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Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk

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Abstract This study examines vigilance as a behavioural indicator of the importance of infanticide risk by comparing the infanticide avoidance hypothesis with the predation avoidance and mate defence hypotheses for wild Thomas's langurs (*Presbytis thomasi*) in Sumatra. We found that all individuals were more vigilant in situations of high predation risk, i.e. lower in the trees and in the absence of neighbours. Females were also more vigilant on the periphery of the group. However, there were variations in vigilance levels that could not be accounted for by the predation avoidance hypothesis. Males without infants showed higher levels of vigilance in areas of home range overlap than in non-overlap areas during the early phase of their tenure, strongly suggesting mate defence. In these areas of home range overlap where Thomas's langur groups can interact, males may attack females and infants, and so the infanticide risk for males and females with infants is likely to be high in these areas. Only females with infants, but not males with infants or females without infants, showed higher vigilance levels in overlap areas than in non-overlap areas; in addition, in overlap areas, females with an infant were more vigilant than females without an infant, while this was not the case in non-overlap areas. Both females and males with infants were more vigilant high in the trees than at medium heights in overlap areas but not elsewhere. These findings can only be explained by the infanticide avoidance hypothesis. In contrast to predator attacks, infanticidal male attacks come from high in the canopy, and only occur in overlap areas. There was a significant sex difference in vigilance, but males were only more vigilant than females without an infant, and not more vigilant than females with an infant. We conclude that vigilance varied mainly in relation to the risk of predation and infanticide. Mate competition only played a role for males during the early phase of their tenure. Predation risk seems to offer the best explanation for vigilance for all individuals in the absence of infants. Both predation risk and infanticide risk played a role for females and males with infants.

Key words Vigilance · Predation · Mate defence · Infanticide · Thomas's langurs · *Presbytis thomasi*

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Introduction

Scanning the environment for predators is often reported to be an important function of vigilance (Vine 1971; Pulliam 1973; McNamara and Houston 1992; Roberts 1996), with predation regarded as the main factor promoting group living in primates (Alexander 1974; van Schaik 1983; Terborgh and Janson 1986; Dunbar 1988). More animals mean more eyes and ears to detect danger and more individuals to 'confuse' the predator (Williams 1966; van Schaik et al. 1983; Landeau and Terborgh 1986). A predator's chances of success are quite slim if the prey detects the predator before it can attack (Caro 1986). The probability of early detection increases greatly as group size increases, provided group members can quickly communicate the presence of a predator (Pulliam and Caraco 1984). Many researchers have reported a reduction in individual vigilance with increasing group size (review: Elgar 1989; Roberts 1996). Furthermore, individuals were found to be more vigilant in positions of higher predation risk: exposed areas on the ground, exposed branches in the canopy, at the periphery of the group, and with less neighbours around (Hamilton 1971; Lipetz and Bekoff 1982; de Ruiter 1986; Roberts 1988; van Schaik and van Noordwijk 1989; Cords 1990; Bednekoff and Ritter 1994; Burger and Gochfeld 1994; Rose and Fedigan 1995).

Mate defence is very common whenever females can be monopolised by males (van Hooff and van Schaik 1992). The influence of mate defence on male vigilance has been reported in several studies (Roberts 1988; Baldellou and Henzi 1992; Rose and Fedigan 1995; Gould et al. 1997). In addition, vigilance can also serve a social purpose reflecting, for example, within-group competition for food (e.g. Keverne et al. 1978; Waite 1987; Caine and Marra 1988).

Research on primates has increasingly shown that conspecifics, especially adult males, can also "prey on" (attack and kill) group members. Since Sugiyama (1965) first reported infanticide by male Hanuman langurs, there have been reports of many other primate species, in which males may kill infants they are unlikely to have sired (review: Hausfater and Hrdy 1984; Struhsaker and Leland 1987; Parmigiani and vom Saal 1994). Therefore, males could influence the distribution of females by the use of infanticide, and females could associate with one particular male in order to reduce this risk (Hrdy 1979; Hausfater and Hrdy 1984; Smuts and Smuts 1993; Brereton 1995; Clutton-Brock and Parker 1995; van Schaik 1996; van Schaik and Kappeler 1997; Sterck et al. 1997; but see Bartlett et al. 1993). Thus, female distribution is influenced by both predation risk and infanticide risk. Because of the extremely high costs of infant loss in terms of reproductive effort, it is expected that, in species with a potential risk of infanticide, this risk will be reflected in both male and female behaviour. This study investigated infanticide risk as a fourth hypothesis to explain patterns of vigilance, in wild Thomas's langurs (*Presbytis thomasi*).

Thomas's langurs

Thomas's langurs live in comparatively small groups with one to six females per group and typically one breeding male. All-male bands (AMBs) and solitary males have also been observed. Both males and females disperse from their natal groups; female secondary dispersal is also common (Sterck 1997; Steenbeek 1999), and the timing of female dispersal may be influenced by infanticide risk (Sterck 1997). Social groups have a limited life-span (Sterck 1997), Steenbeek (1999) describes that most of the time several females associate with a new male and thus form a new group, in which females usually reproduce.

There is no indication of any birth synchrony. Average male tenure lasts about 70 months and ends when all females have left the male in favour of a new male. Almost all females leave the male in the last year of his tenure. Aggressive take-overs are not common.

Adult females only show interest in extra-group males during the early phase of male tenure (before the first infant is born), or before they leave the breeding male during the late phase of his tenure (Steenbeek 1999). Therefore, the infants in a resident male's group are probably his own, although this is not known for sure. Infanticidal attacks by extra-group males and mortally wounded infants have been observed. Sterck (1997) observed one indirect case, where male-female aggression was witnessed and, later, a mortally wounded infant was found. Steenbeek (1996; 1999) witnessed one direct attack, after which the infant died, one indirect case, similar to the one described above, found one dead infant with canine wounds in the belly, and saw several attacks where the resident male and/or the mother could prevent harm to the infant, or where the infant recovered from wounds.

Home ranges of neighbouring groups partly overlap, both with other male + female groups and AMBs. The percentage of overlap ranges from 17 to 64% and corresponds with the time a group spends in the overlap area (this paper). Therefore, it can be assumed that familiarity with the habitat is similar for non-overlap and overlap areas. In overlap areas, groups interact with other groups or males. Between-group interactions can be neutral, but males also chase other individuals. Two types of interactions between groups can be distinguished: (1) groups approach to within 50 m of each other – this is defined as a "group encounter"; (2) males can silently approach a group and suddenly attack the individuals – this is defined as a "male attack". Infanticidal attempts in our Thomas's langurs have only been observed during male attacks, which vary in frequency from 0 to 0.21 per day during the middle of the tenure (Steenbeek 1999). Females never participate in aggressive group encounters, but they do defend their infant when it is being attacked by an extra-group male (Steenbeek 1999). Males have larger canines than females but there seems to be no sexual dimorphism in body size (Sterck 1997).

Dominance relationships are weakly expressed (inside food patches) or not apparent (outside food patches), but the adult breeding male is always dominant to all other group members (Sterck and Steenbeek 1997). Because the patterns of aggression described above offer no evidence that food competition is important, neither within and certainly not between groups, we will concentrate on three hypotheses to explain vigilance behaviour in Thomas's langurs: predation risk, mate defence, and infanticide risk. Table 1 summarises the predictions of the three hypotheses for the occurrence of vigilance relative to local environmental factors: height from the ground, position within the group, number of neighbours, and the presence of the group in areas of the home range which overlap with other langur groups.

