

Loud Calls, Startle Behaviour, Social Organisation and Predator Avoidance in Arboreal Langurs (*Cercopithecidae: Presbytis*)

Vincent Nijman · K.A.I. Nekaris

Anthropology Centre for Conservation, Environment and Development, Oxford Brookes University, Oxford, UK

© S. Karger AG, Basel

**PROOF Copy
for personal
use only**

ANY DISTRIBUTION OF THIS ARTICLE WITHOUT WRITTEN CONSENT FROM S. KARGER AG, BASEL IS A VIOLATION OF THE COPYRIGHT.

Key Words

Alarm calls · Antipredator strategies · Colobine · Crypsis · Indonesia · Leaf monkey

Abstract

Linking predator avoidance and social organisation predicts that large groups are favoured under heavy predation pressure but that small, inconspicuous groups may do equally well by avoiding detection altogether. We explored the relationships between antipredator behaviour (vocalisation, concealment, fleeing), detectability (colouration, group size) and social organisation in arboreal langurs. Three clear antipredation conditions emerged: (1) exemplified by *Presbytis melalophos* – brightly coloured species (red, yellow) with contrasting colours, living in large unimale-multifemale groups (>10 individuals), that vocalised frequently and that flee loudly through the canopy; (2) exemplified by *P. comata* – greyish species (some contrasting colours), living in intermediate, unimale-multifemale or 1-male-1-female groups (approx. 7 individuals), that vocalise infrequently and that flee through the middle forest layers; (3) exemplified by *P. frontata* – dull-coloured species without contrast, living in small unimale-multifemale or 1-male-1-female groups (<5 individuals), that may freeze upon detection, and that may vocalise mainly during the night. Crypsis as an antipredator strategy is restricted to taxa that occur in 1-male-1-female groups. This wide range of antipredator strategies within a monophyletic taxon living in the same general area with a similar suite of predators facing similar predator pressures appears to be unique among the order Primates.

Copyright © 2012 S. Karger AG, Basel

KARGER

Fax +41 61 306 12 34
E-Mail karger@karger.ch
www.karger.com

© 2012 S. Karger AG, Basel
0015-5713/12/0000-0000\$38.00/0

Accessible online at:
www.karger.com/fpr

Vincent Nijman
Oxford Brookes University
Department of Anthropology and Geography
Gipsy Lane, Oxford OX3 0BP (UK)
E-Mail vnijman@brookes.ac.uk

Introduction

One striking feature of the social behaviour of gregarious primates is the existence of alarm calls that signal the presence of predators, and that typically elicit startle behaviour in other members of the group [Fichtel and Kappeler, 2002]. Apart from signalling predator identity [Seyfarth et al., 1980] and location [Zuberbühler, 2000] to group members, these calls may also function as predator deterrence [Zuberbühler et al., 1999] or mobbing recruitment [Wheeler, 2008]. Group size and social organisation appear to reflect ecological forces, including predation pressure [Treves, 1999; Gursky and Nekaris, 2007]. One of the predictions that has arisen from the linkage of predator avoidance and social organisation is that on the one hand large groups are favoured under heavy predation pressure, as greater numbers improve early detection, deterrence and dilution of risk [van Schaik, 1983; van Schaik and van Hooff, 1983; Dehn, 1990], and that, on the other hand, small, inconspicuous groups improve predator avoidance [Watanabe, 1981; Tenaza and Fuentes, 1995; Janson, 1998]. When crypsis is used to avoid predator detection, we expect the animals to blend into their environment, not to have contrasting pelage colours, and to limit vocalising [Bradley and Mundy, 2008; Fichtel, 2007]. With respect to activity patterns, in general, mobile, active animals are expected to employ the early detection strategy [van Schaik and van Hooff, 1983], whereas non-saltatory, slow-moving animals should opt for avoidance [Nekaris, 2001].

Here we focus on langurs of the genus *Presbytis*, a group of primates that have been studied individually but for which no comprehensive overview is present on the relationship between predator avoidance and social organisation (but see van Schaik and Hörstermann [1994] who focussed on the relationship between predation risk and the number of adult males). We start with providing an anecdotal overview of some of the intra- and interspecific variations in alarm calls and escape strategies linking them to the reported social organisation of the respective species. We then present the results of our study of antipredator behaviour towards human observers of 7 langurs of the genus collected in western Indonesia, and link this to pelage colouration and social organisation.

The genus *Presbytis* is a monophyletic taxon, represented by at least 11 species [Groves, 2001] distributed in the Thai-Malay Peninsula, Sumatra, Borneo, Java and associated smaller islands. The adult female body mass is between 5.6 and 8.2 kg [Rowe and Myers, 2010], and all species are almost exclusively arboreal, highly agile and confined to the remaining tall forests in the region. Apart from the 1-male-1-female Mentawai langur *P. potenziani*, most species studied to date live in unimale-multifemale groups, typically comprising 6–16 individuals [Bennett and Davies, 1994; but see Hadi et al., 2012], although larger multimale/multifemale groups have been reported [Curtin, 1980; Sterck and van Hooff, 2000]. Three species have been reported to occur consistently in smaller groups, i.e. the Natuna langur *P. natunae*, white-fronted langur *P. frontata*, and grizzled langur *P. comata*. Recently we [Lamertink et al., 2003] reported on small group sizes in *P. natunae*, and attributed this to the absence of feline predators on the island of Bunguran, allowing it to forage more efficiently with less within-group competition. *P. frontata* lives in small groups, typically comprising <6 individuals [Nijman, 2001]. The data available suggest that both unimale-multifemale and 1-male-1-female groups occur in one population [V. Nijman, unpubl. data]. *P. comata* occurs occasionally in groups with 1 adult male and

1 female, but normally the species lives in typical unimale-multifemale groups [Ruhayat, 1983]; in high altitude forest; the social organisation is similar to that of *P. frontata*, i.e. both unimale-multifemale and 1-male-1-female groups occur in the same population [V. Nijman, unpubl. data].

