



New Experimental Observations of Infanticide and Cannibalism in Northern Tree Shrew *Tupaia belangeri*

Dong-Min Hou, Hong-bi Peng, Wan-Long Zhu* and Zheng-Kun Wang*

Key Laboratory of Ecological Adaptive Evolution and Conservation on Animals-Plants in Southwest Mountain Ecosystem of Yunnan, School of Life Sciences, Yunnan Normal University, Kunming, Yunnan 650500, China.



ABSTRACT

Maternal infanticide and cannibalism, wherein mothers kill and consume their offspring, commonly occur in various animal taxa. The extent of its occurrence in *Tupaia belangeri* remains unclear given the difficulty of observing infanticidal and cannibalistic behaviors. Here, we report observations of maternal infanticide and cannibalism in two female *T. belangeri* in two laboratory experiments. Our footage provides the first video documentation of infanticide, cannibalism, and parental care behavior in *T. belangeri*. Analysis of the video data indicated that the observations were related to nutrition hypothesis, hormone level hypothesis and stress hypothesis. We also suggest that the infanticidal and cannibalistic behaviors of tree shrews might be related to their dietary habits. Although reactions to infants are doubtless affected by the psychological and physiological status of tree shrew mothers as well as the environment, additional work is needed to clarify the relative roles of various factors in shaping maternal behavior post-parturition.

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Authors' Contribution

D-MH and H-BP carried out the experiment. W-LZ and Z-KW conceived of the study and participated in its design, coordination and drafted the manuscript.

Key words

Tupaia belangeri, Infanticide, Cannibalism, Nutrition, Hormone level, Stress, Dietary habits

INTRODUCTION

Infanticide and cannibalism are widespread in the animal kingdom. Several recent studies of infanticide and cannibalism have been conducted in various animals, including primates (Yao *et al.*, 2016), rodents (Schmidt *et al.*, 2015), ungulates (Gray, 2009) and birds (Harris *et al.*, 2016). Most mammals have an instinctive response to protect and nurture their own offspring, as such behavior is favored by natural selection (Rilling and Young, 2014). However, infanticide and cannibalism are the antithesis of offspring care (Hrdy, 2016). Several explanations have been proposed to explain the occurrence of infanticide (Table I) (Kral *et al.*, 2019). Cannibalism is the consumption of all or part of another conspecific (Richardson *et al.*, 2010). In mammals, cannibalism often occurs following infanticide (Culot *et al.*, 2011). Cannibalism of offspring may occur to aid resource acquisition when resources are limited (Bronson and Marsteller, 1985; Hrdy, 1979). In rare cases, infanticide leads to the cannibalization of dead juveniles

(Fox, 1975; Hrdy, 1979). The incidence of cannibalism may be affected by the metabolic requirements of the adults, which can vary with sex, age, and reproductive state (Ebensperger *et al.*, 2000).

Tupaia belangeri (Tupaiidae: Scandentia) is the only member of Tupaiidae in China. As its metabolic system and anatomical structure are more similar to humans than to mice, *T. belangeri* has been widely used as an experimental animal model in biomedical research (Zhu *et al.*, 2010; Hou *et al.*, 2021). It occurs in tropical rain forest, secondary forest, and bush habitat and feeds on insects and fruit (Hou *et al.*, 2018a). Larvae of the genus *Tenebrio* are their preferred food, and fruit is their second choice (Zhang *et al.*, 2017; Peng *et al.*, 2020). Although plant food resources are abundant, animal food resources in their natural habitat are scarce by comparison. They have a strong reproductive capacity, and the number of fetuses generally ranges from 2 to 5 (Yao, 2017).

Here, we provide new behavioral observations of parental infanticide and cannibalism in *T. belangeri* from two different laboratory experiments. The aim of this study was to explore the causes of infanticide and cannibalism in *T. belangeri* and provide insights that could inspire future breeding experiments.

