



# Diel and monthly activity pattern of brown bears and sika deer in the Shiretoko Peninsula, Hokkaido, Japan

Kei KAWAMURA<sup>1)</sup>, Mina JIMBO<sup>1,2)</sup>, Keisuke ADACHI<sup>1)</sup>, Yuri SHIRANE<sup>1,2)</sup>, Masanao NAKANISHI<sup>3)</sup>, Yoshihiro UMEMURA<sup>3)</sup>, Tsuyoshi ISHINAZAKA<sup>3)</sup>, Hiroyuki UNO<sup>4)</sup>, Mariko SASHIKA<sup>1)</sup>, Toshio TSUBOTA<sup>1)</sup>, Michito SHIMOZURU<sup>1)</sup>\*

<sup>1)</sup>Faculty of Veterinary Medicine, Hokkaido University, Hokkaido, Japan

<sup>2)</sup>Hokkaido Research Organization, Hokkaido, Japan

<sup>3)</sup>Shiretoko Nature Foundation, Hokkaido, Japan

<sup>4)</sup>Institute of Agriculture, Tokyo University of Agriculture and Technology, Tokyo, Japan

**ABSTRACT.** Mammals exhibit several types of diel activity pattern, including nocturnal, diurnal, crepuscular, and cathemeral. These patterns vary inter- and intra-specifically and are affected by environmental factors, individual status, and interactions with other individuals or species. Determining the factors that shape diel activity patterns is challenging but essential for understanding the behavioral ecology of animal species, and for wildlife conservation and management. Using camera-trap surveys, we investigated the species distributions and activity patterns of terrestrial mammals on the Shiretoko Peninsula, Hokkaido, Japan, with particular focus on brown bears and sika deer. From June to October 2019, a total of 7,530 observations were recorded by 65 camera-traps for eight species, including two alien species. The diel activity pattern of brown bears was diurnal/crepuscular, similar to that of bears in North America, but different from European populations. Bear observations were more frequent during the autumnal hyperphagia period, and adult females and sub-adults were more diurnal than adult males. In addition, bears inside the protected area were more diurnal than those outside it. These findings suggest that appetite motivation, competitive interactions between conspecifics, and human activities potentially affect bear activity patterns. Similar to other sika deer populations and other deer species, the diel activity patterns of sika deer were crepuscular. Deer showed less variation in activity patterns among months and sex-age classes, while adult males were observed more frequently during the autumn copulation period, suggesting that reproductive motivation affects their activity patterns.

**KEYWORDS:** activity pattern, brown bear, camera-trap, diel rhythm, sika deer

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Most organisms repeat daily cyclical behavior (e.g., activity, feeding, drinking, and sleeping), according to a 24 hr circadian rhythm. This system is regulated by the biological clock, and the expression of rhythm is genetically and spontaneously determined [7]. The circadian rhythm allows animals to operate in a cyclical pattern, which is essential for the survival on earth [6]. Although circadian rhythms can be maintained in the absence of external stimuli, each cycle is slightly longer or shorter than 24 hr; thus, environmental stimuli are required to readjust the rhythm. Among them, the most important factor is the light-and-dark cycle, that is, the optical signal [8]. The pattern formed by these mechanisms is called the diel rhythm. One typical diel rhythm exhibited by most mammals is the sleep and waking cycle.

Surveys of the diel activity patterns of wildlife are important for determining potential factors that affect these rhythms. The diel activity patterns differ among mammalian species [17], and even in the same species, the patterns have been shown to be affected by individual factors. e.g., sex-age classes [24, 26] and reproductive statuses [47], and also by environmental factors, e.g., food availability [15], inter-/intra-specific competitive interactions [34], and human disturbance [12]. Direct and indirect observation methods are typically used to investigate the diel activity patterns of wildlife species. Direct observation is the most classic method for studying animal behavior in wildlife research [23]. However, outcomes of this method can be strongly affected by the presence of the human observer, thus leading to biased results and adverse effects on the entire study population [41]. Indirect observation methods, such as

\*Correspondence to: Shimozuru M: shimozuru@vetmed.hokudai.ac.jp, Faculty of Veterinary Medicine, Hokkaido University, Kita-18, Nishi-9, Kita-ku, Sapporo, Hokkaido 060-0818, Japan

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camera-trap surveys [17] and use of accelerometers in GPS-collars [29], are attracting attention as a way to solve these problems, and such surveys have been used to investigate the activity patterns of several species. Camera-trap surveys require less effort and cost as compared to surveys using GPS-collars that require capture of animals. In addition, camera-trap surveys are suitable for various terrestrial and climatic conditions, and the cameras can even be installed in terrain where direct observation is impossible. Therefore, they are optimal for surveying large areas with a small number of people.