Tilson and Tenaza [1976] reported on the behavioural responses of the 1-male-1-female groups of *P. potenziani* to humans. Adult males perform distraction displays consisting of loud vocalisations accompanied by branch bouncing as they run through the canopy. During this performance, the female and immature young often hide silently and motionless in the canopy for periods up to 45 min before leaving. When males are solitary or when no offspring is present, the langurs flee without giving alarm calls. Under the assumption that this distraction display was unique to *P. potenziani*, Tilson and Tenaza [1976] attributed this predator defence system to the unique situation of the Mentawai Islands, with intense human predation and the lack of counterselection due to the absence of other predators.

For white-thighed langur *P. siamensis*, Curtin [1980] reported similar behaviour to that of *P. potenziani*, i.e. calling and displaying by adult males, drawing aboriginal hunters away from the other group members that remained hidden and silent. Gurmaya [1989, p. 118] reported that Thomas' langur *P. thomasi*, apart from a distraction display that included vocalisations, adult males sometimes vocalised towards humans while hiding in the foliage. Megantara [1989, p. 240], referring to the banded langur *P. femoralis*, did not find analogous behaviours to that of *P. thomasi*, and no apparent distraction displays towards humans were noted. In response to humans, other species have been reported to descend to the ground and to flee through the understory (red langur *P. rubicunda* [Coomans de Ruiter, 1932; Stott and Selsor, 1961]; *P. frontata* and Sarawak langur *P. chrysomelas* [Banks, 1931]; *P. comata* [Bartels, 1937]). Banks [1931] noted that, even when alarmed, Hose's langur *P. hosei* would never descend to the ground but makes prodigious leaps instead. Supriatna et al. [1986] found *P. rubicunda* to be truly arboreal and when alarmed by a human observer, an individual would produce an alarm call, the also vocalising adult male would lead the group away for a short distance, after which the group as a whole would freeze in the trees. Lastly, Davis [1962, p. 62] reported on *P. hosei* that 'when alarmed they make off through the tree tops in a series of spectacular crashing leaps. The arms and legs are spread-eagled, and the animal throws itself into the foliage without aiming at a particular branch'. Later in the same paper, Davis [1962, p. 65] states: 'My observations indicate that [*P. rubicunda*] is more shy than [*P. hosei*]. When a mixed group is alarmed, [*P. rubicunda*] makes off at once in a series of crashing leaps, while [*P. hosei*] may not flee until shot at.'

Methods

Study Areas and Study Species

Data were collected in the period 1994–2007 on the islands of Sumatra, Java and Borneo (table 1; fig. 1). The Sumatran langur *P. melalophos* was studied in the Way Kambas National Park (105°45' E, 4°55' S) and during surveys in the provinces of Lampung and South Sumatra; *P. comata* was studied in the Dieng Mountains, Central Java (109°35' E, 7°06' S) [Nijman, 1997; Nijman and van Balen, 1998], Hose's langur (*P. hosei*) in the Kayan Mentarang National Park, East Kalimantan (115°49' E, 2°53' N) [Nijman, 2004, 2005], *P. rubicunda* and *P. frontata* in the Sungai Wain Protection Forest, East Kalimantan (116°54' E, 1°16' S) [Fredriksson and Nijman,

Table 1. Study species, study areas and study periods

Species	Main study area	Field days (period)	Group density, km ⁻²	Group size	Social organisation
<i>P. melalophos</i>	Way Kambas National Park	19 (1994, 1999, 2001)	–	9.0 ± 2.2 (10) 5–13	unimale-multifemale/ multimale-multifemale
<i>P. rubicunda</i>	Sungai Wain Protection Forest	180 (1999–2005)	3.3 ± 0.7 (4) 2.5–4.0	8.2 ± 2.2 (54) 2–12	unimale-multifemale/ multimale-multifemale
<i>P. hosei</i>	Kayan Mentarang National Park	87 (1996, 2003)	2.0 ± 0.6 (5) 1.0–2.4	8.0 ± 3.0 (16) 2–11	unimale-multifemale
<i>P. thomasi</i>	Ulu Masen	23 (2007)	–	7.2 ± 2.9 (6) 3–11	unimale-multifemale
<i>P. comata</i>	Mts Dieng	130 (1994–2002)	2.4 ± 1.1 (6) 1.2–4.4	7.1 ± 3.6 (24) 2–13	unimale-multifemale/ 1-male-1-female
<i>P. natunae</i>	Bunguran	54 (2001)	2.3 ± 1.1 (3) 1.2–3.4	3.5 ± 2.0 (16) 2–7	unimale-multifemale/ (1-male-1-female?)
<i>P. frontata</i>	Sungai Wain Protection Forest	180 (1999–2005)	1.1 ± 1.2 (4) 0–2.7	2.7 ± 1.2 (11) 2–4	(unimale- multifemale?)/ 1-male-1-female

Densities were obtained by line transect counts. Presented are: number of field days with period in parentheses; group density and size as means ± 1 SD, with sample sizes, number of transects or number of groups in parentheses, and range. Species are ordered according to average group size. – = No transects were walked for *P. melalophos* or *P. thomasi*, but the former species appeared to be common, whereas the latter appeared to be rare in the study area.

