Camera traps reveal interspecific differences in the diel and seasonal activity patterns of cicada nymph predation

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Abstract

Cicadas, a group of large-bodied insects, are preyed upon at both nymphal and adult stages by diverse range of vertebrates such as birds and mammals. Although the behavior of predators toward adult cicadas is well documented, there is a lack of research on the predation on cicada nymphs. In this study, camera-traps deployed in conifer plantations, in which high population densities of cicadas *Lyristes bihamatus* emerge, were used to evaluate the seasonal and diel patterns of predation upon cicada nymphs by three predator species, namely brown bears, red foxes, and jungle crows from May to September in 2018 and 2019 in northern Japan. Among all three species, cicada nymph predation occurred until early August when the final instar nymphs fully emerged. Bears were observed to constantly dig for cicada nymphs until early August, whereas foxes and crows were frequently observed foraging from late July to early August, during the season of *L. bihamatus* emergence. In contract to the powerful digging ability of bears, which facilitates efficient predation upon subterranean cicada nymphs, it is generally difficult for foxes and crows with limited or no digging ability to gain access these nymphs until the period of emergence. Cicada nymph predation by bears and crows was observed primarily during the daytime, despite the typical crepuscular/nocturnal emergence schedules of these insects. Contrastingly, the predatory activities of foxes tended to be nocturnal during the period prior to the beginning of cicada emergence, although subsequently became diurnal during the cicada emergence period. These observations indicate that the temporal activity patterns of cicada nymph predators are determined by interspecific differences in predation abilities and cicada emergence schedules. Accordingly**,** the findings of this study provide evidence to indicate that the timing and duration of trophic interactions between above- and belowground communities might vary among predator species, depending on their predation abilities.

Keywords

Aboveground-belowground linkage, circadian rhythm, *Corvus macrorhynchos,* digging, *Ursus arctos, Vulpes vulpes*

Declarations

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Code availability: The R code used in the current study is available from the corresponding author upon reasonable request.

Introduction

The use of time is one of the most fundamental aspects in animal behavior (Bennie et al., 2014; Fortin et al., 2002; Jones et al., 2001). Temporal patterns of predation are determined by temporal changes in resource availability (e.g. resource phenology) and the temporal foraging strategies of predators (e.g. circadian rhythms and seasonal dietary changes) (Monterroso et al., 2013; Stanek et al., 2017). Temporal patterns of predation can determine the timing and duration of predator-prey interactions (Cunningham et al., 2019; Monterroso et al., 2013). Thus, elucidating the temporal patterns of predation can contribute to deepening our understanding of such interactions.

Cicadas, a group of large-bodied insects, are preyed upon at both the soil-dwelling nymphal and ground-dwelling adult stages by a range of vertebrate species, including birds and mammals (Pons, 2020; Williams and Simon, 1995). The predation on cicadas can be considered a representative example of the phenomenon whereby subterranean prey are actively sought and consumed by aboveground predators (Polis et al., 2003). Adult cicadas are typically consumed by avian predators as resource pulses over short periods of time (ca. ~1 month) (Koenig and Liebhold, 2005). For instance, during July when raising nestlings, parent Mississippi kites (*Ictinia mississippiensis*) in North America prey extensively on adult cicadas (Chiavacci et al., 2014; Glinski and Ohmart, 1983). Contrastingly, cicada nymphs, which remain belowground for several years prior to eventual emergence, are available for predators for relatively longer periods of time. In Mediterranean mixed pinewood, for instance, red foxes (*Vulpes vulpes*) have been observed to consume cicada nymphs from April to August (Lovari et al., 1994), while brown bears forage on cicada nymphs from May to July (Tomita and Hiura, 2020). However, although predatory behavior toward adult cicadas is well documented (Steward et al., 1988; Takakura and Yamazaki, 2007; Vandegrift and Hudson, 2009; Williams and Simon, 1995), there are few studies that have examined the behavior of cicada nymph predators (Lovari et al. 1994).

The availability of cicada nymphs for aboveground predators changes depending on the instar and emergence schedules. For example, whereas the highly nutritional final instar nymphs, which remain in surface soil immediately prior to emergence, can be easily captured by shallow digging, earlier instar nymphs inhabiting deeper soil are inaccessible to aboveground predators. During the cicada emergence period, a large amount of final instar cicada nymphs emerge from the ground, during which time they are readily accessible to a wide range of predators (Storm and Whitaker, 2007). Indeed, some studies have reported that the predators of cicada nymphs consume only those individuals in the final instar. (Storm and Whitaker, 2007; Tomita and Hiura, 2020).

Whereas predators that are suitably equipped for digging can prey on the subterranean final instar nymphs before the beginning of cicada emergence, predators that are poorly adapted for digging tend to be restricted to preying on the nymphs only during the emergence period. Consequently, it might be anticipated that the seasonal patterns of cicada nymph predation would differ among species, depending on their respective predation abilities (i.e., digging). Cicadas typically emerge around twilight zone, thereby largely escaping the attentions of diurnal predators, such as birds (Allard, 1937; Maier, 1982). Given the nocturnal peak of cicada emergence, the diel activity of cicada nymph predators might similarly be expected to show a nocturnal pattern. Thus, the diel patterns of cicada nymph predation might vary not only among predator species, but also in response to cicada emergence schedules even for the same predator species.