The predation risk hypothesis predicts that vigilance levels in Thomas's langurs will be higher where the predation risk is expected to be higher: close to the ground because most predators are terrestrial; at the periphery of the group, compared with the centre; and with few neighbours around. Whether a group is in an area of overlap or non-overlap with other groups should make no difference to vigilance levels, because we have no reasons to assume that the habitat and familiarity with it differ in relation to overlap (see Table 1). The

Table 1 Predictions of the three hypotheses for greater vigilance behaviour in relation to four (*1–4*) local environmental factors, (*5*) sex differences, and (*6*) differences between females with and without infants

	Predation avoidance (males and females)	Mate defence (males only)	Infanticide avoidance	
			Males with infant(s)	Females with infant(s)	Males and females without infant(s)
(1) Height from the ground	Low > high	–	–	–	–
(2) Position in the group	Periphery > centre	–	–	Periphery > centre	–
(3) Number of neighbours	Few > more	–	–	Few > more	–
(4) Overlap versus non-overlap	–	Overlap > non-overlap	Overlap > non-overlap	Overlap > non-overlap	–
(5) Sex difference	Possible	Males > females		Possible	
(6) Difference between females with and without infants	Whole home range: with infant > no infant	–		Only overlap areas: with infant > no infant	

mate defence hypothesis predicts that resident male Thomas's langurs will be more vigilant than females (irrespective of the presence of infants), mainly in areas where they meet extra-group males, i.e. in overlap areas (see Table 1). The infanticide avoidance hypothesis predicts that individuals with infants (both females and resident males) will be more vigilant in overlap areas than in non-overlap areas (Table 1). Furthermore, in these overlap areas, individuals with infants are expected to be more vigilant than individuals without infants. A special case, a group where the adult resident male had suddenly disappeared (Steenbeek 1996), allows for an additional analysis. We can compare vigilance levels before and after the disappearance of the male. We assume that after the disappearance of the resident male, the infanticide risk is extremely high because there is no male to protect the infants. We will try to recognise other conditions which allow differentiation between the predation and infanticide avoidance hypotheses.

Sex differences

Males are reported to be more vigilant than females in several species (Bertram 1980; Gautier-Hion 1980; Cheney and Seyfarth 1981; de Ruiter 1986; Rasa 1989; van Schaik and van Noordwijk 1989; Fragaszy 1990; Baldellou and Henzi 1992; Burger and Gochfeld 1994; Rose and Fedigan 1995; Gould et al. 1997; but see Elgar 1989). van Schaik and van Noordwijk (1989) have suggested that if adult males are better at detecting predators, other individuals may choose to associate with them to increase their safety.

Under the infanticide avoidance hypothesis, one would, at first sight, expect females with an infant to show similar or higher levels of vigilance than males. However, such a difference might disappear due to constraints on vigilance preferentilly affecting females with an infant (e.g. eating, monitoring for food and/or the infant), and males may be extra-vigilant in support of females with infants in order to detect intruding males. So, only under the mate defence hypothesis is a sex difference expected, while it may occur under the predation and infanticide avoidance hypotheses. In other words, a sex difference alone does not discriminate between hypotheses.

Methods

Study area and subjects

This study was conducted at the Ketambe Research Station (3°41′ N, 97°39′ E), Gunung Leuser National Park, situated in Northern Sumatra, Indonesia. The study area, approximately 200 ha, mainly consists of undisturbed primary rain forest (Rijksen 1978; van Schaik and Mirmanto 1985).

The study subjects were wild Thomas's langurs. Potential predators for this species are the python (*Python reticulatus*), the golden cat (*Felis temminckii*), the clouded leopard (*Neofelis nebu-*

losa), and the Sumatran tiger (*Panthera tigris*). These predators are active mainly on the ground and in the understory of the trees. There are no large raptors able to capture adult monkeys (van Schaik and van Noordwijk 1985), but the langurs sometimes give alarm calls for eagles, which are thought to be able to capture infants (Sterck 1996; R. Steenbeek personal observation). Both males and females give alarm coughs when danger is perceived, but only the male makes a long-distance vocalisation (Steenbeek and Assink 1998).

Data were collected on 14 male + female groups, and 5 AMBs. The results contain data from 14 adult resident males, 27 adult females and 7 adult males in AMBs. Because 20 of these 27 adult females transferred from one male to another during this study, a given female may be represented in more than one group. Table 2 shows the group composition of the study groups. When tests concern "females with an infant", the sample only includes females with infants young enough to be potential infanticide victims, i.e. infants younger than 16 months. When the term "extra-group male" is used, it means any male from outside the group: from another male + female group, from an AMB, or a solitary male.

Data collection

Data were collected under the responsibility of Romy Steenbeek (RS) (1993–1995), and Amanda H. Korstjens (1996), by ten different observers. Groups were mostly followed from dawn (when the monkeys left the sleeping tree) until dusk (when the monkeys entered the sleeping tree). Data on individuals were collected with the focal animal method (instantaneous sampling; Martin and Bateson 1986). Every minute, on the minute, the activity, height (in 5-m classes), number of neighbours within 5 m (0, 1, 2, > 2), and position in the group (central or peripheral) of the focal animal were noted. An individual was said to be on the periphery of the group when it did not have group members on one side. Vigilance was measured in terms of the scanning movements of a focal animal. Because it was impossible to reliably observe what the animal was looking at in a tree crown, scanning was defined simply as a head movement of at least 45°, in any direction. Thus, for every focal minute, we noted whether the focal animal had performed either one or more scans, or none (one-zero sampling method; Martin and Bateson 1986). Focal samples with a maximum of 15 min were evenly distributed through the day, and individuals were sampled in a predetermined sequence. If the next focal individual could not be found, the observer was allowed to move on to the next. We attempted to collect focal samples of 15 min before switching to the next animal, but an animal could move out of sight before the 15 min had passed. Such focal records were kept and used, unless the focal sample had lasted less than 3 min. A group was followed for a number of days until the sum of these 15-min focals had exceeded 400 min per adult female. Because adult males could temporarily leave the group, a male was continuously observed for at least 2 consecutive days until a minimum of 600 focal minutes was attained. Thus, one focal period of one group consisted of at least 600 min for the adult male and at least 400 min for every adult female. We collected several focal periods for most groups. In this paper we used a total of 770 h of focal data.

The daily travel route was plotted on a map. Because of seasonal variation in ranging patterns, only maps for the same season were used to determine overlap between groups.

Table 2 Composition of the study groups

Group	Adult males	Adult females	Juveniles	Infants	Total
B2	1	3	3	3	10
B3	1	3	1	0	5
B4	1	6	0	0	7
J1	1	3	5	3	12
J2	1	4	0	0	5
M1	1	3	3	3	10
M2	1	4	1	0	6
M3	1	5	0	0	6
K1	1	4	7	1	13
K2	1	6	0	0	7
N	1	1	1	1	4
A1	1	3	2	1	7
L1	1	2	3	1	7
LR	1	4	0	1	6

Data analysis

Vigilance levels were calculated as the percentage of all 1-min intervals during which one or more scans occurred (Martin and Bateson 1986). One-zero sampling does not give an unbiased estimate of duration or frequency, therefore, we will use the term "vigilance level" or just "vigilance".

The definition of scanning behaviour implies that during feeding, when animals move to search and process food, levels approached 100%. Furthermore, scanning for food or for other reasons could not be distinguished. Because differences in individual feeding times would bias an analysis including feeding minutes, and because the purpose of this paper is to investigate the possible influence of infanticide risk, and not food competition, the analysis only concerns focal minutes during which the individual was not feeding. The total of non-feeding minutes per focal period varied from 200 to 278 min for females and from 279 to 697 min for males. When individuals were not feeding, the main activity was resting. Activities such as moving, grooming or other social behaviour were all below 5% of the time budget. Vigilance levels were calculated for different heights (classes: 0–10 m, 10–20 m, > 20 m), different number of neighbours (0, 1, 2, > 2; within 5 m), different positions in the group (centre vs periphery), and different areas (overlapping vs non-overlapping with areas of other groups). When an individual had less than 25 min in one of these classes, the data point was omitted from the analysis. There is a possible source of error when data for arboreal monkeys are collected in the field: when comparing behaviours at different heights, one should take into account that lower rates of behaviour at greater heights could be becausethese are more easily overlooked. However, this bias, thought to affect all individuals similarly, does not seem to play a major role here, because for certain classes of animals, we did measure an increase in vigilance levels high in the trees.

