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The Activity Patterns of Sympatric Red-Bellied Squirrels (*Callosciurus erythraeus*) and Northern Tree Shrews (*Tupaia belangeri*) using Camera-Traps in Karst Habitat, Guangxi, China

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QHZ conceived and designed the study. GHW, LJW, JFL, ZQ, WY contributed in field data collection and processing. GHW wrote the article. QHZ and CBT modify.

Key words
Red-bellied squirrels (*Callosciurus erythraeus*), Northern tree shrews (*Tupaia belangeri*), Daily activity patterns, Karst habitat, Time niche differentiation.

ABSTRACT

Understanding wildlife activity and the temporal niches of animals is fundamental in revealing the mechanism of niche differentiation among sympatric species and the coexistence of such species communities. However, there is no clarity on whether the activity patterns of the sympatric species red-bellied squirrels (*Callosciurus erythraeus*) and Northern tree shrews (*Tupaia belangeri*) overlap; knowledge on the coexistence mechanism of these animals in the karst habitat is also minimal. Herein, we used camera traps to collect photos and research the activity patterns by using kernel density estimation and coefficient of overlap to explore the animals' time niche differentiation. Both species were found to be typical diurnal animals with two peaks in daily activity (red-bellied squirrels: 07:00-08:00 and 17:00-18:00; Northern tree shrews: 06:00-07:00 and 17:00-18:00). The overlap coefficients of red-bellied squirrels and Northern tree shrews were significantly different in dry season and rainy season. The overlap coefficients between red-bellied squirrels and Northern tree shrews was high (Δ=0.86), with significant differences in both dry season and rainy season. The activity duration of red-bellied squirrels was significantly lower than that of Northern tree shrews (5.49±0.57 vs. 6.80±0.63 s), but the activity temperature was just the opposite (22.19±0.60 vs. 20.82±0.40 ℃). Therefore, we conclude that the sympatric red-bellied squirrels and Northern tree shrews coexist successfully by adjusting their respective activity duration and temperature to reduce interspecific competition.

INTRODUCTION

Comparative studies of sympatric species are essential in understanding their behavioral and ecological adaptations as well as their coexistence mechanisms (Bu *et al*., 2016; Zhou *et al*., 2014). The competitive exclusion principle is often used to explain the conditions under which sympatric species may coexist (Davies *et al*., 2007; Schreier *et al*., 2010). Niche separation appears to have evolved as a mechanism to reduce strong negative effects on each other (e.g., limiting their population sizes), and make the coexistence of different species possible (Jacomo *et al*., 2004; Vieira and Port, 2007). When resources are limiting, sympatric species can mitigate the negative impact of interspecific competition by changing their diet choice, spatial use of the habitat, and activity pattern, for successful coexistence (Davies *et al*., 2007; Dayan and Simberloff, 2005).

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The activity pattern of an animal, which is a relatively stable routine procedure of the animal to complete various necessary activities every day, is the result of the comprehensive adaption of animals to changes in their habitat (Hanya *et al*., 2018). Activity patterns in animals are related directly to a variety of ecological factors, including availability of prey, risk of predation, and competition; studying the activity patterns of sympatric species is helpful to reveal the coexistence mechanism between different species (Ferreguetti *et al*., 2015; Neiswenter *et al*., 2010). Previous studies have found that two sympatric foxes with similar body size and feeding habits mainly reduced the competition for food resources by using different habitats and adjusting their activity patterns; *Lycalopex gymnocercus* reduced its activity at times when the activity of the presumably dominant *Cerdocyon thous* was high (Di-bitetti *et al*., 2009).

Red-bellied squirrels belongs to the squirrel family of rodents and inhabits the evergreen broad-leaved forests of the subtropical mountainous areas. Its diet is mainly composed of plants, fruits, flowers, seeds, and young leaves, and the food composition changes with seasons (Yuan *et al*., 2013). Some studies have shown that red-bellied squirrels to be typical diurnal animals with two activity peaks at 05:00-08:00 and 15:00-18:00 (Yuan *et al*., 2019) or 7:00-8:00 and 17:00-18:00 (Tang *et al*., 2020). Northern tree shrews, belonging to the tree shrew, inhabits the tropical and subtropical evergreen deciduous broad-leaved secondary forests across south Asia, southeast Asia, south and southwest China (Emmons, 2000). Northern tree shrews is an omnivorous animal with two activity peaks at 07:00-08:00 and 16:00-17:00 (Tang *et al*., 2022). Red-bellied squirrels and Northern tree shrews are both arboreal small mammals and sympatric species in the Nonggang National Nature Reserve. Previous studies have shown that there was obvious overlap in the activity patterns of sympatric species (Di-bitetti *et al*., 2009; Hadi *et al*., 2012), but there was no clarity on the coexistence mechanism of red-bellied squirrels and Northern tree shrews and whether their activity patterns also overlaped.