To elucidate the temporal activity patterns of cicada nymph predators, it is necessary to monitor their activity at sites characterized by high levels of predation. In this regard, camera trapping, which is among the most effective non-invasive survey method for studying animal behavior and activity patterns, can provide continuous data on the temporal activities of free-living animals (Burton et al., 2015; Rowcliffe et al., 2014). In the Shiretoko World Heritage (SWH) site, I have found that brown bears dig for cicada nymphs in conifer plantations in which high densities of the cicada (*Lyristes bihamatus*) emerge (Tomita and Hiura, 2021). Camera-traps preliminarily detected that jungle crows (*Corvus macrorhynchos*), red foxes and brown bears frequently visit larch (*Larix kaempferi*) plantations to prey on cicada nymphs (Fig.1). Accordingly, in this study, I evaluated the diel and seasonal patterns of cicada nymph predation by these three predator species, using camera traps at high predation sites in the SWH (Fig. 1, Online Resource; ESM_1-3). Previous studies that have reported cicada nymph predation by these species have already reported (Asabu, 1999; Lovari et al., 1994; Tomita and Hiura, 2020). There are differences in digging abilities among these species: with crows being unable to dig, and brown bears being more effective soil excavators than red foxes. It can be predicted that such interspecific differences in digging ability might yield differences among these species with respect to the seasonal patterns of predation on cicada nymphs. For instance, crows would be restricted to prey on cicada nymphs only during emergence season. Moreover, given the differences in the diel activity patterns of these predator species (Ikeda et al., 2016; Kondo et al., 2010), the diel patterns of cicada nymph predation may also show interspecific variation. Accordingly, I also examined interspecific differences in the diel patterns of cicada nymph predation during the cicada emergence periods. Notably, the average density of emerging cicadas in larch plantations in 2018 (20.20 ± 18.71 / $100m^2$) was lower than that in 2019 (87.07 ± 47.72 / $100m^2$) (Tomita and Hiura, 2021), and thereby provided an opportunity to focus on behavioral differences in cicada nymph predation between two consecutive years in response to differences in the availability of cicada nymphs.

Methods

Study site

This study was conducted on the Horobetsu-Iwaobetsu plateau (total area = 860 ha, 44°09=N, 145°02=E) located in the western parts of the SWH (Fig. 2). The elevation ranged from 120 to 220 m. The annual mean temperature at the study site was 6.2 °C. and the monthly mean temperature ranged from –10.4 °C in February to 15.1 °C in August (1981–2010). The UNESCO certified this area as a World Natural Heritage site because it represents one of the richest northern temperate ecosystems in the world (http://whc.unesco.org/en/list/1193). The natural forests on the site are conifer-broadleaved mixed forests mainly consisting of Sakhalin fir (*Abies sachalinensis*), Mongolian oak (*Quercus crispula*), and maple (*Acer mono*) (Suzuki et al. 2021). The natural forests accounted for 82% of the forest area in the study site. The plantations accounted for 18% of the total forest area. Sakhalin spruce (*Picea glehnii*), larch and Sakhalin fir plantations account for 13%, 4%, and 1%, respectively (Tomita and Hiura, 2021). Two native cicada species, *L. bihamatus* and *Yezoterpnosia nigricosta*, only occur in forest of the SWH and emerge during summer and spring, respectively. In the larch plantations, the emergence densities of *L. bihamatus* were higher than those of *Y.*

nigricosta in both 2018 and 2019. The same investigation for evaluating the density of *L. bihamatus* (Tomita and Hiura, 2021) revealed that the densities of *Y. nigricosta* exuviae in the larch plantations in 2018 and 2019 were 2.06 ± 3.36 / 100m^2 and 3.67± 3.60 / 100m^2, respectively (Tomita *unpublished data*). Thus, I assumed cicada nymph predation occurring within the larch plantations was exclusively for *L. bihamatus*. Hereafter, the term "cicada (s)" is in reference to *L. bihamatus* unless otherwise stated.

Information on the ecology of cicada nymph predators in this area is currently only available for brown bears (Tomita and Hiura, 2021, 2020). Eleven individual bears, including two sub-adults, two solitary female adults, and three females with cub(s) were observed digging for cicada nymphs at the study site in 2018 (Tomita and Hiura, 2020). In 2019, eleven individual bears, including one adult male, one sub-adult, two solitary adult females, and three females with cub(s) were observed digging for cicada nymphs at the study site. Individual identification by each year was based on color, marks, body size, and family structure of the bears. In the study site, brown bear preys on the final-instar nymphs of *L. bihamatus*, but not *Y. nigricosta* and the proportion of *L. bihamatus* nymphs in bear scats was estimated to be 14.3% in 2018 (Tomita and Hiura, 2020). Brown bears only dig for cicada nymphs in the plantation, and the frequency of digging was the highest in the larch plantation compared to other plantation types such as spruce and fir plantations (Tomita and Hiura 2021, Tomita and Hiura *in press*). The emergence density of cicadas in the larch plantation was higher than that in the natural forest and the spruce plantation, and approximately the same amount as that in the fir plantation (Tomita and Hiura, 2021) . Accordingly, I established camera traps in the larch plantations to evaluate the temporal patterns of cicada nymph predation.

Camera-trap survey

In 2017, I conducted a preliminary survey to determine the survey plots by setting camera traps (Tomita & Hiura 2020). As a result, I found eight candidate larch stands where brown bear digging had intensively occurred and cicada emergence density was the highest around other forest stands. These forest stands had a high potential for observing cicada nymph predation events by bears and other predators. From May 15 to September 15 in 2018 and 2019, I set eight survey plots (5 m × 10 m = 50 m^2) in these larch plantations (Fig. 1) and two infrared-triggered cameras (LTL Acorn 5210a; LTL Acorn Outdoors, Green Bay, Wisconsin, USA) in each plot. The plot size was determined based on resolution of cameras to tolerate behavioral observation and the ability of red infrared sensor (c.a. 5 m). I had already conducted a preliminary test for quantifying these abilities of the used sensor cameras beforehand in this study. The cameras were located at the opposite ends of the long side of the survey plot so that the total area of the plot could be observed. The cameras were placed on a larch trunk 1.0 - 1.5 m above the ground and its effective height range is assumed to be about from 0 m to 1.5 m because the camera trap survey was originally designed to observe brown bear behavior. Most exuviae on a tree trunk could be observed under 2 m and, sometimes at 3 m, indicating that most cicadas molted under 2 m height of a tree (Tomita and Hiura, 2021). Thus, it is possible to underestimate the activity of crows over 1.5 m height through overlooking a certain predation by crows outside the camera's range (i.e. over 1.5 m height) even though I can compare the relative values of crow activities among years and seasons owing to the same methods among both years. All cameras were programmed to take 30-second videos with 5-minute intervals to classify the behavioral types of predators and acquire data on the detailed activity time. All videos provided the recording date and time.