Observations were only made after observers had been trained to reach inter-observer reliability (IOR) indices over 90% with RS. These IOR indices were measured again after 5 months of observation. Unfortunately, we found systematic variation in scoring vigilance between different observers. Although this variation was within the 10% IOR limits, some observers scored systematically lower, while some scored systematically higher than RS. Therefore, and because one focal period of one group was always collected by one observer, we decided to analyse the data in a conservative way: For every dataset, the analysis was carried out pair-wise, for every individual within one focal period and, as a result, also within one observer (one-tailed when there was a clear hypothesis, Wilcoxon signed-ranks test; Siegel and Castellan 1988). For example, the dataset of females without an infant contains one focal period for every possible adult female at a moment when she had no dependent infant in the group. In the analysis, these females will only be compared with themselves (within one observer). The dataset of females with a dependent infant consists largely of the same females, but measured at different times and in most cases by a different observer. When there was more than one possible focal period for one individual in one dataset, we choose the one that allowed a comparison between overlap and non-overlap. This seldom left more than one focal period per individual, because overlap could only be calculated if all neighbouring groups were observed in the same season. The total dataset (all males + females) comprised the dataset for males + most of the dataset for females with an infant ($n = 13$ females) + the data for females without an

infant who were not included in the females-with-infant list ($n = 13$ females). A drawback of the pair-wise testing to avoid observer biases is that multivariate tests, comparing between groups for influences such as group size, could not be carried out. Multiple tests on one dataset were corrected with a Bonferroni procedure (Hochberg 1988).

Every individual animal occurs only once in each of the datasets, testing the factors height, position in the group, number of neighbours and overlapping home range area. Because we collected several focal periods for most individuals, the same male or female can occur in the dataset for individuals without infants [they had no infant(s) at that time], as well as in the dataset for individuals with infants [they had infant(s) at the time].

To test for sex differences, every resident male was compared with the average of the adult females in his group. In this case, the same female could be represented in more than one group, but variation among females was relatively low and the average vigilance levels were calculated assuming that groups were independent. Since the same observer collected the data from the group without a male before and after his departure, the two situations could be compared.

Active daylength was defined as the time between leaving a sleeping tree in the morning and entering a sleeping tree in the evening. Because active daylength varied between 661 and 748 min between focal periods, it would not be correct to compare percentages of time spent feeding, and time spent feeding was expressed in minutes per day.

Results

Height above the ground

Table 3 shows median, minimum and maximum values of vigilance levels at different height classes, while Fig. 1 shows the median and quartile values of the differences between classes. The overall analysis shows that vigilance levels were significantly higher at 0–10 m than at 10–20 m (Wilcoxon signed-ranks test: $n = 34$, $z = -4.573$, $P < 0.0001$, corrected for two tests), and also significantly higher at 10–20 m than at >20 m (Wilcoxon signed-ranks test: $n = 38$, $z = -2.371$, $P < 0.01$, corrected for two tests).

When males and females were analysed separately, adult males showed significantly higher vigilance levels at 0–10 m than at 10–20 m (Wilcoxon signed-ranks test: $n = 12$, $T^+ = 77$, $P < 0.005$, corrected for two tests), while there was no difference between the height classes 10–20 m and >20 m ($n = 12$, $T^+ = 42$, n.s.). Both females with an infant and females without an infant also showed significantly higher vigilance levels at 0–10 m than at 10–20 m (Wilcoxon signed-ranks test: $n = 14$, $T^+ = 98$, $P < 0.01$, and $n = 23$; $z = -3.984$; $P < 0.0001$ respectively, corrected for two tests), and both classes of females were also significantly more vigilant at 10–20 m than at >20 m (Wilcoxon signed-ranks test: $n = 15$, $T^+ = 93$, $P < 0.05$, and $n = 26$, $z = -3.099$, $P = 0.001$, respectively, corrected for two tests).

Position in the group

Table 3 shows median, minimum and maximum values of vigilance levels at different positions within the group, while Fig. 2 shows the median and quartile values of the differences between classes. The overall analysis shows that vigilance levels were significantly higher at the periphery of the group than in the centre (Wilcoxon signed-ranks test: $n = 36$, $z = 3.700$, $P < 0.001$).

When males and females were analysed separately, position in the group did not influence adult male vigilance levels (Wilcoxon signed-ranks test: $n = 11$, $T^+ = 47$, n.s.). Both females with infants, and females without infants showed significantly higher vigilance levels when they were at the periphery of the group than in the centre (Wilcoxon signed-ranks test: $n = 13$, $T^+ = 85$, $p < 0.01$, and $n = 25$, $z = -3.915$, $P < 0.0001$, respectively).

Number of neighbours

Table 3 shows median, minimum and maximum values of vigilance levels with a different number of neighbours, while Fig. 3 shows the median and quartiles of the differences between classes. The overall analysis shows that vigilance levels were significantly higher when individuals had no neighbours than when they had 1 neighbour (Wilcoxon signed-ranks test: $n = 38$, $z = -4.010$, $P < 0.001$, corrected for three tests). There was no significant difference between the classes 1 and 2 neighbours (only adjacent classes were tested; Wilcoxon signed-ranks test: $n = 33$, $z = -2.037$, $P = 0.06$, corrected for three tests), but vigilance levels were also significantly higher when individuals had 2 neighbours than when they had >2 neighbours (Wilcoxon signed-ranks test: $n = 24$, $z = -2.357$, $P < 0.05$, corrected for three tests).

When males and females were analysed separately, both adult males and females with an infant showed significantly higher levels of vigilance when they had 0 neighbours than when they had 1 neighbour (Wilcoxon signed-ranks test: $n = 12$, $T^+ = 73$, $P < 0.01$, and $n = 16$, $z = -3.154$, $P < 0.01$, respectively, corrected for three tests). Vigilance levels for both males and females with an infant did not differ for the other two neighbour comparisons (Wilcoxon signed-ranks test; males, 1–2 neighbours, $n = 10$, $T^+ = 29$, n.s., and $2 \rightarrow 2$ neighbours, $n = 7$, $T^+ = 24$, n.s.; females with an infant, 1–2 neighbours, $n = 16$, $z = -1.706$, n.s., and $2 \rightarrow 2$ neighbours, $n = 10$, $T^+ = 37$, n.s., corted for three tests). Females without an infant also showed significantly higher vigilance levels when they had 0 neighbours than when they had 1 neighbour (Wilcoxon signed-ranks test: $n = 26$, $z = -2.553$, $P < 0.01$, corrected for three tests), but in addition, vigilance levels were significantly higher when they had 1 neighbour than when they had 2 neighbours ($n = 21$, $z = -1.851$, $P < 0.05$, corrected for three tests), and again higher when they had 2 neighbours than when they had >2 neighbours ($n = 16$, $z = -3.206$, $P < 0.001$, corrected for three tests).

