RESEARCH ARTICLE

Social Organization of White-Headed Langurs (*Trachypithecus leucocephalus*) in the Nongguan Karst Hills, Guangxi, China

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The number of males per group is the most variable aspect of primate social organization and is often related to the monopolizability of females, which is mainly determined by the number of females per group and their reproductive synchrony. Colobines show both inter-specific and intra-specific variations in the number of males per group. Compared with other colobine species, little is known about the social organization of white-headed langur (*Trachypithecus leucocephalus*), despite its endangered status and unusual limestone habitat. As a part of a long-term study of the white-headed langurs in the Nongguan Karst Hills, Guangxi, China, we quantitatively investigated their social organization by analyzing census data from 1998 to 2003. The population censuses revealed that the predominant social organization of bisexual groups was the one-male group, similar to a previous report on this species and many other Asian colobines. In such groups, one adult male associated with 5.1 adult females, 0.1 sub-adult males, 2.6 juveniles and 2.9 infants on average, with a mean group size of 11.7 individuals. In addition, three multi-male groups were recorded, consisting of 2–3 adult males, 1–5 adult females, 0–2 sub-adult males, 0–7 juveniles and 0–2 infants. They did not contain more adult females than the one-male groups and were unstable in group membership. The langurs outside bisexual groups were organized into small nonreproductive groups or lived as solitaries. The nonreproductive groups averaged 1.3 adult males, 1.3 sub-adult males and 2.6 juveniles. Juvenile females were present in such groups on 52.4% of all occasions. As predicted by the monopolization model, the prevalence of the one-male pattern in this species may mainly be attributed to the small number of females in the group. The possible reasons for the occurrence of multi-male groups and the presence of juvenile females in nonreproductive groups are also discussed. Am. J. Primatol. 71:206–213, 2009.

Key words: Asian colobine; one-male group; group composition; monopolizability of females; group size

INTRODUCTION

The white-headed langur (*Trachypithecus leucocephalus*) is among the most endangered primate species in the world and endemic to China. They are restricted to the limestone hills in a triangular area of southern Guangxi province (22°06'–22°42'N, 107°–108°E), with a total number of 700–800 individuals mainly found in the Nongguan Karst Hills in Chongzuo County and the Nonglin Karst Hills in Fusui County [Ran, 2003; Wang & Jin, 2004; Wang et al., 2005]. As this species was first described by Tan [1957], debates about its taxonomic status have continued on whether it is an independent species [Eudey, 1987; Lu & Li, 1991], or a subspecies of the Francois’ langur (*T. francoisi*) [Li & Ma, 1980; Shen & Li, 1982; Wang et al., 1997]. Recently, Groves [2001] listed six closely related langur taxa into the *T. francoisi* group, and recognized the white-headed langur as a subspecies of the golden-headed langur (*T. poliocephalus*) in Vietnam. This opinion was agreed by other researchers [Brandon-Jones et al., 2004].

Although its precise taxonomic status remains unresolved, study of the white-headed langur is important because of its endangered status and its special limestone habitat. Their unusual habitat requirements may lead to differences in behavioral ecology from other colobine species. Moreover, knowledge on their socioecology will be useful for conservation purpose. However, only limited information is available on this species. Previous studies are mainly conducted in the Nonglin Karst Hills in

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Received 30 July 2008; revised 10 October 2008; revision accepted 11 October 2008
DOI 10.1002/ajp.20637
Published online 10 November 2008 in Wiley InterScience (www.interscience.wiley.com).

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Fusui County, focusing primarily on activity budget, locomotion, feeding ecology and habitat quality [Huang & Li, 2005; Huang et al., 2002, 2003, 2007; Li, 1993; Li & Rogers, 2004a, 2005a, b, 2006; Li et al., 2003]. Information on the social organization of this species has been limited to one study of the Nonglin population [Li & Rogers, 2004b]. Based on brief observations, they suggested that the principal mating system of white-headed langurs was one-male, but one multi-male group was found in the same population. This study provides basic understanding on the species’ social organization, but lacks any quantitative data and is unable to explain the intra-specific variation in the number of adult males per group. Compared with the Nonglin population, little is known about the langurs in the Nongguan Karst Hills.