Behavior classification

Behavior of brown bear and red fox was categorized into three types: digging, moving (i.e., only walking), and foraging on the ground (e.g. climbing tree and/or capturing cicada nymphs on tree trunks). Given that the purpose of tree climbing in foxes is predation on arboreal prey (Mella et al., 2018; Murdoch et al., 2004) and such prey of red fox is only cicada nymphs in the study site (Tsukada and Nonaka 1996, Tomita *personal observation*), this behavior was regarded as cicada nymph predation. Crow behavior was categorized into two types: predation and searching for cicada nymphs. Crows perching on a tree branch were regarded to be searching for cicada nymphs. The reasons for this consideration were: (1) the crows several meter from the ground could only be resting or searching for foods, because moving of crows is only by flight and (2) the crows would not perch on a tree branch for rest, because crows were captured by camera-traps only during the daytime (see Fig. 3e) and crows usually rest at night (Kondo et al., 2010).

Data analysis

To assess the seasonal activity patterns of predation on cicada nymphs, I defined the following as independent events: (1) consecutive videos of different individuals of the same or different species, and (2) consecutive videos of individuals of the same species taken more than 0.5 hours apart (O'Brien et al., 2003). Event frequency was defined as the number of independent events per trap-night. I divided the survey period into three seasons: the pre-emergence period (from May 15 to July 14), cicada emergence period (from July 15 to August 9), and the post-emergence period (from August 10 to September 15). Because the first observed dates of cicada exuviae are 13 July and 15 July in 2018 and 2019, respectively, I set the cicada emergence period as 14 July. This date are roughly consistent with Hayashi and Saisho (2011). Because cicada emergence in Japan generally continues about 3-4 weeks (namely, 21-28 days) (Hayashi and Saisho, 2011; Sato and Sato, 2015), I set the cicada emergence period from 15 July to 9 August (25 days). One-way ANOVA and Tukey's multiple comparison tests were used to compare the event frequencies across cicada emergence periods. Multiple comparison was performed when the ANOVA indicated a significant difference ($P < 0.05$). These analyses were applied to each behavior of each species.

To assess the diel patterns of cicada nymph predation, I calculated video frequency (the number of videos per hour) as the index of animal activity levels (Ikeda et al., 2016; Tobler et al., 2008). To consider the changes in daylength across seasons, I divided the daily time periods into two categories: daytime (from sunrise to sunset) and night-time (from sunset to sunrise) for each cicada emergence period according to the information on the sunset and sunrise times provided by the National Astronomical

Observatory of Japan (https://eco.mtk.nao.ac.jp/koyomi/). During the pre-emergence period, the average sunrise and sunset times are 3:45 (3:37 - 3:54) and 18:54 (18:34 - 19:02), respectively. During the cicada emergence period, the average sunrise and sunset times were 4:02 (3:50 – 4:15) and 18:48 (18:31 – 18:56), respectively. For the pre-emergence and cicada emergence periods, daytime and nighttime were defined as 4:00-19:00 and 19:00-4:00, respectively. I didn’t perform statistical analysis for the data on diel activity patterns during the post-emergence period because there were few videos captured during this period (Table 2, 3). Data on diel activity patterns was pooled between 2018 and 2019. Generalized linear mixed models (GLMMs) with log link and Poisson error distribution, and with year as a random factor were used to compare the video frequency between daytime and nighttime. These analyses were applied to each behavior of each species. All statistical analyses were conducted using R version 3.5.1 (R Core Team, 2018).

Results

In 2018, 411 videos and 311 events were recorded: 111 videos and 71 events for brown bears, 299 videos and 239 events for red foxes, and 1 video for crows. In 2019, 369 videos and 321 events were recorded: 112 videos and 73 events for brown bears, 181 videos and 175 events for red foxes, and 76 videos and 68 events for crows. The number of videos and event frequencies for each behavior across the three species in 2018 and 2019 are listed in Table 1. I did not perform statistical analyses on data on brown bear foraging, behaviors of crows in 2018, and the diel activity patterns of all species in the post-emergence period due to low video frequencies.

Seasonal patterns of cicada nymph predation

All species were mainly recorded during the pre-emergence and emergence periods in both survey years (Fig. 3).

Brown bears

In 2018, the event frequency of digging was the highest in the pre-emergence period (TukeyHSD, $P < 0.05$), but there was no significant difference in the frequency of this behavior across cicada emergence periods in 2019 (ANOVA, $F_{1,85} = 0.62$, $P =$

0.432; Fig. 3a, b). In 2018, there was no significant difference in the event frequency of moving across cicada emergence periods (ANOVA, $F_{2,121} = 1.572$, $P = 0.212$), but the frequency was higher in the emergence period than in the pre-emergence period in 2019 (ANOVA, $F_{1,85} = 10.20$, $P = 0.002$; Fig. 3a, b, Tables 2 and 3). There was a larger proportion of digging behavior to the total event frequency in the pre-emergence period than in the emergence period in both years. In 2018, this proportion in pre-emergence and emergence periods was 0.81 and 0.55, respectively. In 2019, this proportion in pre-emergence and emergence periods was 0.78 and 0.37, respectively.

Red fox

Digging occurred during the pre-emergence and emergence periods, and the event frequency in the pre-emergence period was significantly higher than that in the emergence period in 2018 (ANOVA, $F_{1,85} = 4.24$, $P = 0.042$; Fig.3c), but there was no significant difference in 2019 (ANOVA, $F_{1,85} = 0.48$, $P = 0.491$; Fig. 3d). The event frequency of moving was the highest in the emergence period, and the difference in the frequency of moving between the pre-emergence and post-emergence periods was not significant in either year (TukeyHSD, $P < 0.05$). Foraging was observed only during the emergence period. There was a larger proportion of digging behavior to the total event frequency in the pre-emergence period than in emergence period. In 2018, this proportion in pre-emergence and emergence periods was 0.32 and 0.02, respectively, while in 2019, it was 0.29 and 0.03, respectively.