2004] and *P. thomasi* in the Ulu Masen forest, Aceh (95°38' E, 5°18' N). Data on *P. natunae* from Bunguran (108°14' E, 3°55' N) was made available by M. Lammertink and U. Setioringi [Lammertink et al., 2003]. Additional surveys were conducted in various parts of Java, Sumatra, Borneo and the Thai-Malay Peninsula, including the period 2008–2010. The total survey effort approximated 600 days in lowland forests <800 m above sea level where *Presbytis* was found to be present. Throughout this paper, we adopt the taxonomy of Groves [2001], recognising that especially *P. hosei* in fact comprises up to 3 species [Nijman and Meijaard, 2008; Nijman, 2010].

Most study areas are covered in primary or old secondary rain forest with a more or less closed canopy. In Sumatra, Java and Bunguran parts of the study areas consisted of a matrix of selectively logged forest with a less continuous canopy, and in Sumatra, also forest gardens. All these forests allowed the langurs to use arboreal pathways through the canopy.

P. hosei in Kayan Mentarang National Park is occasionally hunted to obtain bezoar stones (visceral secretions found in langurs that are used in traditional medicine and that fetch high prices). *P. melalophos* more so than *P. natunae* are occasionally caught for the domestic pet trade, the latter mostly haphazardly near settlements or in people's forest gardens. In the other study areas, no hunting or capturing of *Presbytis* occurred. Other than humans, there are no natural predators for primates on Bunguran. Predators on the other islands include tigers (*Panthera tigris*; Thai-Malay Peninsula, Sumatra and formerly Java), leopards (*Panthera pardus*; Thai-Malay Peninsula, Java), clouded leopards (*Neofelis nebulosa* and *N. diardi*; Thai-Malay Peninsula, Sumatra, Borneo), dhole (*Cuon alpinus*; Thai-Malay Peninsula, Sumatra, Java), various hawk eagles (*Spizaetus* spp.; Thai-Malay Peninsula, Sumatra, Borneo, Java) and eagles of the genus *Aquila* (Thai-Malay Peninsula). A small and intermediate-sized hawk eagle (*Spizaetus nanus* and *S. alboniger*) occur on Siberut, the largest of the 4 Mentawai Islands, but not on the other 3 islands; no eagles of the genus *Spizaetus* occur on Bunguran.



Fig. 1. Langurs of the genus *Presbytis* showing differences in pelage colouration and contrast. Clockwise from top left: white-fronted langur *P. frontata* from South Borneo, Hose's langur *P. hosei* from North Borneo, red langur *P. rubicunda* from East Borneo, Sumatran langur *P. melalophos* from South Sumatra, Thomas' langur *P. thomasi* from North Sumatra. Based on photographs of M. Janda, C. Prudente, G.M. Fredriksson, M. Jimenez, N. Rowe.

Data Acquisition

We collected data on the antipredator behaviour while conducting population assessments along transects in the forest and during general surveys (details in Lammertink et al. [2003], Nijman [2001, 2004, 2005], Nijman and van Balen [1998]). In none of the areas were the primates habituated to human observers and in general all were relatively shy (table 2). Judging by the locations we encountered groups and their composition, most groups were included only once in the analysis. Encounters with the same groups in long-term study areas were separated in time, and we consider encounters with these groups as independent events. Upon encounter the

Table 2. Responses of 6 species of *Presbytis* to a human observer, with percentages of total in parentheses

Species	n	Vocal	Freezing	Fleeing		
				canopy	middle	low/ground
<i>P. melalophos</i>	10	7 (70)	0 (0)	7 (70)	2 (20)	0 (0)
<i>P. rubicunda</i>	54	45 (83)	0 (0)	33 (61)	14 (26)	2 (4)
<i>P. hosei</i>	24	5 (21)	0 (0)	6 (25)	10 (42)	0 (0)
<i>P. comata</i>	38	11 (29)	1 (3)	7 (18)	13 (34)	2 (5)
<i>P. natunae</i>	10	5 (50)	0 (0)	–	–	–
<i>P. frontata</i>	17	7 (41)	6 (35)	0 (0)	2 (12)	12 (71)

Species are ordered according to average group sizes, with the largest group sizes listed on top. n = Number of groups observed; Vocal = number of these that responded with loud calls, and not to the total number of groups that were heard vocalising prior to detection.

observer (mostly V.N., and mostly walking singly) collected data on group size (only ‘complete counts’ when there was a great degree of certainty that all individuals in a group were counted included here), the langurs’ positions in the tree, and their reaction when they noted the observer’s presence. As the primary aim of us being in the forest was not to study antipredator behaviours, we normally behaved as inconspicuously as possible, walking slowly, and not trying to disturb the langurs, although by merely being present we obviously did. We consider the following 3 behavioural patterns.

Vocalising. This refers mostly to loud calls (that also have been referred to as long calls or long-distance calls) [Cheney, 1987; Hohmann and Fruth, 1995]. The relatively stereotyped vocalisations are used almost exclusively by adult males and carry over long distances. The exception is *P. potenziani*, where male and female exchange loud calls in so-called duets [Tilson and Tenaza, 1976]. In most species, loud calls consist of several notes and their presentation is often accompanied with relatively stereotyped positional and locomotor displays (e.g. jumping with stiff legs, branch shaking). Loud calls appear to be elicited by external stimuli such as intergroup encounters, loud calls from neighbouring groups, loud noises, and the appearance of birds of prey or potential terrestrial predators (including humans) [Curtin, 1980; Ruhiyat, 1983; Gurmaya, 1989; Megantara, 1989; Fuentes, 1996; Wich, 2002; Wich and Sterck, 2003; Fam and Nijman, 2011].

Freezing. Animals may hide silently and remain motionless for prolonged periods before moving slowly away or fleeing. Freezing is an active behaviour and is distinctly different from that when individuals remain motionless for brief periods between engaging in one type of behaviour and another. During freezing by definition the animals remain silent.

