RAFFLES BULLETIN OF ZOOLOGY **68**: 654–661
Date of publication: 27 July 2020
DOI: 10.26107/RBZ-2020-0080
http://zoobank.org/urn:lsid:zoobank.org:pub:73D7256A-159C-4117-BD43-102069A12891

Activity pattern and resource use of two *Callosciurus* species in different habitats in northeastern Thailand

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Abstract. Some squirrel species can adapt to areas of extensive human activities. However, few studies have compared the behaviour of such squirrels in human activity areas with that in their natural forest areas in the tropics. This study describes the activity pattern and resource use of *Callosciurus finlaysonii* and *C. caniceps* in a small residential area located in the dry evergreen and dry dipterocarp forests in Sakaerat Biosphere Reserve, Thailand, by using route census survey. Both species were active in the morning and evening, just as they are in the forests, but the frequency of detection of *C. finlaysonii* was higher than that of *C. caniceps*. Intraspecific interactions were frequently observed in *C. finlaysonii*; however, interspecific interactions were not observed. *Callosciurus finlaysonii* used buildings and electric wires located above ground in open areas as pathways, whereas *C. caniceps* was not observed in open areas. *Callosciurus finlaysonii* consumed a greater diversity of food items than *C. caniceps*, including fruits, leaves, flowers, and seeds, whereas *C. caniceps* fed mainly on fruits/seeds. The present study showed that *C. finlaysonii* can use human activity areas. *Callosciurus finlaysonii* probably use the human activity area owing to the presence of fewer natural predators, its ability to survive in different type of environments, as well as its wide feeding habits, and the presence of fewer competitors. However, it was observed that *C. caniceps* scarcely used human modified areas.

Key words. activity pattern, callosciurine squirrels, human activity, resource use, Southeast Asia, tropical seasonal dry forest

INTRODUCTION

Human activities affect the physical and chemical environment, population, and community characteristics of wildlife, and inflict structural and functional changes in ecosystems (McDonnell & Pickett, 1990). Although the population sizes of some animal species dramatically decrease due to human activities, other species adapt to artificially modified habitats (McKinney, 2002; Ditchkoff et al., 2006; Goddard et al., 2010; Galbreath et al., 2014; Parker et al., 2014).

Some squirrels (Rodentia: Sciuridae) can adapt to areas where human activities are prevalent (human activity areas), such as urban parks. For example, some squirrel species such as eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*) have increased population density in urban habitats compared to natural habitats (Manski et al., 1980; Mccleery et al., 2008). Some species also become less vigilant of humans in urban habitats, such as eastern gray squirrels (Cooper et al., 2008), fox squirrels (Mccleery, 2009), and Eurasian red squirrels, *S. vulgaris* (Uchida et al., 2015). The absence of natural predators, availability of suitable food in sufficient quantities, and the presence of fewer competitors are factors considered to favour the adaptation of squirrels to human activity areas (Duckett, 1982; van der Merwe et al., 2005; Devan, 2010).

Squirrels have become highly diversified in the Southeast Asian region (Corlett, 2007), where several forest types exist, and multiple diurnal squirrel species occur sympatrically in each forest type (Lekagul & McNeely, 1988; Francis, 2008; Phillipps, 2016). For example, 25 (14 diurnal and 11 nocturnal) and 14–18 squirrel species occur in the Peninsular Malaysia tropical rainforests and tropical forests in Lao PDR, respectively (Medway, 1983; Duckworth et al., 1999). Within this region, the coexistence mechanism of squirrels in the various types of forests (Saiful et al., 2001a, b; Shafique et al., 2006; Koyabu et al., 2009; Kobayashi et al., 2019b), the effect of wildfires on their population (Walker & Rabinowitz,

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Accepted by: Marcus A. H. Chua

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ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

1992; Kobayashi et al., 2017), and their roles in ecosystems (Yumoto et al., 2000; Kitamura et al., 2008; Bobadilla et al., 2016; Kobayashi et al., 2019a) have been documented. With the rapid deforestation and human modification of natural landscapes in Southeast Asia (Sodhi et al., 2010; Stibig et al., 2014), human-modified areas and urban habitats present a novel environment for squirrels. Devan (2010) reported the behaviour of *Callosciurus notatus* in an urban green area in Singapore and suggested that the availability of various environments and predator-free habitat can enable this species to inhabit this habitat type. However, there are no studies comparing the characteristics of these species in human activity areas and natural habitats.