MATERIALS AND METHODS

Observation of individual behavior

This study involves two experiments. In the first experiment the individual behavior was observed. *T.*

* Corresponding author: zwl_8307@163.com, wangzk_123@163.com
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belangeri were captured at the boscage of Luquan County, Yunnan Province in the spring of 2017 and maintained at the School of Life Sciences, Yunnan Normal University, Kunming, China. The animals (n=6, ♀3: ♂3) were acclimated to ambient temperature 25±1°C, kept under a 12L:12D light/dark cycle, and were provided water *ad libitum* for whole process of the experiment. Individual behavior (activity behavior, resting behavior, feeding behavior, modifying behavior) was observed for 28 d. Animals were provided with adequate larvae of *Tenebrio molitor* and apples during the pre-parturition period. As it was clear that only one *T. belangeri* were pregnant before the experiment, observations of the pre-parturition and post-parturition behavior in *T. belangeri* were made; the physiological state of the infants was also determined. The purpose of experiments 1 was to observe the behavior of tree shrews, and see (Hou *et al.*, 2018b; c; 2019) for relevant experimental results.

Effects of light on behavior, memory and oxidative stress

The effects of light intensity on the behavior, learning memory, and oxidative stress of *Tupaia belangeri* was observed in the second experiment. *T. belangeri* were captured at the boscage of Luquan County, Yunnan Province in the summer of 2019 and maintained at the School of Life

Sciences, Yunnan Normal University, Kunming, China. The animals (n=6 of each group, ♀6: ♂12) were acclimated to ambient temperature 25±1°C, kept under a 12L: 12D light/dark cycle, and were provided water *ad libitum* for whole process of the experiment. The animals were randomly divided into three groups: 50-W illumination group, 100-W illumination group, and 200-W illumination group. The appropriate/natural brightness under general rearing conditions of tree shrews was 15-W. During the experiment, the animals were placed in behavioral arena, and an incandescent lamp was suspended at 120 cm above the device for light stimulation. Experiments were run from 9:00 to 17:00 daily and individual behavior (activity behavior, resting behavior, feeding behavior, modifying behavior) was observed for 28 d. Animals were fed daily from 7:00 to 8:00 and from 18:00 to 19:00. Tree shrews showing infanticide and cannibalism behavior were in the 200-W illumination group; however, the experimental animals in this group did not appear to be pregnant prior to the start of the experiment. But over time, one animal was found to be pregnant. The purpose of experiments 2 was to investigate the effects of different light intensities on the behavior changes, learning memory ability and oxidative stress in *T. belangeri*, and see (Peng *et al.*, 2021) for relevant experimental results.

Table I. List of hypotheses explaining the occurrence of infanticide and cannibalism in mammals.

Hypothesis	Definition and description	References
Exploitation	The infanticidal animal benefits from consumption or use of the victim.	Agrell <i>et al.</i> , 1998; Hrdy, 1979
Resource competition	The infanticidal animal competes with other adult individuals for physical resources such as food or nest sites.	Agrell <i>et al.</i> , 1998; Hrdy, 1979; Manning <i>et al.</i> , 1995
Food scarcity	Cannibalism may be an interaction that reduces population size before acute resource shortage causes severe physiological stress.	Fox, 1975
Compensate of pregnancy	Cannibalistic behaviour after a short period of maternal care is that it allows mothers to compensate for the costs of pregnancy.	Elgar and Crespi, 1992
Paternal manipulation	By killing the infant, parents improve chances for their own survival or the survival of their existing offspring, or they may gain greater net reproductive fitness in the future. In addition, parents may manipulate the offspring sex ratio via infanticide.	Hrdy, 1979; Ebensperger, 1998
Nutrition	The nutritional hypothesis for cannibalism posits that the act of consuming a conspecific provides participating individuals with nutritional benefits that might improve future reproductive success.	Fox, 1975; Klug and Bonsall, 2007
Adoption avoidance	An individual commits infanticide to avoid adopting and providing parental care, especially allosuckling, to unrelated offspring.	Ebensperger, 1998
Sexual selection	Infant killing is directed at offspring unlikely to be descendants of the killer, so reducing the reproductive success of competitors and increasing the nfanticidal individual's own opportunities to breed.	Agrell <i>et al.</i> , 1998; Hrdy, 1979; Palombit, 2015
Non-adaptive behaviour	Infanticide is a mistake or a result of stress, frustration, or even a consequence of aggression to third parties or self-destruction, etc.	Hrdy, 1979; Cassini, 1998; Palombit, 2015
Accidental behaviour	This would seem more likely to be an attempt to remove the newborn rather than a deliberate attempt to kill and eat the neonate.	Singh and Garcia, 2015; Smith and Smith, 2019

Note: Some of the descriptions of hypotheses are quoted from Kral *et al.*, 2019.

