

Influence of intra- and inter-specific competitions on food hoarding behaviour of buff-breasted rat (*Rattus flavipectus*)

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Food hoarding behavior of sympatric conspecific rodents has been extensively documented during the last decades, while research concerning the influence of intraand inter-specific competition on hoarding behaviour of rodents is limited. We investigated food hoarding behaviour of buff-breasted rat (Rattus flavipectus) under conditions of semi-natural enclosures in the tropical rain-forest of the Xishuangbanna area (altitude 475-2430 m, 21°09'-22°36'N, 99°58'-101°50'E), Yunnan Province, Southwest China. The main goal of this study was to understand the influence of intra- and inter-specific competition on food hoarding behaviour of rodents. Seeds of Lithocarpus truncatus (Fagaceae), with woody and hard seed coat, were selected and marked as a food item in this experiment. The result showed that: (1) R. flavipectus mainly exhibited food hoarding behaviour in larder form; and (2) the presence of intra-specific competitors significantly increased larder hoarding in R. flavipectus, while an inter-specific competitor. Chinese white-bellied rat (*Niviventor confucianus*). exerted no significant influence on food hoarding behaviour of subjects. These results indicated that rodent species would adjust their food hoarding behaviour in the presence of competitors, and intra-specific competition has a greater effect than inter-specific competition.

KEY WORDS: *Rattus flavipectus*, seed hoarding, intra- and inter-specific competition, *Lithocarpus truncatus*, Xishuangbanna.

INTRODUCTION

Many species of rodent hoard seeds which they feed on periods of food shortage (SMITH & REICHMAN 1984; VANDER WALL 1990; HURLY & LOURIE 1997; JENKINS & BRECK 1998). Food hoarding enhances the chance of animal survival during periods of food scarcity (SMITH & REICHMAN 1984; CLARKSON et al. 1986; VANDER WALL 1990, 1995; LEE 2002), and gives hoarders an advantage over non-hoarders (CHENG et al.

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2005a). There are two types of hoarding behaviour: scatter-hoarding, where animals store their food in numerous small caches; and larder-hoarding, which entails storing repeated loads of food in a single place. Scatter- and larder-hoarding are polarisation of food hoarding in animals (VANDER WALL 1990; LI & ZHANG 2001).

The selection of food hoarding pattern in animals, larder- or scatter-hoarding, is influenced by numerous factors including conspecific and/or heterospecific competition, body size of the hoarder, food availability and pilfering (VANDER WALL 1990; GERHARDT 2005). Competition is regarded as an important factor influencing food hoarding in rodents (SANCHEZ & REICHMAN 1987; VANDER WALL 1990). They have evolved a range of strategies to reduce loss in stored food, such as avoiding storing food in the presence of conspecific or heterospecific individuals (BURNELL & TOMBACK 1985; CARRASCAL & MORENO 1993; LAHTI & RYTKONEN 1996; BROTONS 2000; BUGNYAR & KOTRSCHAL 2002). For example, Merriam's kangaroo rats (Dipodomys *merriami*) living in an environment with predominant conspecific competitors scatterhoard more than those living in an environment with fewer conspecific competitors or in the presence of heterospecific competitors (MURRAY et al. 2006). It has also been reported that the presence of conspecific flock has a negative influence on caching behaviour in food-hoarding bird species (GAMMON & BAKER 2004). Caching grey squirrels (Sciurus carolinensis) remain sensitive to the presence of conspecific individuals until the cache is completed and they respond flexibly to conspecifics according to the type of food they stored (HOPEWELL & LEAVER 2008).

According to the Competition Theory (SANCHEZ & REICHMAN 1987), animals would like to speed up the hoarding process and might change their food hoarding behaviour when competitors are coming into sight. A number of cache protection strategies may be deployed by hoarding animals, such as caching in areas of low conspecific density (CLARKSON et al. 1986; BUGNYAR & KOTRSCHAL 2002), or waiting until would-be pilferers are distracted or out of sight (HEINRICH 1999). Some species are also known to return alone to hide caches in the presence of conspecifics, and re-cache them in new places unbeknown to potential thieves (HEINRICH 1999; EMERY & CLAYTON 2001). Western scrub-jays (*Aphelocoma californica*) preferred to hide items in distant sites when watched by another jay, but used near and distant sites equally when the observer's view was obscured by a screen (DALLY et al. 2005). Animals thus adopted reciprocal strategy on preying and protected more food. The difference in food hoarding behaviour among species, to food hoarding animals, is an important matter for alleviating competition of food resources for coexistence (JENKINS & BRECK 1998).

