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# The extremely small body size of Williamson's mouse deer (*Tragulus williamsoni*) allows coexistence with sympatric larger ungulates through temporal avoidance

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Research on the coexistence of congeneric species is essential for understanding community assemblages. Smaller competitors are expected to avoid larger ones, either spatially or temporally, to reduce interspecific competition. According to the spatial scaling law, the greater the difference in body size, the weaker the competitive interactions of the competitors. However, this is not confirmed in the guild of tropical forest ungulates. In this study, we assessed the competitive interactions of Williamson's mouse deer (*Tragulus williamsoni*), an endangered species and one of the smallest ungulates in the world, with sympatric larger ungulates. We hypothesized that: 1) because of its extremely small body size, competition with the larger ungulates would be relatively weak, allowing spatial co-existence but still requiring temporal avoidance, and 2) the strength of avoidance would increase with decreasing differences in body size. We set up 238 camera traps from January 2017 to January 2021 to survey Williamson's mouse deer and the sympatric larger ungulate species, that is, northern red muntjac (*Muntiacus vaginalis*), wild boar (*Sus scrofa*), Chinese serow (*Capricornis milneedwardsii*), and sambar (*Rusa unicolor*), in the protected areas of Mengla County, southwestern China. We then performed spatio-temporal analyses, including occupancy models, daily activity patterns, and a time interval analysis. Spatially, there was no significant avoidance. Temporally, Williamson's mouse deer had different daily activity patterns and direct temporal avoidance of all larger ungulate species. The lack of spatial avoidance and strong temporal avoidance supported our first hypothesis, but the stronger avoidance of much larger species ran counter to our second hypothesis. Our results revealed the coexistence mechanism between Williamson's mouse deer and sympatric larger ungulates and suggested that the difference in body size is limited in explaining the

competitive interactions of tropical forest ungulates due to the effects of multiple ecological processes. This deepens our understanding of the relationship between species trait differences and community assembly in tropical forest ecosystems.

#### KEYWORDS

body size, coexistence, daily activity pattern, direct temporal avoidance, interspecific competition, occupancy, sympatric ungulates

## Introduction

Research on the mechanisms of species coexistence is crucial in community ecology and fundamental for understanding the maintenance of biodiversity. Species coexistence refers to the state of two or more species in the same place at the same time (Holt, 2013), which is accompanied by various interspecific interactions, such as competition, predation, parasitism, and mutualism (Hellmann, 2013). Interspecific competition is the main driver of the coexistence of sympatric species, especially congeneric species (MacArthur and Levins, 1967; Chesson, 2000); close competitors attempt to monopolize limited resources and thereby reduce the fitness of each other (Farris et al., 2020). According to the competitive exclusion principle, that is, sympatric species with completely the same niche cannot coexist, interspecific competition forces sympatric species to differentiate their ecological and evolutionary processes, thus shifting their fundamental niches to realized niches and achieving a steady state of coexistence. The degree of overlap among realized niches is usually considered a key indicator of the strength of interspecific competition (Wissinger, 1992; Wandrag et al., 2019).

For animal guilds, niche theory emphasizes that resources, space, and time are the three major niche axes partitioned by competitors (Schoener, 1974). Sympatric species should either reduce the overlap of resources to alleviate exploitation competition or reduce the likelihood of encounters through spatial and temporal avoidance to alleviate direct interference competition (Case and Gilpin, 1974). First, the differentiation of resource use is fundamental for alleviating interspecific competition since resource overlap is the prerequisite for the formation of competition (Chesson, 2000). This implies that sympatric species can achieve coexistence by exploiting different resources at the same sites and at the same time. Second, sympatric species can achieve coexistence by avoiding co-occupying sites with each other (Karanth et al., 2017), which implies that they can exploit the same resources at the same time in different sites, thus resulting in a “checkerboard” distribution pattern (Stone and Roberts, 1990). Additionally, sympatric species with low competitive strength can avoid using sites with abundant competitors (Pimm et al., 1985). Third, sympatric species may achieve coexistence through variation in their daily activity patterns (reducing activity overlap and staggering activity peaks) (Kronfeld-Schor and Dayan, 2003),

which implies that they can exploit the same resources in the same sites at different time periods. However, the daily activity patterns of sympatric species, especially congeneric species, usually cannot be completely separated due to widely shared physiological rhythms (Pilorz et al., 2018), which may result in a high likelihood of encounters between them. Finally, a way to reduce the likelihood of an encounter is to avoid each other temporally by delaying using sites that were just used by another species (Niedballa et al., 2019). This is because longstanding interactions will promote the evolution of the capacity to identify the occurrence of competitors through a range of sensory modes.

Interspecific competition is usually asymmetric in that larger species are generally expected to be superior competitors due to their stronger ability to monopolize resources (Morin and Johnson, 1988), leading to them excluding smaller species spatially and temporally (e.g., interference competition) (Karanth et al., 2017). Body size is also considered an important factor affecting the competitive strength of sympatric species (Leyequién et al., 2007) because it is associated with many ecological traits and thus can summarize the difference in niche characteristics among species (Wilson, 1975). Fundamentally, different-sized species have dissimilar resource requirements and foraging strategies (Dickman, 1988). Large species usually consume large-sized and lower-quality food types, while small species specialize in consuming small-sized and higher-quality food types (Cromsig and Olf, 2006). Therefore, theoretically, the dissimilarity of body size between competitors is negatively associated with the degree of competitive strength (Leyequién et al., 2007). Furthermore, the difference in body size may be the potentially unifying first principle to explain community assembly, according to “spatial scaling laws” (Ritchie and Olf, 1999). In this case, competitors may coexist if the mean body length and body mass ratios are greater than 1.3 and 2.0, respectively (Hutchinson, 1959; Bowers and Brown, 1982). This means that the larger species will not competitively exclude the smaller species if their body sizes are extremely different (i.e., exceed the ratios), thus achieving steady coexistence at the shared sites (Roughgarden, 1983), although temporal avoidance may continue to occur (Roth, 1981).

Based on the above theoretical background, we conducted the first spatio-temporal analysis focused on the coexistence between larger ungulates and the Williamson’s mouse deer (*Tragulus williamsoni*), an endangered species and one of the smallest deer

species in the world. Williamson's mouse deer has thus far only been recorded in northern Thailand (Phrae Province) and southwestern China (Yunnan Province), and it might be one of the least-known mammal species in the world (Meijaard et al., 2017). In Yunnan, this species is only distributed in the transboundary area between China and Laos in Mengla County, with few records and little information about its ecology. Although it has been identified as an endangered species and a national first-class protected animal species in China, research on this species is scarce (Luo et al., 1999; Cao et al., 2010). Its breeding ecology, daily activity patterns, movements, home range, social organization and interactions with other species are still unknown (Meijaard, 2011). There are four larger ungulate species that are also distributed in Mengla County, starting with the species closest in size, although all are much larger than Williamson's mouse deer: northern red muntjac (*Muntiacus vaginalis*), wild boar (*Sus scrofa*), Chinese serow (*Capricornis milneedwardsii*), and the largest species, sambar (*Rusa unicolor*) (Table 1). We generally hypothesized that Williamson's mouse deer would display either spatial or temporal avoidance of these species, with the intensity of avoidance correlated to its size-difference with the other species.