The aim of this study was to identify the activity pattern and resource use of two sympatric diurnal squirrels (*C. finlaysonii* and *C. caniceps*) in a small residential area located in tropical dry forest. Kobayashi et al. (2019b) reported the resource use of these two tree squirrels in the contiguous dry dipterocarp (DDF) and dry evergreen forests (DEF) around the residential area of this study. Therefore, we specifically compared the resource use patterns in the human activity area with those in the surrounding natural forests to evaluate the capacity of each species to cope with human-modified habitats.

MATERIAL AND METHODS

Study site. This study was conducted in a small residential area, which is the headquarter area (HQ; approximately 2 ha) of Sakaerat Biosphere Reserve in Nakhon Ratchasima, northeastern Thailand (Fig. 1). The Sakaerat Biosphere Reserve contains both DDF and DEF, and the HQ is located in the border of two types of forests. Several native trees (e.g., *Shorea obtusa* in DDF and *Hopea ferrea* in DEF) with >20 m height grew inside the HQ area, in addition to several planted ornamental herbs and shrubs. A plant nursery was located near one building. Small (<2 m^2) artificial ponds were located near the main building and nursery. In the HQ area, there are guest houses, buildings for researchers, restaurants, and factory buildings, with less than 20 residents including staff and researchers, with one dog as a pet which is kept in a doghouse. During business days, 50–150 students visit and stay for science training courses that are held from early morning to night. The study region is a seasonal forest; December to February is the dry season when monthly precipitation is less than 50 mm (Sakurai et al., 1998).

Study species. Ten Sciuridae species (five diurnal and five nocturnal species) have been recorded in the Sakaerat Biosphere Reserve (Thailand Institute of Scientific and Technological Research, 2001; Trivedi et al., 2018). In this study, we focused on diurnal species. However, because Indochinese ground squirrels (*Menetes berdmorei*), black giant squirrels (*Ratufa bicolor*), and Burmese striped tree squirrels (*Tamiops macclellandi*) were not observed, we chose Finlayson's squirrels (*Callosciurus finlaysonii*) and gray-bellied squirrels (*C. caniceps*) as our target species. Although *C. finlaysonii* has a disputed taxonomy and can generally be divided into several subspecies (Boonkhaw et al., 2017) with different coat colours (Lekagul & McNeely, 1988), only *C. f. bocourti*, with a white coat, occurs in this study area (Thailand Institute of Scientific and Technological Research, 2001). In contrast, *C. caniceps* is grey ventrally and brown elsewhere with a black tipped tail. In addition, *C. finlaysonii* (cf. range of body weight is 220–250 g; Bertolino et al., 2004) is smaller than *C. caniceps* (cf. mean body weight of adult male is 347 g and that of adult female is 329 g; Saiful et al., 2001a). Although morphological data for these species are lacking at this site, the two species can easily be distinguished visually. These two species share several food items and species, but *C. finlaysonii* consumes a greater variety of food than *C. caniceps* (Kobayashi et al., 2019b). In addition, *C. caniceps* uses lower (height above ground) and dense vegetation (Kobayashi et al., 2019b).