The karst habitat of southwestern China is among the most spectacular examples of tropical-subtropical karst formations. It is rich in animal resources (Li *et al*., 2021), but due to the poor local environment, it is difficult to collect detailed information on the activity patterns of animals using conventional methods. However, camera traps represent a non-invasive technology, and abundant data are obtained in short sampling periods, and with lower financial costs than the traditional method of capturing and recapturing the individuals. Thus, it has been proposed as an effective tool for studying and monitoring wildlife activity patterns (Luo *et al*., 2019). In this study, we used camera traps to collect detailed information of red-bellied squirrels and Northern tree shrews in Nonggang National Nature Reserve to analyze the differences in the activity patterns of these two species and explore their coexistence mechanism.

MATERIALS AND METHODS

Study site

Field monitoring was performed from January to December 2017 at the Nonggang National Nature Reserve (106°42’28″-107°04’54″E; 22°13’56″-23°39’09″N) in the Guangxi Zhuang Autonomous Region, southwest China. The nature reserve has a typical karst landscape consisting of peak-cluster depressions and valleys, and consists of three areas: Longshan (3644.8 hm^2), Longhu (1008.0 hm^2) and Nonggang (5424.7 hm^2) (Li *et al*., 2020). The regional climateis dominated by the mid-subtropical zonal monsoon with a mean temperature of 20.8-22.4 ℃ and is situated at altitudes in the range of 400-600 m above sea level. There are large temporal and spatial differences in rainfall, with distinct dry and rainy seasons, the dry season ranging from April to September and the rainy season from October to March. This area is a typical representation of the karst forest ecosystem in the northern edge of tropical China, with a variety of endangered animals, such as *Trachypithecus francoisi*, *Macaca assamensis*, and *Moschus berezovskii* (Yao *et al*., 2021).

Data collection

One hundred and twenty infrared cameras (Loreda,710) were set up in Nonggang National Nature Reserve, in a total area of 120 km^2. Considering the habitat characteristics, landscape, and camera safety, the cameras were set up in places with high occurrence of animal activities, such as tracks, water sources, and fecal excretion areas. The camera parameters were set such that 3 shots could be obtained in a row, with the shooting time interval of 1s, and the sensitivity being medium. Cameras were directly tied to tree trunks at a height of 0.5 m from the ground. Photo data were collected every 3 months; batteries were checked; and batteries, memory cards, and damaged cameras were replaced if needed to ensure continuous normal monitoring. All photos and camera site details were uploaded to the wildlife monitoring data processing system (http://cameradata.ioz.ac.cn); subsequently, the species were automatically grouped according to their identification, and data analysis was conducted.

Independent photos of red-bellied squirrels and Northern tree shrews obtained with an interval of at least 30 min between adjacent photos of the same individual at the same camera site were screened (O'Brien *et al.*, 2003). Then, using kernel density estimation, the animals' daily activity pattern was analyzed by taking their actual activity duration in the independent photos as the sample data. Animal behavior events were randomly sampled in a continuous time distribution cycle of 24 h. The method of kernel density estimation does not attach any assumptions to the data distribution and studies the distribution characteristics of data from the sample itself so as to describe the animals' activity patterns in a specific period of time (Ridout and Linkie, 2009; Chen *et al.*, 2019).

The overlap area ratio of distribution curve was calculated using the overlap package Δ (Δ=0: completely separated, Δ=1: complete overlap) to analyze the overlapping degree of the animals' activity patterns in dry and rainy seasons (Azevedo *et al.*, 2018; Chen *et al.*, 2019), and the compare function in the activity package was then used to analyze the difference in their activity patterns in dry and rainy seasons (Rowcliffe, 2016). When discussing the overlap of daily activity patterns of the two species, in order to ensure the sympatric the camera site data recorded for a single species was deleted, while that recorded for both species at the same site was retained (Liu *et al.*, 2019). The statistically significant difference for all tests was set as P<0.05, and the analysis and mapping of all data were in R3.6.1 (R Core Team, 2019).