The Shiretoko Peninsula, located in eastern Hokkaido, Japan, is famous for its rich diversity of ecosystems and species. Due to various unique natural features, the area from the central portion of the peninsula to Shiretoko Cape, including Shiretoko National Park (hereinafter SNP), was registered as Japan's third World Natural Heritage site in 2005. By contrast, at the base of the peninsula, agriculture and dairy farming are actively conducted on vast areas of land. In addition, fisheries are a major industry along the coast of the peninsula. The Shiretoko Peninsula is home to many animals, including 29 species of terrestrial mammals [28]. Among these, Hokkaido brown bears (*Ursus arctos yesoensis*) and sika deer (*Cervus nippon yesoensis*) are representative large terrestrial mammals with abundant populations. These two species occupy important positions in this small peninsula in terms of ecosystem conservation and human-wildlife conflicts. For example, brown bears play an important role in material circulation between the sea and land, by foraging marine animals and defecating in the forest, and act as seed dispersers [55]. By contrast, deer overpopulation has caused serious damage to vegetation, and population control measures have been implemented in and around SNP. Furthermore, due to the close proximity of areas of human activity and wildlife habitats, various human-wildlife conflicts, such as bear intrusions into cities and traffic accidents involving deer, have become a serious problem on the Shiretoko Peninsula. Clarification of their diel activity patterns can contribute to reduce risk of dangerous encounter with bears, e.g., by alerting people to the active time of brown bears, and also to develop an effective strategy for population control of deer. Therefore, knowledge of their diel activity patterns and influencing factors is essential not only for understanding their behavioral ecology, but also for wildlife conservation and management. To the best of our knowledge, studies on diel activity patterns of brown bears and sika deer in Hokkaido are limited in number and in locations (south-west part of Hokkaido) [16, 17]. In these studies, brown bears were categorized as cathemeral and deer were as crepuscular.

The brown bear is a large, solitary carnivore that reigns at the top of the food chain in Hokkaido. They are non-territorial, suggested by the fact that their home ranges overlap both inter- and intra-sexually [22]. More than 500 bears are estimated to inhabit this small peninsula, suggesting that this area harbors one of the highest densities of brown bears in the world [31]. The bears are omnivorous and exhibit seasonal changes in diet; they feed mainly on herbs, newborn fawns, insects, and berries from early summer to midsummer, and on salmon and acorns from late summer to autumn [55]. In general, bears begin hibernating in November–December and emerge from their dens between March and May [49]. They are seasonal breeders, with mating occurring from late spring to early summer [58]. Pregnant females give birth to 1–3 cubs during the next hibernation period [59]. Offspring become independent from their mother between the ages of 1.5 to 3.5 years [51]. Males and females become reproductive between ages of 3 to 5 years [59, 65], but males take longer to mature physically (around eight years of old; [56]) and have reproductive opportunities [53]. Generally, the diel activity patterns of brown bears have been reported as crepuscular or diurnal, but the patterns differ depending on habitat conditions and individual status [14]. In this study, we addressed two hypotheses: 1) due to significant seasonal differences in food availability in this peninsula, i.e., scarce in summer and abundant in autumn [55], bears during the autumnal hyperphagia period were expected to show increased activity or different diel activity pattern, and 2) to avoid intraspecific competition in highly populated bear habitats where encounters with conspecifics are very frequent, vulnerable bears (e.g., immature individuals and bears with offspring) were expected to show different activity patterns to adult males and solitary adult females.

