

1 **Title page**

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3 **Extra interesting phenomenon in the experiment: infanticide and**
4 **cannibalism in *Tupaia belangeri***

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15 **Abstract:** Maternal infanticide and cannibalism, whereby a mother killing and consumes her own
16 offspring, occurs in various animal taxa. The ability of the tree shrew (*Tupaia belangeri*) to kill and
17 consume conspecifics is accepted, but the extent of its occurrence is not fully understood due to
18 difficulty in observation and uneven reporting. Here we discover extra interesting phenomenon and
19 that two tree shrew respectively eating the neonate in two different experiments. This was the first
20 recorded of evidence by video clip that both infanticide/cannibalism and caring behavior for their
21 infants in *T. belangeri*. Through the analysis of video data, we conclude that the occurrence of
22 cannibalism behavior is more inclined to the nutrition hypothesis. In addition, we also speculated
23 for the first time that the infanticide and cannibalism of tree shrews is related to their dietary habits/

24structures. Although reactions to infants are doubtless influenced by tree shrew mothers'
25physiological or psychological stress status and environmental stimulation, the specific reasons of
26these phenomena need further studies.

27**Key words:** *Tupaia belangeri*, infanticide and cannibalism, nutrition hypothesis, dietary
28habits/structures, compensate of pregnancy, non-adaptive behaviour

29

30**Introduction**

31 It's an ubiquitous phenomenon that the occurrence of infanticide and cannibalism behavior
32in wild animals. In recent years, there have been in-depth studies on infanticide and cannibalism
33behavior in primates (Badescu *et al.*, 2016; Yao *et al.*, 2016), rodents (Haapakoski *et al.*, 2015;
34Schmidt *et al.*, 2015), ungulates (Gray, 2009; Bartos *et al.*, 2015), fishes (Jindal *et al.*, 2017), birds
35(Harris *et al.*, 2016) and other fields. Most mammalian populations have an instinctive response to
36protect and nurture their own offspring, which is to make their own genetic genes continue to pass
37on to their offspring, continue and expand their own population (Rilling & Young, 2014).
38However, infanticide and cannibalism are opposite to the protect and nurture behavior in some
39mammals (Hrdy, 2016).

40 Infanticide is the killing of infants by conspecifics (Agoramoorth & Mohnot, 1988). It was an
41interesting behavioural phenomenon from many viewpoints, several basic explanations for
42adaptive infanticide have been proposed: exploitation/cannibalism, resource competition, paternal
43manipulation, adoption avoidance, sexual selection and non-adaptive behaviour/pathology
44(Table 1) (Kral *et al.*, 2019). It may be divided into active killing or behaviours resulting in the
45death of offspring in terms of mode of occurrence; and parental or non-parental from the
46perspective of performance subjects (Smith, RL & Smith, P, 2019). Some scholars put forward that

47the breeding systems for some species or members of populations can promote behaviors such as
48infanticide, which have important consequences for individuals and populations (Haines *et al.*,
492018).

50 Cannibalism, the consumption of all or part of another individual or own cubs of the same
51species (Richardson *et al.*, 2010; Nishikawa, *et al.*, 2020). In mammals, the cannibalism is
52commonly associated with infanticide (Polis *et al.*, 1984), and it often follows appeared infanticide
53(Culot *et al.*, 2011). The maternal cannibalism of deceased infants is the most common situation
54(Tian *et al.*, 2016). Cannibalism of cubs may occur to reclaim limited resources or obtain
55additional resources during times of hardship (Bronson & Marsteller, 1985; Hrdy, 1979; Trulio,
561996). In rare cases, infanticide leads to cannibalisation of the dead juveniles (Fox, 1975; Hrdy,
571979). The incidence of cannibalism may be affected by the different metabolic requirements of
58the adults, which is due to the variable of gender, age and reproductive states of the adults
59involved (Ebensperger *et al.*, 2000).