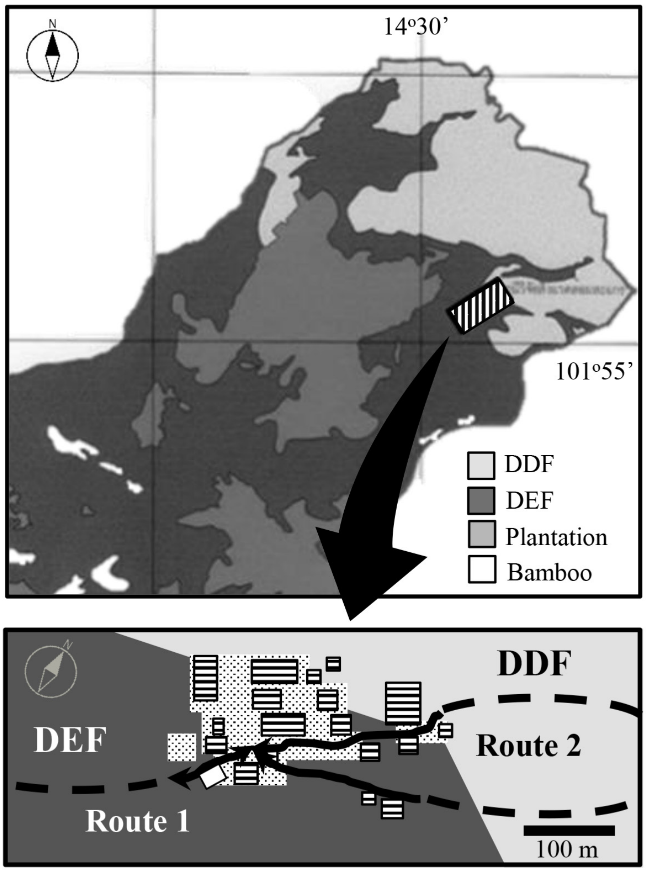

Fig. 1. Location of the study site in the headquarters (HQ) of the Sakaerat Environmental Research Station and census routes. Upper figure shows the location of Sakaerat Biosphere Reserve and the bottom figure shows an enlarged view of the HQ. Solid lines show the census route of the present study, broken lines show paved survey route of the previous study (Kobayashi et al., 2019b), broken line shows non-paved survey route of the previous study (Kobayashi et al., 2019b) in natural forests (DDF: dry dipterocarp forest in light grey; DEF: dry evergreen forest in dark grey). Dotted areas in the bottom figure are relatively open spaces with few trees, white square is the nursery, and striped squares are buildings.

Route census survey. Route census surveys were conducted to describe the activity pattern and resource use of the two squirrel species in the HQ. The surveys were conducted from 19 February to 30 March 2016, from 4 to 14 March 2017, and from 7 to 14 April 2017. Two survey routes were set and surveys were conducted one by one on successive days (Fig. 1). Route 1 was 100 m long and Route 2 was 500 m long; because each survey route was short, the data of Route 1 and Route 2 on successive days were combined (total route length: 600 m) into one set for analysis. In total, 24 sets of route census series were conducted in the morning (start time: 0620–0630 hours), 15 sets at midday (start time: 1220–1250 hours), and 22 sets in the early evening (start time: 1630–1640 hours). Route start and end points were reversed on successive days. Observation range was 20 m at each side from the route path.

Surveys involved walking slowly along the route, recording and observing squirrel's behaviour (feeding, drinking, interacting, nesting, grooming, traveling, alarming, resting, others/unknown), position (trunk, primary branch, secondary branch, vine, ground, roof, electric wire, other artificial matters, others/unknown), and height above ground level. Food items and species consumed by squirrels were recorded when feeding behaviours were observed. Distances between routes and observed individuals and heights above ground level were measured using a laser distance meter (Leica DISTO™ X310; Leica, Germany).

Data analysis. All statistical analyses were performed in R version 3.5.0 (R Core Team, 2018). Activity pattern was compared using the Steel-Dwass test and the frequency of detection was compared using the Welch's *t*-test. In addition, to compare the population density between human activity area (HQ: this study) and nearby DDF and DEF forests (previous study; Kobayashi et al., 2019b), the "estimated population density" was calculated as follows:

$$\text{Estimated population density} = \frac{\text{The number of observed individual}}{\text{The observed area calculated by the route length and observed range}}$$

Fisher's exact test was used to compare the proportion of squirrels observed at different heights and consumption of food items which was based on the number of observations. Niche width (Feisinger et al., 1981) and niche overlap (Slobodchikoff & Schulz, 1980) were calculated using the height of the tree used by the squirrels and the food items as follows:

$$\text{Niche width} = \frac{1}{\sum \mathrm{P_i^2}}$$

$$\text{Niche overlap} = \frac{\sum \mathrm{P_{ih}P_{jh}}}{\sqrt{\sum \mathrm{P_{ih}^2}}\sqrt{\sum \mathrm{P_{jh}^2}}}\ .$$