Jungle crow

The event frequency of foraging and searching was significantly higher in the cicada emergence period than in the pre-emergence period (TukeyHSD, $P < 0.05$; Fig. 3e, Table 3). There were no videos of crows during the post-emergence period.

Diel patterns of cicada nymph predation

In both survey years, almost all videos of brown bears and jungle crows were recorded during the daytime (Figure S1). The video frequencies of each behavior for both species was significantly higher during the daytime than the nighttime, regardless of the cicada emergence season (GLMM, $P < 0.001$; Fig. 4a,c). For red foxes, the frequency of digging captured by video did not significantly differ between the daytime and nighttime during both periods (GLMM, $P > 0.1$). During the cicada emergence period, the video frequency of fox foraging in the daytime was significantly higher than the nighttime (GLMM, $P = 0.031$). The video frequency of foxes moving was significantly higher in the daytime than the nighttime during the emergence period (GLMM, $P < 0.001$; Fig.4b). In contrast, the frequency was lower during the nighttime than the daytime during the pre-emergence period (GLMM, $P < 0.001$; Fig, 4b).

Discussion

In both survey years, brown bears, red foxes, and jungle crows were mainly observed in study plots during the pre-emergence and emergence periods, and were generally absent post-emergence period (Fig.3), thereby indicating that cicada nymph predation continued until the end of cicada emergence. This would tend to confirm that final instar nymphs, the most accessible prey across the cicada nymphal stages, are the main targets of the three assessed predators. The seasonal predation patterns of foxes were similar to those of crows, but differed from those of bears. Given their superior digging ability, brown bears are able to gain access to the nymphs for longer periods than other predators, whereas red foxes and jungle crows with limited or no digging ability are typically restricted to preying on nymphs during the period of cicada emergence. Thus, interspecific differences in the seasonal patterns of cicada nymph predation tend to reflect interspecific differences in predation ability (i.e., digging). In the case of brown bears and red foxes, the proportion of digging behavior to the total event frequency during the emergence period was greater than that during the pre-emergence period (Fig. 3a-d), indicating a temporal change in the mode of cicada nymph predation from digging to predation on the ground in response to the sequence of events in cicada emergence schedule.

Temporal patterns of cicada nymph predation by brown bears

In 2018, the event frequency of brown bears during the cicada emergence period was lower than that during the pre-emergence period (Fig.3a), even though the energy expenditure for predation on cicada nymphs might have the lowest during the cicada emergence period, when bears could have readily preyed upon the nymphs without digging. This seemingly counter-intuitive observation may be attributable to the lower importance of nymphs for bears during the cicada emergence period compared with that during the pre-emergence period. At the SWH site, from late July, brown bears start foraging on nuts of the Japanese stone pine (*Pinus pumila*), which are present in subalpine areas (at an elevation of approx. 600-1,100 m) (Shirane et al., 2021). Accordingly, the main foraging habitat of bears may change from forests to subalpine areas during the cicada emergence period; and consequently, there might be a reduction in cicada nymph predation by bears during this period, even though the emerging cicada nymphs would be readily accessible to bears. However, in 2019, the event frequency during the cicada emergence period did not differ significantly from that during the pre-emergence period (Fig.3b). Given that the cicada emergence densities at the study site in 2019 were higher than those in 2018 (Tomita and Hiura, 2021), I speculate that bears may have prolonged the duration of cicada nymph predation in 2019 owing to the higher availability of nymphs. Indeed, the foraging behavior of brown bears, which consume diverse food items across multiple ecosystems, changes depending on the food availability from coastal to alpine areas (Shirane et al. 2021). More detailed information on food availability across ecosystems is required to deepen our understanding of how bears utilize these resources.

In the present study, brown bears were mostly recorded by camera traps during the daytime, indicating that they are diurnal predators of cicada nymphs (Fig. 4a). The diel patterns of brown bear foraging activities are usually diverse (Klinka and Reimchen, 2002; Munro et al., 2006). Given that brown bears are active throughout the day (Ikeda et al., 2016; Kaczensky et al., 2006), they would divide their activity time during the day according to the type of food item and foraging behavior (Munro et al., 2006).

However, human activities make the activity time of brown bears nocturnal (Kaczensky et al., 2006; Wheat and Wilmers, 2016). Nevertheless, despite the fact that many people visit the study site for sightseeing (Shimozuru et al., 2020) and most of the survey plots are located near to roads that are frequently used by humans (Fig.2), I observed that cicada nymph predation by bears occurred diurnally, coinciding both temporally and spatially with human activities. Thus, it would appear that human activities at this study site have yet to promote a temporal shift in bear foraging behavior. The potential reason is human habituation. In Southeast Alaska, USA, for instance, the activity patterns of human-habituated bears have become diurnal, whereas non-habituated bears are mainly active during the night (Wheat and Wilmers, 2016). In the present study area, bears have been released from hunting pressure following the designation of the site as a protected area, even though park managers frequently drive away bears appearing along the roadside into the forest (Shimozuru et al., 2020). Such a situation may lead to human habituation of bears. Another plausible explanation for the observed diurnal activity of brown bears is a sex-related difference in diel activity that females show a greater extent of diurnal activity than males, which could be attributable to the avoidance of infanticide by male bears (Schwartz et al., 2010). This sex difference in diurnal activity of foraging behavior is consistent with the findings of Tomita and Hiura (2020), who found that the brown bears observed digging for cicada nymphs mainly consist of solitary females or females accompanied by cubs.

Temporal patterns of cicada nymph predation by red foxes

The foraging behavior of red foxes mainly consist of moving, which is inferred to be indicative of searching for cicada nymphs, as the frequency of movement was observed to be the highest during the period of cicada emergence and lowest during the post-emergence period. Given that the home range size of red foxes at the study site has been shown not to change from May to August (Tsukada, 1997; Tsukada and Nonaka, 1996), a higher event frequency in the cicada emergence period than that in the pre-emergence period can be interpreted as an increase in the intensity of cicada nymph predation rather than an increase in their overall activity levels. The life history of red foxes isn’t likely to influence their seasonal patterns of cicada nymph predation because juvenile foxes become independence from their parents during autumn and winter seasons(Yoneda and Maekawa, 1982), which were not assessed in the camera trap survey of the present study.