To understand the social system of the white-headed langur, a long-term project was conducted in the Nongguan Karst Hills in Chongzuo County, beginning in December 1996. As a part of this comprehensive study, in this article, we analyze the results from regular population censuses conducted between 1998 and 2003. From a comparative perspective, we aim to present quantitative data on the social organization and group composition of the little-studied white-headed langurs in the Nongguan Karst Hills on a long-term scale.

METHODS

Study Site

The white-headed langurs were studied in the Nongguan Karst Hills (22°15′–22°17′N, 107°29′–107°32′E, 150–430 m above sea level), a 22 km² area within the Chongzuo Precious Animal Nature Reserve, Guangxi, China (Fig. 1). The site receives an average annual rainfall of 1,152 mm, which occurs in a seasonal pattern: a dry season from November through March with <=50 mm monthly rainfall and a rainy season from May to August with >=150 mm monthly rainfall. The mean temperature is 22.8°C with a maximum of 28.7°C in July and a minimum of 15.0°C in January [Chongzuo Weather Bureau, 1998–2004, unpublished data].

The study site is typical karst, with steep limestone hills rising over the flatlands, providing a relatively safe habitat for the langurs. The habitat is highly fragmented by human activity. Almost all the flatlands and valleys around the hills have been cultivated by the local people to grow sugarcane, rice, corn and peanuts, whereas most of the original

Fig. 1. Study site of the Nongguan Karst Hills in Chongzuo County, Guangxi, China.
tropical monsoon forest on the hills and slopes has been replaced by secondary shrub vegetation owing to firewood collection by villagers. The langurs inhabit the limestone hills and rarely come down to the flatlands, so crop raiding and provisioning are never seen. No other primate species are sympatric within the study area. Only a few potential predator species have survived in the study area owing to human activity, such as leopard cat (*Felis bengalensis*), yellow-throated marten (*Martes flavigula*) and golden eagle (*Aquila chrysaetos*). Locally extinct are tiger (*Panthera tigris*), leopard (*P. pardus*), and clouded leopard (*Neofelis nebulosa*). Poaching was the main threat to the langur population in the past, but has been prohibited in the study area since 1998 [Wang & Jin, 2004].

### Age/Sex Classification

During population censuses, we categorized the langurs into six age/sex classes: adult males, adult females, sub-adult males, juvenile males, juvenile females and infants.

The langurs show little sexual dimorphism in body size, so we identified the sexes mainly by the color and shape of the perineal region. In males, this region is covered by black hair extending back to the fused ischial callosities, whereas in females this triangular region is hairless and skin-colored, which clearly contrasts with the surrounding black hair and can be clearly seen from a distance. This method was applicable in sex determination in the adults, sub-adults and juveniles during the census work. However, it was hard to apply to the infants, because of the slight contrast between the pale skin color and their yellow hair. Thus, distinguishing sex among infants was much more difficult but could still be achieved after repeated observations, by the pendentulous penis in male infants.

Age/sex classes were assigned mainly by body size and pelage color pattern. Adult males have full head–body length and shoulder width. They are easily discriminated by the discernable penis when facing observers. Adult females have a somewhat smaller head–body length and shoulder width than adult males, and can be distinguished from nulliparous juvenile females by elongated nipples, which imply recent suckling. Sub-adult males are a little smaller and much more slender than the adults, usually with a visible glans and protruding snout because of developing canine teeth. Juveniles are much smaller (less than two-thirds that of the adult) and have more white patches on their shoulders, limbs, feet and tail than the adults and sub-adults. Infants are distinguished by the differential pelage color and suckling behavior. Langurs are born with flamboyant orange pelage and pale skin. After about 3 months, the coat begins to grow darker and the skin turns black. The pelage becomes yellow–brown at about 1 year and gradually changes into the adult black-and-white pattern after 1.5–2 year, at which time they are weaned and reclassified as juveniles [Weaning age: 19–21 months, Zhao et al., 2008].