P_i in the niche width formula indicates the proportion of observations of a species found in *i*th unit of the resource set. Niche width ranges from 1 (when a species use one resource exclusively) to N (when the species use all resources with equal proportion). P_{ih} and P_{ij} in the niche overlap formula indicates the proportion of observations of each species in the *h*th unit of a certain resource dimension. Niche overlap ranges from 0 (no overlap) to 1 (complete overlap).

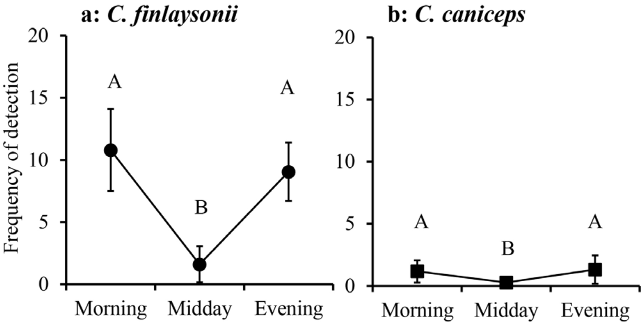

Fig. 2. Frequencies of detection of active (a) *Callosciurus finlaysonii* and (b) *C. caniceps* in each survey time. Data are displayed as mean ± SD. Different letters in the figure indicate a significant difference (Steel-Dwass test; $P < 0.05$).

Table 1. Results of Steel-Dwass test comparing for frequencies of detection within the observed time.

	t	p-value
C. finlaysonii		
morning vs. midday	5.200	<0.001
morning vs. early evening	1.845	0.155
midday vs. evening	5.136	<0.001
C. caniceps		
morning vs. midday	3.380	0.002
morning vs. early evening	0.349	0.935
midday vs. evening	3.117	0.005

RESULTS

In total, *C. finlaysonii* was observed 510 times (morning: 259, midday: 51, evening: 200) and *C. caniceps* was observed 64 times (morning: 28, midday: 7, evening: 29). Both species were active in the morning and the early evening, but the number of active individuals decreased at midday (Steel-Dwass test; $P < 0.05$, Fig. 2, Table 1). The frequency of detection of *C. finlaysonii* was higher than that of *C. caniceps* irrespective of time (Welch's *t*-test; morning: $t_{26.38} = 13.48$, midday: $t_{16.58} = 3.29$, and evening: $t_{30.46} = 13.57$, $P < 0.05$, Fig. 2). The estimated population density of *C. finlaysonii* was 3.5 ± 1.1/ha (mean ± SD) and that of *C. caniceps* was 0.4 ± 0.3/ha in the morning.

As for the behaviour of *C. finlaysonii*, traveling, feeding, and interaction were frequently observed in the morning and evening, while 50% of observed individuals were resting on the branch or trunk at midday (Fig. 3a). Although the frequency of detection of *C. caniceps* was low, the proportion of the different behaviours observed varied throughout the day. Feeding and traveling behaviour by *C. caniceps* were mainly observed in the morning, in addition to interaction (n = 3, intraspecific interactions) that was not observed at other times (Fig. 3b). At midday, many individuals would rest but they sometimes emitted an alarm call before the observer found individuals (Fig. 3b). The proportion of feeding behaviour was higher in the morning (48.3%) and evening (62.1%) compared to midday (14.3%) in *C. caniceps*,