Whereas during the pre-emergence period, the diel patterns of red fox predation on cicada nymphs were broadly consistent, predatory activity was observed to be significantly higher during the daytime than at night during the period of emergence (Fig. 4b). Given that cicada emergence is usually crepuscular and nocturnal (Allard, 1937; Maier, 1982), the nymphs would be readily accessible to ground-searching foxes at these times of the day during the emergence period. However, even though cicada emergence usually continues throughout night, the predatory activity of foxes tended to be concentrated in the evening between 16:00 and 18:00, with the frequency of predatory events decreasing thereafter. I speculate that foxes depend primarily on the visual cues for predation on cicada nymphs and hence would be able to detect the location of nymphs more accurately prior to sunset. Accordingly, the diel patterns of cicada nymph predation by foxes might be determined by a combination of the circadian patterns of cicada emergence and the sensory properties of foxes. Consistent with this supposition, the diel activity patterns of red foxes in a Mediterranean mixed forest in Italy have been observed to change in response to the circadian patterns of prey animals (Lovari et al., 1994).

Temporal patterns of cicada nymph predation by jungle crows

Given that jungle crows forage exclusively during the hours of daylight (Kondo et al., 2010), the diel patterns of cicada nymph predation by these crows are generally consistent with their overall diel activity patterns. An increase in the event frequency of jungle crows from pre-emergence to cicada emergence periods indicates that they ambush the emerging cicada nymphs. Pons (2020) reported that the true cicadas (Cicadidae) preyed upon by avian predators consist primarily of adults. However, final instar cicada nymphs, which would be more readily captured than adults, could have potential value as a food resource for birds. The use of final instar cicada nymphs as prey by avian predators may be underestimated owing to the shorter periods during which nymphs are available to birds compared with adult cicadas.

Interestingly, my camera traps captured crows only a single time in 2018 when the cicada emergence density was lower than in 2019, although this might represent an underestimate of the absolute frequency of predatory events, considering the likelihood cicada nymph predation by crows at sites beyond the detection range of the installed cameras. In North America, numerous avian predators, including American crows (*Corvus brachyrhynchos*), only have the opportunity to prey on periodical cicadas once every 13 or 17 years, and never prey on cicadas during the intervening non-emergence years (Koenig and Liebhold, 2005). Although at the present study site, the temporal availability of prey does not differ as markedly as that for avian predators of periodical cicadas, jungle crows might plastically determine whether to prey on cicada nymphs in response to annual fluctuations in cicada emergence density.

Importance of the seasonal use of plantations by insectivorous vertebrates for evaluating their role as wildlife habitats

The findings of this study revealed seasonal changes in the frequency of plantation visits by cicada nymph predators, namely brown bears, red foxes, and jungle crows. The frequency of these visits was found to peak in the period between May and August, with a subsequent reduction in visitations from August to September (Fig. 3). These observations accordingly indicate that larch plantations serve as a foraging habitat for cicada nymph predators over a limited period of the year from late spring to late summer. Recently, there has been growing evidence that plantations are a more valuable source of wildlife habitats than previously thought (Brockerhoff et al., 2008; Lindenmayer and Hobbs, 2004). Nevertheless, although numerous studies have indicated that plantations play an important role as foraging habitats for wildlife (e.g., Lantschner et al. 2012; Castaño-Villa et al. 2019; Tomita and Hiura 2021), there is currently a lack of evidence regarding the effects of seasonal changes on this role.

Given a seasonal fluctuation of the availability of insects such as cicadas, the value of plantations for insectivorous vertebrates as foraging habitats would also be expected to change throughout the year. Accordingly, in term of evaluating the role of plantations as wildlife habitats the seasonal differences in the use of plantations by wildlife certainly warrants greater consideration.

Do the timing and duration of aboveground-belowground trophic interactions vary depending on predator functional traits ?

Although energy flow from belowground to aboveground communities via predation is a key process in terrestrial food webs (Bardgett and Wardle, 2010; Scheu, 2001), the associated temporal aspects such as the timing and duration of predator-prey interactions across these communities are poorly understood (Bardgett et al., 2005). Cicada nymph predation by aboveground predators is a form of aboveground-belowground trophic interactions (Polis et al. 2003). This study found interspecific differences in the seasonal patterns of cicada nymph predation, indicating that the timing and duration of aboveground-belowground trophic interactions differ among predator species, depending on their predation abilities. Accordingly, to gain a more in-depth understanding of the temporal aspects of trophic interactions between above- and belowground communities, we should focus to a greater extent on the interspecific differences among predator functional traits, such as body size and predatory ability (e.g., digging).

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Tables

Table 1 The number of videos and the event frequency of each behavior of brown bears, red foxes, and jungle crows in 2018 and 2019. The event frequency is defined as the number of independent events. A row “Moving/Searching” represent "Moving" for bears and foxes, but for crows, it indicates "Searching".

Species	Frequency	Year	Behavior			
			Digging	Foraging	Moving/ Searching	Total
Brown bear *Ursus arctos*	events	2018	53	0	18	71
		2019	45	3	25	73
	videos	2018	88	0	23	111
		2019	78	3	31	112
Red fox *Vulpes vulpes*	events	2018	26	14	199	239
		2019	14	11	150	175
	videos	2018	29	14	256	299
		2019	14	11	156	181
Jungle crow *Corvus macrorhynchos*	events	2018	–	1	0	1
		2019	–	11	57	68
	videos	2018	–	1	0	1
		2019	–	15	61	76

Table 2 The event frequency in each behavior of the brown bear (*Ursus arctos*), the red fox (*Vulpes vulpes*), and the jungle crow (*Corvus macrorhynchos*) among cicada emergence schedules ((pre-emergence: May 15 to July 14, emergence: July 15 to August 9, post-emergence: August 10 to September 15) in 2018. The event frequency is defined as the number of independent events per trap-night.