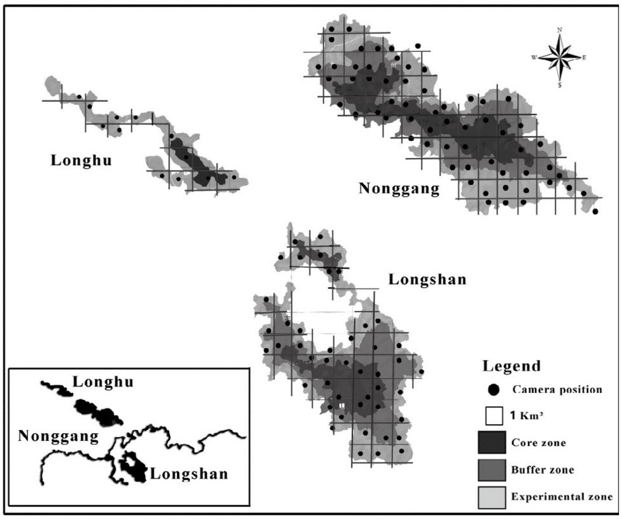

Fig. 1. The distribution of camera positions in Nonggang National Nature Reserve.

RESULTS

Daily activity patterns of red-bellied squirrels and Northern tree shrews

During the monitoring period, a total of 866 independent photos of red-bellied squirrels (677 records) and Northern tree shrews (189 records) were obtained at 85 camera sites. Both species were typical diurnal animals with two peaks in daily activity (red-bellied squirrels: 07:00-08:00 and 17:00-18:00; Northern tree shrews: 06:00-07:00 and 17:00-18:00) (Fig. 2a, b). In addition, a large number of photos of red-bellied squirrels were taken by camera traps from 21:00 to 0:500, indicating that the animal was relatively inactive for lesser time periods.

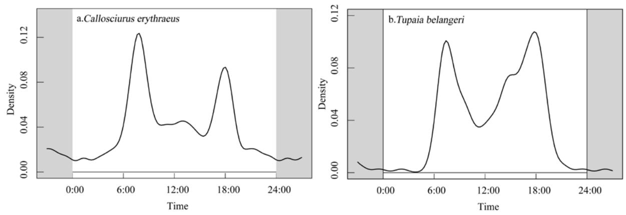

Fig. 2. Daily activity pattern of red-bellied squirrels (a) and Northern tree shrews (b).

The overlap coefficient of activity patterns of red-bellied squirrels was significantly different between the dry season (280 records) and rainy season (397 records) (Δ=0.51, P<0.001). The peak activity in the morning and afternoon of the dry season (07:00-08:00, 17:00-18:00) was 1h later than that in the rainy season (06:00-07:00, 16:00-17:00) (Fig. 3a). The overlap coefficient of activity patterns of Northern tree shrews was significantly different between the dry season (88 records) and rainy season (101 records) (Δ=0.75, P=0.001), The peak activity in the morning of the dry season (07:00-08:00) was 1 h later than that in the rainy season (06:00-07:00) (Fig. 3b).

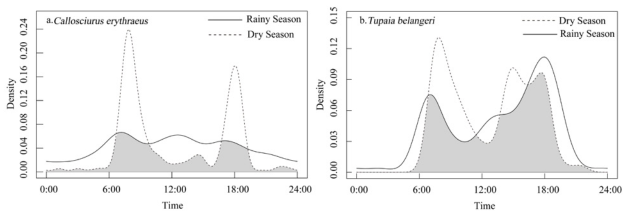

Fig. 3. Seasonal changes in the daily activity pattern of red-bellied squirrels (a) and Northern tree shrews (b).

Overlap of daily activity patterns between red-bellied squirrels and Northern tree shrews

Only 279 independent photos of red-bellied squirrels (117 records) and Northern tree shrews (162 records) were taken at 26 camera sites at the same time. There was no significant difference between their daily activity pattern curves (Δ=0.86, P=0.16), indicating that the similarity of their daily activity patterns was high (Fig. 4a). However, there were significant differences in the activity patterns of the two species between the dry season (Δ=0.72, P=0.012) and rainy season (Δ=0.73, P<0.001) (Fig. 4b, c).

The activity duration of red-bellied squirrels was significantly lower than that of Northern tree shrews (5.49±0.57 vs. 6.80±0.63 s) (Fig. 5a); however, the activity temperature of the former was higher than that of the latter (22.19±0.60 vs. 20.82±0.40°C) at the same site (Fig. 5b).