Flight. Typically, when animals flee, they move rapidly away from the observer, (i) upwards to the canopy and use arboreal pathways, or (ii) they may flee through the middle forest layer, or (iii) they may descend to ground level and flee through the undergrowth or over the forest floor. Although the distinction between the three levels of flight (canopy, middle, or lower and floor) is somewhat arbitrary, the height of the forests (with canopy levels mostly at >30–40 m) in practice allows rather accurate judgement. During flight individuals may vocalise.

Analysis

As to avoid pseudoreplication [Martin and Bateson, 2007], for analysis the group instead of the individual was considered the appropriate unit of measurement. Loud calls were mostly given by 1 or more adult-sized males, but often the other group members responded. Freezing, described below, was mostly performed by most if not all group members, and while fleeing

most members follow the same or similar pathways (all upwards to the canopy or all downwards to the forest floor). Indeed, it has been suggested that one of the primary functions of alarm calls is to increase the synchronisation of flight [Charnov and Krebs, 1975]. Hence, group members are mostly engaged in the same activity supporting the assumption that in these situations individuals in a group do not behave independently.

As a means to explore the relations between antipredator behaviour, crypsis, pelage colouration, group sizes and social organisation, we conducted a hierarchical cluster analysis for all 10 of the 11 langurs (insufficient data were available for *P. chrysomelas*). Six variables (vocal behaviour during non-stress situations; dominant frequency of exhalation notes; concealment; the amount of contrast or colourfulness in the pelage and face; the amount of time spent on the ground or at low levels; group size; social organisation) were coded from 1 (least common, or smallest) to 3 (most common, or largest) based on data from the current study and from the literature (see Appendix). We selected the unweighted pair group method with arithmetic mean, implemented in SPSS, as the hierarchical clustering method, where at each step the nearest two clusters are combined into a higher-level cluster.

As little is known about the nature of the (statistical) population from which the samples are drawn, and in order to increase the generality of the conclusions, non-parametric statistical tests were used [Siegel, 1956]. Yates' correction for continuity was applied in the χ^2 test when appropriate. As we made multiple comparisons, we used a Bonferroni technique [Sokal and Rohlf, 1995] to limit the overall experiment-wise error, with significance accepted when $p < 0.01$ in a two-tailed test.

Results

Startle Response and Fleeing Routes

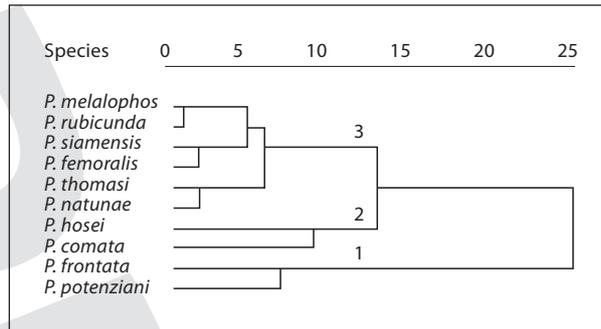
Data from *P. thomasi* were limited and sample sizes were too small for the species to be included in parts of the analysis. Fleeing upwards to the canopy was the most common startle response in *P. melalophos* and *P. rubicunda*, whereas *P. hosei* and *P. comata* mostly fled through the middle forest layer. These species, and also *P. natunae*, when fleeing, would normally jump from branches leaping from one tree to another, making a lot of noise and clearly drawing attention to themselves. *P. frontata* most frequently descended to the undergrowth before fleeing, whereas this pathway was chosen by two groups each for *P. rubicunda* and *P. comata*. Fleeing in *P. frontata* was almost silent. *P. thomasi* was the most terrestrial of the langurs, but this was not as a startle response: when on the ground they would flee into the trees.

Fleeing routes differed significantly between the 5 species (middle and low/ground level pooled as to avoid too many low expected values: $\chi^2 = 26.5$, d.f. = 4, $p < 0.001$), and for each of the individual species, the distribution of fleeing routes (canopy, middle, and low/ground) was not equal ($\chi^2 > 8.3$, d.f. = 1, $p < 0.005$). *P. rubicunda* significantly used the canopy more than the other species combined ($\chi^2 = 12.9$, d.f. = 1, $p < 0.001$), whereas the same tendency was observed in *P. melalophos* ($\chi^2 = 3.4$, d.f. = 1, $p < 0.07$). *P. frontata* used the middle and lower layer significantly more than other species ($\chi^2 = 14.9$, d.f. = 1, $p < 0.001$).

Freezing

Freezing behaviour as defined above was observed in 2 species only, *P. frontata* and *P. comata*. Especially in *P. frontata* freezing was common, and indeed was recorded significantly more often than in the other species combined ($\chi^2 = 38.2$, d.f. = 1, $p < 0.001$). In *P. frontata* at all times (during feeding, resting and travelling) groups

Fig. 2. Hierarchical cluster analysis using average linkage (unweighted pair group method with arithmetic mean) using predator detection- or avoidance-related variables for 10 species of *Presbytis*.



remained cohesive. Upon detecting the human observer, the group would either remain silent or softly vocalise, and then they would gently retreat into the foliage. Rarely would the adult male produce loud calls, and if he did, these were, in comparison with the other members of the genus, short in duration. Alternatively, upon detection, the group members would hide silently and remain motionless for prolonged periods (up to 55 min) before moving slowly away or fleeing.