A majority of studies on food hoarding of rodents have focused on the differences in seed choice (JOHNSON & JORGENSEN 1981; KERLEY & ERASMUS 1991; CHENG et al. 2005b; LU & ZHANG 2008) and the differentiation in microhabitats where seeds were hoarded (PRICE 1977; BROWN 1988; BOUSKILA 1995; LEAVER & DALY 2001). The influence of intra- and inter-specific competition on the hoarding behaviour of rodents has rarely been addressed. We think that, in the field, rodent species are very likely to encounter intra- and inter-specific competitors during their foraging activities. Consequently, rodents have to adjust their hoarding behaviour in the presence of competitors. We thus intended to evaluate how rodents justify their food hoarding behaviour under different competitive patterns. To investigate this question, here we used the buff-breasted rat (*Rattus flavipectus*), which is widely distributed in tropical rain forests, tropical seasonal moist forests and buildings in the Xishuangbanna area, Yunnan, Southwest China. It is one of the dominant species in the local community of small mammals (SHOU 1962). As an omnivorous species under natural conditions, food items consumed by *R. flavipectus* include seeds, nuts, acorns and crop seeds (SHOU 1962). In this study, seeds of *Lithocarpus truncatus* were used as a food item to study the food hoarding behaviour of *R. flavipectus*. The aims of this study are to document the pattern of food hoarding of *R. flavipectus* and investigate the effects of intra- and inter-specific competitions on food hoarding behaviour of this animal.

STUDY AREA

This study was conducted in the Xishuangbanna region (altitude 475–2430 m, 21°09'-22°36'N, 99°58'-101°50'E) of Yunnan province, Southwest China. The region has mountain-valley topography with the Hengduan Mountains running north-south, and about 95% of the region is covered by mountains and hills. The Mekong River flows through the centre of this area, and the region contributes more than 20 important tributaries, resulting in many river valleys and small basins (LI et al. 2008). The climate is influenced by warm-wet air masses from the Indian Ocean in summer, continental air masses of subtropical origin in winter, resulting in a rainy season from May to October, and a dry season from November to April (ZHANG 1988). The annual rainfall ranges from 1200 to 1800 mm. The annual temperature is 15.2 °C. The annual sunshine has a mean of 800~1000 h (CHEN 2000; XIAO et al. 2004). Within the tropical rain forest in the Xishuangbanna region, there are plenty species of shrub, tropical lianas and trees including Cleistanthus sumatranus, Sumbaviopsis albicans, Celtis philippensis var. wightii, Dracaena cochinchinensis, Bombax insignis (ZHU 2007). Nonetheless, the local ecosystem has been severely disturbed by economic activities such as artificial cutting and slash-and-burn cultivation by local people over past decades. The current forest coverage is no more than 30%, about 25% lower than in the 1950s. The decrease of aboriginal forests led to the reduction of the rain forest's function and the species diversity in this area.

MATERIALS AND METHODS

Experimental animals

All experimental animals, buff-breasted rat (*R. flavipectus*) and Chinese white-bellied rat (*Niviventor confucianus*), were captured with live traps ($12 \text{ cm} \times 12 \text{ cm} \times 25 \text{ cm}$, made of steel wire, baited with peanuts) from January–March 2009. Immediately after capture, animals were weighed, numbered and individually maintained in plastic boxes ($37 \text{ cm} \times 26 \text{ cm} \times 17 \text{ cm}$). Animals were given free access to corn and water throughout the holding period. Lighting reflected natural day lengths during the study period. A total of 12 healthy non-pregnant adult *R. flavipectus* (body weight 151.28 ± 4.28 g, mean \pm SE) were used as experimental subjects. The other 8 healthy adult *R. flavipectus* were used as intra-specific competitors, while 12 healthy adult *N. confucianus* (with body weight 69.75 ± 3.62 g, mean \pm SE) were used as inter-specific competitors. Each experimental subject was used only once, whereas the competitors could be used repeatedly in the whole experimental period. All experimental animals were fed every day for a week before the tests to habituate them to the food. The current animal study was approved by the Ethics Committee of Zhengzhou University. The protocol of the investigation was in accordance with the principles outlined in the China Practice for the Care and Use of Laboratory Animals.