The experimental procedures were approved by the Animal Care and Use Committee of the School of Life Sciences, Yunnan Normal University (No. 13-0901-011).

Behavioral observation

For behavioral observation the behavioral arena is a special instrument made of a transparent acrylic plate, and a real-time surveillance camera was located at the top of the behavioral arena. Animals were also provided with a box for feeding in the device. The animal houses was equipped with a 15-W incandescent lamp. After each experiment, 75% alcohol was used to wipe and disinfect the device.

Data analysis

The video data obtained by the real-time surveillance camera were stored on a hard disk. Because the hard disks were typically full after 7 d, the data were extracted from the hard disks every 7 d. Video software was used to analyze tree shrew behavior.

RESULTS

Pre-parturition and post-parturition behavior

Prior to delivery in experiment 1, tree shrews did not engage in strenuous activities, spent most of their time licking their abdomen and pudenda, and occasionally fed. Births occurred rapidly during the delivery period, and body movements were infrequent. Consequently, it was impossible to determine the specific birth order and birth time of the five infants. Following delivery, adults spent approximately 18 min licking the head and body parts of the infants and 5 min licking their pudenda and other body parts. During this period, we observed tree shrews cover the infants with small pieces of paper is shown in [Video 1](#). Thereafter, the animals frequently fed.

In experiment 2, tree shrews often engaged in strenuous activities, and they did not lick their pudenda prior to delivery. Tree shrews exhibited various body movements during the delivery period. The birth order and birth time of the three infants were noted. The tree shrews licked No. 2-1 for only approximately 3s during the entire delivery period. Following delivery, tree shrews were highly active and frequently fed.

Infanticide and cannibalism information

In experiment 1, no infanticide was observed, and all five infants died of natural causes ([Table II](#)). However, cannibalism was only observed for No.1-3 the day after delivery. The entire body of the infant was consumed at one time, and the consumption of this individual took approximately 740s.

In experiment 2, infanticide and cannibalism were observed for three infants 66s after delivery ([Table II](#)). Cannibalism occurred immediately after infanticide. It took approximately 185s for the entire body of No.2-1 to be consumed. It took 221 s for the entire body of No.2-2 to be consumed, 135 s for all of the body parts except the head, and 86 s for the head, and the body parts were consumed before the head. It took approximately 133 s for the entire body of No. 2-3 to be consumed, 101 s for the head, and 32 s for the remaining body parts, and the head was consumed before the body parts. See [Video 2](#) for details of cannibalism in *T. belangeri*.

DISCUSSION

The metabolic levels of hormones such as oxytocin and steroids are especially high during the second half of pregnancy and can affect maternal behavior ([Saltzman and Maestripieri, 2011](#); [Bercovitch, 2020](#)). Animals can go from treating an infant cadaver as alive to treating it as food, and these behavioral changes might be mediated by physiological changes in hormone levels ([Watson and Matsuzawa, 2018](#)). *T. belangeri* covered the infants with small pieces of paper, which resembled the way that human mothers often show love for their children. However, some *T. belangeri* mothers also killed and consumed their young. The occurrence of cannibalism at the end of pregnancy might thus reflect a gradual weakening of the mother-infant relationship and a change in hormone metabolism ([Trapanese et al., 2020](#)). [Elgar and Crespi \(1992\)](#) suggested that the occurrence of cannibalism following a short period of maternal care might be driven by mothers compensating for the energy consumed during pregnancy. Our observations support this hypothesis in experiment 1: the tree shrews took care of their offspring post-parturition, and cannibalism occurred long after parturition ([Table II](#)). Thus, the first explanation for cannibalism might be that the hormone levels of the tree shrews changed during pregnancy.