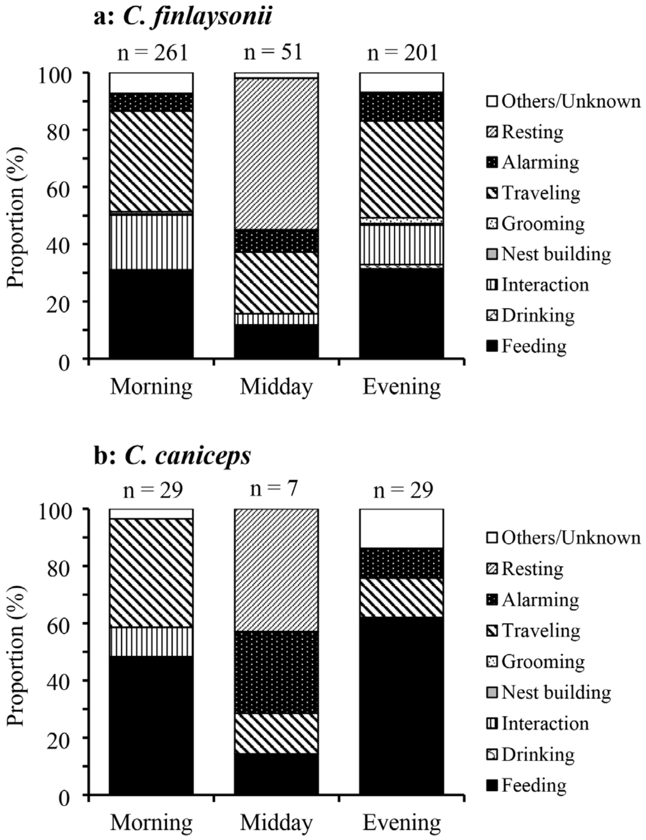

Fig. 3. Proportion of observed behaviours of (a) *Callosciurus finlaysonii* and (b) *C. caniceps* throughout the day.

and it was generally higher than that of *C. finlaysonii* (11.8–31.3%) (Fig. 3).

More than 80% of squirrels of both species were observed on trunks, primary branches, secondary branches and vines; secondary branches were the most frequently used, accounting for more than 50% of observations for *C. caniceps* (Fig. 4). *Callosciurus finlaysonii* used electric wires, entered the restaurant at the HQ, and moved on roofs. Most of these individuals used these artificial structures as pathways. *Callosciurus caniceps* entered vacant small houses but they were not observed in the buildings that people frequently used. When feeding, *C. finlaysonii* was frequently (60.1%) observed on a secondary branch, while *C. caniceps* were observed on primary and secondary branches, 72.7% and 66.7%, respectively. Both species were observed at various heights. *Callusciusus finlaysonii* was most often seen below a 10 m height (56.2% of observation), while *C. caniceps* was most often (38% of observations) seen at 15–19 m height above ground level. The frequencies of vertical space use differ between species (Fisher's exact test; $P < 0.05$, Fig. 5). Niche overlap was 0.86, and niche width of *C. finlaysonii* was 2.32 (n = 466) and that of *C. caniceps* was 0.92 (n = 61).

Feeding behaviour of *C. finlaysonii* was observed 143 times and that of *C. caniceps* was observed 35 times. Number of food items and species consumed by *C. finlaysonii* was greater than that of *C. caniceps* (Table 2). Both species ate human snacks and leftover food such as watermelon, and frequently consumed fruits/seeds, accounting for 45.5%

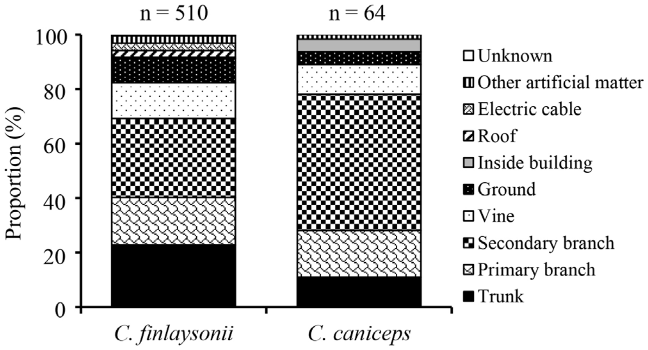

Fig. 4. Observed positions of (a) *Callosciurus finlaysonii* and (b) *C. caniceps*.