We carried out a field survey in three protected areas in Mengla County, using noninvasive camera traps, and then implemented spatial-temporal analyses. Spatially, we performed single-species and two-species occupancy models to examine the spatial avoidance of Williamson's mouse deer to the larger ungulates, that is, the association of Williamson's mouse deer's occupancy with the relative abundance and presence of larger ungulates. Temporally, we conducted a daily activity pattern and a time interval analysis to examine the temporal avoidance of Williamson's mouse deer to the larger ungulates. We specifically hypothesized that:

1. Temporal avoidance plays a more important role than spatial avoidance for Williamson's mouse deer to alleviate interspecific competition with larger ungulates, as their competition with other species is not very intense because of their extremely small body size.

2. The strength of avoidance increases with decreasing difference in body size (avoidance of northern red muntjac > wild boar > Chinese serow > sambar).

## Materials and methods

### Study area

This study was conducted at the Mengla and Shangyong subreserves of the Xishuangbanna National Nature Reserve and Yiwu Prefectural Nature Reserve in Mengla County, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, southwestern China (21°08'~22°25' N, 100°50'~101°06' E). This region borders Laos and harbors rich biodiversity and provides important habitats for some key protected animal species in China, such as Indochinese tiger (*Panthera tigris corbetti*), Indochinese leopard (*Panthera pardus delacouri*), Asian elephant (*Elephas maximus*), clouded leopard (*Neofelis nebulosa*), Owston's civet (*Chrotogale owstoni*), as well as Williamson's mouse deer, yet anthropogenic disturbance is severe. Large amounts of tropical forests in this region have been displaced by cultivation (i.e., croplands and rubber plantations) and urbanization (e.g., cities, towns, villages, roads) since the 1950s (Zhang et al., 2019), which potentially affects the habitat use of Williamson's mouse deer and other ungulate species in this region.

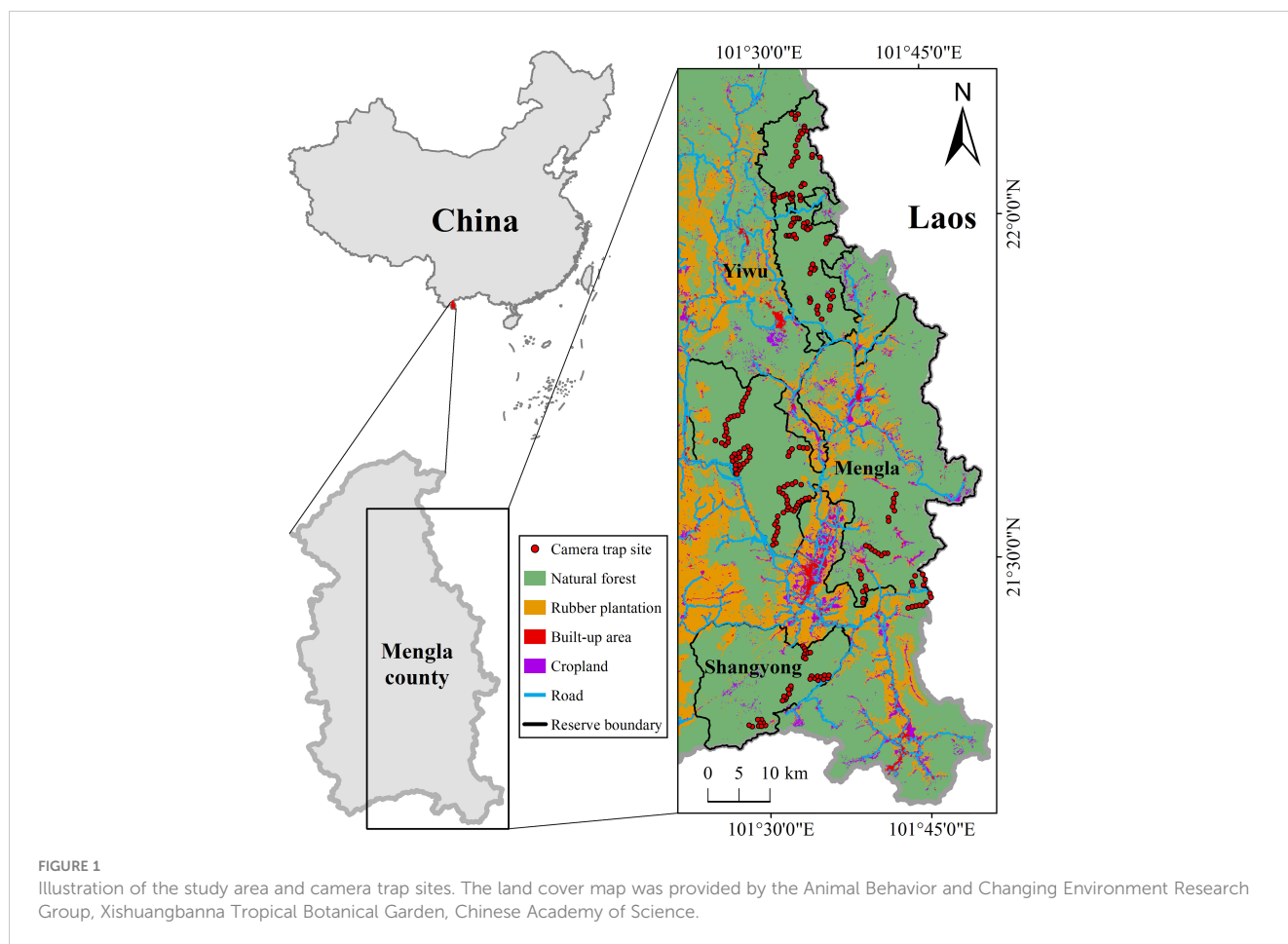
### Camera trap survey

We used camera traps to monitor the ungulate species in the three protected areas (Mengla, Shangyong, and Yiwu) in Mengla County from January 2017 to January 2021 (Mengla: from January 2017 to June 2020; Shangyong: from November 2018 to January 2021; Yiwu: from July 2017 to October 2020). A total of 238 camera-trapping sites were set up along transects (Figure 1). The transects

TABLE 1 Body size, body mass, threatened status and summary of the camera trap survey (n = 238) of the five ungulate species.