Species	Behavior	Pre-emergence	Emergence	Post-emergence
Brown bear *Ursus arctos*	Digging	0.09426±0.15588[a]	0.02885±0.10190[b]	0.00338±0.02025[b]
	Foraging	0	0	0
	Moving	0.02254±0.05356[a]	0.02404±0.05024[a]	0.00676±0.02866[a]
Red fox *Vulpes vulpes*	Digging	0.04713±0.07625[a]	0.01442±0.04073[b]	0
	Foraging	0.00205±0.01600[a]	0.06250±0.12374[b]	0
	Moving	0.09836±0.1481[a]	0.68269±0.53529[b]	0.03041±0.05437[a]
Jungle crow *Corvus macrorhynchos*	Foraging	0	0.00100±0.03175	0
	Searching	0	0	0

Means ±SD are presented. Tukey test was used for a multiple-comparison correction. Different superscript letters indicate significant differences in the event frequency of each behavior among cicada emergence periods, tested by the multiple-comparison correction.

Table 3 The event frequency in each behavior of brown bears, red foxes, and jungle crows among the cicada emergence schedules (pre-emergence: May 15 to July 14, emergence: July 15 to August 9, post-emergence: August 10 to September 15) in 2019. The event frequency is defined as the number of independent events per trap-night.

Species	Behavior	Pre-emergence	Emergence	Post-emergence
Brown bear *Ursus arctos*	Digging	0.07172±0.14336[a]	0.04808±0.07966[a]	0
	Foraging	0.00205±0.01601[a]	0.00962±0.03397[a]	0
	Moving	0.01844±0.05513[a]	0.07212±0.10108[b]	0
Red fox *Vulpes vulpes*	Digging	0.02254±0.05356[a]	0.01442±0.04073[a]	0
	Foraging	0	0.05289±0.08784	0
	Moving	0.11271±0.12850[a]	0.42789±0.37943[b]	0.02027±0.05523[a]
Jungle crow *Corvus macrorhynchos*	Foraging	0.00615±0.02726[a]	0.06731±0.20381[b]	0
	Searching	0.05533±0.14528[a]	0.1394±0.18482[b]	0

Means ±SD are presented. Tukey test was used for a multiple-comparison correction. Different superscript letters indicate significant differences in the event frequency of each behavior among cicada emergence periods, tested by the multiple-comparison correction.

Figure legends

Figure 1 Photographs associated with cicada nymph predation in the study site. (a) brown bear digging for cicada nymphs; (b) jungle crows on tree branches and ground; (c) red fox digging for cicada nymph; (d) red fox climbing on a *Larix kaempferi* tree for searching cicada nymphs (e) a fox's scat containing exoskeleton of cicada nymphs. Photographs (a-d) were taken by camera traps set in the *L. kaempferi* plantations.

Figure 2 Location of the survey plots superimposed on a map of the study site. Bold and thin lines indicate roadway and forest road, respectively.

Figure 3 The event frequencies of each behavior of brown bears (a-b), red foxes (c-d), and jungle crow (e) among the cicada emergence periods (pre-emergence: May 15 to July 14, emergence: July 15 to August 9, post-emergence: August 10 to September 15) in 2018 (a, c) and 2019 (b, d, e). Event frequency is defined as the number of independent events per trap-night. For bears and foxes (a-d), black, dark gray and gray bars indicate digging, moving (only walking), foraging on the ground (e.g., climbing tree and/or capturing nymph on tree trunk), respectively. For crows (e), black and gray bars indicate searching and foraging behaviors, respectively.

Figure 4 Diel activity patterns in brown bears (a), red foxes (b), and jungle crows (c) during the pre-emergence (May 15 to July 14, left panel) and cicada emergence (July 15 to August 9, right panel) periods. The video frequency was defined as the number of videos per hour. Dark shaded areas indicate the nighttime (19:00-4:00) in the pre-emergence and cicada emergence periods. For bears and foxes (a,b), black, dark gray and gray bars indicate digging, moving (only walking), foraging on the ground (e.g., climbing tree and/or capturing nymph on tree trunk), respectively. For crows (c), black and gray bars indicate searching and foraging behaviors, respectively.

