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BRIEF REPORT

Possible Audience Effect in Thomas Langurs (Primates; *Presbytis thomasi*): An Experimental Study on Male Loud Calls in Response to a Tiger Model

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Recent research indicates that animal vocalizations can refer to objects in the outside world, and that call production may be controlled by the sender depending on the type of audience involved. Our research on wild male Thomas langurs (Primates: *Presbytis thomasi*) shows that these males call as a response to a tiger model when they are in a group, but do not call when they are solitary. This is the first experimental study on wild primates to demonstrate that the presence or absence of an audience influences calling behavior. Our results indicate that males in mixed-sex groups give more loud calls than solitary males when exposed to a predator model. This suggests that giving loud calls in response to predators is not purely a reflex and may be controlled in some way by the sender. Am. J. Primatol. 60:155–159, 2003.

Key words: Thomas langur; predation; possible audience effect

INTRODUCTION

Since Darwin's [1872] first study on the subject, the control over expression of emotion by humans has been contrasted with uncontrolled expressions by animals, including nonhuman primates. However, a number of studies do not support the view that emotional expression in animals is uncontrolled. These studies indicate that the likelihood that an individual will vocalize depends on the presence and identity of the listeners (i.e., whether the listener is male or female, kin or not, etc.)—the so-called ''audience effect'' [Sherman, 1977; Cheney & Seyfarth, 1985, 1990; Marler et al., 1986; Gyger et al., 1986]. Most detailed experimental work on the audience effect has been conducted in birds [Marler & Mitani, 1988], and primates have received little attention in this regard. However, it has been shown that the identity of the listeners affects call rates in captive vervet monkeys (*Cercopithecus aethiops*) [Cheney & Seyfarth, 1985], and anecdotal evidence suggests that in this species the presence of an audience affects call rates in wild individuals [Cheney & Seyfarth, 1990].

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In these types of studies, a subject is usually exposed in different social conditions to a predator model, such as a raptor in the bird experiments [Gyger et al., 1986] or a researcher wearing a surgical gown and mask and carrying a net in the vervet monkey case [Cheney & Seyfarth, 1985]. Examples of social conditions under which subjects are exposed to a predator model include a male being tested alone or with a mate [Gyger et al., 1986], and a mother being tested with related or unrelated offspring, as in the experiment by Cheney and Seyfarth [1985]. When the test subjects differ in their alarm calling response depending on the context, this is called an audience effect. The explanation of this difference is that in some species individuals give alarm calls to warn conspecifics (i.e., do not alarm call when solitary), and in some species, such as vervet monkeys, individuals are more likely to give alarm calls to warn related rather than unrelated conspecifics.

Our study subject was the medium-sized arboreal Thomas langur (*Presbytis thomasi*). This primate is endemic in the tropical rain forest of northern Sumatra, Indonesia [Sterck, 1997]. Thomas langurs live in one-male, multi-female groups (called mixed-sex groups), but solitary males also occur [Sterck, 1997]. Both males in groups and solitary males produce a so-called ''loud call'' [Steenbeek & Assink, 1998] that plays a role in intergroup communication [Wich et al., 2002a, b]. Loud calls are also given in reaction to the presence of predators, such as tigers (*Panthera tigris*) [Steenbeek et al., 1999]. Acoustical analyses have shown that loud calls emitted during between-group encounters and in response to a predator are very similar acoustically. However, loud calls given in response to groups that are far away appear to differ acoustically from calls in between-group encounters and calls in response to predators [Wich et al., 2003]. Two encounters of Thomas langurs with a tiger have been observed. On one occasion the langurs ascended to the canopy and moved in the opposite direction to that of the tiger. On the other occasion the females ascended and left, while the male followed the tiger over a short distance (S.A. Wich, personal observation, and S.E. Koski, personal communication). During each encounter the male (from different mixed-sex groups) gave two loud calls. The different grouping constellations provided an opportunity to study the audience effect for a wild primate in its natural habitat.

METHODS

Experiments were conducted in two study areas in the Leuser Ecosystem, northern Sumatra, Indonesia: Ketambe and Bukit Lwang. The Thomas langurs in Ketambe (3°41′N, 97°39′E) were studied continuously during 1988–2001, and all individuals of the study population were individually recognized and well habituated to the presence of human observers. The Ketambe area consists of primary tropical rain forest [Rijksen, 1978; van Schaik & Mirmanto, 1985]. At Ketambe a total of six males in six different mixed-sex groups, and four solitary males were tested. The Thomas langurs in Bukit Lawang (3°30′N, 98°6′) were studied in the early 1980s [Gurmaya, 1986] and have been studied by us since 1998. This area consists of a mosaic of primary and secondary forest with rubber plantations on its fringes [Gurmaya, 1986]. Six males in six different mixed-sex study groups, and three solitary males in this area are well habituated to the presence of humans because they encounter local farmers on a regular basis in the plantations. Data from these two populations were combined for the analyses.