Species	Body length (m)	Body mass (kg)	Body length ratio	Body mass ratio	Threatened status		Camera trap survey		
					IUCN red list	China's red list	Recorded sites	Independent events	Co-occupied sites with WMD
Northern red muntjac	1.09	28.5	2.32	8.14	LC	NT	236	11,729	32
Wild boar	1.35	125	2.87	35.71	LC	LC	226	3,972	32
Chinese serow	1.55	122.5	3.3	35	-	VU	99	468	9
Sambar	1.9	222.5	4.04	63.57	VU	NT	53	471	7
Williamson's mouse deer	0.47	3.5	-	-	DD	EN	32	921	-

The body length and body mass data were extracted from "A dataset on the morphological, life-history and ecological traits of the mammals in China" (Ding et al., 2022); the IUCN red list information from <https://www.iucnredlist.org/> (IUCN, 2022); China's red list information from the "Red List of China's Vertebrates" (Jiang et al., 2016). "WMD" is the abbreviation of Williamson's mouse deer. The taxonomic status of the Chinese serow remains controversial, hence it is not listed in the IUCN red list.



primarily followed abandoned human or mammal trails, with the inclusion of sampling sites from the core to the edge of each of the protected areas. To ensure sampling independence, the minimum distance between any two adjacent camera trap sites that were concurrently operating was 500 m. Camera traps (Loreta L710, Yi'an Weishi Technology Co, Ltd, Shenzhen) were mounted at 0.5–2 m aboveground on the trunk of trees without baits or lures. The monitoring system of the camera traps was set to work 24 hours per day with high sensitivity, and three photographs were taken at each trigger without a delay. To reduce the disturbance of the observers, the batteries and SD cards for storing animal photographs were changed only every six months. After we collected the camera photographs, we recorded for each photograph the GPS location, species names (including livestock and humans), capture dates, and capture times within the day.

## Additional environmental covariates

We used the relative abundance index (hereafter RAI) of the larger ungulates (RAI of northern red muntjac, RAI of wild boar, RAI of Chinese serow, RAI of sambar and RAI of all ungulates) as the major variables. Moreover, to eliminate the false signal of spatial interaction between Williamson's mouse deer and the sympatric larger ungulates (Pollock et al., 2014; D'Amen et al., 2018), we

added additional environmental covariates that can potentially affect the occupancy of Williamson's mouse deer into the analyses. A total of 12 site-level covariates were selected (see more detailed description and data resources in Table S1), including two covariates that could reflect habitat quality (tree density and normalized difference vegetation index, NDVI), four covariates that could reflect topographical variation (elevation, slope, aspect and topographic position index, TPI), and six covariates that represent different types of anthropogenic disturbances (distance to nearest road, distance to nearest built-up area, distance to nearest cropland, distance to nearest plantation land, RAI of local people presence, and RAI of livestock presence). We also added site-level annual average temperature to explain the variation in detection probability because temperature has a potential effect on the detection capability of camera traps, and is often considered to influence detectability (Wang et al., 2018; Wang et al., 2021). All covariates were standardized with a mean of 0 and a standard deviation of 1.

## Statistical analysis

Consecutive photographs of a given species at the same camera site within 30 minutes were not considered independent detections to avoid overestimating true occurrences of animals

(O'Brien et al., 2003). The RAI of each species in each camera site was denoted by the number of independent detections recorded within 100 trapping days (Jenks et al., 2011), as it is an efficient index to represent the abundance of forest ungulates (Rovero and Marshall, 2009). Matrixes of detection history with 30 days as a sample segment for analysis were created for each species using the *camtrapR* package (Niedballa et al., 2016) for occupancy modeling. All analyses were conducted with R software 4.1.0 (R Core Team, 2022).

To examine how the relative abundance of sympatric larger ungulates affects the occupancy of Williamson's mouse deer, single-species occupancy models were implemented by using the *occu* function in the *unmarked* package (Fiske and Chandler, 2011). Five full models were established with annual average temperature as the detection variable, and then differing occupancy variables: 12 covariates, 12 covariates + RAI of northern red muntjac, 12 covariates + RAI of wild boar, 12 covariates + RAI of Chinese serow and 12 covariates + RAI of sambar. All variance inflation factor (VIF) values of the occupancy variables were under 5 in the full models, as measured by the *vif* function, which indicates little collinearity (Akinwande et al., 2015). After the collinearity check of each full model, the candidate models were established with all possible combinations of the occupancy variables and then compared based on the Akaike information criterion (AIC) (Burnham and Anderson, 2002). Models with a  $\Delta AIC < 2$  from the top model (the model with the lowest AIC) were selected for weighted model average calculation by using the *model.avg* function in the *AICcmodavg* package (Mazerolle, 2020). The full averaged coefficients and 95% confidence intervals were finally reported. The variables were considered significant if their 95% confidence intervals did not cross 0 and the full averaged P value was  $< 0.05$ . We also modeled the four ungulate species separately with the same model selection procedure (only with the 12 covariates) in order to provide the precondition of establishment for the following two-species occupancy models (see below). For model validation, we ran goodness-of-fit tests, that is, calculating the Sum of Squared Errors, Freeman-Tukey Chi-squared test, and Pearson's Chi-squared test with 1,000 bootstraps for the top model, using the *parboot* function (Fiske and Chandler, 2011). All P-values of goodness-of-fit tests were greater than 0.05, which supports the goodness of fit for our occupancy modeling (Table S2).

We further used conditional two-species occupancy models to determine the spatial interaction between Williamson's mouse deer and the larger ungulate species (Richmond et al., 2010). This model categorizes the species pair as a dominant competitor A and a subordinate competitor B, and allows the estimation of three occupancy parameters,  $\psi_A$ ,  $\psi_{BA}$ , and  $\psi_{Ba}$ , and 5 detection parameters,  $p_A$ ,  $r_A$ ,  $p_B$ ,  $r_{BA}$ , and  $r_{Ba}$  (see the details in Richmond et al., 2010). The species interaction factor (SIF) can be calculated by the three occupancy parameters, as follows:

$$SIF = \frac{\psi_A \psi_{BA}}{\psi_A (\psi_A \psi_{BA} + (1 - \psi_A) \psi_{Ba})}$$