Table 3 Median, minimum and maximum values of vigilance levels under different environmental factors (*n* number of individuals; *Median*, *Minimum* and *Maximum* values refer to the percentage of minutes out of the total minutes within one class during which scanning behavior occurred)

Factor	All individuals			Males			Females with an infant			Females without an infant		
	n	Median (%)	Minimum–Maximum (%)	*n*	Median (%)	Minimum–Maximum (%)	*n*	Median (%)	Minimum–Maximum (%)	*n*	Median (%)	Minimum–Maximum (%)
Height												
0–10 m.	34	100	83.4–100	12	99.7	93.1–100	14	94.5	83.4–100	23	100	87.8–100
10–20 m.	38	86.4	73.1–100	12	86.3	78.0–98.3	16	86.7	70.0–97.1	26	83.7	71.8–100
>20 m.	38	83.2	50.7–100	12	88.6	50.7–96.7	15	76.9	51.5–100	26	75.4	53.3–100
Position												
Center	36	84.9	67.1–99.4	11	86.5	69.0–95.5	13	82.1	74.9–94.6	26	80.0	67.1–99.4
Periphery	36	92.8	74.0–100	11	92.5	81.1–100	13	93.8	79.1–100	25	93.7	74.0–100
Neighbours (<5 m)												
0 neighbors	38	93	71.8–100	12	93.3	82.1–98.9	16	91.5	75.3–99.3	26	93.5	71.8–100
1 neighbor	38	85.7	62.2–100	12	85.0	69.2–98.4	16	85.5	59.4–95.6	26	86.0	61.0–100
2 neighbors	33	78.8	46.7–100	10	89.3	53.2–100	16	76.4	45.6–100	21	80.1	46.7–100
>2 neighbors	25	75.0	45.0–100	8	78.5	69.8–100	10	76.9	45.0–91.7	18	66.2	44.4–80.9
Male												
<5 m							13	80.3	52.2–91.7	22	74.4	52.2–100
>5 m							13	87.3	69.7–100	22	76.6	57.7–100
Overlap												
Overlap[a]	Early phase of tenure			7	92.8	80.9–100						
Non-overlap[a]	Early phase of tenure			7	87.7	73.0–97.5						
Overlap	35	97.3	55.6–100	10	97.2	78.9–100	13	100	85.9–100	25	89.3	55.6–100
Non-overlap	35	90.3	48.0–100	10	97.7	83.5–100	13	85.8	50.0–100	25	86.7	48.0–100

[a] Measurement during the early phase of male tenure, when there were no infants in the group

Proximity to the adult male

When the effect of the proximity to the adult male was analysed, both females with and females without an infant were significantly less vigilant when the adult male was within 5 m than when he was further away (Wilcoxon signed-ranks test: $n = 14$, $T^{+} = 100$, $P < 0.01$, and $n = 24$, $z = -2.601$, $P < 0.01$, respectively, two-tailed). However, because this effect could be caused by any neighbour, irrespective of its age or sex, the analysis was repeated, but only for minutes when the female had at least one neighbour. By comparing minutes with the adult male as a neighbour with minutes with other individual(s) as a neighbour, we more specifically tested the effect of the presence of the adult male himself. Table 3 shows median, minimum and maximum values of vigilance levels for females when the male is present within 5 m or not, while Fig. 3 shows the median

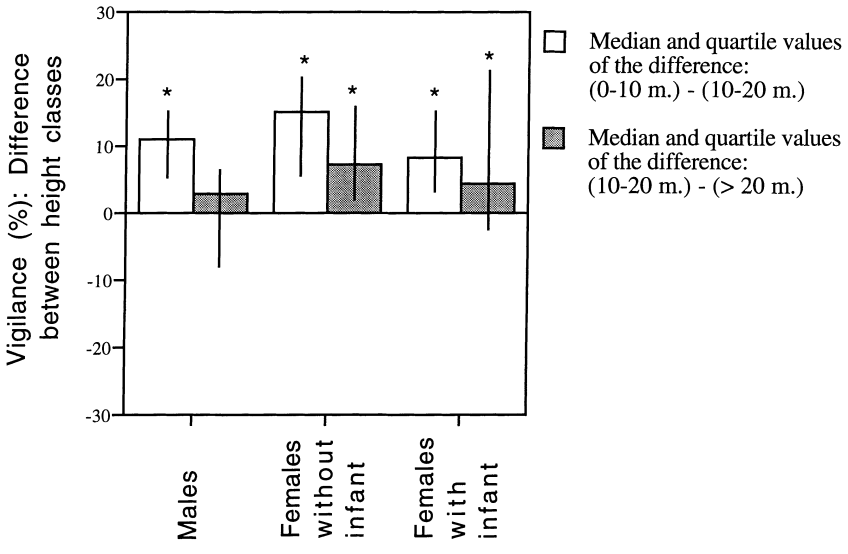

Fig. 1 The difference in vigilance levels between height classes. *Bars* represent the median value and *lines* represent the quartile values. Significant differences between the two classes are marked with an *asterisk* (see text for details)

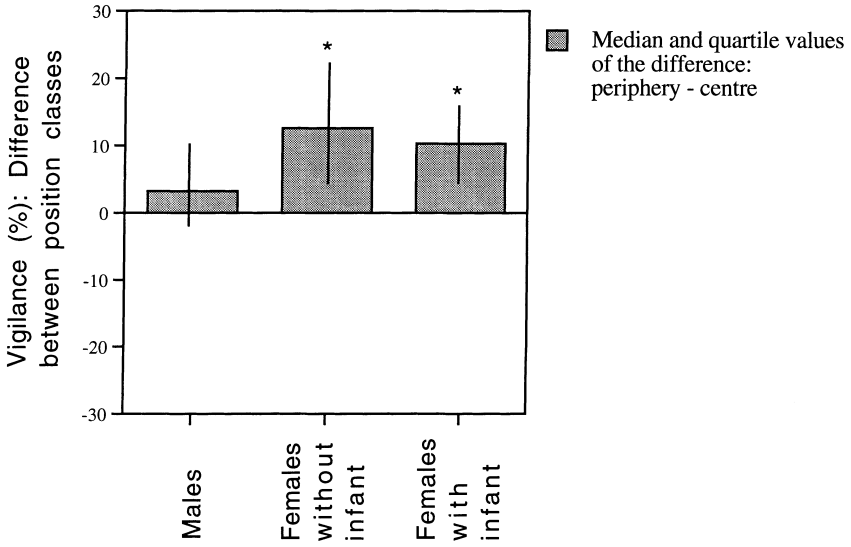

Fig. 2 The difference in vigilance levels between positions in the group. *Bars* represent the median value and *lines* represent the quartile values. Significant differences between the two classes are marked with an *asterisk* (see text for details)

and quartiles of the differences between classes, after controlling for the presence of at least one neighbour. These results show that only females with an infant were significantly less vigilant when the adult male was present within 5 m (Wilcoxon signed-ranks test: $n = 13$, $T^{+} = 83$, $P < 0.01$, two-tailed), whereas females without an infant were not (Wilcoxon signed-ranks test: $n = 21$, $z = -0.713$, $P = 0.47$, two-tailed).

Overlap versus non-overlap in the home range

A preliminary analysis on home range overlap showed that during the middle of the tenure, the percentage of the home range which overlaps with other groups had a median value of 31.3% and varied from 16.7 to 63.9% ($n = 6$ groups). During the middle of the tenure, the percentage of time spent in overlap areas had a median value of 37.3% and varied from 26.3 to 57.5% ($n = 7$ groups). There was a significant positive correlation between the percentage of overlap and the time that groups spent in overlap areas ($n = 9$, including 3 groups during the early phase of the tenure; Spearman $r = 0.72$, $P = 0.03$).Therefore, it can be assumed that familiarity with the habitat is similar for non-overlap and overlap areas.

The overall analysis showed higher vigilance levels in overlap areas than in non-overlap areas (Wilcoxon signed-ranks test: $n = 30$, $z = 2.571$, $P < 0.01$), although when the sexes were tested separately, neither males nor females showed a significantly higher level of vigilance in overlap areas than in non-overlap areas (Wilcoxon signed-ranks test; males: $n = 12$, $T^{+} = 51$, n.s.; females with an infant: $n = 13$, $T^{+} = 52$, n.s.; females without an infant: $n = 26$, $z = -0.572$, n.s.).