Individuals were identified by age/sex class, coat color pattern, face/body shape and injuries. Adult females were also identified by the black blotches on the skin-colored area at the perineum. Infants were also recognized by the strong bond with their mothers. Note that all the individual identifications were done with great caution. Several physical and behavioral traits were always combined to identify the animals, usually within a given social or geographic context. And individual identifications were conducted by experienced observers.

### Data Collection and Analysis

The langur population in Nongguan has been under observation since December 1996. Preliminary observations were conducted in a random way to collect basic information from December 1996 to January 1997 and March–May 1997 [Zhang, 1998]. Since January 1998, this population has been systematically monitored through regular population censuses and focal group observations by various researchers from Peking University. From 1998 to 2003, each year at least one population census was carried out to assess the age/sex composition of as many groups as possible. The censuses were intensively conducted in the northern part of the Nongguan Karst Hills (about 10 km², Fig. 1). Because of the terrain and the unhabituated nature of the langurs, observations were normally made at a distance of 50–200 m through binoculars (LEICA TRINOVID 8 x 42BN) or a spotting scope (LEICA APO-TELEVID77 20–60 x). This study complied with the protocols approved by the Guangxi Forestry Administration and adhered to the legal requirements of China.

Most langurs live in groups and select small caves or cracks on the cliffs as sleeping sites. Each group has several fixed sleeping sites and leaves the site in the early morning and moves back at dusk. The sleeping sites are easily recognized by the reddish-brown excrement markings on the rock surface below them [Huang & Li, 2005; Huang et al., 2003; Wang et al., 2005]. During the population censuses, we looked for such sleeping sites along the trails and searched for the langur groups around the sleeping sites. When a group was detected, data concerning group size and age/sex composition were repeatedly recorded. Each sleeping site was thoroughly searched at least twice. Groups were recognized by identified individuals, relatively stable group composition and home range.

In this study, we chose results of the censuses conducted between January and March from 1998 to 2003 to calculate the percentage of each group type,
the distribution of adult males among different
group types, and age/sex composition of each group
type. During these months, the vegetation was
sparsest and the visibility was highest, thus the
results were most accurate. Note that the same
group may occur in the results of several censuses
but were at different phases in group composition, so
they were treated as different ones during the course
calculation.

Kruskal–Wallis tests were used to compare the
mean group size and the mean number of adult
females in one-male groups across time. Statistical
tests were two-tailed, with $P < 0.05$ taken as the
threshold for significance (SPSS 15.0).

RESULTS
Social Organization at Group Level

According to censuses from 1998 to 2003, most
of the langurs in Nongguan were group-living,
whereas some males lived as solitaries. Group-living
langurs commonly lived in bisexual groups or
nonreproductive groups (Table I). Nonreproductive
groups referred to the groups without adult females.
In the censuses of 1998 and 1999, 92.3 and 85.7% of
the bisexual groups were one-male groups, while one
and two multi-male groups were recorded, respecti-
vely. Thereafter, bisexual groups were exclusively
one-male. Bisexual groups were accompanied by
nonreproductive groups in all the censuses except
in 1999. Overall, 72.4% of the group-living adult
males in the population lived in one-male groups,
5.7% in multi-male groups and 21.9% in nonrepro-
ductive groups.

Besides the group-living langurs, solitary males
were occasionally encountered during the censuses.
Owing to the difficulty in individual recognition of
solitary males, we only recorded the number of
sightings, and this number to a great extent
depended on the duration of the censuses. The
relatively small number of the sightings of solitary
males in 2003 was attributed to the short census
period (Table I).