60 *Tupaia belangeri* is a member of Tupaiidae of Scandentia, which is the only representative of
61Tupaiidae in China. As the metabolic system and anatomical structure of *T. belangeri* are closer to
62humans than mice, they are widely used in biomedical research as a new experimental animal
63model (Wilson *et al.*, 1994; Zhu *et al.*, 2010; Hou *et al.*, 2021). It generally lives in tropical rain
64forest, secondary forest and bush, and feeds on insects and fruits in wild forest. Tree shrews
65especially like larva of tenebrio, fruit is the second choice. Although plant food resources are
66abundant, but there are few animal food resources suitable for tree shrews in the wild
67environment. It have strong reproductive capacity, and the number of fetuses is generally 2 to 5
68(Yao, 2017).

69 In the present study, we provide details and extended thinking of a behavior observation of
70 parental infanticide and subsequent cannibalism in two different experiments about *T. belangeri*.
71 The purpose of this study was to explore the reasons of infanticide and cannibalism behavior of
72 tree shrews, and provide rationale for future breeding experiments of *T. belangeri*.

73 **Materials and methods**

74 *Original experiment 1: Observation on individual behavior of tree shrews*

75 *T. belangeri* were captured at the bosage of Luquan County, Yunnan Province in the spring
76 of 2017, and maintained at the School of Life Sciences, Yunnan Normal University, Kunming,
77 China. The animal acclimated to ambient temperature $25\pm 1^{\circ}\text{C}$, 12L: 12D, water was provided *ad*
78 *libitum* and domestication for 7 days. Then individual behavior was observed for 28 days. They
79 were provided with adequate larvae of *Tenebrio molitor* and apple in pre-parturition period. Before
80 the experiment, the pregnant state of the experimental animals was obvious, therefore, it is
81 necessary to observe the pre-parturition and post-parturition behavior in *T. belangeri* after delivery
82 and physiological state of infants.

83 *Original experiment 2: Effects of light intensity on behavior, learning memory and* 84 *oxidative stress of Tupaia belangeri*

85 *T. belangeri* were captured at the bosage of Luquan County, Yunnan Province in the summer
86 of 2019, and maintained at the School of Life Sciences, Yunnan Normal University, Kunming,
87 China. The animal acclimated to ambient temperature $25\pm 1^{\circ}\text{C}$, 12L: 12D, water was provided *ad*
88 *libitum* and domestication for 7 days. The animals were randomly divided into three groups: 50W
89 illumination group, 100W illumination group, 200W illumination group. During the experiment,
90 the animals were placed in the behavior observation device, and incandescent lamp was suspended

91at 120 cm above the device for light stimulation, the experiment time was 9:00-17:00 every day,
92each group lasted for 28 days. They were fed daily from 7:00 to 8:00 and 18:00 to 19:00. Tree
93shrews with infanticide and cannibalism behavior were in 200W illumination group, and before
94the experiment, the pregnant state of the experimental animals was not obvious, so it was not
95found.

96*Behavior observation*

97 The behavior observation device is a special instrument made of transparent acrylic plate
98(Fig. 1), there is a real-time surveillance camera on the top in behavior observation device (ES-
99N6009). The behavior observation device is also provided with a box for feeding. The mainonnette
100is equipped with 15W incandescent lamp for normal lighting. After each experiment, 75% alcohol
101was used to wipe and disinfect the behavior observation device.

102*Data analysis*

103 The video data obtained by the real-time surveillance camera is stored in the video capture
104hard disk, because the data will be covered within 7 days, so it is necessary to copy the data in
105time, then use the video software for observation and analysis, and recorded the behavior of tree
106shrews.

107**Result**

108*The pre-parturition and post-parturition behavior*

109 In the experiment 1, the pre-parturition disposition was gentle of tree shrews, there were
110almost no strenuous activities, and it was mostly licked their abdomen and pudenda, and
111occasionally feeding behavior. The scope of birth sites was relatively concentrated during delivery
112period of *T. belangeri*, and no extensive body movement. Therefore, it is impossible to observe the
113specific birth order and time of the five infants. The post-parturition disposition was also gentle,

114there was about 18 min to licked the head and body parts of the infants after delivery, then it to
115licked own pudenda and other body parts about 5 min. During this period, we observed the tree
116shrew covered the infants with small pad paper (Video. 1). After that, a large number of feeding
117behaviors were observed.