We controlled for height, position and number of neighbours by analysing minutes at medium height, in the centre of the group (females only), and without

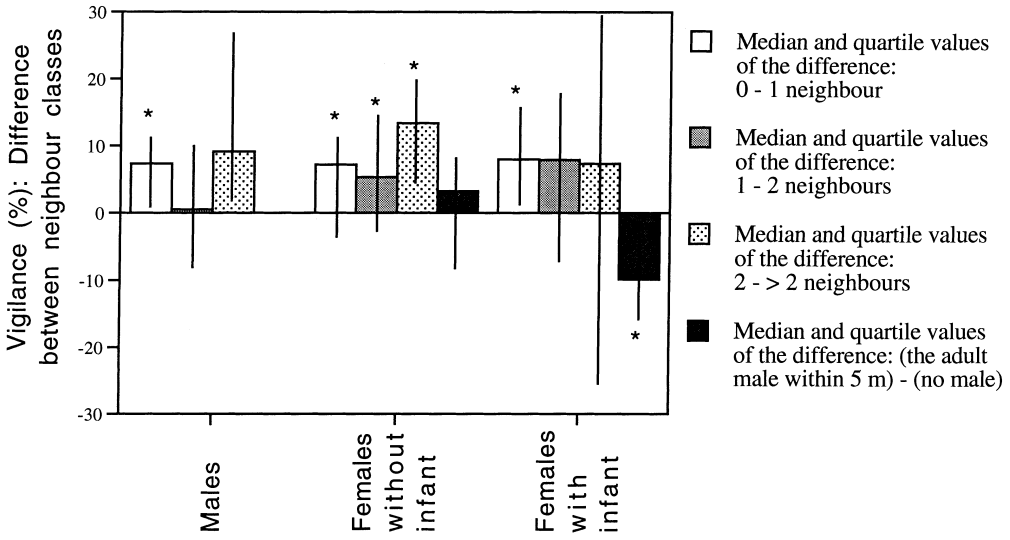

Fig. 3 The difference in vigilance levels between classes of neighbours. *Bars* represent the median value and *lines* represent the quartile values. Significant differences between the two classes are marked with an *asterisk* (see text for details)

neighbours. When there were too few minutes without neighbours we choose minutes with 1 neighbour. Table 3 shows median, minimum and maximum values of controlled vigilance levels in overlap and non-overlap areas, while Fig. 4 shows the median and quartiles of the differences between classes, after controlling for the environmental factors. We found the following significant differences. (1) Resident males during the early phase of their tenure (no infants yet) were more vigilant in overlap areas than in non-overlap areas (Wilcoxon signed-ranks test: $n = 7$, $T^+ = 28$, $P < 0.01$), but males with infants were not (Wilcoxon signed-ranks test, $n = 9$, $T^+ = 25$, n.s.). (2) Females with an infant were more vigilant in overlapping areas than in non-overlapping areas (Wilcoxon signed-ranks test: $n = 11$, $T^+ = 66$, $P < 0.001$), but females without an infant were not (Wilcoxon signed-ranks test: $n = 25$, $z = -01.019$, n.s.).

Sex difference

Table 4 shows median, minimum and maximum values of vigilance levels for males and females, while Fig. 5 shows the median and quartile values of the difference between males and females.

Table 4 shows that males were significantly more vigilant than females when the overall dataset was tested (Wilcoxon signed-ranks test: $n = 11$, $T^+ = 63$, $P < 0.01$). Table 4 further shows that males were significantly more vigilant than females in the centre of the group (corrected for two tests), and in overlap areas (corrected for two tests). There was a trend for males to be more vigilant than females above 20 m, and with 2 or > 2 neighbours.

Where we found a significant sex difference, we analysed the sex difference separately for females with an infant and females without an infant. Males were significantly more vigilant than females without an infant in the total dataset, in the centre of the group, and in overlap areas (Wilcoxon signed-ranks test: $n = 9$, $T^+ = 45$, $P < 0.01$; $n = 9$, $T^+ = 45$, $P < 0.01$; $n = 10$, $T^+ = 54$, $P < 0.01$, respectively, corrected for four tests). Males were never significantly more vigilant than females with an infant.

To test if males and females spent their time in a different way, we investigated the variable time spent feeding. Males spent significantly less time feeding than females (Wilcoxon signed-ranks test: $n = 12$, $T^+ = 75$, $P < 0.01$).

A comparison between females with and females without an infant

In the overall dataset, females with an infant were significantly more vigilant than females without an infant (Wilcoxon signed-ranks test: $n = 5$, $T^+ = 15$, $P < 0.05$). More specifically, females with an infant were significantly more vigilant than females without an infant in overlap areas (Wilcoxon signed-ranks test: $n = 5$, $T^+ = 15$, $P < 0.05$), whereas they were not in non-overlap areas (Wilcoxon signed-ranks test: $n = 5$, $T^+ = 14$, n.s.).

The group without a male

Data were subdivided into three different periods, as in Steenbeek (1996). Period 1 represents the normal situation before the adult male had disappeared (background phase). Period 2 represents the first 60 days after the adult male had disappeared (avoidance phase), and the third period represents the time when the females initiated friendly interactions with neighbouring extra-group males (period 3 + 4 of Steenbeek 1996). Although the

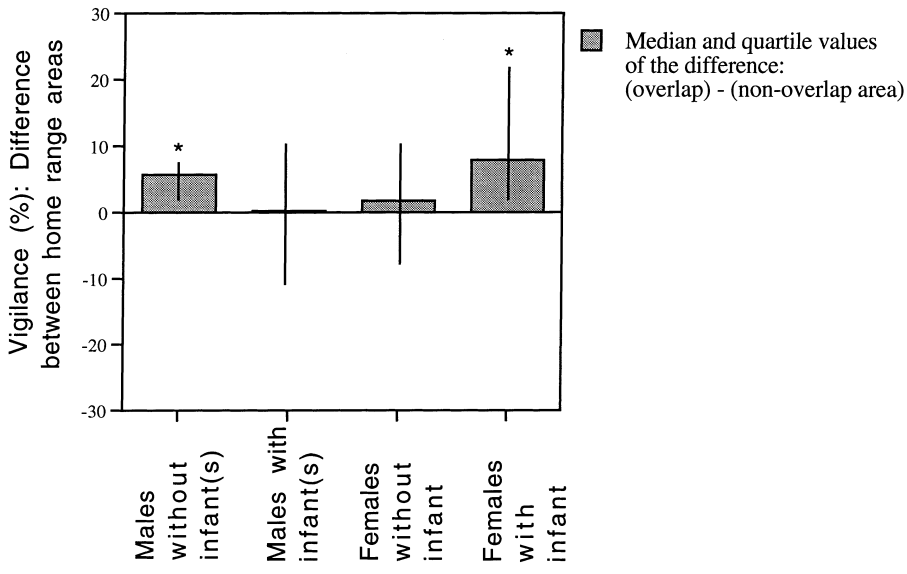

Fig. 4 The difference in vigilance levels between areas of the home range. *Bars* represent the median value and *lines* represent the quartile values. Significant differences between the two classes are marked with an *asterisk* (see text for details)

Table 4 Sex differences in vigilance levels under different environmental factors. *Median*, *Minimum* and *Maximum* values refer to the percentage of minutes out of the total minutes within one class during which scanning behavior occurred (*WSR* Wilcoxon signed-ranks test, *M* males, *F* females)

Factor	*n*	WSR test statistics	Difference	Males		Females	
				Median	Minimum–Maximum	Median	Minimum–Maximum
All data	11	$T^+ = 63$**	M > F	89.1	85.4–96.3	82.6	73.1–90.7
Height							
0–10 m.	10	$T^+ = 36.5$		99.3	93.1–100	97.9	88.3–100
10–20 m.	11	$T^+ = 48$		86.4	82.7–98.3	87.7	75.8–97.1
> 20 m.	11	$T^+ = 54$		89.8	50.7–96.7	74.5	58.8–100
Position							
Center	10	$T^+ = 53$**	M > F	88.1	84.4–95.5	80.9	71.7–88.2
Periphery	10	$T^+ = 29$		93.0	81.1–100	90.6	83.0–98.8
Neighbors							
0 neighbors	12	$T^+ = 52$		93.3	82.1–98.9	90.8	79.8–99.0
1 neighbor	12	$T^+ = 45$		84.9	69.2–98.4	84.2	62.0–93.1
2 neighbors	10	$T^+ = 45$		89.3	53.2–100	76.1	50.0–96.9
> 2 neighbors	7	$T^+ = 26$		82.0	69.8–100	73.5	52.8–85.8
Overlap							
Overlap	11	$T^+ = 58$*	M > F	91.3	81.2–99.4	85.1	67.8–92.3
Non-overlap	11	$T^+ = 38$		88.8	82.1–100	89.3	74.6–94.3
Feeding							
Min/day	12	$T^+ = 75$**	F > M	24.5	19.1–32.1	35.0	22.4–45.0

* $P < 0.05$; ** $P < 0.01$

sample size is too small for a statistical test, Fig. 6a shows that, overall, vigilance levels strongly increased for the three females with an infant and the one without after the adult male had disappeared, and that levels decreased again when females started to have friendly relationships with neighbouring males. Figure 6b shows about the same pattern, after controlling for height and number of neighbours.