Social Composition of One-Male Groups

The age/sex composition of one-male groups in
each census from 1998 to 2003 is shown in Table II.
There were no differences either in the mean group
size (Kruskal–Wallis test: $\chi^2 = 2.597$, df = 5,
$P > 0.05$), or the mean number of adult females
(Kruskal–Wallis test: $\chi^2 = 6.199$, df = 5, $P > 0.05$)
across time. On average, a one-male group consisted
of one adult male, 5.1 adult females, 0.1 sub-adult
male, 2.6 juveniles and 2.9 infants, with a mean
group size of 11.7 individuals.

Social Composition of Multi-Male Groups

Three instances of multi-male groups were also
recorded in the population over the course of the
study: Group GYN, Group GY, and Group SHY. In
the census of 1998, group GYN was documented to
have three adult males, three adult females and two
new-born infants. This group was first identified in
January 1997, with four adult males and three adult
females [Zhang, 1998]. During the course of the
census in 1998, two new-born infants were recorded
in January and then one adult male disappeared
from the group in March. When we revisited the
group in the census of 1999, it had become a one-
male group with one adult male, three adult females
and two infants. Because the males were not
individually identified, the process from multi-male
to one-male was unknown.

In the census of 1999, group GY was recorded
with two adult males, one adult female, one sub-
adult male, four juvenile males and three juvenile
females. Group GY formed in April 1998, by several

### TABLE I. Social Organization of the White-Headed Langurs in Nongguan Karst Hills

<table>
<thead>
<tr>
<th>Year</th>
<th>Work day</th>
<th># of groups</th>
<th># of indivs.</th>
<th># of groups</th>
<th># of indivs.</th>
<th># of groups</th>
<th># of indivs.</th>
<th>Total # of groups</th>
<th>Total # of indivs.</th>
<th>Size</th>
<th>AM/AF</th>
<th>Sightings of solitary males</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>65</td>
<td>12</td>
<td>132</td>
<td>1</td>
<td>8</td>
<td>4</td>
<td>17</td>
<td>17</td>
<td>168</td>
<td>9.2</td>
<td>1:3.0</td>
<td>10</td>
</tr>
<tr>
<td>1999</td>
<td>59</td>
<td>12</td>
<td>137</td>
<td>2</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>21</td>
<td>137</td>
<td>11.3</td>
<td>1:4.3</td>
<td>14</td>
</tr>
<tr>
<td>2000</td>
<td>45</td>
<td>14</td>
<td>181</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>15</td>
<td>18</td>
<td>196</td>
<td>11.5</td>
<td>1:3.5</td>
<td>15</td>
</tr>
<tr>
<td>2001</td>
<td>59</td>
<td>17</td>
<td>204</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>19</td>
<td>20</td>
<td>223</td>
<td>11.2</td>
<td>1:4.7</td>
<td>17</td>
</tr>
<tr>
<td>2002</td>
<td>61</td>
<td>17</td>
<td>204</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>25</td>
<td>30</td>
<td>229</td>
<td>10.4</td>
<td>1:3.1</td>
<td>17</td>
</tr>
<tr>
<td>2003</td>
<td>29</td>
<td>17</td>
<td>180</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>23</td>
<td>32</td>
<td>213</td>
<td>9.3</td>
<td>1:3.7</td>
<td>3</td>
</tr>
</tbody>
</table>

$N$, number of individuals; AM, adult male; AF, adult female.

*solitary males were excluded from calculation because the actual number was unknown, making the sex ratio more female-biased than the real population adult sex ratio.
individuals who were evicted from a one-male group after male take-over and at least six individuals of unknown history [Zhang, 2002]. It was under focal observation from August 1998 to July 2000. The group was relatively stable in group composition until the only adult female died in November 1999, and the group turned into a nonreproductive group with three juvenile females [Zhang, 2002].