118 In the experiment 2, the pre-parturition disposition was irascible of tree shrews, and with a lot
119of strenuous activities. There was no behavior of licking the pudendal part of the abdomen. There
120was a wide range of body movement during delivery period of *T. belangeri*, the birth order and
121time of the three infants were observed. It was observed that the tree shrew licked to No.2-1 only
122about 3 seconds in the whole delivery period. The post-parturition disposition was also irascible of
123tree shrews, and activities were increased. After that, a large number of feeding behaviors were
124observed.

125*Infanticide and cannibalism information*

126 In the experiment 1, there was no infanticide in the tree shrew, and all the five infants died
127naturally (Table 2). But there was the cannibalism behavior, it only occurred on No.1-3. The time
128of cannibalism was the next day after delivery. Whole body of infants were eaten at one time
129without residue, it takes about 740 s.

130 In the experiment 2, the tree shrews had infanticide and cannibalism to their three infants
131when 66 s after delivery (Table 2). Cannibalism behavior occurred immediately after infanticide. It
132takes about 185 s to cannibalised the whole body of No.2-1 at one time. It was divided into two
133times when cannibalised No.2-2 and total time used 221 s, it takes about 135 s to cannibalised all
134the body parts except the head for the first time, and about 86 s to cannibalised the residual head
135for the second time. It was also divided into two times when cannibalised No.2-3 while the order

136was different, it takes about 101 s to cannibalised the head for the first time (Video. 2), and about
13732 s to cannibalised the cannibalised the remnant for the second time, and the total time used 133
138s.

139Discussion

140 The metabolic levels of hormones such as oxytocin and steroids are especially high in the
141second half of pregnancy and play a role in the maternal behavioral expression (Saltzman &
142Maestriperieri, 2011; Bercovitch, 2020). Animals would go through the process of treating a infant
143cadaver from as if it were alive to treating it as a food, and these might be due to behavioral
144changes caused by physiological changes of hormone levels (Watson & Matsuzawa, 2018). If
145cannibalism occurs at the end of pregnancy, it is consistent with the gradual weakening of mother-
146infant relationship and the decline of hormone metabolism (Saltzman & Maestriperieri, 2011;
147Trapanese *et al.*, 2020). Elgar & Crespi (1992) considered that in case of the cannibalistic
148behaviour after a short period of maternal care, it might be that the mothers compensating for the
149energy consumed during pregnancy. Our observation supports this hypothesis in experiment 1: the
150tree shrews would take care of its cubs at the time of post-parturition, and then the cannibalistic
151behaviours occurs after a long time (Table 2). The first reason might be that the tree shrews'
152hormone levels had changes during pregnancy, thus this leads to the occurrence of cannibalism. It
153is necessary and significant to determine the hormone levels of *T. belangeri* during pregnancy in
154the future of cannibalism.

155 *T. belangeri* are omnivorous and have partiality for larvae of *Tenebrio molitor* (Peng *et al.*,
1561991). Sufficient food was provided in the early stage of experiment 1 and the whole process in
157experiment 2. In the literature, food scarcity is considered one of the main factors related to

158infanticide and cannibalistic behaviour in animals (Getto *et al.*, 2005; Duarte *et al.*, 2010). The
159cannibalistic behaviours occurred at a condition where food resources were ample, which is
160contradict with ecological theory that cannibalism mostly occurs where resources are finite (Meek
161& Brown, 2017). However, the phenomenon fits the nutritional hypothesis well (Hrdy, 1979;
162Ebensperger, 1998), since the cannibalism behavior assumes that eating the the same animal
163provides nutritional benefits for the participating individuals, and may increase the success rate of
164reproduction in the future (Fox, 1975; Klug & Bonsall, 2007; Nishikawa *et al.*, 2020). Therefore,
165the event presented in this study can be explained by this hypothesis. In mammals, pregnancy
166increases daily energy consumption by 20%-30% (Aiello & Wells, 2002). There was no
167carnivorous food in the later stage of experiment 1 and the whole process of experiment 2. The
168second reason might be that tree shrews might have been motivated by desire for carnivorous
169food, we thus suggest that the necessity of carnivorous food resources might have favoured the
170event of cannibalism. In addition, we also speculated for the first time that the infanticide and
171cannibalism of tree shrews is related to their dietary habits/structures.