Interestingly, average resting height decreased from period 1 to period 2 from 18.3 m to 10.8 m and increased again in period 3 to 13.4 m. The average number of neighbours decreased from period 1 to period 2 from 0.42 to 0.24 and increased again in period 3 to 0.6. Position in the group could not be compared over the three phases because it was not reliably scored at the beginning of the project. Overlap versus non-overlap could not be compared, because the females avoided other groups in the second period to such an extent that there were no data for normal overlap areas. In addition, during phases 2–4, males from neighbouring groups travelled through the whole home range of the group lacking a male, so the entire home range should be considered overlap (for details see Steenbeek 1996).

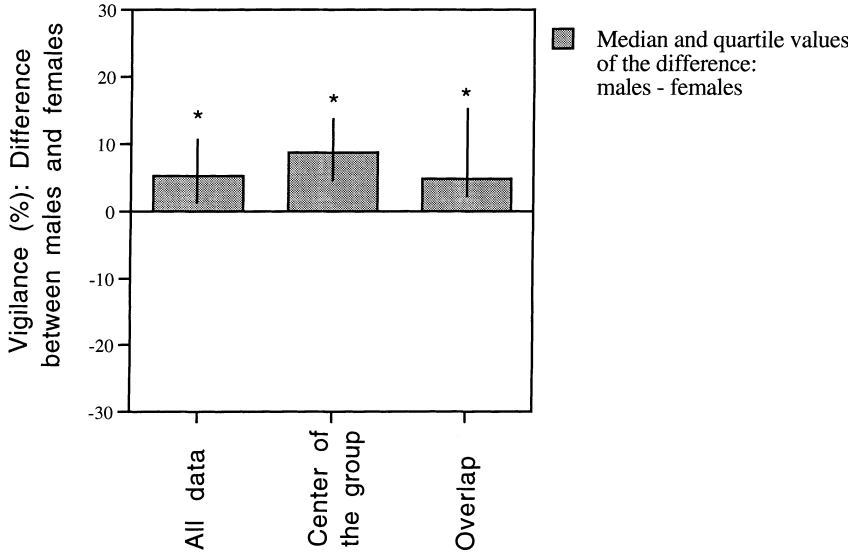

Fig. 5 Sex differences in vigilance levels. *Bars* represent the median value and *lines* represent the quartile values. Significant differences between the two classes are marked with an *asterisk* (see text for details)

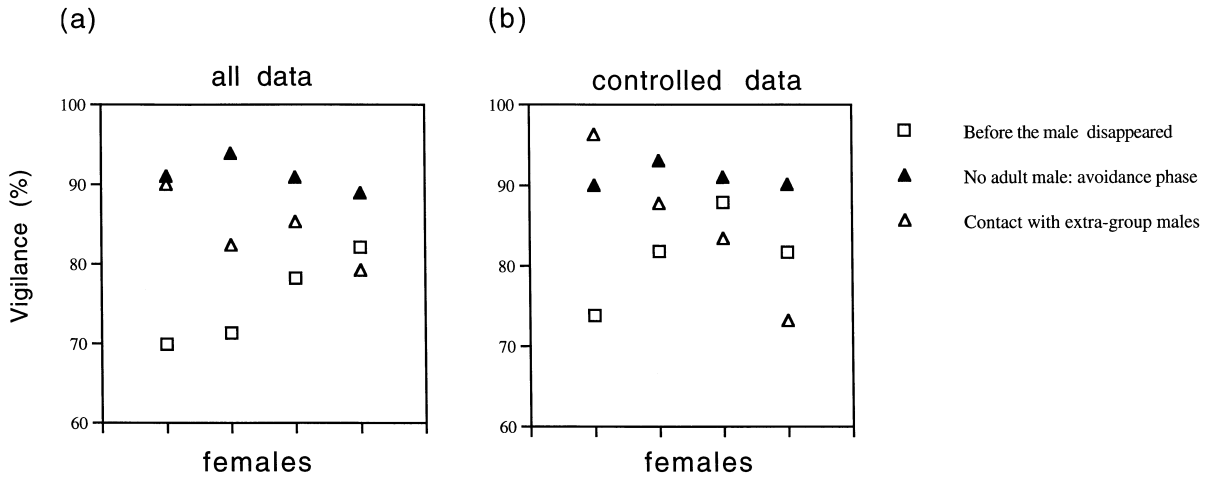

Fig. 6 The relation between the presence and absence of the adult male and vigilance levels in the group without a male: all data (**a**), and data controlled for height and number of neighbours (**b**). Every vertical trio of symbols (*one square*, *one open* and *one black triangle*) represents one female. The fourth female did not have an infant at the time

Predation avoidance as opposed to infanticide avoidance

It is possible that in the group without a male, females decreased their average resting height following the loss of the group's male in order to reduce the chance of being detected and attacked by extra-group males. If height influences the chance of being detected and consequently of being attacked, we expect a positive correlation between average height and attack rate. This effect should be most pronounced in situations where most or all group members suffer from these attacks, i.e. in AMBs and the group without a male. In AMBs, which experience significantly higher attack rates and wounds than male + female groups (Steenbeek 1999), there was a significant positive correlation between average height and the rate of being attacked ($n = 7$, $r = 0.79$, $P < 0.05$). Furthermore, adult AMB members were significantly more vigilant at 0–10 m than at 10–20 m (as was found for individuals in male + female groups), but they were also significantly more vigilant above 20 m than at 10–20 m (see Table 5). Our first set of analyses concerning height indicates that both sexes are most vigilant at low canopy heights (0–10 m), and that females are more vigilant at 10–20 m than at heights above 20 m. This is consistent with the predation avoidance hypothesis, i.e. this risk decreases with increasing canopy height. However, our observations for the group without a male and the extrapolation from AMBs suggest that the risk of being attacked by extra-group males (and the associated risk of infanticide) *increases* with canopy height. An additional analysis on the dataset of all groups was carried out in order to distinguish between these two height effects. The data were separated for males versus females, infants versus no infants and overlap versus non-overlap. For these eight data sets, we first analysed differences in vigilance levels between the height classes 0–10 m and 10–20 m. Table 5 shows that all individuals showed significantly lower levels of vigilance at 10–20 m than at 0–10 m, except for males with infants in their group in non-overlap areas (but four out of five males did show less vigilance). Second, we analysed differences between the height classes 10–20 m and above 20 m. Females with an infant and males with infant(s) in their group showed significantly *higher* levels of vigilance above 20 m than at 10–20 m, but only in overlap areas. Females without an infant showed significantly *lower* levels of vigilance above 20 m than at 10–20 m, irrespective of overlap (see Table 5), i.e. they confirmed to the overall pattern of decreasing vigilance with increasing height.

A comparison between vigilance levels at 0–10 m and > 20 m for both sexes with infants in the overlap area showed that there was no significant difference [males: $n = 5$ (1 tie), $T^{+} = 12$, n.s.; females: $n = 4$ because of 5 ties of 100%].