Another multi-male group, group SHY, was also recorded in the census of 1999. At that time, the group consisted of two adult males, five adult females, two sub-adult males and one new-born infant. But the infant had disappeared when we revisited this group in April. In August, group SHY split into a one-male group, which consisted of one adult male and five adult females, and a nonreproductive group comprising three adult males [Pan et al., unpublished data].

Overall, a multi-male group comprised 2.3 ± 0.6 adult males, 3.0 ± 2.0 adult females, 1.0 ± 1.0 sub-adult male, 2.3 ± 4.0 juveniles and 1.0 ± 1.0 infant, with a size of 9.7 ± 1.5 individuals. The multi-male groups did not have more adult females than the one-male groups.

Social Composition of Nonreproductive Groups

The nonreproductive groups averaged 1.3 adult males, 1.3 sub-adult males and 2.6 juveniles, with a mean size of 5.2 individuals (Table II). The size of nonreproductive groups was smaller than that of bisexual groups. In general, a nonreproductive group consisted of adult, sub-adult, and juvenile males. Sometimes a nonreproductive group only had duos or trios of adult and/or sub-adult males. However, up to three juvenile females were present in such groups on 11 occasions (52.4% of all occasions). Among the individuals found in nonreproductive groups, 82.6% were males of all age classes except infants and 17.4% were juvenile females.

As previously noted, group GY became such a group with three juvenile females in November 1999. In July 2000, when the three juvenile females began estrous, extra-group males continuously harassed the group. Finally, an invading male took over the group and evicted all the male members of the group [Zhang, 2002].

DISCUSSION

In Asian colobines, the modal pattern of bisexual groups is the one-male group [Kirkpatrick, 2007; Newton & Dunbar, 1994]. A previous report on the white-headed langurs in the Nonglin Karst Hills in Fusui County suggested that the principal mating system of this species is one-male [Li & Rogers, 2004b]. In the Nongguan Karst Hills, repeated population censuses revealed that the predominant social organization of bisexual groups was also the one-male group, and this pattern was stable on a long-term scale. A one-male group typically contained 5.1 adult females, which is similar to the langurs in Fusui County [3–9 females, Li & Rogers, 2004b].

Former analyses identified monopolizability of females as the key factor responsible for the distinction between one-male and multi-male groups [Clutton-Brock & Harvey, 1977; Emlen & Oring, 1977; van Schaik & van Hooff, 1983; Wrangham, 1980]. The number of females in a group and their degree of reproductive synchrony have been

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**TABLE II. Age/sex Composition of One-Male Groups and Nonreproductive Groups in Nongguan Karst Hills**