Figure 1

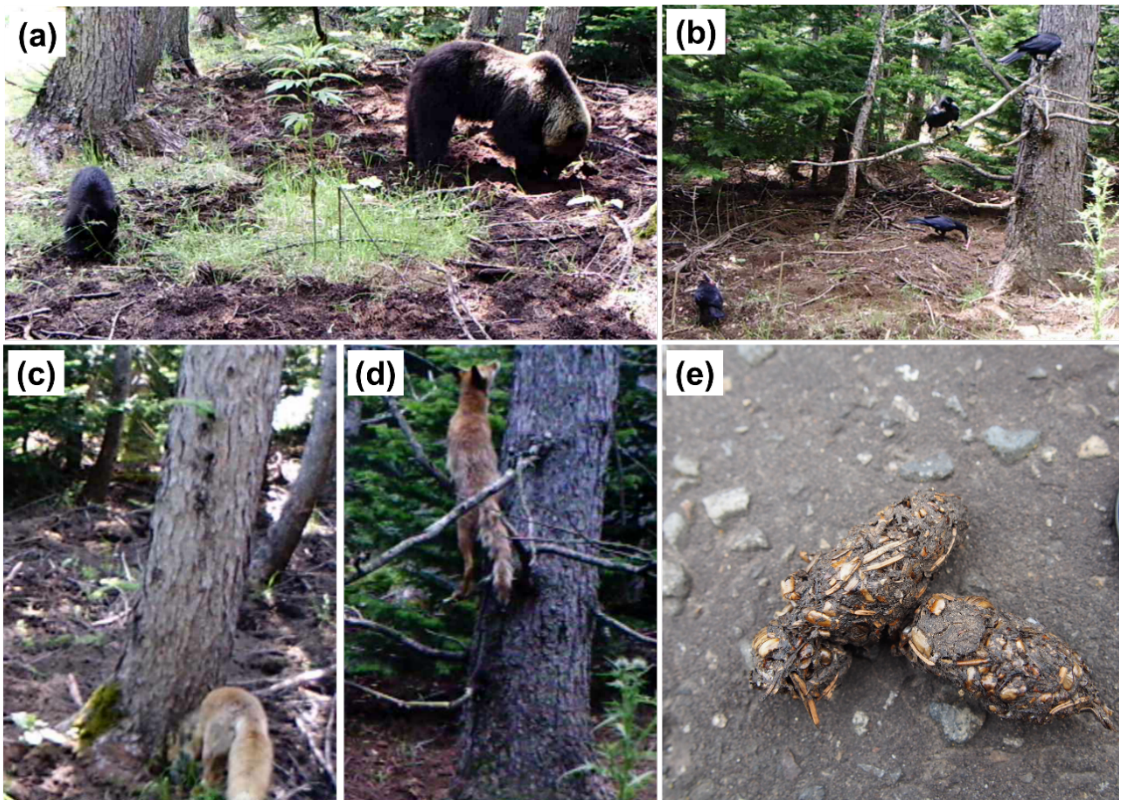


Figure 2

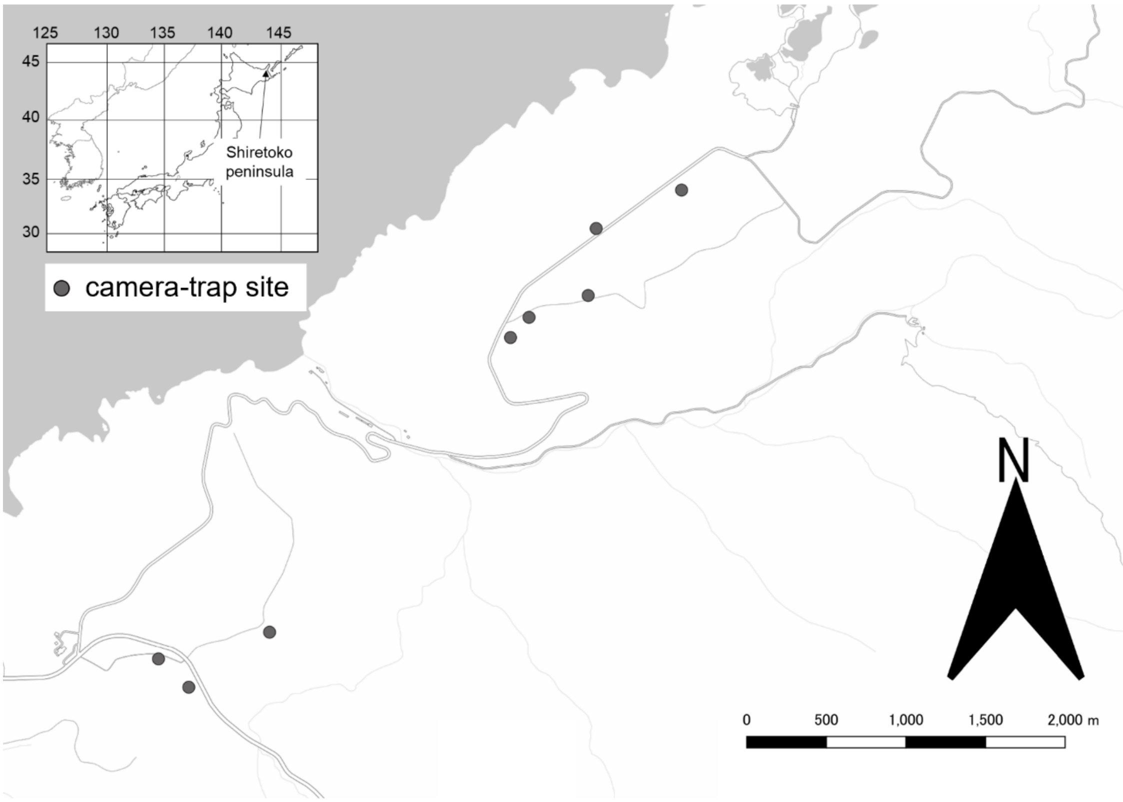

125
130
135
140
145
45
40
35
30
Shiretoko
peninsula
camera-trap site
N
0
500
1,000
1,500
2,000 m