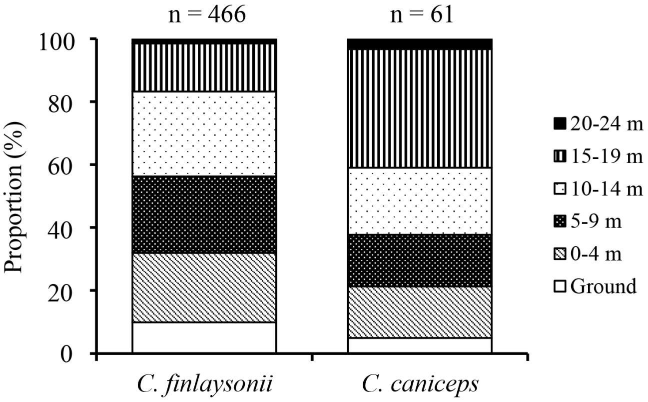

Fig. 5. Frequency of observed height range of *Callosciurus finlaysonii* and *C. caniceps*.

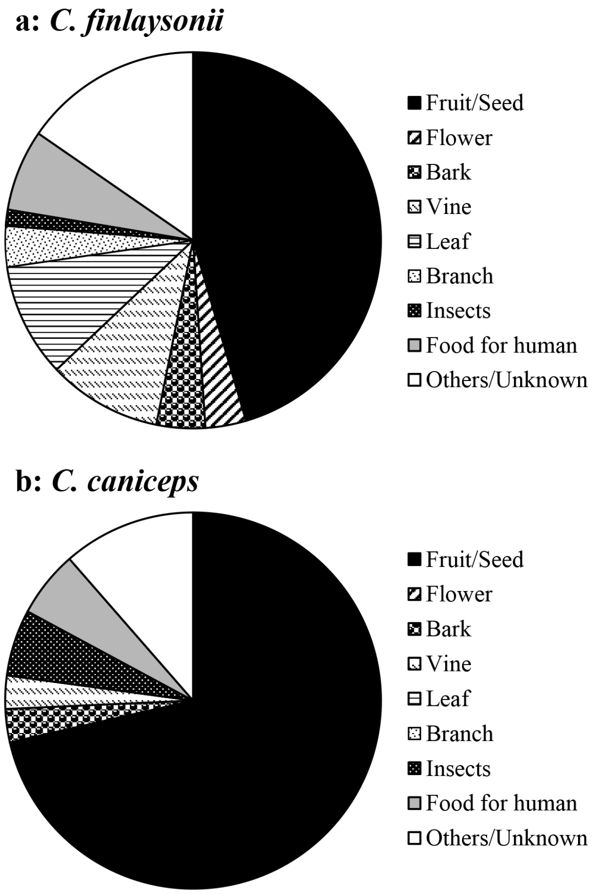

Fig. 6. Proportion of food items consumed by (a) *Callosciurus finlaysonii* (n = 143) and (b) *C. caniceps* (n = 35).

Table 2. Food items and species consumed by *Callosciurus finlaysonii* and *C. caniceps*.

Species	Food item	*C. finlaysonii*	*C. caniceps*
Plants			
Albiza adratissima	Seed	+	
	Bark	+	
Bombax onceps	Leaf	+	
Croton oblongifolius	Fruit	+	
Dalbergla nigrescans	Bark	+	
Datbergia cochinchinensis	Bark	+	
Entada sp.	Vine	+	
Fabaceae (Mimosoideae)	Branch	+	
Fabaceae sp.1	Vine	+	
Fabaceae sp.2	Fruit	+	
Ficus sp.	Fruit	+	+
Hopea ferrea	Flower	+	
Melientha suavis	Fruit	+	
Parkia sumatrana	Flower	+	
Shorea obtuse	Bark	+	
Shorea sp.	Bark		+
Sterculia pexa	Fruit	+	+
	Seed	+	+
Wrightia arborea	Fruit	+	
	Flower	+	
Xylia xylocarpa	Branch	+	
Tree sp.1	Fruit	+	
Tree sp.2	Fruit	+	
Tree sp.3	Fruit	+	
Tree spp. (>2 spp.)	Fruit	+	+
	Bark	+	
	Branch	+	
	Leaf	+	
Vine sp.1	Fruit	+	
Vine sp.2	Fruit		+
Vine spp. (>3 spp.)	Fruit	+	+
	Stem	+	+
	Leaf	+	
Animals			
Formicidae sp.		+	+
Human related food			
Snack		+	+
Fruits (e.g., watermelon)		+	
Rice and wheat material (e.g., bread, rice ball)		+	

