warning displays multimodal? *Behavioral Ecology and*

369   *Sociobiology* **67(9)**, 1425-1439.

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

371 4-5.

372 Skelhorn, J., and Rowe, C. (2006). Predator avoidance learning of prey with secreted or stored defences

373 and the evolution of insect defences. *Animal Behaviour* **72**, 827-834.

374 Sody, H.J.V. (1989). Diet of Javanese birds. In 'Henri Jacob Victor Sody (1892-1959), his life and work.'

375 (Ed J.H. Becking.) pp. 164-221 (Brill: Leiden.)

376 Starcevic, A., Moura-da-Silva, A.M., Cullum, J., Hranueli, D., and Long, P.F. (2015). Combinations of long

377 peptide sequence blocks can be used to describe toxin diversification in venomous

378 animals *Toxicon* **95**, 84-92.

379 Weldon, P.J., and McNease, L. (1991). Does the American alligator discriminate between venomous and

380 nonvenomous snake prey. *Herpetologica* **47(4)**, 403-406.

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

382 London.)

383 Wiens, F., and Zitzmann, A. (1999). Predation on a wild slow loris (*Nycticebus coucang*) by a reticulated

384 python (*Python reticulatus*). *Folia Primatologica* **70**, 362-364.

385

386   Table 1. Ethogram for responses of Changeable Hawk-eagles *Nisaetus cirrhatus* and Crested Serpent-

387   eagles *Spilornis cheela* to food items treated with control or Greater Slow Loris *Nycticebus coucang*

388   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.

389

390

391 **Table 2**. Responses of five Crested Serpent-eagles *Spilornis cheela* and ten Changeable Hawk-eagles

392 *Nisaetus cirrhatus* towards chicken pieces in combination with neutral scents (blank and lavender),

393 Greater Slow Loris *Nycticebus coucang* scent, or its venom (brachial gland exudate on its own or

394 incubated in saliva). Medians and interquartile ranges are presented for Latency (time in seconds

395 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

396

398

399

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*,

403