Chapter 8

The audience effect in Primates: an experimental study on male calls in response to a tiger model

With E.H.M. Sterck

(Proceedings of the Royal Society of London B in review)
Abstract

The traditional view in animal communication research asserts that animal vocalisations merely express emotion and are not under voluntary control. Recent research, however, indicates that animal vocalisations can refer to objects in the outside world and that call production can be under control of the sender depending on the type of audience. 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 primate study showing that the presence or absence of an audience influences calling behaviour. Our results indicate that call production in primates is under control of the callers and not merely express emotion.

Introduction

Since Darwin (1872), the control over expression of emotion by humans has been contrasted with uncontrolled expressions by animals, including non-human primates. Such a view is still expressed in claims that animal calls are "quite automatic and impossible to suppress" (Bickerton 1990) or not much more than just "groans of pain" (Griffin 1981). Two major lines of evidence challenge this view. First, an increasing body of research shows that primate vocalisations refer to objects, especially predator types, in the outside world (Struhsaker 1967; Seyfarth et al. 1980; Zuberbühler et al. 1997; Zuberbühler 2001). Second, some studies indicate that the likelihood that an individual vocalises depends on the presence and identity of the listeners (such as kin or no kin, and sex), the so called "audience effect" (Sherman 1977; Cheney & Seyfarth 1985, 1990; Gyger et al. 1986). Most detailed experimental work on the audience effect concerns birds (Marler & Mitani 1988). In primates the audience effect has received little attention. However, it has been shown that the identity of the listeners affects call rates in vervet monkeys (*Cercopithecus aethiops*, Cheney & Seyfarth 1985) and anecdotes exist for this species that the...
presence of an audience affects call rates (Cheney & Seyfarth 1990). Our study is the first to experimentally investigate the influence of the presence or absence of an audience on the production of vocalisations in a wild primate.

Our study object 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 inter-group 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). An encounter of Thomas langurs with a tiger was observed twice. On one occasion the langurs ascended to the canopy and left the encounter location, on the other occasion the females ascended and left, while the male followed the tiger over a short distance (S. A. Wich, pers. obs., S. E. Koski, pers. comm.). 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. The Thomas langurs in one area (Ketambe 3°41’N, 97° 39’E) have been studied continuously from 1988-2001 and all individuals of the study population were individually recognised and were 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 six mixed-sex groups and four solitary males were tested. The Thomas langurs in the other area (Bukit Lawang, 3 30’N, 98 6’E) 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). The mixed-sex study groups (n=6) and solitary males (n=3) were well habituated. Data from these two populations were lumped 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 an emotional reaction to novel objects of similar size and shape. To this end, mixed-sex groups were exposed to a fake tiger skin and a white cotton blanket with coloured stripes. Second, we examined whether the presence of an audience affected the production of loud calls by exposing solitary males to the tiger skin and the blanket. For each experiment we recorded the number
of loud calls produced, whether the group or solitary male ascended or descended the trees, and whether they approached or retreated from the stimulus (tiger skin or blanket). The fake skin and blanket were exposed 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 notice the stimulus by staring at it, the human observer carrying the fake skin or blanket slowly moved out of sight. Two other observers collected the behavioural data. 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. Statistics were one-tailed, because we expected that males reacted more strongly to the fake tiger skin than the blanket and that males in mixed-sex groups called but that solitary males remained silent.

**Results**

The results of the first experiment on mixed-sex groups indicate 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 signed rank test: \( p=0.002, n=12 \) groups, Table 1). After being exposed to the tiger skin the monkeys also significantly more often ascended the trees (11 out of 12 cases) than after exposure to the blanket (5 out 12 cases) (Fischer’s Exact test: \( p=0.02 \)). In addition, the males significantly more often avoided the tiger skin (10 out of 12 cases) than the blanket (4 out of 12 cases) (Fischer’s Exact test: \( p=0.02 \)).

When the fake tiger skin and blanket were exposed to solitary males (2nd experiment, \( n=7 \) males) no loud calls were made in either of the experiments (Wilcoxon signed rank test: 7 ties, \( p=1.0 \)). Nevertheless, after being exposed to the tiger skin the solitary males tended to ascend the trees (7 out of 7 cases).

| Table 1. Results of tiger model exposure to solitary males and males in groups |
|---------------------------------|-----------------|-------------------|
|                                 | Fake tiger skin | Blanket           |
| Males in group (\( n=12 \))     | 2 (1, 3)        | 0 (0, 0)          |
| Males solitary (\( n=7 \))      | 0 (0, 0)        | 0 (0, 0)          |

Table 1. Median number of loud calls given by males in the experiments. Median values are presented here with the 25th and 75th percentiles between brackets.
more often than when exposed to the blanket (4 out of 7 cases) (Fischer's Exact test: p=0.10). Similarly, they retreated significantly more often from the location of the fake tiger skin (7 out of 7 cases) than when exposed to the blanket (3 out of 7 cases) (Fischer's Exact test: p=0.10).

Although the behavioural response (ascend/descend and approach/retreat) is the same for group living males 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). Thus, the fake tiger skin is perceived as a real threat.

**Discussion**

These experiments convincingly show an effect of the presence or absence of an audience on call production by wild Thomas langur males. Solitary male Thomas langurs do not make loud calls when exposed to a predator model, whereas those in mixed-sex groups do. Hence, Thomas langur males can manipulate their response and loud call production is under voluntary control (Marler & Evans 1996). In addition, these experiments also indicate that loud calls are produced to warn conspecifics (Zuberbühler et al. 1997) and not to alert the predator (Zuberbühler et al. 1997, 1999), since in the latter case calls are always expected when the fake tiger skin is presented and not only by males in groups.

Thus, in contrast to Darwin's view (1872), Thomas langurs show that primates may control the expressions of their emotions and oppose Bickerton's (1990) opinion than animal calls are "impossible to suppress".