T. belangeri are omnivorous and prefer to consume *T. molitor* larvae ([Peng et al., 1991](#)). Sufficient food was provided in the early stage of experiment 1 and 2. However, there was a shortage of animal food resources (*T. molitor* larvae) in the later stage of the experiment, plant food resources (apple) was still abundant. Food scarcity is considered one of the main factors driving infanticide and cannibalism in animals ([Getto et al., 2005](#); [Duarte et al., 2010](#)). Cannibalism has often been observed to occur when food resources are abundant, which contradicts ecological theory predicting that cannibalism mostly occurs where resources are scarce ([Meek and Brown, 2017](#)). However, these observations

are consistent with the nutrition hypothesis (Hrdy, 1979; Ebensperger, 1998), which predicts that cannibalism might be selectively favored because consuming conspecifics provides nutritional benefits that may increase future fitness (Klug and Bonsall, 2007; Nishikawa *et al.*, 2020). This hypothesis may also explain the observations in our study. Meat was not provided as food late in experiment 1 and 2. Thus, tree shrews might have been motivated by the desire to consume meat. Generally, the need for carnivores to consume meat might lead to cannibalism. We suggest that the infanticide and cannibalism of tree shrews might

be related to their dietary habits, namely their preference for consuming *Tenebrio molitor* larvae.

According to Fox (1975), physiological or psychological stress has been associated with infanticide and cannibalism. Maternal cannibalism has also been suggested to be induced by unnatural laboratory environments and thus represents a non-adaptive behavior (Fedurek *et al.*, 2020). Stressful conditions can lead to a higher incidence of infanticide (Rimbach *et al.*, 2012). The biological responses of rodents may be affected by abnormal environments, such as temperature, photoperiod, and noise (Besch, 1980).

Table II. Notes on infanticide and cannibalism in *Tupaia belangeri* from two laboratory experiments.

Information	Experiment 1	Experiment 2
Original goal	Observation on individual behavior of <i>T. belangeri</i>	Effects of light intensity on behavior, learning memory and oxidative stress of <i>Tupaia belangeri</i>
Date	2017.4.10-2017.5.8	2019.8.22-2019.9.19
Type of feed	Larvae of <i>Tenebrio molitor</i> and apple	Standard solid feed
Experimental condition	Normal environment	200W illumination
Start time of parturition	4.16 09:59:20	8.25 10:33:48
End time of parturition	4.16 10:05:23	8.25 10:35:51
Duration of parturition (s)	363	123
Time ranges of lick behavior	4.16 10:09:53-10:38:28	8.25 10:34:12-10:34:15
Birth time in infants	The scope of birth sites was relatively concentrated, it was impossible to observe the birth time of each infants	8.25 10:33:51 No.2-1 8.25 10:34:18 No.2-2 8.25 10:35:51 No.2-3
Litter size	5	3
Number of infanticides	0	3
Number of cannibalism	1	3
Death time in infants	4.16 19:00:52 No.1-1 4.16 22:28:37 No.1-2 4.17 04:22:48 No.1-3 4.17 08:34:24 No.1-4 4.17 10:56:06 No.1-5	8.25 10:36:57 No.2-1 8.25 10:46:01 No.2-2 8.25 14:03:02 No.2-3
Manner of death in infants	Natural death	Be killed by mother
Time ranges of cannibalism	4.17 14:15:02-14:27:22 Cannibalised of No.1-3	8.25 10:36:57-10:40:02 Cannibalised of No.2-1 8.25 10:46:01-10:48:16 Cannibalised of No.2-2 8.25 11:59:09-12:00:35 Cannibalised the remnant of No.2-2 8.25 14:03:02-14:04:43 Cannibalised of No.2-3 8.25 16:34:47-16:35:19 Cannibalised the remnant of No.2-3

Note: Because it was impossible to observe the birth time of each infant, they were referred to as No.1-X and No.2-X in accordance with their death time in experiment 1 and experiment 2, respectively.

Tree shrews were clearly restless under the high strength of illumination in experiment 2; this, coupled with the fact that they killed their offspring and consumed them shortly after delivery, is consistent with the non-adaptive behavior hypothesis. The third possible explanation for the infanticidal and cannibalistic behaviors is that they reflect a response to psychological stress under abnormal environments (200-W illumination).

In summary, our study provides the first analysis of infanticide and cannibalism in *T. belangeri* as well as the first evidence of nursing and caring behaviors. Nutrition hypothesis, hormone level hypothesis and stress hypothesis are all related to the observations of cannibalism, which we expect is might related to the dietary habits of *T. belangeri*. In addition, because of the limited number of experimental animal samples, we need to further expand the number of samples to further determine which hypothesis led to this phenomenon.

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Supplementary material

There is supplementary material associated with this article. Access the material online at: <https://dx.doi.org/10.17582/journal.pjz/20210820090809>

Statement of conflicts of interest

The authors declare no conflicts of interest.

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