Seed collection and marking

Lithocarpus truncatus (Fagaceae) exist widely in the tropical rain-forest (our study area). The seed has a woody and hard coat. Mature intact seeds $(1.19 \pm 0.31 \text{ g}, \text{mean} \pm \text{SE}, n = 50 \text{ in})$

fresh weight) were collected during the fruiting periods. Seeds were marked following the method of ZHANG & WANG (2001). A tiny hole was drilled in each seed and a small, light plastic label (3 cm long and 2 cm wide) was connected to a 10 cm long fine wire. The labels were coded using a waterproof pen. They were easily seen after animals buried the seeds because the label remained on the soil surface. The labels did not significantly change the food hoarding behaviour of these rodents due to their negligible weight (0.1 g) relative to the weight of the food items (LU & ZHANG 2004; XIAO et al. 2004, 2006).

Enclosure design

Four semi-natural enclosures (length \times width \times height = 10 m \times 10 m \times 1.5 m) were constructed in an artificial rubber forest that has been used in many studies (LU & ZHANG 2005b, 2008; WANG et al. 2007; ZHANG & ZHANG 2007). The enclosure walls were constructed of bricks and the floor was concrete covered to prevent subjects from escaping by digging underground. The top of the enclosures was covered with wire mesh to prevent predators coming from outside, and the escape of the experimental animals. A 20 cm deep layer of soil was placed over the bottom of the enclosure to allow the animals to bury hoarded seeds. A wire nest box (40 cm \times 30 cm \times 20 cm) with a small open door was placed in one corner of each enclosure for the subjects. A water dish was placed next to each nest box. All food items were provided in a wooden feeder that was located in the centre of each enclosure. To define the position of seeds, we virtually divided each enclosure into four quadrants, and referred to the quadrant containing the nest box as quadrant II.

Experimental design

One week before experiments, all subjects were fed with L. truncatus seeds to habituate them to the food. All subjects were deprived of food for 6 hr prior to being placed into the enclosures, and allowed to adapt to the new environment for about 3 hr before the seeds were provided. One experimental round comprised four sequential days including: habituation day (Day 0), control day (Day 1), intra-specific competition day (Day 2) and inter-specific competition day (Day 3). In the morning (at 10:00) of the habituation day (Day 0), one R. flavipectus wasere randomly assigned to each enclosure. Forty marked L. truncatus seeds were then placed in the feeder at about 16:00. In the morning (at 08:00–09:00) of control day (Day 1), the experimental subjects were remained kept in the enclosures, while all the seeds released on day 0 (including eaten, removed and remaining) were taken out and the nest-box was cleaned up and the water in the water dish was replaced. At 16:00 on Day 1, another 40 marked seeds of L. truncatus were placed in the feeder. In the morning (at 08:00–09:00) of the next day (Day 2), the status and location of each marked seeds were checked and recorded following LU & ZHANG (2005a, 2005b): (i) eaten in situ (EI): the tagged seeds were eaten at or near the feeder; (ii) eaten after removal (ER): the tagged seeds were eaten on the ground surface after removal; (iii) buried in soil (B): the tagged seeds were buried in soil and they were intact; (iv) entered nest (EN): the tagged seeds were transported into the nest box; (v) abandoned on the surface (AS): the tagged seeds were abandoned intact on the ground surface after removal; and (vi) intact in situ (IS): the tagged seeds were intact in situ. Data from this day were referred to as control. Then, all the seeds released on Day 1 (including eaten, removed and remaining) were taken away and the nest box was cleaned up and the water in the water dish was replaced, while the tested subject remained in the enclosure. At 16:00 on Day 2, another 40 marked seeds of L. truncatus were placed in the feeder. Then a single individual of R. flavipectus was confined to a nest box placed in the opposite corner to the nest box of the hoarder. The experimental subject could sense the competitor's presence, but the two animals could not touch one other. We repeated seed checking and recording as we did on the morning of Day 3. Data from this experimental day were regarded as intra-specific competition. To minimise the odour effect of the previous competitor, the soils were mixed well before the next step. At 16:00 on Day 3, the intra-specific competitors were taken out from each enclosure, and an adult N. confucianus that

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was confined in its nest box, referred to as the inter-specific competitor, was put into each enclosure. In the morning of Day 4, checking and recording were done, and data from this experimental day were regarded as inter-specific competition. This was the end of the first experimental round. Tested animals and competitors were then taken out of enclosures, all the seeds released on Day 3 were taken away, the nest-box was cleaned up, and the water in the water dish was replaced, and the soils in each enclosure were mixed again. The enclosures were not used for at least one day before the next experimental round.