Discussion

Predation avoidance

As predicted under the predation avoidance hypothesis, we indeed found that vigilance levels were highest in those positions most sensitive to predation, such as low in the trees, at the periphery of the group (only for females), and in the absence of neighbours. For males and females with infant(s), vigilance levels were lower in the presence of one neighbour than when none were present, and for females without an infant, vigilance levels decreased as the number of neighbours increased.

Males were more vigilant than females, especially in the centre of the group. If males were simply more alert than females and if their vigilance was solely related to predation risk, then the sex difference would be expected at positions with the highest predation risk, i.e. close to the ground, at the periphery and with few neighbours around. At first sight, it appears that males are most in

Table 5 The relation between vigilance and height for males versus females, infants versus no infants, and overlap versus non-overlap areas: median values and test results (n* number of non-tied pairs used in the Wilcoxon signed-ranks test, *neg* decrease in vigilance from the first to the second height class, *pos* increase in vigilance from the first to the second height class)

Sex	Infant	Height class						Test results					
		0–10 m		10–20 m		> 20 m		0–10 m vs 10–20 m			10–20 m vs > 20 m		
		n	Median	n	Median	n	Median	n*	Statistics		n*	Statistics	
Non-overlap area													
Males	None	7	100	7	82.3	7	91.8	7	$T^+ = 28$**	neg	7	$T^+ = 23$	
Males	With	8	100	9	98.1	9	100	5	$T^+ = 12$		6	$T^+ = 12$	
Females	None	20	100	21	82.9	21	72.7	20	$z = -3.659$***	neg	20	$z = -6.061$**	neg
Females	With	11	100	12	93.2	11	76.9	10	$T^+ = 52$**	neg	11	$T^+ = 40$	
Overlap area													
Males	None	5	100	7	90.4	7	89.7	5	$T^+ = 15$*	neg	7	$T^+ = 16$	
Males	With	6	100	9	89.6	9	96.6	6	$T^+ = 21$*	neg	9	$T^+ = 42$**	pos
Females	None	18	100	23	85.8	21	75.0	18	$z = -3.576$***	neg	18	$z = -3.006$	neg
Females	With	11	100	12	82.3	10	100	10	$T^+ = 58$***	neg	10	$T^+ = 47$*	pos
AMB males		8	100	8	79.9	7	100	7	$T^+ = 28$**	neg	6	$T^+ = 28$**	pos

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

vigilant in circumstances where the predation risk is relatively low. However, when females were feeding on the ground, males were often observed a few meters above them scanning the environment. Poysa (1987), Boinski (1988), and van Schaik and van Noordwijk (1989) have pointed out that a reduction in time spent vigilant leaves more time to forage. Because females spent significantly more time feeding than males, it is possible that females benefit from male protection through vigilance while they feed. But the protection could still be against both predation and infanticide risk. Females with infants decreased vigilance levels in the proximity of the adult male, so this protection factor may be most important for females with infants.

Mate defence

Greater vigilance by males than by females is predicted by the mate defence hypothesis. Under this hypothesis it was also expected that males, but not females, would increase vigilance in areas of range overlap. However, we found that only males during the early phase of their tenure were more vigilant in overlap than in non-overlap areas. This may be related to female behaviour. Females may take a while to complete transfer to a new male, and are not continuously associated with him during the early phase of his tenure. Females sometimes copulated with extra-group males during the first few months after a new group was formed. Therefore, it seems that male vigilance is related to the interest that females have in extra-group males, which reflects mate competition. After females have given birth, they no longer seem interested in extra-group males.

The results support the predation avoidance hypothesis, but also suggest that vigilance by males that have just started a new group is at least partly directed toward mate defence.

Infanticide avoidance

Several patterns are consistent with both the predation avoidance and the infanticide avoidance hypotheses. Comparisons between overlap versus non-overlap areas, and between females with versus females without an infant enable us to distinguish between these two possible functions of vigilance. Two findings support the infanticide avoidance hypothesis. First, females with an infant showed higher vigilance levels in overlap areas than in non-overlap areas, whereas females without an infant did not. Second, in overlap areas, females with an infant were more vigilant than females without an infant, while this was not the case in non-overlap areas. Because predators are not expected to distinguish between overlap and non-overlap areas, these results are best explained by the infanticide avoidance hypothesis. In contrast, males with infant(s) in the group did not show higher vigilance levels in overlap areas compared

to non-overlap areas, which is not consistent with the infanticide avoidance hypothesis.

The finding that individuals with infants, but not individuals without infants, were more vigilant at heights >20 m than at 10–20 m in overlap areas again supports the infanticide avoidance hypothesis. The results are more conclusive for females than for males. Males are sometimes observed in a sentinel position, scanning the surroundings, so this finding could reflect both the risk of being seen high in the canopy (more likely for females) as well as an attempt to get a view of possible threats.

Sex differences

The detailed results on sex difference indicate that, except for the early phase of tenure, there may be no functional difference in vigilance between the sexes. Males were only more vigilant than females without infants, and did not differ significantly from females with infants. Furthermore, females with an infant were more vigilant than females without an infant. The sex differences are, therefore, due to relatively low vigilance levels of females without infants.

Differential effects of the three hypotheses

The results from the group without a male led to the prediction that the risk of being detected and possibly attacked by extra-group males, and hence the infanticide risk, can be decreased by resting lower in the canopy. We could confirm this in the analysis of the AMBs: they were attacked significantly more often at greater heights. Because most AMB members are wounded by resident males sooner or later, and because AMB members usually flee when they encounter a resident male (Steenbeek 1999), this result really seems to reflect the risk of being detected. Steenbeek (1996) suggested that predation risk did not influence female decisions in the group without a male, because after the adult male had disappeared females reduced group size by forming subgroups. The function of the subgroups was not clear. The most likely explanation is a conflict of interest. One of the subgroups stayed away from the borders of the home range, and travelled little. This subgroup contained a mother with an almost weaned male infant, one newly weaned juvenile female and a juvenile male. These are, except for the mother, the individuals most at risk in an attack. A possible interest of at least one of the subgroups may have been to avoid detection. So, in a situation where infanticide risk was extremely high, i.e. when there was no male to protect the infants, variation in vigilance was more strongly related to factors correlated with infanticide risk than variation in predation risk.

The results in Table 5 show that predation risk seems to be the main factor influencing vigilance at low heights, and remains the dominant factor for individuals without infants at other heights. However, in overlap areas, where there is a risk of being attacked, individuals with infants increase vigilance when moving from medium (10–20 m.) to high (>20 m.) heights. Raptors, able to capture infants only, are not expected to distinguish between overlap and non-overlap areas, so predation risk from aerial predators cannot account for this result. However, the chance of being detected by extra-group males, and hence the infanticide risk, is higher in overlap areas. Males in AMBs show the same vigilance pattern as individuals with infants, supporting the idea that individuals with infants are primarily vigilant for possible attacks by extra-group males at heights >20 m.

In conclusion, we can say that vigilance (when not feeding) varied mainly in relation to the risks of both predation and infanticide, except for males during the early phase of their tenure, when male mate competition also played a role. Predation risk offers the best explanation for vigilance for all individuals in the absence of infants. Both predation risk and infanticide risk played a role for females and males with infants, but the evidence seems stronger for females than for males. Predation risk offers the best explanation for vigilance at low heights throughout the whole home range, while the risk of being detected and possibly attacked by extra-group males offers the best explanation for vigilance high in the canopy (>20 m) in areas of overlap with other langur groups (i.e. where there is a risk of being attacked). Females with infants show reduced vigilance levels when the adult male is in nearby. These analyses strongly suggest that Thomas's langur groups are protective associations of females around a male (as suggested by van Schaik 1996; Sterck et al. 1997; van Schaik and Kappeler 1997) to reduce both infanticide and predation risk.