Vocal Behaviour

The frequency of producing loud calls upon detecting a human observer differed significantly between the 6 species ($\chi^2 = 19.5$, d.f. = 5, $p < 0.005$). *P. rubicunda* was significantly more vocal than the other 5 species ($\chi^2 = 15.4$, d.f. = 2, $p < 0.001$). Both *P. hosei* and *P. comata* were less vocal than the other species combined ($\chi^2 = 5.4$, d.f. = 1, $p < 0.02$ and $\chi^2 = 5.3$, d.f. = 1, $p < 0.02$ for *P. hosei* and *P. comata*, respectively). This difference was also apparent during non-distress situations: throughout the day, *P. rubicunda*, *P. melalophos*, *P. thomasi* and *P. natunae* could be frequently heard vocalising, whereas this was much rarer in *P. hosei* and *P. comata*. Nocturnal calling (i.e. between 20.00 and 1.00 h) was frequent in *P. frontata*, but calls were heard rarely during the day, whereas *P. natunae* was recorded calling from 4.00 to 10.00 h (sunrise at Bunguran is at approx. 5.30 h).

Antipredator Conditions

When considering vocal behaviour (amount and frequency of exhalation notes), concealment when detecting a human observer (freezing, coming down to low levels), detectability of the langurs (colouration, contrast, group size) and social organisation, the different *Presbytis* species divide into 3 distinct clusters (fig. 2). The first, most basal, cluster comprises *P. frontata* from Borneo and *P. potenziანი* from the Mentawai Islands, these being the species living in the smallest group sizes, of dull colouration without contrasts (brownish in *P. frontata* and black in *P. potenziანი*) and use concealments as a form of predator avoidance. The easternmost populations of *P. comata* are blackish; if given a score of 1 for pelage colouration *P. comata* clusters with this first group. The second cluster comprises *P. comata* from Java and *P. hosei* from Borneo. Both are grey-backed with a contrasting white belly (more pronounced in the sexually dimorphic white-headed males of the western populations of *P. hosei*), that live in intermediate group sizes, and that alarm call infrequently

when detected by human observers. Finally, the third cluster comprises colourful species from Sumatra, the Thai-Malay Peninsula and Borneo, which live in large unimale-multifemale or multimale-multifemale groups, often high up in the canopy. They rely on early detection for predator avoidance, and their loud calls can be heard frequently both in distress and non-distress situations. When the social status of *P. natunae* is changed from unimale-multifemale to 1-male-1-female groups, it no longer clusters with the third cluster but becomes a fourth single-species one, basal to second and third clusters. Although data was limited for *P. chrysomelas*, it appears most similar to *P. rubicunda*, *P. melalophos* and *P. siamensis*, and hence we predict *P. chrysomelas* to be part of the third cluster.

Discussion

There were distinct differences in the reaction of the 6 *Presbytis* species when they encountered a human observer. In most species one or more individuals emitted loud calls after which all group members would noisily flee upwards into the canopy or through the middle forest layer. *P. rubicunda* always fled through the canopy or, to a lesser extent, the middle layer, although historical accounts from other parts of its range mention that it descends to the ground and flees through the understorey (West Kalimantan [Coomans de Ruiter, 1932]; Sabah [Stott and Selsor, 1961]). Descending to ground level and fleeing through the understorey was common in *P. frontata* but has only been reported by Banks [1931]. For the easternmost populations of *P. comata*, Bartels [1937] reported that when pursued, they would drop to the understorey and escape through the dense undergrowth, probably partly along the ground. In the present study, this response was observed only in 5% of all cases; if this is representative for the startle response of the species in general, this explains why this is not observed in short studies, e.g. Melisch and Dirgayusa [1996]. In general, and for all species, escape was highly synchronised and only rarely would a group split up in subgroups or would individuals differ markedly in their response.

The conspicuous vocal behaviour in *Presbytis* most likely functions to signal detection and unprofitability directly to the predator. In a visually dense environment, loud calls in response to a potential predator provide a conspicuous and unambiguous acoustic signal to the predator to indicate detection and the futility of a further hunting attempt. Even though the langurs do draw attention to themselves, the continuous scaffolding of the rain forest canopy will still allow them to enjoy an enormous locomotor advantage over a ground-dwelling predator. Such conspicuous vocal behaviour is costly both energetically and because it attracts other predators, for example large eagles or felids. Predation on colobines in Asia has been rarely documented [Hart, 2007; Fam and Nijman, 2011]: hawk eagles appear to be an important threat. Hawk eagles mainly adopt a strategy of still hunting, waiting at a perch in the upper canopy for prey (such as langurs) to pass by, and perform a surprise attack from above. Vocalising may attract an eagle to the general area where the langurs are, but, given that many eagles rely on surprise for the actual kill, it may not pose a disadvantage for the langurs.

Vocalising in *P. frontata*, because of its cryptic lifestyle and frequent fleeing through the undergrowth, probably has not been favoured as a predator deterrence effect. It most likely functions as an interspecific warning mechanism only.

The data from the present study strongly suggest that *P. frontata* evolved a predator avoidance strategy based on crypsis. As such it deviates importantly from that of most other members of the genus, as well as from all other sympatric primates. It is perhaps best comparable with the mode of predator avoidance as found in *P. potenziანი*, simakobu (*Simias concolor*) [Watanabe, 1981] and de Brazza's monkeys (*Cercopithecus neglectus*) [Gautier-Hion and Gautier, 1978]. This antipredator strategy may have played an important role in the evolution of a monogamous (with a 1-male-1-female social organisation) or monandrous social system (with both 1-male-1-female and unimale-multifemale groups in the same population [Tenaza and Fuentes, 1995]). Gautier-Hion and Gautier [1978] suggested that if primates avoid predators primarily by concealment, then it pays to form small social units, with ultimately monogamous family groups as the most extreme outcome. As such it has been suggested that for de Brazza's monkeys, concealment as an antipredator strategy resulted in a monandrous social system. Thus, the cryptic way of predator avoidance has so far been reported in 3 species (*P. potenziანი*, *P. frontata* and to a lesser degree *P. comata*), and these same 3 species are the only that live in 1-male-1-female groups. The likelihood that this arises due to chance in a group of 11 species is very small indeed (Fisher's exact probability test, $p = 0.006$).