SIF = 1 suggests that the species pair is spatially independent, SIF > 1 suggests that species B is more likely to co-occur with species A than expected under the hypothesis of independence (i.e., spatial aggregation), and SIF < 1 suggests that species B is less likely to co-

occur with species A than expected under the hypothesis of independence (i.e., spatial avoidance). We modeled the species pairs composed of Williamson's mouse deer and each of the sympatric ungulate species. We considered the larger ungulates as the dominant species (species A) and Williamson's mouse deer as the subordinate species (species B), and established four candidate models for each species pair, corresponding to four hypotheses: 1) the occupancy and detection of Williamson's mouse deer are affected by the presence of larger ungulates, while the larger ungulates are independent from Williamson's mouse deer ( $\psi_A$ ,  $\psi_{BA}$ ,  $\psi_{Ba}$ ,  $p_A = r_A$ ,  $p_B$ ,  $r_{BA} = r_{Ba}$ ); 2) only the occupancy of Williamson's mouse deer is affected by the presence of larger ungulates, while the larger ungulates are independent from Williamson's mouse deer ( $\psi_A$ ,  $\psi_{BA}$ ,  $\psi_{Ba}$ ,  $p_A = r_A$ ,  $p_B = r_{BA} = r_{Ba}$ ); 3) only the detection of Williamson's mouse deer is affected by the presence of larger ungulates, while the larger ungulates are independent from Williamson's mouse deer ( $\psi_A$ ,  $\psi_{BA} = \psi_{Ba}$ ,  $p_A = r_A$ ,  $p_B$ ,  $r_{BA} = r_{Ba}$ ); and 4) Williamson's mouse deer and the larger ungulates are independent from each other ( $\psi_A$ ,  $\psi_{BA} = \psi_{Ba}$ ,  $p_A = r_A$ ,  $p_B = r_{BA} = r_{Ba}$ ). We did not hypothesize the effect of larger ungulate detection on Williamson's mouse deer's detection since we used a long sample segment (30 days). The detection variable, annual average temperature, and the significant occupancy variables from single-species occupancy models were added to each candidate two-species occupancy model. The candidate models with  $\Delta AIC < 2$  from the top model were selected for weighted model average calculation. The mean predicted value  $\pm$  conditional 95% confidence intervals of the parameter's coefficients were finally reported. Williamson's mouse deer was considered significantly aggregated (or avoided) with the presence of larger ungulates if the conditional 95% confidence intervals were higher (or lower) than 1. All the two-species occupancy models were conducted by using the program PRESENCE (<https://www.mbr-pwrc.usgs.gov/software/presence.html>).

Nonparametric kernel density estimations were used to examine the overlap of the daily activity patterns of Williamson's mouse deer and the sympatric larger ungulates. The captured clock time of day of independent events was transformed to circular solar time by using the *solartime* function in the *activity* package (Rowcliffe, 2022). The overlap of the activity pattern was measured by calculating the coefficient of overlap D-hat ( $\Delta$ ) with the *overlapEst* function in the *overlap* package (Ridout and Linkie, 2009), in which a range from 0 (no overlap) to 1 (complete overlap) was generated.  $\Delta_4$  was used since the number of detections of all species was  $> 50$ . The overlap was considered high when  $\Delta > 0.75$ , moderate when  $0.5 < \Delta < 0.75$ , and low when  $\Delta < 0.5$  (Monterroso et al., 2014). We also performed randomization tests by using the *compareCkern* function to test the significant difference in the daily activity patterns of Williamson's mouse deer and the larger ungulates. We repeated the analysis for Williamson's mouse deer with the different species of larger ungulates.

We performed time interval analyses to understand whether Williamson's mouse deer displays direct temporal avoidance of the sympatric larger ungulates in their co-occupied sites. Two types of time intervals were calculated at each camera trap site: 1) the time interval from the detection of a given ungulate species to the next

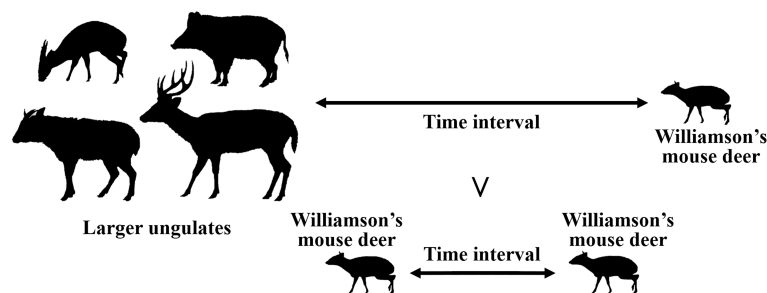


FIGURE 2

Illustration of direct temporal avoidance. It suggests direct temporal avoidance if the time intervals of a given ungulate species to the next Williamson's mouse deer detection were longer than between successive Williamson's mouse deer detections. The illustrations of ungulate species in this figure were drawn by R-CH, following illustrations in Smith and Xie (2009).

detection of Williamson's mouse deer, and 2) the time interval between two successive detections of Williamson's mouse deer (Figure 2). Because of nonnormality, one-tailed Wilcoxon rank sum tests were performed to determine whether the time intervals of a given ungulate species to the next detection of Williamson's mouse deer were significantly longer than those of two successive detections of Williamson's mouse deer. A significant test result suggests that interspecific temporal avoidance exceeded temporal avoidance between conspecifics (Harmsen et al., 2009; de Oliveira et al., 2020), which would imply that Williamson's mouse deer does show direct temporal avoidance of the given ungulate species. We repeated these analysis procedures for Williamson's mouse deer with the different larger ungulate species. We also calculated the avoidance ratios by using the time interval from the detection of a given ungulate species to the next detection of Williamson's mouse deer divided by that between two successive detections of Williamson's mouse deer to determine the difference in the avoidance strength of Williamson's mouse deer to different-sized larger ungulate species.

## Results

From January 2017 to January 2021, a total of 105,087 camera-trapping days were obtained from 238 camera-trap sites. The range of each site's camera-trapping days was 78–1118 (mean  $\pm$  SD =  $441.54 \pm 248.64$ ), and only two sites had less than 100 days (78 and 94). A total of 17,561 independent events of all five ungulate species were obtained (Table 1), of which 921 independent events of Williamson's mouse deer were recorded at 32 camera trap sites. Of this total, 32, 32, 9 and 7 sites were co-occupied with northern red muntjac, wild boar, Chinese serow and sambar, respectively. The other species were all found at more camera trap sites than Williamson's mouse deer (Table 1).

## Occupancy interactions

The results of single-species occupancy models showed that the occupancy probability of Williamson's mouse deer was only significantly associated with elevation, in which it was higher in

the lowlands (coefficient [95% CI] =  $-1.26 [-1.97, -0.56]$ ,  $P < 0.001$ ), when interactions with other ungulates were not included (Table S3). The relative abundance of all larger ungulate species had no significant effects on the occupancy probability of Williamson's mouse deer (northern red muntjac: coefficient [95% CI] =  $0.4 [-0.026, 0.83]$ ,  $P = 0.066$ ; wild boar: coefficient [95% CI] =  $0.026 [-0.19, 0.25]$ ,  $P = 0.81$ ; Chinese serow: coefficient [95% CI] =  $-0.5 [-1.83, 0.83]$ ,  $P = 0.46$ ; sambar: coefficient [95% CI] =  $0.0046 [-0.11, 0.12]$ ,  $P = 0.94$ ) (Figure 3).