Our experiments consisted of two parts. First, we aimed to establish that loud calls are produced in reaction to the presence of predators, and are not simply a reaction to novel objects of similar size and shape. To this end, mixed-sex groups

TABLE I. Number of loud calls in the experiments

Mixed-sex group males (n = 12)	Tiger skin	Blanket	Solitary males (n = 7)	Tiger skin	Blanket
Ketambe group 1	1	0	Ketambe male 1	0	0
Ketambe group 2	2	0	Ketambe male 2	0	0
Ketambe group 3	3	0	Ketambe male 3	0	0
Ketambe group 4	3	0	Ketambe male 4	0	0
Ketambe group 5	0	0	Bukit Lawang male 1	0	0
Ketambe group 6	1	0	Bukit Lawang male 2	0	0
Bukit Lawang group 1	3	0	Bukit Lawang male 3	0	0
Bukit Lawang group 2	2	0	Bukit Lawang male 4	0	0
Bukit Lawang group 3	2	0			
Bukit Lawang group 4	3	0			
Bukit Lawang group 5	2	0			
Bukit Lawang group 6	1	0			
Median (25th, 75th percentile)	2 (1, 3)	0 (0, 0)		0 (0, 0)	0 (0, 0)

were exposed to a fake tiger skin and a white cotton blanket with thin black, red, and green stripes. The fake skin and blanket were shown to the monkeys by a human observer carrying the skin or blanket over his shoulders and the rest of his body while walking on all fours. When one of the monkeys was observed to stare at the stimulus, the human observer carrying the fake skin or blanket slowly moved out of sight. Two other observers collected the behavioral data. Second, we examined whether the presence of an audience affected the production of loud calls by also exposing solitary males to the tiger skin and the blanket. For each experiment we recorded the number of loud calls produced, whether the mixed-sex group or solitary male ascended or descended the trees (vertical locomotion), and whether the mixed-sex group or solitary male moved in the direction of the observer with the stimulus (tiger skin or blanket) or not (horizontal locomotion). All experiments were conducted between 1998 and 2001. Groups were never exposed to more than one stimulus on the same day or on two consecutive days. Six of the mixed-sex groups and four solitary males were first exposed to the fake tiger skin and then to the blanket, whereas the other six groups and three solitary males were exposed to the opposite sequence. The order of stimulus presentation did not affect the results. The statistics were one-tailed, because we expected that the males would react more strongly to the fake tiger skin than the blanket, and that a male in a mixed-sex group would call, while the solitary males would remain silent.

RESULTS

The results of the first experiment on mixed-sex groups indicated that loud calls were produced as a reaction to a predator. The males produced significantly more loud calls in response to the fake tiger skin than to the blanket (Wilcoxon's signed-rank test: $P = 0.002$, $n = 12$ groups, Table I).

The monkeys were significantly more likely to ascend the trees after they were exposed to the tiger skin (11 of 12 cases) than after exposure to the blanket (five of 12 cases) (Fischer's Exact test: $P = 0.02$). In addition, the males were significantly more likely to retreat from the location of the tiger skin (10 of 12

cases) than from that of the blanket (four of 12 cases) (Fischer's Exact test: $P = 0.02$).

Each solitary male was exposed one time each to the fake tiger skin and the blanket (second experiment, n = 7 males). The number of loud calls produced by solitary males during these two occasions did not differ, because on both occasions the solitary males did not give any loud calls (Wilcoxon's signed-rank test: 7 ties, $P = 1.0$). Nevertheless, the solitary males tended to ascend the trees more often after they were exposed to the tiger skin (seven of seven cases) than after they were exposed to the blanket (four of seven cases) (Fischer's Exact test: $P = 0.10$). Similarly, they retreated significantly more often from the location of the fake tiger skin (seven of seven cases) than from that of the blanket (three of seven cases) (Fischer's Exact test: $P = 0.04$).

Although the behavioral responses (ascend/descend and move toward/away from the location of the stimulus) were similar for males in mixed-sex groups and solitary males, loud calls were only given to the fake tiger skin by group-living males (Mann-Whitney U-test: n1 = 12, n2 = 7, U = 3.5, $P = 0.0003$).