and 71.4% of observed food items for *C. finlaysonii* and *C. caniceps*, respectively (Fig. 6). Only *C. finlaysonii* ate flowers and leaves (Table 2). Niche width based on food items of *C. finlaysonii* was 3.86 and larger than that of *C. caniceps* (1.88). The niche overlap of food items was 0.95 and the proportion of consumed food items was not significantly different between species (Fisher's exact test; $P = 0.09$).

DISCUSSION

The activity pattern, estimated population density, behaviour, and observed position and height of two squirrel species were compared between the HQ (this study) and the two types of natural forests (DDF and DEF) around the HQ reported previously (Kobayashi et al., 2019b) (Table 3). *Callosciurus finlaysonii* was active in morning and evening just like in the forests; however, the estimated population density in the HQ area was higher than in either forest. One possible reason is that *C. finlaysonii* in the HQ may be more visible because they are used to human presence and do not avoid them as in natural forests. In addition, the proportion of active individuals at midday of this species in the HQ (10.0%) area was higher than in natural forests (DDF: 3.9%, DEF: 4.4%; Kobayashi et al., 2019b). Some individuals were observed using artificial structures (rooftops, electric cables, etc.) that

Table 3. Activity pattern, population density, diet, and habitat use of *Callosciurus finlaysonii* and *C. caniceps* in a head quarter area (HQ), dry dipterocarp forest (DDF), and dry evergreen forest (DEF). The estimated population density was calculated as (the number of observed individual)/(the observed area calculated by the route length and observed range) and data in the morning was shown.

	Active time	**Estimated population density in the morning (ha-1)**	**Food items**	**Niche width of food items**	**Most utilised position**	**Mainly utilised height**	**Reference**
C. finlaysonii							
HQ	Morning and Evening	3.5 ± 1.1	Fruit/Seed	3.86	Trunk, Branch	0–20 m	Present study
DDF		0.7 ± 0.2	Fruit/Seed	2.78	Branch	10–15 m	Kobayashi et al. (2019b)
DEF		0.8 ± 0.4	Various	6.85	Branch	5–20 m	Kobayashi et al. (2019b)
C. caniceps							
HQ	Morning and Evening	0.4 ± 0.3	Fruit/Seed	1.88	Branch	15–20 m	Present study
DDF		0.0 ± 0.0	–	–	–	–	Kobayashi et al. (2019b)
DEF		0.8 ± 0.3	Fruit/Seed, Bark	4.32	Ground	0 m	Kobayashi et al. (2019b)

did not occur in the forests, and the observed height above ground level in the HQ was different from that in DDF, although it was similar to that in DEF (Table 3). *Callosciurus caniceps* was also active in the mornings and evenings, just as in the forests, but the estimated population density in the HQ was smaller than in the DEF and higher than in the DDF (Table 3). Behaviours observed in the HQ area were different from those observed in the DEF—particularly this species did not often use the ground in the HQ compared to DEF, although feeding was the most frequently observed in both habitats. This is probably because this species is shyer to human presence. According to these comparisons, the density and behaviours of both squirrel species in the HQ area were different from those in the forests.

Callosciurus finlaysonii seems to be more flexible in behaviour and use of human-modified habitats than *C. caniceps* as indicated by the higher estimated population density of *C. finlaysonii* in the HQ area than in natural forests and the lower estimated density of *C. caniceps* in HQ than in DEF (Table 3). The likely reasons are that 1) human activity areas are open, whereas *C. caniceps* prefers dense vegetation (Tamura, 1995) that is not available in human activity areas including the HQ area of this study, and 2) the availability of food items is limited in the HQ area because the food niche width of *C. caniceps* is relatively small (Kobayashi et al., 2019b).