We did not deploy two-species occupancy models to analyze the avoidance of Williamson's mouse deer to the presence of northern red muntjac and wild boar. This is because its recorded sites were fully covered by those of the two larger ungulates, which suggested no avoidance of them. The averaged estimates of the two-species models showed that Williamson's mouse deer had significant aggregation with Chinese serow (SIF [95% CI] =  $1.041 [1.019, 1.064] > 1$ ), and it was independent from the presence of sambar (SIF = 1) (Table 2).

## Daily activity pattern

The daily activity pattern of Williamson's mouse deer was significantly different from that of the sympatric larger ungulates (all  $P < 0.001$ ), with moderate overlap with northern red muntjac ( $\Delta 4 = 0.63$ ), wild boar ( $\Delta 4 = 0.66$ ) and Chinese serow ( $\Delta 4 = 0.54$ ) and low overlap with sambar ( $\Delta 4 = 0.44$ ) (Figure 4). The daily activity pattern of Williamson's mouse deer was typically crepuscular with 2 peaks at 9:00:00 and 18:00:00 and a trough at 13:00:00. The other four species of larger ungulates had varied degrees of nocturnal activity, with inapparent peaks in the morning and twilight. In particular, sambar was mainly active at night without any obvious peaks and only had an obvious trough in the afternoon.

## Direct temporal avoidance

The time intervals of the detection of any larger ungulate species to the next Williamson's mouse deer were significantly longer than those of the successive detections of Williamson's mouse deer (all

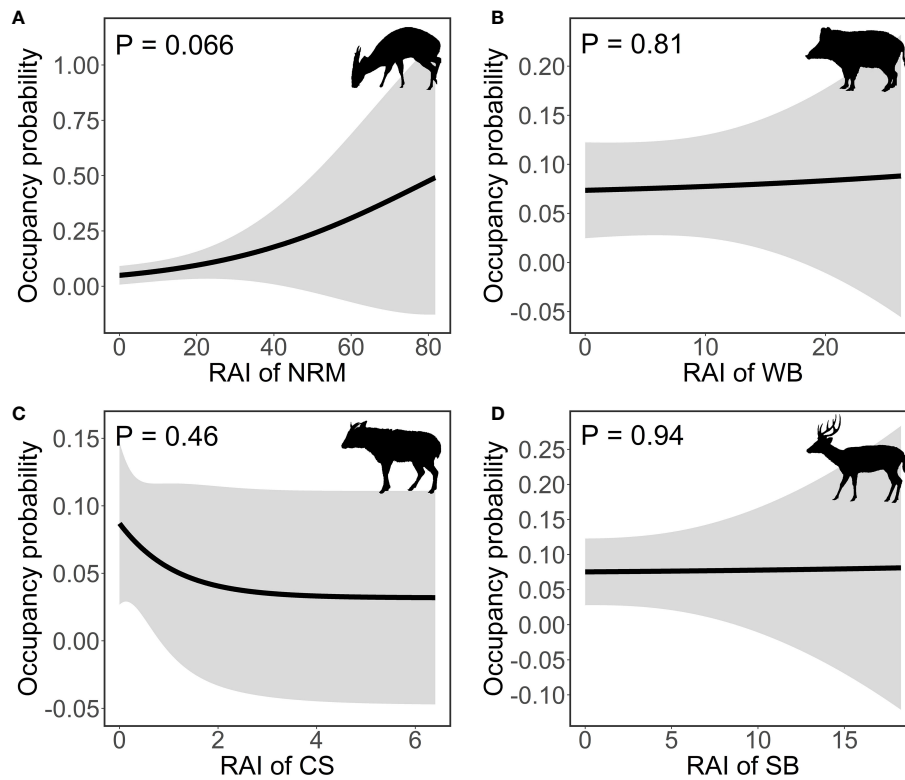


FIGURE 3

The association between the occupancy probability of Williamson’s mouse deer and the relative abundance of northern red muntjac (A), wild boar (B), Chinese serow (C) and sambar (D). The black lines and the grey areas are fitted lines and 95% confidence intervals, respectively. NRM, WB, CS, SB are the abbreviations of northern red muntjac, wild boar, Chinese serow and sambar, respectively. The illustrations of ungulate species in this figure were drawn by R-CH, following illustrations in Smith and Xie (2009).

$P < 0.05$ ) (Figure 5), which means that the interspecific temporal avoidance exceeded temporal avoidance between conspecifics, suggesting that Williamson’s mouse deer do display direct temporal avoidance to these species. Moreover, the strength of avoidance to Chinese serow (avoidance ratio = 3.36) > sambar (avoidance ratio = 3.026) > northern red muntjac (avoidance ratio = 1.96) > wild boar (avoidance ratio = 1.53).

## Discussion

In this study, we identified for the first time how Williamson’s mouse deer coexists with the sympatric larger ungulates, northern red muntjac, wild boar, Chinese serow, and sambar with the analyses of long-term camera-trapping data from Mengla County, southwestern China. Williamson’s mouse deer had no spatial

TABLE 2 The setting and comparison of candidate two-species occupancy models.

Species pair	Candidate model	K	AIC	$\Delta$ AIC	AIC weight
CS–WMD	$\psi_A, \psi_{BA}, \psi_{Ba}, p_A=r_A, p_B, r_{BA}=r_{Ba}$	12	2503.57	0	0.6
	$\psi_A, \psi_{BA}=\psi_{Ba}, p_A=r_A, p_B, r_{BA}=r_{Ba}$	10	2504.35	0.78	0.4
	$\psi_A, \psi_{BA}=\psi_{Ba}, p_A=r_A, p_B=r_{BA}=r_{Ba}$	8	2569.17	65.6	0
	$\psi_A, \psi_{BA}, \psi_{Ba}, p_A=r_A, p_B=r_{BA}=r_{Ba}$	10	2571.01	67.44	0
SB–WMD	$\psi_A, \psi_{BA}=\psi_{Ba}, p_A=r_A, p_B, r_{BA}=r_{Ba}$	12	1808	0	0.63
	$\psi_A, \psi_{BA}, \psi_{Ba}, p_A=r_A, p_B, r_{BA}=r_{Ba}$	14	1811.17	3.17	0.13
	$\psi_A, \psi_{BA}=\psi_{Ba}, p_A=r_A, p_B=r_{BA}=r_{Ba}$	10	1811.24	3.24	0.12
	$\psi_A, \psi_{BA}, \psi_{Ba}, p_A=r_A, p_B=r_{BA}=r_{Ba}$	12	1811.41	3.41	0.11