The second round of the experiment was conducted hereafter. Another 4 animals were introduced into each enclosure, and the procedures were repeated. A total of 12 adult *R. flavipectus* were tested in this research. Our experiments were conducted from February–March 2009.

Statistics and analysis

All data were analysed using SPSS for Windows (Version 16.0). We combined the data from males and females. The Wilcoxon test was used to determine the differences between the data: (1) of intra-specific competition and control treatment; and (2) with and without competition.

RESULTS

Food hoarding strategy of R. flavipectus

To study the food hoarding strategy of R. flavipectus, we first counted the number of seeds with different fates based on the categories described earlier. Under natural conditions, when rodents encounter a food source they will treat it in different ways, for example, hoarding it, feeding on it or abandoning it. The fate of the seeds reflects the rodents' ability in protecting their storage and under field conditions the strong protection of food coincides with a large amount of storage. In this study, seeds that were transported into the nest box (EN) were considered as larder-hoarding, and seeds that were buried in the soil (B) of the enclosures were defined as scatter-hoarding, which is in line with the definition in previous studies (SMITH & REICHMAN 1984; VANDER WALL 1990; JENKINS & BRECK 1998). On the control day (Day 1, without competition), R. flavipectus removed total 152 (EN) among 480 marked seeds of L. truncatus into the nest-box from the feeder (Table 1). Six (EI) seeds were eaten in situ and five (ER) seeds were eaten after removal. Although 10 (AS) marked seeds were found abandoned on the soil surface along the wall of the enclosures, no seed was separately buried by animals in soil within enclosures (Table 1), indicating no scatter-hoarding. This result suggested that larder-hoarding was the main form adopted by *R. flavipectus* during food hoarding.

Effect of intra-specific competition on food hoarding of R. flavipectus

On the intra-specific experimental day (Day 2), in the presence of intra-specific interaction, *R. flavipectus* moved a total of 256 seeds into the nest box for larder-hoarding (Table 1). Intra-specific competition significantly increased the number of larder-hoarded seeds (Z = -2.268, P = 0.023) by our experimental animals. There were fewer IS (intact in situ) seeds (Z = -2.317, P = 0.021) than without competitors on

Table 1.

Experiment group	Status of seeds						
		IS	EN	EI	ER	В	AS
Control	Mean ± SE Range Total	$25.6 \pm 2.8 \\ 0-38 \\ 307$	$12.7 \pm 3.0 \\ 0-40 \\ 152$	0.5 ± 0.2 0-2 6	$0.4 \pm 0.2 \\ 0-2 \\ 5$	0 0 0	$0.8 \pm 0.4 \\ 0-3 \\ 10$
Intra-specific competition	Mean ± SE Range Total	$16.3 \pm 2.9 \\ 0-34 \\ 196$	$21.3 \pm 3.2 \\ 5-40 \\ 256$	$0.3 \pm 0.1 \\ 0-1 \\ 3$	$0.3 \pm 0.1 \\ 0-1 \\ 3$	0 0 0	$1.6 \pm 0.6 \\ 0-6 \\ 19$
Inter-specific competition	Mean ± SE Range Total	$21.6 \pm 3.0 \\ 0-38 \\ 259$	$16.0 \pm 3.0 \\ 2-40 \\ 192$	0.4 ± 0.2 0-2 5	$0.9 \pm 0.5 \\ 0-6 \\ 11$	0 0 0	1.1 ± 0.4 0-4 13

Status of Lithocarpus truncatus seeds after treatment by Rattus flavipectus.

Note: IS: intact in situ; EN: entered nest; EI: eaten in situ; ER: eaten after removal; B: buried in soil; AS: abandoned on the surface.