Vigilance can serve a variety of purposes, and infanticide avoidance should receive attention in other species. For example, in white-faced capuchins, male vigilance appears to be directed primarily toward males in other groups (Rose and Fedigan 1995; Gould et al. 1997). Furthermore, the alpha male who was assumed to have sired most of the offspring, was the most vigilant individual. One case of a male killing an infant was observed in white-faced capuchins (Rose 1994), and male take-overs are a source of mortality for infants in this species (Fedigan et al. 1996). The same holds for vervet monkeys, although the evidence for infanticide is indirect (Cheney 1981; Fairbanks and McGuire 1987; Isbell et al. 1990). Again, male vigilance was directed at extra-group males, and again the alpha male was the most vigilant individual (Baldellou and Henzi 1992). So, infanticide risk could be an additional factor explaining vigilance patterns in these species.

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References

Alexander RD (1974) The evolution of social behaviour. Annu Rev Ecol Syst 5:325–383

Baldellou M, Henzi SP (1992) Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. Anim Behav 43:451–461

Bartlett TQ, Sussman RW, Cheverud JM (1993) Infant killing in primates: a review of observed cases with specific reference to the sexual selection hypothesis. Am Anthropol 95:958–990

Bednekoff PA, Ritter R (1994) Vigilance in Nxai pan springbok, *Antidorcas marsupialis*. Behaviour 129:1–11

Bertram BCR (1980) Vigilance and group size in ostriches. Anim Behav 28:278–286

Boinski S (1988) Sex differences in the foraging behaviour of squirrel monkeys in a seasonal habitat. Behav Ecol Sociobiol 23:177–186

Brereton AR (1995) Coercion-defence hypothesis: the evolution of primate sociality. Folia Primatol 64:207–214

Burger J, Gochfeld M (1994) Vigilance in African mammals: differences among mothers, other females, and males. Behaviour 131:153–169

Caine NG, Marra SL (1988) Vigilance and social organization in two species of primates. Anim Behav 36:897–904

Caro TM (1986) The functions of stotting in Thomson's gazelles: some tests of the hypotheses. Anim Behav 34:663–684

Cheney DL (1981) Intergroup encounters among free-ranging vervet monkeys. Folia Primatol 35:124–146

Cheney DL, Seyfarth RM (1981) Selective forces affecting predator alarm calls of vervet monkeys. Behaviour 76:25–61

Clutton-Brock TH, Parker GA (1995) Sexual coercion in animal societies. Anim Behav 49:1345–1365

Cords M (1990) Vigilance and mixed-species association of some East African forest monkeys. Behav Ecol Sociobiol 26:297–300

Dunbar RIM (1988) Primate social systems. Crook Helm, London

Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol Rev 64:13–33

Fairbanks LA, McGuire MT (1987) Mother-infant relationships in vervet monkeys: response to new adult males. Int J Primatol 8:351–366

Fedigan LM, Rose LM, Avila RM (1996) See how they grow. Tracking Capuchin monkey (*Cebus capucinus*) populations in a regenerating Costa Rican dry forest. In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive radiations of neotropical primates. Plenum, New York, pp 289–307

Fragaszy DM (1990) Age and sex differences in the organisation of behaviour in wedge-capped capuchins (*Cebus olivaceus*). Behav Ecol 1:81–94

Gautier-Hion A (1980) Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. J Anim Ecol 49:237–269

Gould L, Fedigan LM, Rose LM (1997) Why be vigilant? The case of the alpha animal. Int J Primatol 18:401–414

Hamilton W D (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Hausfater G, Hrdy SB (1984) Infanticide: comparative and evolutionary perspectives. Aldine, New York

Hochberg Y (1988) A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75:800–802

Hooff JARAM van, Schaik CP van (1992) Cooperation and competition: the ecology of primate bonds. In: Harcourt AH, Waal FBM de (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 357–389

Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13–40

Isbell AL, Cheney DL, Seyfarth RM (1990) Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. Behav Ecol Sociobiol 27:351–358

Keverne EB, Leonard RA, Scruton DM, Young SK (1978). Visual monitoring in social groups of talapoin monkeys (*Miopithecus talapoin*) Anim Behav 26:933–944

Landeau L, Terborgh J (1986) Oddity and the 'confusion effect' in predation. Anim Behav 34:1372–1380

Lipetz VE, Bekoff M (1982) Group size and vigilance in pronghorns. Z Tierpsychol 58:203–216

Martin P, Bateson P (1986) Measuring behaviour. Cambridge University Press, Cambridge, UK

McNamara JM, Houston AI (1992) Evolutionarily stable levels of vigilance as a function of group size. Anim Behav 43:641–658

Parmigiani S, Saal FS vom (1994) Infanticide and parental care. Harwood, Chur

Poysa H (1987) Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. Behaviour 103:108–122

Pulliam HR (1973) On the advantages of flocking. J Theor Biol 38:419–422

Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size? In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 122–147

Rasa OA (1989) Behavioural parameters of vigilance in the dwarf mongoose: social acquisition of a sex-biased role. Behaviour 110:125–145

Rijksen HD (1978) A field study on Sumatran orang utans (*Pongo pygmaeus abelii*, Lesson 1827): ecology, behaviour and conservation. Veenman, Wageningen

Roberts G (1996) Why individual vigilance declines as group size increases. Anim Behav 51:1077–1086

Roberts SC (1988) Social influences on vigilance in rabbits. Anim Behav 36:905–913

Rose LM (1994) Benefits and costs of resident males to females in white-faced capuchins (*Cebus capucinus*). Am J Primatol 32:235–248

Rose LM, Fedigan LM (1995) Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. Anim Behav 49:63–70

Ruiter J de (1986) The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). Behaviour 98:240–258

Schaik CP van (1983) Why are diurnal primates living in groups? Behaviour 87:120–144

Schaik CP van (1996) Social evolution in primates: the role of ecological factors and male behaviour. Proc Br Acad 88:9–31

Schaik CP van, Kappeler PM (1997) Infanticide risk and the evolution of male-female association in primates. Proc R Soc Lond B 264:1687–1694

Schaik CP van, Mirmanto E (1985) Spatial variation in the structure and litterfall of a Sumatran rain forest. Biotropica 17:196–205

Schaik CP van, Noordwijk MA van (1985) Evolutionary effect of the absence of felids on the social organisation of the macaques on the island of Simeuleu (*Macaca fascicularis*). Folia Primatol 44:138–147

Schaik CP van, Noordwijk MA van (1989) The special role of male *Cebus* in predation avoidance and its effect on group composition. Behav Ecol Sociobiol 4:265–276

Schaik CP van, Noordwijk MA van, Warsono B, Sutriono E (1983) Party size and early detection of predators in Sumatran forest primates. Primates 24:211–221

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. Adv Study Behav 22:1–63

Steenbeek R (1996) What a maleless group can tell us about the constraints on female transfer in Thomas's langurs (*Presbytis thomasi*). Folia Primatol 67:169–181

Steenbeek R (1999) Female choice and male coercion in wild Thomas's langurs. PhD thesis, Utrecht University

Steenbeek R, Assink P (1998) Individual differences in male long-distance calls of wild Thomas langurs (*Presbytis thomasi*) Folia Primatol 69:77–80

Sterck EHM (1996) The langurs of Gunung Leuser National Park. In: Schaik CP van, Supriatna J (eds) Leuser: a sanctuary. Depok Yayasan Bina Sains Hayati, Indonesia, pp 280–293

Sterck EHM (1997) Determinants of female dispersal in Thomas langurs. Am J Primatol 42:179–198

Sterck EHM, Steenbeek R (1997) Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. Behaviour 134:749–774

Sterck EHM, Watts DP, Schaik CP van (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Struhsaker TT, Leland L (1987) Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, (eds) Primate societies. University of Chicago Press, Chicago, pp 83–97

Sugiyama S (1965). On the social change of Hanuman langurs (*Presbytis entellus*) in their natural condition. Primates 6:381–418

Terborgh J, Janson CH (1986) The socioecology of primate groups. Annu Rev Ecol Syst 17:111–135

Vine I (1971) Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. J Theor Biol 30:405–422

Waite TA (1987) Vigilance in the white-breasted nuthatch: effects of dominance and sociality. Auk 104:429–434

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton, NJ

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