<table>
<thead>
<tr>
<th>Year</th>
<th>Adult female (0–3)</th>
<th>Sub-adult male (0–6)</th>
<th>Juvenile (0–3)</th>
<th>Infant (0–9)</th>
<th>Group size (0–13)</th>
<th>Adult male (1–7)</th>
<th>Sub-adult male (1–6)</th>
<th>Juvenile male (2–12)</th>
<th>Juvenile female (2–13)</th>
<th>Group size (2–24)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>5.5 ± 2.3</td>
<td>0</td>
<td>2.0 ± 2.3</td>
<td>2.5 ± 2.2</td>
<td>11.0 ± 5.1</td>
<td>2.0 ± 0.0</td>
<td>0</td>
<td>1.3 ± 0.5</td>
<td>1.0 ± 0.8</td>
<td>4.3 ± 1.0</td>
</tr>
<tr>
<td>1999</td>
<td>5.2 ± 2.4</td>
<td>0</td>
<td>2.8 ± 2.4</td>
<td>2.5 ± 2.2</td>
<td>11.4 ± 5.0</td>
<td>2.3 ± 0.6</td>
<td>0.3 ± 0.6</td>
<td>1.3 ± 2.3</td>
<td>1.0 ± 1.7</td>
<td>5.0 ± 4.4</td>
</tr>
<tr>
<td>2000</td>
<td>5.2 ± 2.1</td>
<td>0.9 ± 0.9</td>
<td>2.7 ± 3.1</td>
<td>4.0 ± 2.4</td>
<td>12.9 ± 6.2</td>
<td>1.0 ± 0.0</td>
<td>2.7 ± 0.6</td>
<td>1.3 ± 1.2</td>
<td>1.3 ± 1.5</td>
<td>6.3 ± 2.5</td>
</tr>
<tr>
<td>2001</td>
<td>4.8 ± 2.5</td>
<td>0.1 ± 0.5</td>
<td>3.1 ± 3.2</td>
<td>3.1 ± 2.4</td>
<td>12.0 ± 7.3</td>
<td>0.8 ± 0.4</td>
<td>1.8 ± 1.1</td>
<td>1.4 ± 1.3</td>
<td>1.0 ± 1.7</td>
<td>5.0 ± 2.4</td>
</tr>
<tr>
<td>2002</td>
<td>5.1 ± 2.4</td>
<td>0.2 ± 0.8</td>
<td>2.9 ± 2.6</td>
<td>2.8 ± 1.9</td>
<td>12.0 ± 5.3</td>
<td>0.8 ± 0.4</td>
<td>1.7 ± 1.0</td>
<td>2.5 ± 3.4</td>
<td>0.5 ± 0.8</td>
<td>5.5 ± 3.9</td>
</tr>
<tr>
<td>2003</td>
<td>4.8 ± 3.5</td>
<td>0.2 ± 0.8</td>
<td>1.9 ± 2.4</td>
<td>2.6 ± 2.6</td>
<td>10.6 ± 6.9</td>
<td>1.3 ± 0.7</td>
<td>1.3 ± 1.2</td>
<td>1.7 ± 2.1</td>
<td>0.9 ± 1.1</td>
<td>5.2 ± 2.8</td>
</tr>
<tr>
<td>Overall</td>
<td>5.1 ± 2.6</td>
<td>0.1 ± 0.5</td>
<td>2.6 ± 2.7</td>
<td>2.9 ± 2.3</td>
<td>11.7 ± 6.0</td>
<td>1.3 ± 0.7</td>
<td>1.3 ± 1.2</td>
<td>1.7 ± 2.1</td>
<td>0.9 ± 1.1</td>
<td>5.2 ± 2.8</td>
</tr>
</tbody>
</table>
identified as important determinants of male monopolization potential [Andelman, 1986; Dunbar, 1988; Mitani et al., 1996; Nunn, 1999; Ridley, 1986]. For Asian colobines, there are both inter-specific and intra-specific variations in the number of males per group. In the hanuman langurs (Semnopithecus entellus), data for 23 populations show that the percentage of one-male groups is, indeed, related to the number of females per group and breeding seasonality [Srivastava & Dunbar, 1996]. Theoretically, a single hanuman langur male is able to monopolize up to 12 adult females [Newton, 1988]. However, in other langur subgenera, although multi-male groups are regularly observed, the monopolization ability of females is always high because the number of females per group is on average smaller and birth seasonality is less pronounced than the hanuman langurs [Sterck & van Hooff, 2000]. In the case of the white-headed langurs, although the number of females per group varied considerably (range: 1–14), the typical one-male group only consisted of 5.1 adult females, which was small enough to be defensible. Thus, the prevalence of the one-male groups in this species is probably owing to the relatively small number of females in the group, as predicted by the monopolization model. But in one case, an adult male was able to monopolize as many as 14 adult females, so additional information about the degree of reproductive synchrony in this species is still needed to understand the maximum limit of the number of females per group that can be monopolized by one male.