The only other species that lives in small, possibly 1-male-1-female, groups is *P. natunae*. This species evolved on an island (Bunguran) without feline, canine or avian predators, and, unlike the likewise predator-free Mentawai Islands home to *P. potenziანი*, the indigenous human population does not hunt primates. Concealment did not seem to be part of its behavioural repertoire, although Indrawan and Rangkuti [2001] reported that 1 of 19 groups detected was 'fleeing and hiding'. The impression was that the species was rather vocal [M. Lammertink, pers. commun.; Indrawan and Rangkuti, 2001]. As indicated by Lammertink et al. [2003], this suggests that in this species small group sizes probably evolved as to forage more efficiently with less within-group competition as opposed to predator avoidance. A similar scenario can be envisaged for *P. potenziანი*. Tilson [1977] speculated that predation by humans is responsible for 1-male-1-female groups in *S. concolor*, another colobine endemic to the Mentawai Islands, suggesting that crypsis is the best defence against the specific long-distance hunting technique of the human predators. However, most closely related taxa on the islands of Sumatra, Borneo and Java live in unimale-multifemale or multimale-multifemale groups, although people must have started hunting there much longer ago than on the Mentawai Islands [van Schaik and van Hooff, 1983; Meijaard et al., 2010]. Hence, the 1-male-1-female grouping of *P. potenziანი* is almost certainly due to the absence of large non-human predators rather than to the presence of human predators [van Schaik and van Hooff, 1983].

Although the data we collected were observational only and experiments would be necessary to provide stronger evidence, it seems that clear species-specific startle responses are found in *Presbytis* accompanied by species-specific patterns of vocalisation. These behavioural responses in turn are correlated with physical characteristics in pelage colouration and pelage contrast, and are in part linked to social organisation. As such some species consistently deploy a tactic of early predator detection, deterrence and dilution of risk, while their congeners deploy a tactic of remaining inconspicuous avoiding detection by predators. This wide range of predator avoidance within a monophyletic taxon, living in the same general area with a similar suite of predators facing similar predator pressures, appears to be unique among

the order Primates. (It is perhaps comparable only to the guenons *Cercopithecus*; they however range over a wider geographic area and a wider range of habitats facing distinctly different predation pressures [Jaffe and Isbell, 2011].) It furthermore clearly disproves the dictate that mobile, active animals should employ an early detection strategy.

Appendix: Hierarchical Cluster Analysis

Seven variables (vocal behaviour during non-stress situations; call frequency; concealment; the amount of contrast or colourfulness in the pelage and face; the amount of time spent on the ground or at low levels; group size; social organisation) were coded from 1 (least common, or smallest) to 3 (most common, or largest) based on data from the current study and from the literature.

Vocal Behaviour during Non-Stress Situations

Those species that rarely called during daytime or that called almost exclusively during the night received a score of 1, those that called infrequently a score of 2, those that called frequently, often in calling rounds, a score of 3 (online suppl. table 1; for all online suppl. material, see www.karger.com/doi/10.1159/000339647).

Dominant Frequency in the Exhalation Notes

Loud Calls. Position of dominant frequency in last exhalation note, measured across the whole duration of the last exhalation note. Sound recordings were digitized with a sample rate of 22 kHz, sonograms were generated using Canary 1.2.4 [Charif et al., 1995] and frequencies were coded as 1 = <1,250 Hz, 2 = >1,250–<2,100 Hz, 3 = >2,100 Hz. Data from T. Geissmann, J. Vermeer, V. Nijman [unpubl. manuscript].

Crypsis

Species that upon detection do behave conspicuously, or that approach the observer, received a score of 1; those that behave more reservedly, but that normally do not exhibit freezing behaviour received a score of 2; those species that show freezing behaviour received a score of 3.

Colouration

Within the genus *Presbytis*, and within some species more than in others, there is a large amount of variation in pelage colouration (bright yellow, red, to black and earthy colours), contrast between belly and dorsum (white belly and darker dorsum), as well as colouration of the head (contrasting with the body, longitudinal stripes, naked patches) and face (contrasting overall colour or eye rings). Species with an overall earthy or black uniform body colour, no contrast between belly and dorsum, no bright face, and no or few contrasting head patterns received a score of 1; intermediates between 1 and 3 received a score of 2; species with vivid colouration (bright yellow, red, cruciger patterns), or with a strong contrast between belly and dorsum (white belly and darker dorsum), longitudinal head stripes or contrasting face (contrasting overall colour or vivid eye rings) received a score of 3. In certain species (e.g. *P. melalophos*, *P. siamensis*, *P. comata*), some geographic populations are more strikingly coloured than others, but rarely did subspecies receive different scores. The exception is *P. comata*, where the western and central populations received a score of 2 (being grey with varying amounts of black, with a contrasting white belly) and the easternmost populations that received a score of 3 (being largely black, with small amounts of white). Scoring was done independently by K.A.I.N. and V.N., based on photographs in Rowe [1996] and well-documented photographs available on the Internet, and drawings made by V.N. of museum specimens.

Amount of Time Spent on the Ground or at Low Level

Species that rarely, if ever, descended to the ground, and that when fleeing generally used the upper canopy received a score of 1; those species that occasionally descended to the ground, and that when fleeing, in addition to the canopy level, used the middle or low levels received a score of 2; those species that frequently spent time at low levels, that when fleeing frequently used the low level or the ground, and that rarely used the upper canopy, received a score of 3. While *P. thomasi* spends more time on the ground than some of its congeners, it is mostly observed in the upper canopy and when startled does not come down to low levels: we gave it an intermediate score of 2.