172 Depending on the description by Fox (1975), physiological or psychological stress has been
173associated with infanticide and cannibalism. other scholars also suggested that maternal
174cannibalism is caused by unnatural laboratory environments, and therefore represents a non-
175adaptive behavior (Tokuyama *et al.*, 2017; Fedurek *et al.*, 2020). Stressful conditions can account
176for a higher incidence of infanticide (Rimbach *et al.*, 2012). The biological responses of rodents
177may be influenced by abnormal environments, such as temperature, photoperiod, and noise
178(Besch, 1980). Our results indicate that the tree shrew were very restless under high strength of
179illumination in experiment 2, and almost in a short time had infanticide and cannibalism after

180delivery, which most closely accords with the non-adaptive behavior hypothesis base on the stress.
181The third reason might be that tree shrews have psychological stress under abnormal environments
182(200W illumination). Future research, could examine the abnormal environment hypothesis via
183advanced scientific and technological for infanticide and cannibalism of *T. belangeri*.

184 Interestingly, our observation showed an interesting, endearing and meaningful scene was
185that the *T. belangeri* covered the infants with small pad paper, it's similar to mothers' love for
186children in human (Video. 1). At the same time, unfortunately, we recorded the action of cruelty
187that infanticide and cannibalism behavior in tree shrews (Video. 2). This was the first recorded of
188evidence by dynamic picture that both infanticide/cannibalism and caring behavior for their
189infants in *T. belangeri*. By comparing the conditions and results of experiment 1 and 2, it can be
190inferred that the cause of infanticide and feeding behavior of tree shrews may be more inclined to
191the nutrition hypothesis, and the hormone level hypothesis and stress hypothesis may also be the
192main reasons, but the specific regulatory mechanism needs further study.

193 In conclusion, our observation of infanticide and cannibalism in *T. belangeri* is thus
194significant as both the first depth analysis of infanticide and cannibalism in this species, but also as
195the first documented evidence by video of nursing or caring behaviours. The occurrence of
196cannibalism behavior is more inclined to the nutrition hypothesis, but we also speculate that it is
197related to their dietary habits/structures in *T. belangeri*. Although reactions to infants are doubtless
198influenced by tree shrew mothers' physiological or psychological stress status and environmental
199stimulation, the specific reasons of these phenomena need further studies.

200Data Accessibility

201video data files: figshare doi: <https://doi.org/10.6084/m9.figshare.14273666.v1>

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322**Table 1.** 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 & 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 & 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 infanticidal 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 Nogueira <i>et al.</i> , 1999 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 & Garcia, 2015 Smith, RL & Smith, P, 2019

323Note: Some of them are quoted from Kral *et al.*, 2019

324**Table 2.** Infanticide and cannibalism information of tree shrew in two 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

325Note: Because it's impossible to observed the birth time of each infants, so they were named by

326No.1-X according to the order of death time in the experiment 1; the infants were named by No.2-

327X according to the order of birth time in the experiment 2.

328**Ethics statement**

329All applicable the Animal Care and Use Committee of the School of Life Sciences, Yunnan

330Normal University for the care and use of animals were followed (No. 13-0901-011).

331

332**Conflict of interest statement**

333The authors declare no conflict of interest.

334

335**Funding statement**

336This research was financially supported by National Science Foundation of China (No. 31760118),

337Young and Middle-aged Academic and Technical Leaders Reserve Talents Project of Yunnan

338Province (2019HB013) and Young Top-Notch Talent for “Ten Thousand Talents Program” of

339Yunnan (YNWR-QNRC-2019-047).

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341**Figure 1.** The behavior observation device sketch map

342

343**Supporting Information**

344**Video 1.** Cover the infants with small pad paper in tree shrew

345**Video 2.** Infanticide and cannibalism behavior in tree shrew