DISCUSSION

The results of the current experiments showed an effect of the presence or absence of an audience on call production by wild Thomas langur males. Solitary male Thomas langurs did not give loud calls when exposed to a predator model, whereas those in mixed-sex groups did. Even though the sample size for solitary males was fairly small (n = 7), we believe the results are solid, since all solitary males showed the same response (i.e., none of the solitary males gave any loud calls). These results are similar to those obtained in experiments with domestic chickens (*Gallus domesticus*), in which solitary males gave less alarm calls than when they were with conspecifics [Gyger et al., 1986]. They also agree with a previous study of wild vervet monkeys, in which it was observed that solitary males did not give alarm calls to predators [Cheney & Seyfarth, 1990]. However, there are two possible explanations for the difference between the loud-call behaviors of the mixed-sex group males and the solitary males. The first is that Thomas langur males can manipulate their response according to whether an audience is present or absent, and loud call production is likely under voluntary control [Marler & Evans, 1996]. The second is that solitary males may have adopted a cryptic antipredator strategy, and that therefore they refrain from giving loud calls. The latter explanation, however, seems unlikely in the case of Thomas langurs because solitary males do not hide or silently move away from the tiger skin—rather, they move away from the tiger skin with as much jumping-about as shown by males in mixed-sex groups. The most likely explanation for the difference in loud call behavior may therefore be the lack of an audience for a solitary male. It should be noted that there is no reason to assume that males in mixed-sex groups simply give loud calls in response to female vocalizations, since males often give loud calls before females gave alarm calls.

Zuberbühler et al. [1997, 1999] suggested that primates give alarm calls to those predators that are likely to give up hunting when they are detected. Following this hypothesis, Thomas langurs males (whether solitary or in mixed groups) would be expected to give loud calls when they encounter a tiger. That Thomas langur males only call when they are in mixed-sex groups, may indicate that tigers do not give up hunting when the prey gives alarm calls. However,

further studies of tiger hunting behavior are needed to provide conclusive evidence on this topic.

Thus, in contrast to Darwin's view [1872], the behavior of Thomas langurs suggests that primates may control the expression of their emotions. This may indicate that at least some part of primate communication is more than a mere reflex.

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REFERENCES

Cheney DL, Seyfarth R. 1985. Vervet monkey alarm calls: manipulation through shared information? Behaviour 93:150–166.

Cheney DL, Seyfarth R. 1990. How monkeys see the world: inside the mind of another species. Chicago: University of Chicago Press. 377 p.

Darwin C. 1872. The expression of the emotions in man and mammals. London: Murray. VI, 374 p.

Gurmaya K. 1986. Ecology and behaviour of *Presbytis thomasi* in Northern Sumatra. Primates 27:151–172.

Gyger M, Karakashian S, Marler P. 1986. Avian alarm calling: is there an audience effect? Anim Behav 34:1570–1572.

Marler PM, Dufty A, Pickert R. 1986. Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? Anim Behav 34: 194–198.

Marler PM, Mitani J. 1988. Vocal communication in primates and birds: parallels and contrasts. In: Todt P, Goedeking P, Symmes D, editors. Primate vocal communication. Berlin: Springer-Verlag. p 3–14.

Marler PM, Evans C. 1996. Bird calls: just emotional displays or something more? Ibis 138:26–33.

Rijksen HD. 1978. A field study on Sumatran orangutans (*Pongo pygmaeus abelii* Lesson 1872). Wageningen: H. Veenman & Zonen, B.V. 421 p.

Sherman PW. 1977. Nepotism and the evolution of alarm calls. Science 197: 1246–1253.

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

Steenbeek R, Assink PR, Wich SA. 1999. Tenure related changes in wild Thomas' langurs: II: Loud calls. Behaviour 136: 627–650.

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

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

Wich SA, Assink PR, Becher F, Sterck EHM. 2002a. Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of location. Behaviour 139:65–78.

Wich SA, Assink PR, Becher F, Sterck EHM. 2002b. Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. Behaviour 139:79–87.

Wich SA, Koski S, de Vries H, van Schaik CP. 2003. Individual and contextual variation in Thomas langur male loud calls. Ethology 109:1–13.

Zuberbühler K, Noë R, Seyfarth RM. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. Anim Behav 53:589–604.

Zuberbühler K, Jenny D, Bshary R. 1999. The predator deterrence function of primate alarm calls. Ethology 105:477–490.