Group Size

Although there is considerable variation in group sizes within species, when sample sizes are large enough, some species consistently occur in smaller or larger group sizes than others. Species that occurred in average group sizes of 5 or less individuals, and never more than 6 individuals, received a score of 1; species that mostly occurred in group sizes between 6 and 8 individuals, occasionally in smaller or larger groups, received a score of 2; species that occurred in group sizes of more than 8, and frequently in groups of more than 10 individuals received a score of 3.

Social Organisation

Species that have only been reported as unimale-multifemale or multimale-multifemale received a score of 1; species that have been reported as monandrous, i.e. with both 1-male-1-female and unimale-multifemale groups in one population, received a score of 2; species that occur mainly or exclusively in 1-male-1-female groups received a score of 3. *P. natunae* lives in small groups, but it is not clear if these are unimale-multifemale or 1-male-1-female: we gave it a score of 1 but ran a separate analysis with a score of 3.

Acknowledgments

We thank the Indonesian Institute for Sciences and the Indonesian Ministry of Forestry for allowing us to conduct fieldwork in Indonesia. Institutional help over the years was received from, amongst others, WWF-Indonesia (Jakarta, Samarinda), Bird Life Indonesia Programme (Bogor), Fauna and Flora International Indonesia Programme (Bogor, Banda Aceh), Pusat Informasi Lingkungan Indonesia (Bogor), Badan Pengelolaan Hutan Lindung Sungai Wain (Balikpapan) and Mitra Dieng (Pekalongan). Funding was received from Primate Conservation Inc., the Society for the Advancement of Science in the Tropics and the Netherlands Foundation for International Nature Protection. Many people helped us with data collection over the years: here we single out Martjan Lammertink and Utami Setiorini for their work on Bunguran. Susan Cheyne and Dawn Burnham are thanked for inviting us to contribute to this special issue and Andy Gray for help with formatting. Two reviewers provided extensive comments forcing us to express ourselves less ambiguously and thereby greatly improving the clarity of the paper.

References

- Banks E (1931). A popular account of the mammals of Borneo. *Journal of the Malayan Branch of the Royal Asiatic Society* 9: 1–139.
- Bartels M (1937). Zur Kenntnis der Verbreitung und der Lebensweise javanischer Säugetiere. *Treubia* 16: 149–164.
- Bennett EL, Davies AG (1994). The ecology of Asian colobines. In *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (Davies AG, Oates JF, eds.), pp 129–171. Cambridge, Cambridge University Press.

- Bradley BJ, Mundy NI (2008). The primate palette: the evolution of primate coloration. *Evolutionary Anthropology* 17: 97–111.
- Charif RA, Mitchell S, Clark CW (1995). Canary 1.2.4 user's manual. Ithaca, Cornell Laboratory of Ornithology.
- Charnov EL, Krebs JR (1975). Evolution of alarm calls: altruism or manipulation? *American Naturalist* 109: 107–112.
- Cheney DL (1987). Interactions and relationships between groups. In *Primate Societies* (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds.), pp 267–281. Chicago, University of Chicago Press.
- Coomans de Ruiter L (1932). Het roode bergaapje en andere slankapen. In *Borneo's wonderwereld, schetsen over dieren en planten*, pp 34–45. Batavia, Nederlandsch-Indische Natuurhistorische Vereniging.
- Curtin SH (1980). Dusky and banded leaf monkeys. In *Malayan Forest Primates: Ten Years' Study in Tropical Rainforest* (Chivers DJ, ed.), pp 107–145. New York, Plenum Press.
- Davis DD (1962). Mammals of the lowland rain-forest of north Borneo. *Bulletin of the National Museum of Singapore* 31: 5–129.
- Dehn MM (1990). Vigilance for predators: detection and dilution effects. *Behavioural Ecology and Sociobiology* 26: 337–342.
- Fam SD, Nijman V (2011). *Spizaetus* hawk-eagles as predators of arboreal colobines. *Primates* 52: 105–110.
- Fichtel C (2007). Avoiding predators at night: antipredator strategies in red-tailed sportive lemurs (*Le-pilemur ruficaudatus*). *American Journal of Primatology* 69: 611–624.
- Fichtel C, Kappeler PM (2002). Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology* 51: 262–275.
- Fredriksson GM, Nijman V (2004). Habitat use and conservation of two elusive ground birds (*Carpococcyx radiatus* and *Polyplectron schleiermacheri*) in the Sungai Wain Protection Forest, East Borneo. *Oryx* 38: 297–303.
- Fuentes A (1996). Feeding and ranging in the Mentawai langur (*Presbytis potenziani*). *International Journal of Primatology* 17: 525–548.
- Gautier-Hion A, Gautier JP (1978). Debrazza's monkey: an original strategy. *Zeitschrift für Tierpsychologie* 46: 84–104.
- Groves CP (2001). *Primate Taxonomy*. Washington, Smithsonian Institution Press.
- Gurmaya KJ (1989). Ecology, behavior and sociality of Thomas' leaf monkey in north Sumatra. *Comparative Primatology Monographs* 2: 53–170.
- Gursky SL, Nekaris KAI (2007). *Primate Anti-Predator Strategies*. New York, Springer.
- Hadi S, Ziegler T, Waltert M, Syamsuri F, Mühlenberg M, Hodges JK (2012). Habitat use and trophic niche overlap of two sympatric colobines, *Presbytis potenziani* and *Simias concolor*, on Siberut Island, Indonesia. *International Journal of Primatology* 33: 218–232.
- Hart D (2007). Predation on primates: a biogeographical analysis. In *Primate Anti-Predator Strategies* (Gursky SL, Nekaris KAI, eds.), pp 27–59. New York, Springer.
- Hohmann G, Fruth B (1995). Loud calls in great apes: sex differences and social correlates. In *Current Topics in Primate Vocal Communication* (Zimmermann E, Newman JD, Jürgens U, eds.), pp 161–184. New York, Plenum Press.
- Indrawan M, Rangkuti F (2001). Development, biodiversity and the conservation status of banded langur in Natuna Islands, Indonesia. *Tropical Biodiversity* 7: 151–163.
- Jaffe KE, Isbell LA (2011). The guenons: polyspecific associations in socioecological perspective. In *Primates in Perspective* (Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds.), 2nd ed., pp 277–300. Oxford, Oxford University Press.
- Janson CH (1998). Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. *Behaviour* 135: 389–410.
- Lammertink M, Nijman V, Setiorini U (2003). Population size, Red List status and conservation of the Natuna leaf monkey *Presbytis natunae* endemic to the island of Bunguran, Indonesia. *Oryx* 37: 472–479.
- Martin P, Bateson P (2007). *Measuring Behaviour: An Introductory Guide*, 3rd ed. Cambridge, Cambridge University Press.
- Megantara E (1989). Ecology, behavior and sociology of *Presbytis femoralis* in east central Sumatra. *Comparative Primatological Monographs* 2: 171–301.
- Meijaard E, Welsh A, Ancrenaz M, Nijman V, Wich SA, Marshall AJ (2010). Orangutan encounter rates from Wallace to the present suggest the species was once more abundant. *PLoS One* 5: e12042.
- Melisch R, Dirgayusa IWA (1996). Notes on the grizzled leaf monkey (*Presbytis comata*) from two nature reserves in West Java, Indonesia. *Asian Primates* 6: 5–11.
- Nekaris KAI (2001). Activity budget and positional behaviour of the Mysore slender loris: implications for slow climbing locomotion. *Folia Primatologica* 72: 228–241.