“K” is the number of parameters, “ $\Delta$ AIC” is the difference in AIC relative to the top model (the model with lowest AIC). “Species A” is the dominant species (Chinese serow or sambar) in each model, while “Species B” is the subordinate species (Williamson’s mouse deer). CS, SB and WMD are the abbreviations of Chinese serow, sambar and Williamson’s mouse deer, respectively. “ $\psi_A, \psi_{BA}, \psi_{Ba}, p_A=r_A, p_B, r_{BA}=r_{Ba}$ ”: the occupancy and detection of Williamson’s mouse deer are affected by the presence of larger ungulates, while the larger ungulates are independent from Williamson’s mouse deer; “ $\psi_A, \psi_{BA}=\psi_{Ba}, p_A=r_A, p_B=r_{BA}=r_{Ba}$ ”: only the occupancy of Williamson’s mouse deer is affected by the presence of larger ungulates, while the larger ungulates are independent from Williamson’s mouse deer; “ $\psi_A, \psi_{BA}, \psi_{Ba}, p_A=r_A, p_B=r_{BA}=r_{Ba}$ ”: only the detection of Williamson’s mouse deer is affected by the presence of larger ungulates, while the larger ungulates are independent from Williamson’s mouse deer; “ $\psi_A, \psi_{BA}=\psi_{Ba}, p_A=r_A, p_B=r_{BA}=r_{Ba}$ ”: Williamson’s mouse deer and the larger ungulates are independent from each other.

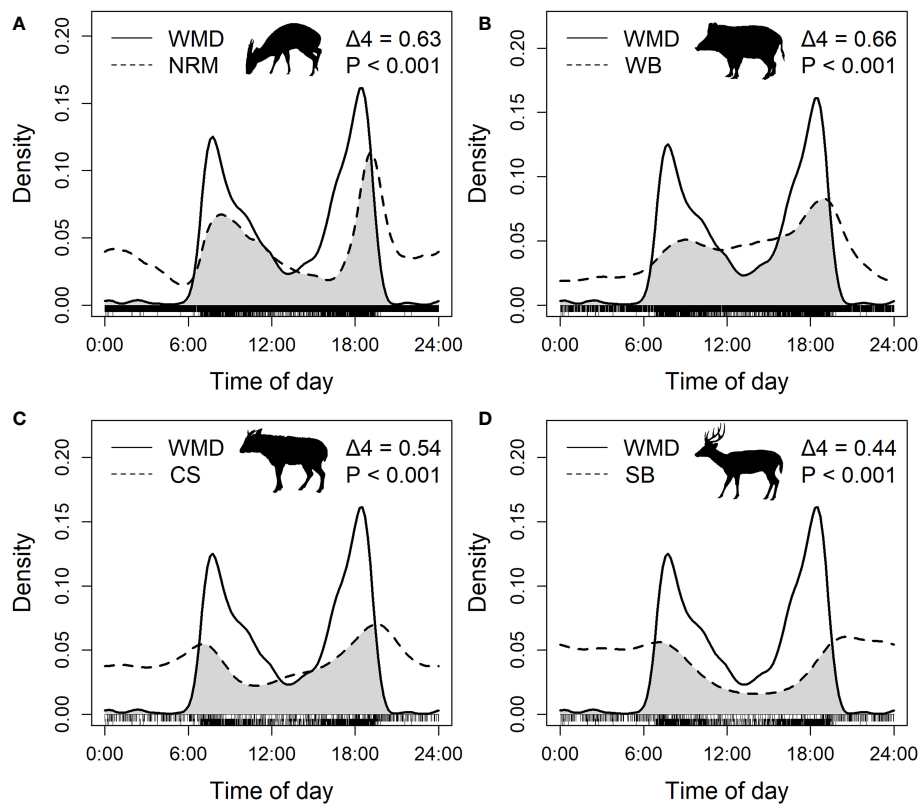


FIGURE 4

Overlap and difference in the daily activity pattern of Williamson's mouse deer and northern red muntjac (A), wild boar (B), Chinese serow (C) and sambar (D). The grey areas are the overlap areas. NRM, WB, CS, SB, WMD are the abbreviations of northern red muntjac, wild boar, Chinese serow, sambar, and Williamson's mouse deer, respectively. The illustrations of ungulate species in this figure were drawn by R-CH, following illustrations in Smith and Xie (2009).

avoidance of all larger ungulate species but avoided them temporally, which supported our first specific hypothesis that temporal avoidance plays a more important role than spatial avoidance for Williamson's mouse to coexist with the sympatric larger ungulates, because its competition with them is relatively weak due to the extreme difference in body size. However, Williamson's mouse deer had stronger avoidance of the much larger species, which was contrary to our second hypothesis that the strength of avoidance would increase with decreasing differences in body sizes.

## No evidence of spatial avoidance

It is usually considered that spatial avoidance is more frequent and important for alleviating interspecific competition than the other two major niche axes, i.e., resource and time (Schoener, 1974). Spatial avoidance would seem to indicate such intense competition that the species are unable to be present together at the same location, whereas in other forms of competition the species are able partition the resources, or temporal access to them. However, our results showed the occupancy probability of Williamson's mouse deer was not negatively associated with the presence and relative

abundance of the larger ungulates, which indicates that Williamson's mouse deer did not avoid the larger ungulate species spatially. This suggested that spatial avoidance may not play a major role in the coexistence of Williamson's mouse deer with the sympatric larger ungulates. This lack of spatial avoidance could largely be explained by temporal avoidance (i.e., differing in daily activity patterns and direct temporal avoidance; see below) (Kronfeld-Schor and Dayan, 2003). In addition, the differentiation in dietary niches may be another important reason that facilitates the steady coexistence of sympatric competitors (du Preez et al., 2017).