Although the modal pattern of bisexual groups in this species is the one-male group, three multi-male groups were recorded in our study. This intra-specific variation in the number of males per group was also documented in the langurs in Fusui County [Li & Rogers, 2004b]. But owing to the short observation period, the only multi-male group in the Nonglin Karst Hills was not followed long enough to determine whether it was a reproductive group or just temporary phases in a demographic development. In the Nongguan population, the multi-male groups did not contain more females than the one-male groups, suggesting that they are not a strategy to maintain access to more females. In many other colobine species, the multi-male groups may either be age-graded or temporarily occur during male replacement [reviewed by Sterck & van Hooff, 2000]. In our study, groups GY and SHY were associated with male take-over and all three multi-male groups finally became one-male groups or nonreproductive groups, indicating their transitory and unstable nature. The only multi-male group reported in the Nonglin Karst Hills also formed after a male take-over [Li & Rogers, 2004b]. Age-graded multi-male groups may also have the chance to happen in this population, because sub-adult males occurred in the one-male groups on five occasions, implying the relatively long male tenure in this species and the possibility for young males maturing in their natal groups. Therefore, as in most other langur species, the multi-male group in this species is a temporary adaptive strategy in response to complex demographic processes.

Other than the bisexual groups, solitary males and nonreproductive groups mainly consisting of males were also described in white-headed langurs, indicating that the males are the “dispersing sex”, as in many other Asian colobines [Kirkpatrick, 2007; Newton & Dunbar, 1994]. However, unlike the all-male bands described in the Nonglin population, juvenile females were present in nonreproductive groups on 11 occasions in Nongguan, indicating that immature female dispersal occurs in this species, although they only accounted for a small portion of all the individuals in such groups. Similar situations have been described in other colobine species, such as Nasalis larvatus, T. auratus, T. johnii and Presbytis thomasi [Steenbeek et al., 2000; Yeager & Kool, 2000]. This kind of group may be formed by the immatures of both sexes expelled from one-male groups by the new resident male after take-over, as in the cases of the purple-faced langur (T. vetulus) [Rudran, 1973] and the Thomas’s langur (P. thomasi) [Steenbeek et al., 2000], or by all-male bands joined by large juvenile females, who were presumed to have left their natal groups to avoid inbreeding, as in the case of the proboscis monkey (N. larvatus) [Murai, 2004]. In this species, the nonreproductive groups were elsewhere referred to as male-immature groups and formed by the ousted male and all his male offspring after male take-over [Zhao & Pan, 2006]. In some cases, older female infants were forced to wean and also left with the ousted male to avoid infanticide [Wang, 2004]. As in group GY, when these females approached sexual maturity, the group became unstable because of continuous male harassment and finally turned into a one-male group by male take-over.

In conclusion, we suggest that the prevalence of one-male groups in this species may be mainly attributed to the small number of females in the group. Low predation risk, within-group feeding competition and infanticide might also contribute to small group size in this langur population, but more data are needed to test these hypotheses.

ACKNOWLEDGMENTS

For contribution to the data collection of this long-term study we are very grateful to Lei Zhang, Yingyi Zhang and Lizhong Zhu. Our thanks go to the local guide, Mr. Qihai Chen and the staff in Chongzuo Eco-park for assistance in the field. The local government of Guangxi Province and Chongzuo County supported the field work. Thanks also go to the Weather Bureau of Chongzuo County for sharing
the climate data. We thank Dr. Carola Borries, Prof. Kunio Watanabe and Prof. Terry Harrison for helpful comments and discussion. Special thanks are extending to the editors and two anonymous reviewers for their valuable suggestions on editing the manuscript. We gratefully acknowledge our colleagues in the Giant Panda and Wildlife Conservation Research Center for their thoughtful discussions on the subject. Thanks go to Dr. Iain C. Bruce for revising the language. The study was financially supported by the 985 Project of Peking University, the Margot Marsh Biodiversity Foundation, and Conservation International. This study complied with the protocols approved by the Guangxi Forestry Administration and adhered to the legal requirements of China.

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