- Nijman V (1997). On the occurrence and distribution of *Presbytis comata* (Desmarest 1822) (Mammalia: Primates: Cercopithecidae) on Java, Indonesia. *Contributions to Zoology* 66: 247–256.
- Nijman V (2001). *Forest (and) Primates: Conservation and Ecology of the Endemic Primates of Java and Borneo*. Wageningen, Tropenbos Foundation.
- Nijman V (2004). Effects of habitat disturbance and hunting on the endemic Hose's leaf monkey *Presbytis hosei* (Thomas 1889) (Mammalia: Primates: Cercopithecidae) in East Borneo. *Contributions to Zoology* 73: 283–291.
- Nijman V (2005). Decline of the endemic Hose's langur *Presbytis hosei* in Kayan Mentarang National Park, East Borneo. *Oryx* 39: 223–226.
- Nijman V (2010). Ecology and conservation of the Hose's langur group (Colobinae: *Presbytis hosei*, *P. canicrus*, *P. sabana*): a review. In *Behavior, Ecology and Conservation of Indonesian Primates* (Gursky S, Supriatna J, eds.), pp 269–284. New York, Springer.
- Nijman V, Meijaard E (2008). Zoogeography of primates in insular Southeast Asia: species-area relationships and the effects of taxonomy. *Contributions to Zoology* 77: 117–126.
- Nijman V, van Balen S (1998). A faunal survey of the Dieng Mountains, Central Java, Indonesia: status and distribution of endemic primate taxa. *Oryx* 32: 145–156.
- Rowe N, Myers M (eds.) (2010). *All the World Primates*. <http://www.alltheworldsprimate.com> (accessed March 1, 2012).
- Ruhayat Y (1983). Socio-ecological study of *Presbytis aygula* in West Java. *Primates* 24: 344–359.
- Seyfarth RM, Cheney DL, Marler P (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210: 801–803.
- Siegel S (1956). *Non-Parametric Statistics*. New York, McGraw-Hill.
- Sokal RR, Rohlf FJ (1995). *The Principles and Practice of Statistics in Biological Research*. New York, Freeman & Co.
- Sterck EHM, van Hooff JARAM (2000). The number of males in langur groups: monopolizability of females or demographic processes. In *Primate Males* (Kappeler PM, ed.), pp 120–129. Cambridge, Cambridge University Press.
- Stott K, Selsor CJ (1961). Observations of the maroon leaf monkey in North Borneo. *Mammalia* 25: 184–189.
- Supriatna J, Manullang BO, Soekara E (1986). Group composition, home range, and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting Reserve, Central Kalimantan, Indonesia. *Primates* 27: 185–190.
- Tenaza RR, Fuentes A (1995). Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. *International Journal of Primatology* 16: 295–310.
- Tilson RL (1977). Social organization of simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. *Journal of Mammalogy* 58: 202–212.
- Tilson RL, Tenaza RR (1976). Monogamy and duetting in an Old World monkey. *Nature* 263: 320–321.
- Treves A (1999). Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology* 48: 113–126.
- Van Schaik CP (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120–144.
- Van Schaik CP, Hörstermann M (1994). Predation risk and the number of adult males in a primate group: a comparative test. *Behavioural Ecology and Sociobiology* 35: 261–272.
- Van Schaik CP, van Hooff JARAM (1983). On the ultimate causes of primate social systems. *Behaviour* 85: 91–117.
- Watanabe K (1981). Variations in group composition and population density in the two sympatric Mentawai leaf-monkeys. *Primates* 22: 145–160.
- Wheeler BC (2008). Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigrinus*. *Animal Behaviour* 76: 1465–1475.
- Wich SA (2002). *The Structure and Function of Thomas Langur Loud Calls*. PhD thesis, Utrecht University.
- Wich SA, Sterck EHM (2003). Possible audience effect in Thomas langurs (Primates; *Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology* 60: 155–159.
- Zuberbühler K (2000). Referential labeling in Diana monkeys. *Animal Behaviour* 59: 917–927.
- Zuberbühler K, Jenny D, Bshary R (1999). The predator deterrence function of primate alarm calls. *Ethology* 105: 477–490.