Figure 3

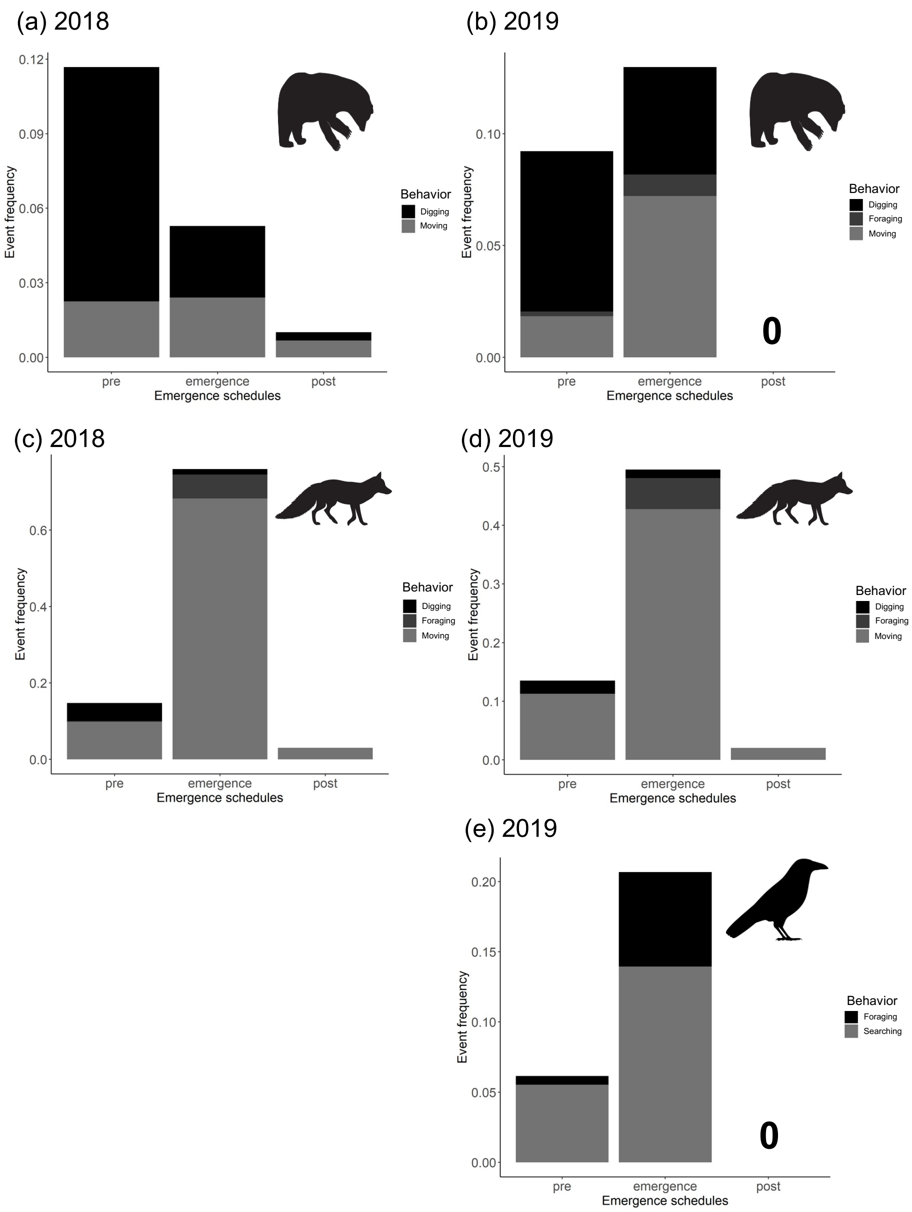
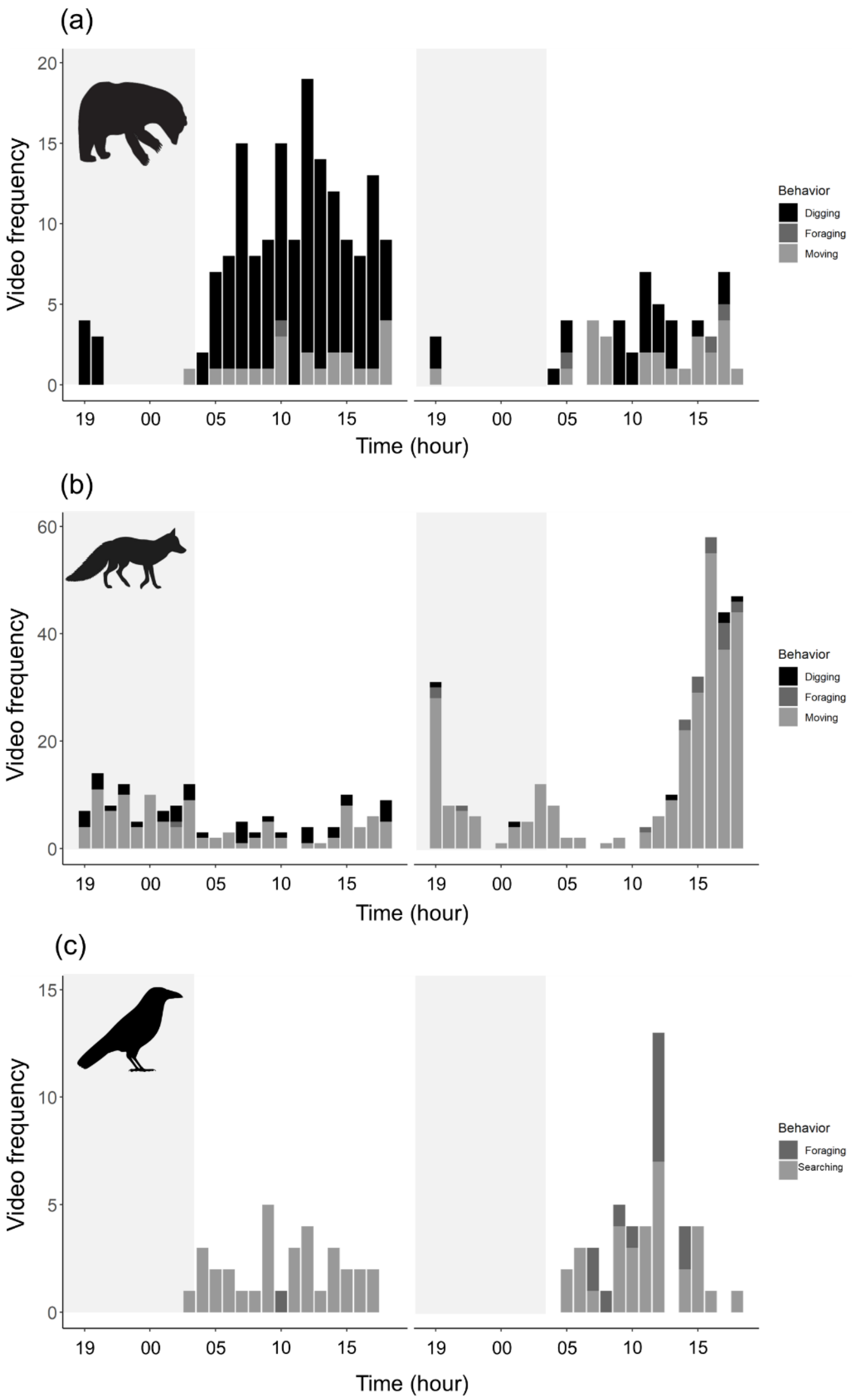

(a) 2018
(b) 2019
(c) 2018
(d) 2019
(e) 2019
Event frequency
Emergence schedules
pre
emergence
post
Behavior
Digging
Foraging
Moving
Searching
0

Figure 4


(a)
Video frequency
20
15
10
5
0
19
00
05
10
15
Time (hour)
Behavior
Digging
Foraging
Moving
(b)
Video frequency
60
40
20
0
19
00
05
10
15
Time (hour)
Behavior
Digging
Foraging
Moving
(c)
Video frequency
15
10
5
0
19
00
05
10
15
Time (hour)
Behavior
Foraging
Searching