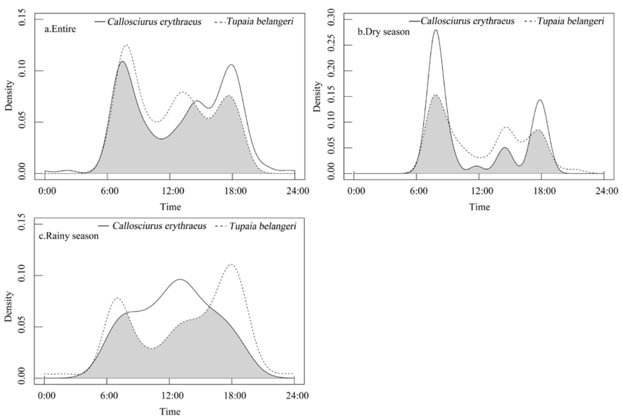

Fig. 4. Overlapping of the daily activity patterns of the entire (a); dry season (b); rainy season (c), between red-bellied squirrels and Northern tree shrews.

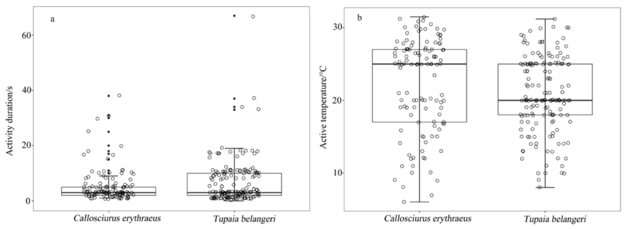

Fig. 5. Comparison of activity duration (a) and temperature (b) between red-bellied squirrels and Northern tree shrew.

DISCUSSION

Activity pattern is not only a part of the evolutionary adaptation of animals, but also a survival strategy in response to environmental changes (Wang *et al*., 2019). It is comprehensively affected by many factors such as, food resources, interspecific competition, and weather conditions (Yao *et al*., 2021). Our study results (Fig. 2a, b), in a manner similar to another study, showed that red-bellied squirrels and Northern Tree Shrew were typical diurnal animals (Tang *et al*., 2020, 2022; Yuan *et al*., 2019). However, different studies observed different activity peaks for these animals, which may be related to the different judgment methods of activity peaks used in different studies. Earlier studies divided 1 d into 12 time periods of 2 h duration, and the activity pattern of animals was reflected by calculating relative abundance of the animals' activity in the different time periods. This study directly took the time recorded by camera traps as the basic data and expressed the activity peak of animals; this method can obtain more accurate evaluation results even with less sample data (Mills *et al*., 2019; Porfirioa *et al*., 2016). The activity intensity of the two animals decreased significantly at noon (Fig. 2a, b), which may be the result of their long-term adaptation to the karst habitat. Due to the long-term lack of surface runoff in karst habitat and the maximum temperature at noon in hot summer, reducing activities appropriately can avoid the high temperature at noon and reduce the loss of water in the body (Tang *et al*., 2020).

The activity patterns of red-bellied squirrels and Northern Tree Shrew were significantly different between the dry and rainy seasons (Fig. 3a, b), and the activity peak in the dry season was later than that in the rainy season, which may be related to seasonal changes in day and night. In the karst habitat, the daytime duration in the dry season is significantly shorter than that in the rainy season (Wang *et al*., 2019; Yao *et al*., 2021), and the lower environmental temperature in the dry season also promotes animals to adjust their activity time accordingly. Furthermore, it may also be related to seasonal changes in food resources. The availability of food resources in the dry season is low in this habitat, and the animals appropriately reduce their activity intensity to save more energy to deal with the adverse impact of food shortage. The sympatric species *Trachypithecus leucocephalus* also showed a similar activity pattern (Zhou *et al*., 2010).

The overlap coefficient of daily activity pattern between red-bellied squirrels and Northern Tree Shrew was high (Δ=0.86) (Fig. 4a), indicating that there is a great overlap in their respective activity patterns. However, there were significant differences between their activity pattern curves in dry and rainy seasons, and the overlapping coefficient of activity pattern was high (Fig. 4b, c), indicating that the time niche differentiation between them was high during dry and rainy seasons. Therefore, they may reduce the competition for food resources and space utilization by adjusting the activity intensity between dry and rainy seasons, so as to achieve coexistence. These results are similar to those of other animals in the same area (Li *et al*., 2021; Yao *et al*., 2021). red-bellied squirrels avoided or alleviated the competition with Northern Tree Shrew by reducing its activity duration and choosing higher temperature periods for its activity (Fig. 5a, b). Furthermore, red-bellied squirrels increased the intensity of nocturnal activity (Fig. 2a), which may also be in order to avoid competition with sympatric species.

Therefore, the time niche differentiation and subtle food differentiation of red-bellied squirrels and Northern tree shrew in the karst habitat were one of the ecological evolutionary mechanisms these animals developed for their coexistence.

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Statement of conflict of interest

The authors have declared no conflict of interest.

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