Fig. 1. — Seed fate status of seeds of *Lithocarpus truncatus* after hoarding by *Rattus flavipectus* under the conditions of control, intra-specific competition and inter-specific competition. IS: intact in situ; EN: entered nest; EI: eaten in situ; ER: eaten after removal; B: buried; AS: abandoned on the surface.

Day 1. Fewer seeds were eaten in situ and after removal when the intra-specific competitors existed (Table 1). There were no significant differences in the number of EI (Z = -1.000, P = 0.317), ER (Z = -1.414, P = 0.157) and AS seeds (Z = -1.199, P = 0.230) between Day 2 and Day 1 (Fig. 1). On intra-specific day (Day 2), no seeds were scatter-hoarded. The most of ER seeds were found near the edge of enclosures (Fig. 2b). The majority of AS seeds were located between the nest box and the feeder (Fig. 3b), possibly because they were dropped in the course of transportation. These data suggested that intra-specific competition significantly increased the larder-hoarding of *R. flavipectus*.



Fig. 2. — Distribution of *Lithocarpus truncatus* seeds eaten by *Rattus flavipectus* after removal within the enclosure. (a) Control; (b) intra-specific competition; (c) inter-specific competition.



Fig. 3. — Distribution of *Lithocarpus truncatus* seeds abandoned on the soil surface by *Rattus flavipectus* within enclosures. (a) Control; (b) intra-specific competition; (c) inter-specific competition.

Effect of inter-specific competition on food hoarding of R. flavipectus

When confronted with competition from inter-specific individuals on the interspecific day (Day 3), *R. flavipectus* transported 192 marked seeds into the nest box for larder-hoarding, which was more than on the control day but less than on the intra-specific competition day. The increase of EN seeds was not statistically significant compared to the no competition day 1 (Z = -0.890, P = 0.373) (Table 1). Compared with data on Day 1, the variations in IS seeds (Z = -1.139, P = 0.255), EN seeds (Z = -0.890, P = 0.373), EI seeds (Z = -0.378, P = 0.705), ER seeds (Z = -1.186, P = 0.236), and AS seeds (Z = -0.638, P = 0.524) were all insignificant (Fig. 1). These data suggested that although inter-specific competition increased large-hoarding of *R. flavipectus*, the difference was insignificant.

Comparison of intra- and inter-specific competition on food hoarding of R. flavipectus

When we compared the effect of intra- and inter-specific competition on food hoarding, we observed a significant difference in the number of EN seeds (Z = -1.989, P = 0.047), suggesting that intra- and inter-specific competition have different effects

on larder-hoarding. There were no significant differences in the number of IS seeds (Z = -1.581, P = 0.114), EI seeds (Z = -0.816, P = 0.414), ER seeds (Z = -1.511, P = 0.131), and AS seeds (Z = -1.850, P = 0.395) between Day 1 and Day 2 (Fig. 1).

DISCUSSION

Animals have various food hoarding behaviours that change with age, sex, features of the food, season and predation risk (VANDER WALL 1990; LEAVER 2004). Larder-hoarding allows rodents to guard food from pilfering, while scatter-hoarding provides potential resources if nests are overtaken or destroyed. Here, our results showed that *R. flavipectus* showed only larder-hoarding behaviour with or without the competition. The choice of food hoarding strategy is influenced by the hoarders' ability to defend stored food (VANDER WALL & JENKINS 2002). Inter-species dominant status is generally correlated with a larger body size. In the tropical rain-forest in the Xishuangbanna area, species of *R. flavipectus* have a relatively bigger body size compared with other rodent species; they thus might protect their hoarded food more effectively. Therefore, our results support the hypothesis that animal species that have larger bodies are more capable of defending stored foods and may tend to show larder hoarding (LU & ZHANG 2008).