There may be four likely reasons for the relatively high abundance of *C. finlaysonii* in the human activity area (i.e., the HQ area). First, the presence of few or no predators, which are likely to be carnivores, raptors, and snakes (Tamura, 1989, 2011; Tamura & Yong, 1993). Although the actual predators of *C. finlaysonii* are unknown, all of these predators occur in the contiguous forests but may not get close to human activity areas. Second, the use of different habitat types by *C. finlaysonii* as shown by a similar use of DDF, where the forest floor was covered by grasses or a few seedlings and the canopy was relatively open, and the DEF, where the forest floor had no grasses and the canopy was dense (Kobayashi et al., 2019b). Lekagul & McNeely (1988) also pointed out that *C. finlaysonii* used various habitats such as open wood, coconut plantations, and dense forests. This wide range of habitat types used by *C. finlaysonii* suggests that this species can use human activity areas. Third, food availability seems adequate for this species which consumes various food items including leftover food by humans (Kobayashi et al., 2019b; present study). Thus, the HQ is a good feeding place for *C. finlaysonii*. The last reason is the low abundance of competitors. *Callosciurus caniceps* dominated *C. finlaysonii* in natural DEF, but was not frequently observed in the HQ area compared to its presence in the DEF (Kobayashi et al., 2019b). Thus, less abundance of *C. caniceps* in the HQ area may favour the presence of *C. finlaysonii*.

The observation of certain behaviours of *C. finlaysonii* at midday that were more frequently recorded in the HQ area than in natural forests may be due to the higher population density in the HQ area. For example, the number of active individuals and frequency of interactions were higher in HQ than in DDF and DEF at midday (Kobayashi et al., 2019b). In addition, in *C. erythraeus*, active time is limited to morning and evening as they rest at daytime when enough food is available (Tamura, 2011). Furthermore, a plant pollinator survey by Kobayashi et al. (2018) indicated that *C. erythraeus* visited flowers in the morning and evening in the forests, but also in the daytime in urban sites (Kobayashi et al., 2018). The behaviours of *C. finlaysonii* observed in the HQ area at midday may be caused by intraspecific competition because of the limited food and the large number of individuals.

The behaviour of *Callosciurus finlaysonii* in this study in Thailand differs from that of the same species in Italy and Japan, where it has settled as an invasive species in urban parks (Bertolino et al., 1999; Oshida et al., 2007). For example, the proportion of feeding time was higher in Italian parks than in the present study and the trunk was used less frequently, while primary branches were used more often in Italy (Bertolino et al., 2004); however, it is noted that observation methods differed between studies. Although many factors such as weather conditions and food availability may influence behaviour, the difference in intensity of human activity may also contribute to the differences in behaviour of *C. finlaysonii* in Italy and Japan compared to this study as those sites were surrounded by houses or non-natural forest such as orchard and garden (Bertolino et al., 2004). Furthermore, it is worth noting that *C. erythraeus* and *C. notatus* also occur in urban areas and both species use different types of natural habitats (Tamura, 1995; Saiful et al., 2001a; Lurz et al., 2013). Thus, *Callosciurus* species that use open habitats in their natural habitat may have the ability to use the more open human activity areas.

In this study, the frequency of detection of *C. caniceps* was lower in the human activity areas compared to adjacent forests (DDF and DEF) despite the low level of human activity and fragmentation impacts. Considering the home range size of *Callosciurus* squirrels is 0.3–2.7 ha (Tamura et al., 1989; Saiful et al., 2001a), the studied squirrels may be able to visit both natural forests and human modified areas. This suggests that deforestation and human modification of forest habitats can have a negative impact on the species. Deforestation poses a serious threat to animal and plant conservation in Southeast Asian countries, such as Thailand (Sodhi et al., 2010; Wohlfart et al., 2014). Hence, understanding the impacts of anthropogenic landscape changes on animal behaviour and ecology is essential for conservation and management of forest biodiversity.

ACKNOWLEDGEMENTS

We are grateful to Naoki Kato (Kyoto University) and staff at Sakaerat Environmental Research Station for supporting this study. We also thank two anonymous reviewers for giving us valuable comments. This study was partly supported by JSPS KAKENHI (Grant Number: 16H05771) and Centre of Excellence on Biodiversity, Thailand (BDC-PG2-159009).

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