The diet of Williamson's mouse deer is unclear (Meijaard, 2011), but it should be much different from the larger ungulates due to the extreme difference in body size (Cromsig and Olf, 2006). From interviews of local villagers in Mengla, a previous paper described the food selection of Williamson's mouse deer to mainly include fallen fruits of wild figs (*Ficus* spp.), *Phyllanthus emblica* and *Phyllanthi fructus*, and the tender leaves of *Alpinia kwangsiensis* and *Phrynium capitatum* (Cao et al., 2010). If it is similar to other species of mouse deer, such as Javan mouse deer (*Tragulus javanicus*) and lesser mouse deer (*T. kanchil*), Williamson's mouse deer's diet may generally consist of small fallen fruits from *Ficus*, shoots, tender leaves from understory



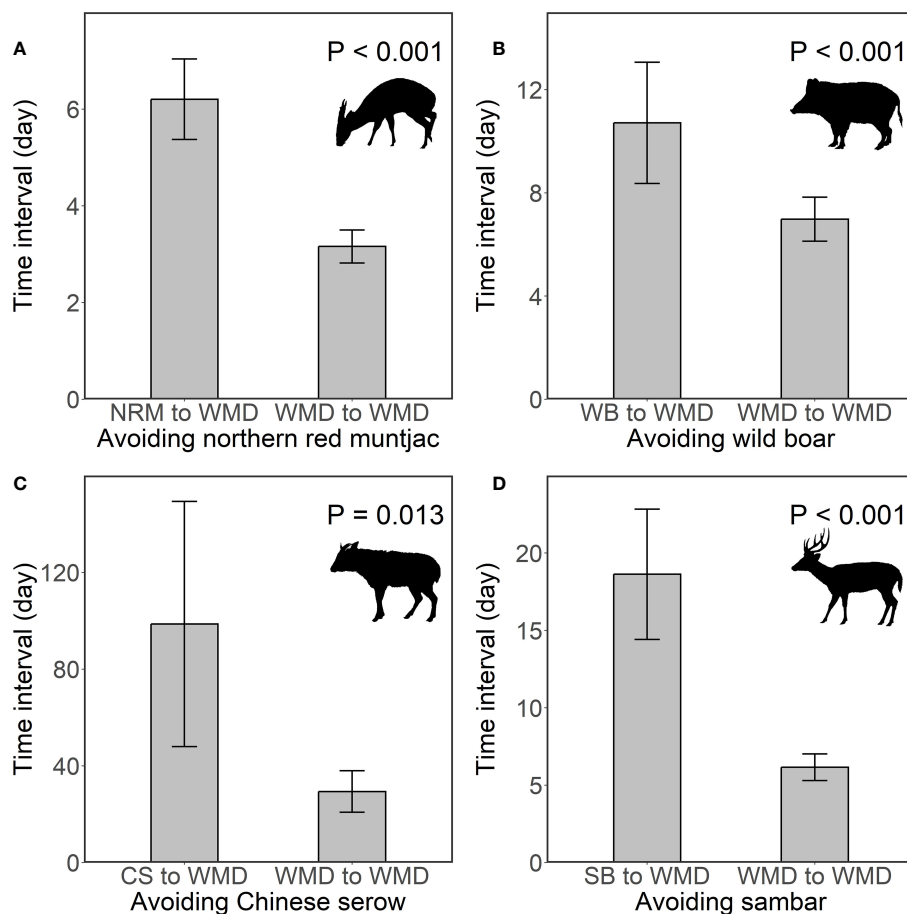


FIGURE 5

The direct temporal avoidance of Williamson's mouse deer to northern red muntjac (A), wild boar (B), Chinese serow (C) and sambar (D). The bars and error bars represent mean values and standard errors, respectively. NRM, WB, CS, SB, WMD are the abbreviations of northern red muntjac, wild boar, Chinese serow, sambar, and Williamson's mouse deer, respectively. The illustrations of ungulate species in this figure were drawn by R-CH, following illustrations in Smith and Xie (2009).

plants and small mushrooms (Matsubayashi et al., 2003; Meijaard, 2011). In contrast, the diets of larger ungulates are wider and more opportunistic (Ahrestani et al., 2016). The four larger ungulate species can also consume fallen fruits and understory plants, but they are not restricted to items that are of low height and small size, as are the small deer, and can consume more species of plants or other food items. For example, sambar can browse tender leaves, twigs and large fruits of larger plants (Ahrestani et al., 2016); wild boar even frequently consume small animals, such as earthworms, snakes, frogs, small rodents, and ground-dwelling birds (Ballari and Barrios-García, 2014). A previous study in Singapore showed that the presence of wild boar and sambar had no effect on the occupancy of lesser mouse deer, which may be partially explained by different food selection (Khoo et al., 2021).

The occupied sites of Williamson's mouse deer were all covered by northern red muntjac and wild boar, and it was statistically aggregated with the presence of Chinese serow, which suggests that Williamson's mouse deer is positively associated with these species in its space use. It is possible that Williamson's mouse deer could

reduce predation risk by co-occurring with the important prey of larger carnivores according to the "dilution effect" hypothesis (Dehn, 1990). In particular, the northern red muntjac is much more abundant than other species in our study area, and the number of independent detection events is almost three times (2.95 times) that of the second most abundant species, the wild boar (Table 1), and muntjac may be the major prey of the Asian golden cat (*Catopuma temminckii*) and dhole (*Cuon alpinus*) (Kamler et al., 2012; Kamler et al., 2020). This may be why Williamson's mouse deer had a near-significant positive association with the relative abundance of northern red muntjac. Additionally, although wild boar, Chinese serow and sambar may be important prey terms of the Asian golden cat, dhole and clouded leopard (*Neofelis nebulosa*) (Kamler et al., 2012; Kamler et al., 2020; Rasphone et al., 2022), the neutral associations with the relative abundance of wild boar, Chinese serow and sambar and the presence of sambar may be due to Williamson's mouse deer having a trade-off between the benefits of reducing predation risk and habitat damage (reduced food availability and destruction of

the refuges of Williamson's mouse deer) by the abundant larger ungulates (Foster et al., 2014).

## Temporal avoidance is more important than spatial avoidance

Although the possible dietary niche differentiation and dilution effects may be important reasons to explain the positive and neutral spatial associations between Williamson's mouse deer and the sympatric larger ungulates, the temporal avoidance (i.e., differing in daily activity pattern and direct temporal avoidance) we assessed in this study provides an alternative way of avoiding competition from the perspective of niche theory.

Subordinate competitors commonly partition niches temporally with the dominant competitor (Schoener, 1974), and this is often found in ungulate guilds (de Pinho et al., 2022; You et al., 2022). In this study, Williamson's mouse deer had significantly different daily activity patterns from the four sympatric larger ungulate species. The four larger ungulate species have more active times at night with inapparent peaks in the morning and twilight, especially sambar, which has primary nocturnal activities without any apparent peaks and only has a trough in the afternoon. Williamson's mouse deer, in this region, is a typically crepuscular species, a finding which was different from the nocturnal activity pattern mentioned in a previous study in the same area that did not use camera traps (Cao et al., 2010). Similarly, another camera-trap study also reported that lesser mouse deer have a bimodal and crepuscular activity pattern (Khoo et al., 2021), which was different from the nocturnal pattern reported by earlier studies. Here the mouse deer was more active at night, which was different from the sympatric wild boar and sambar, which showed more diurnal and unimodal activities. This may suggest that Williamson's mouse deer shift their daily activity pattern to avoid the sympatric larger ungulates. The moderate and low overlaps (< 0.7) and different activity peaks imply that Williamson's mouse deer can use the co-occupied sites with the larger ungulates at different time periods of the day, which efficaciously reduces the likelihood of encounter, thus facilitating the coexistence between them (Kronfeld-Schor and Dayan, 2003).