When we started this study, according to VANDER WALL (1990), we proposed three possible consequences about the influence of intra-specific competition on food hoarding behaviour. First, in the presence of conspecific competitors, food hoarders may hoard fewer food items in order to decrease the likelihood of pilferage as pilferage has been shown to be a general phenomenon among different conspecific individuals (Kallander 1978; James & Verbeek 1983; Sanchez & Reichman 1987; Stone & BAKER 1989; DALY et al. 1992; MAPPES 1998; PRESTON & JACOBS 2001; CHENG et al. 2005b). Consequently, the presence of conspecific competitors could restrain the food hoarding behaviour to minimise the possibility that the caches would be pilfered. Second, the presence of conspecific competitors would stimulate experimental animals to possess and hoard more seeds, and then their food hoarding behaviour would be strengthened. For example, the presence of a conspecific competitor promoted Edward's rats (Leopoldamys edwardsi) to not only bury more seeds but also bury these seeds much farther away from where the seeds were released (or where the seeds dropped on the ground) (CHENG et al. 2005b). When white-footed mice (Peromyscus leucopus) were kept in the same cages, they decreased the number of seeds buried distinctly (SANCHEZ & REICHMAN 1987). The smell of conspecific individuals has also been shown to make bank voles hoard more food at the end of the breeding season (MAPPES 1998). Third, for the food hoarders that are social or cooperative, the presence of conspecific competitors would stimulate food hoarding behaviour. For instance, one honey bee in a group of 30-50 individuals will hoard more food than one does in a group of 10 (RINDERER & BAXTER 1978); for male and female grey squirrels (Sciurus carolinensis), related squirrels lived significantly closer to one another than unrelated squirrels (SPRITZER & BRAZEAU 2003). In our experiment, in the presence of intra-specific competitors, experimental animals removed significantly more seeds into the nest box for larder-hoarding. Although the presence of inter-specific competition also increased EN seeds, it was not statistically significant. This result suggests that intra-specific competition remarkably enhances the food hoarding behaviour of R. flavipectus. Therefore, our data support the second hypothesis.

The interactions among conspecific individuals do not behave in a single way. There might be competition as well as cooperation. Merriam's kangaroo rats (*Dipodomys merriami*) living in a system where competitors are predominantly conspecific rodents scatter-hoard more seeds than those individuals living in a system where conspecifics are less abundant and heterospecific competitors are also present (MURRAY et al. 2006). Communal caching has also been documented for acorn woodpeckers (*Melanerpes formicivorus*), taiga voles (*Microtus xanthognathus*), Mongolian gerbils (*Meriones unguiculatus*), beavers (*Castor canadensis*) and numerous social insects (MUMME & DEQUEIROZ 1985; VANDER WALL 1990). In this study, we showed that *R. flavipectus* increased the number of seeds that were transported into the nest box when conspecific individuals came into sight whereas we did not observe any cooperation between conspecific individuals of *R. flavipectus*.

The coexistence of ecologically similar rodent species has been a subject of interest for decades (LEAVER & DALY 2001), but most of the studies have been focused on differentiation of food composition (CHENG et al. 2005a; WAUTERS et al. 2005), food hoarding forms (LEAVER & DALY 2001; PRICE & MITTLER 2006) and the change in feeding space and time (WAUTERS et al. 2005). The investigation into the change in food hoarding behaviour remains in controversy. The results from our study indicate that *N. confucianus* have no significant influence on the food hoarding behaviour of *R. flavipectus* (Z = -0.890, P = 0.373). The reason may be that *R. flavipectus* have a larger body size than *N. confucianus*, and thus could protect their larderhoarded food effectively. In a future experiment, it would be of interest to see whether a larger heterospecific rodent would produce a different result. In this study, intraspecific but not inter-specific competition significantly strengthened the larder-hoarding (Z = -1.989, P = 0.047), suggesting that the effect of intra-specific competition on larder-hoarding behaviour of *R. flavipectus* is greater than that of inter-specific competition.

In several previous studies concerning the effects of competition on food hoarding behaviour, the control groups awere arranged in parallely with the tested groups throughout the experiment period (PRESTON & JACOBS 2001; CHENG et al. 2005b). The results from the current research provided some information about adjustments in rodent food hoarding behaviour under conditions in the presence of inter- and intra-specific competitions.

In conclusion, our study documented the caching pattern and its variation on *R. flavipectus* under enclosure conditions with and without competition. *R. flavipectus* performed only larder-hoarding for food storage regardless of competition. An environment with competition enhances the food hoarding of *R. flavipectus*, and intraspecific competition has a greater effect than inter-specific competition. The variation in food hoarding behaviour of *R. flavipectus* under natural conditions needs to be further investigated.

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