Although the differentiation of daily activity patterns is an effective way to alleviate interspecific competition, the overlapping of daily activity time periods also implies that the subordinate species still have a low probability of encountering the dominant species (Kronfeld-Schor and Dayan, 2003). Our time interval analysis showed that Williamson's mouse deer had direct temporal avoidance of the larger ungulates in the co-occupied sites. This suggested that direct temporal avoidance also helps Williamson's mouse deer relieve competitive pressure from larger ungulates. Prolonged interactions may enable Williamson's mouse deer to identify the tracks of larger ungulates by signs, scent and vocalizations. This avoidance strategy has rarely been found among the interactions of wild ungulates (Kavčić et al., 2021; Staudenmaier

et al., 2021), although it has been found in the response of wild ungulates to livestock (Feng et al., 2021).

## Stronger avoidance to much larger species

According to our second specific hypothesis, the coexistence of congeneric species with small differences in body size would prompt fiercely competitive interactions (Leyequién et al., 2007), which means that the smaller northern red muntjac should have had the strongest spatio-temporal exclusion to Williamson's mouse deer, followed by wild boar, Chinese serow, and sambar. However, Williamson's mouse deer had stronger avoidance of the much larger species spatially and temporally, which contradicts this hypothesis.

Spatially, Williamson's mouse deer had positive associations with the presence of the three smaller ungulate species but had a neutral association with sambar (the largest species). Temporally, Williamson's mouse deer had lower overlaps of daily activity patterns (wild boar [0.66] > northern red muntjac [0.63] > Chinese serow [0.54] > sambar [0.44]) and stronger direct temporal avoidance (wild boar [avoidance ratio = 1.53] < northern red muntjac [avoidance ratio = 1.96] < sambar [avoidance ratio = 3.026] < Chinese serow [avoidance ratio = 3.36]) with/of the much larger ungulate species, which was contrary to the expectation that the more similar the body sizes, the stronger the competition (Roughgarden, 1983). One possible reason is that sufficiently different body sizes represent sufficient differentiation of niches between sympatric species (Wilson, 1975), resulting in an unclear pattern between differences in body sizes and the degree of spatio-temporal competitive interactions. Previous studies pointed out that competitors can steadily coexist spatially if the body size ratio exceeds thresholds that were considered near 1.3 for body length and 2.0 for body mass (Hutchinson, 1959; Bowers and Brown, 1982). In Mengla, the sympatric larger ungulate species is much larger than Williamson's mouse deer; for example, the body size and body mass of northern red muntjac, the next smallest ungulate species, are 2.32 and 8.14 times those of Williamson's mouse deer, which implies that it has extremely different niches, representing distinct morphology and physiology (Helaouët and Beaugrand, 2009). Moreover, the sambar may utilize more open sites compared to Williamson's mouse deer due to its extremely large body size, with a standing height reaching two meters from the foot to the antler. This difference in microhabitat preference may explain why Williamson's mouse deer was positively associated with the presence of the three smaller ungulate species but neutrally associated with sambar. Another possible reason is that the strength of interspecific competition between the species may be related to multiple ecological factors instead of purely the difference in body size. Evaluation of interspecific competition focusing only on body size could miss processes such as the larger species excluding the smaller species in multiple ways (such as through habitat damage), or competitors having imperceptible symbiotic

relationships (such as predator dilution effects). Consequently, we highlight that interspecific competition in this community appears to be more complicated than we expected, and the difference in body size is limited in explaining the coexistence of tropical forest ungulates.

## Conservation implications

Our study also can provide the first evidence of the relationship between Williamson's mouse deer and anthropogenic disturbance. Fortunately, none of the anthropogenic variables had negative effects on Williamson's mouse deer (Table S3). Williamson's mouse deer may have good adaptability in disturbed habitats, similar to common ungulate species such as muntjac and wild boar. According to studies of other species of mouse deer, these kinds of deer can occupy disturbed habitats. For example, Javan mouse deer can use dense tea plantations (Farida et al., 2006). Similarly, lesser mouse deer prefer fragmented and logged forest patches over continuous primary forests (Hazwan et al., 2022), and they can occupy fragmented urban forests and even prefer small fragments (Khoo et al., 2021).

Our study was conducted in protected areas with low levels of human disturbance. However, the potential habitats of Williamson's mouse deer may also exist outside of protected areas, which we will be assessing in the future. Consistent with previous findings, our results showed that Williamson's mouse deer prefer to use lowlands, and they may prefer to use sites closer to water resources (Cao et al., 2010). We thus suggest that future investigations of the population of Williamson's mouse deer in nonprotected areas should mainly focus on lowlands closer to water. In Mengla County, the northern red muntjac and wild boar are becoming problematic to local ecosystems (e.g., damaging the local habitats and excluding the local species) due to their overabundance caused by habitat fragmentation and the declining population of larger predators (Cao and Zhang, 2022), which is hard to control and manage. However, we emphasize that these two species have no spatial exclusion from Williamson's mouse deer. In summary, our study provides important information for understanding the threats to the population of Williamson's mouse deer, which can guide management and conservation.

## Conclusions

Based on a long-term camera trap survey, we assessed the spatio-temporal avoidance of Williamson's mouse deer to sympatric larger ungulates and the relationship between the strength of avoidance and body size differences. Spatially, there was no spatial avoidance. Temporally, the species had different daily activity patterns and direct temporal avoidance of all larger ungulate species. This suggests that temporal avoidance can play

an important role in alleviating interspecific competition with sympatric larger species. Furthermore, we found results that run contrary to the body size–competition hypothesis (the more similar body sizes, the stronger competitive interactions), because Williamson's mouse deer had a stronger avoidance of the much larger species (sambar and Chinese serow). Our results provide the first evidence of a coexistence mechanism between Williamson's mouse deer and sympatric larger ungulates. We highlight that the difference in body size has limited power to explain the coexistence of tropical forest ungulates, because natural competitive interactions may be related to multiple ecological processes.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

The animal study was approved by the State Forestry Administration of China and in accordance with the legal requirements of China. The study was conducted in accordance with the local legislation and institutional requirements.

## Author contributions

R-CH, LW and R-CQ designed the study. R-CH processed and analyzed the data. R-CH wrote the first draft of the manuscript. R-CH, LW, KL, EG and R-CQ revised the manuscript. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1125840/full#supplementary-material>

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