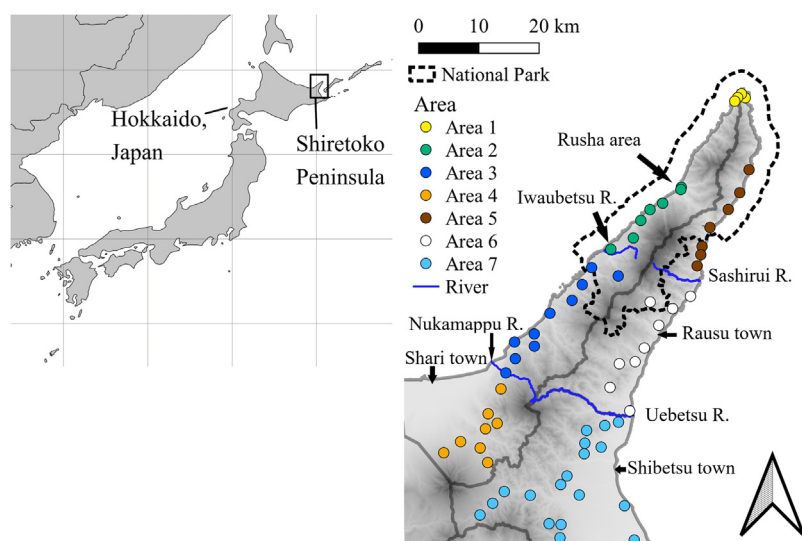
Sika deer are herbivorous mammals that live in a herd. They are also seasonal breeders; mating occurs in autumn, from October to November [60], and adult males keep multiple females during the breeding season and defend their mating territories from other males [30]. Females give birth to a fawn in early summer (June–July) of the following year [60]. The mother and her fawn would then remain together in the same herd, and male deer become independent of their mother after the age of 2 years [33]. Adult deer are rarely attacked by brown bears, but starving deer and newborn fawns are important food items for bears in spring and summer, respectively [21, 64]. On the Shiretoko Peninsula, excluding the national park, deer killing for management of areas near farmland was permitted throughout the study period, and additionally, hunting starts in October. Deer species are generally considered crepuscular, including sika deer [17]. We predicted that, in contrast to brown bears, significant differences in diel activity patterns would not be seen among months or sex-age classes, because they rely mainly on grass available from summer to autumn, and because they live in a herd consisting of multiple sex-age classes.

In the present study, we used camera-trap surveys to investigate the distributions and activity patterns of terrestrial wild mammals on the Shiretoko Peninsula, with particular focus on two representative large mammals—brown bears and sika deer. Our primary objective was to assess their diel activity patterns and examine how internal factors, including individual status (sex, age, presence or absence of offspring), and external factors, including seasonality, affect those patterns. In addition to the species-specific hypotheses described above, we addressed how human activities affect their activity patterns by analyzing data obtained in areas affected by human activity of varying intensity (inside or outside SNP).

## MATERIALS AND METHODS

### Study area

We conducted field survey on the Shiretoko Peninsula (approximately 1,760 km<sup>2</sup>, 43°50'–44°20'N, 144°45'–145°20'E), Hokkaido, Japan (Fig. 1). The study area included Shiretoko National Park (Fig. 1; 386.4 km<sup>2</sup>), where hunting is prohibited. Similar to our previous study [57], the area was divided into seven portions based on the four rivers where salmon run up, to obtain an overview of the



**Fig. 1.** Map of Shiretoko Peninsula, Hokkaido, Japan, from Geospatial Information Authority of Japan (<https://maps.gsi.go.jp/>). The left was Japanese islands, including Hokkaido, and the right was the Shiretoko Peninsula. The colored symbols indicate the sites of camera-trap, blue lines indicate four rivers (Iwaubetsu River, Nukamappu River, Sashirui River, and Uebetsu River), and the area in dash line indicates the Shiretoko National Park.

less likely to affect deer behavior because no signs of attraction (e.g., sniffing behavior) or avoidance were observed. Fluorescent flagging tape was placed at a height of 2 m as a visual guide for the estimation of bears' height when they stood upright for tree-rubbing. Cameras (HykeCam SP2, Hyke Co., Ltd., Asahikawa, Japan) were used for monitoring the hair traps. The installation was done according to our previous studies, which was optimized for shooting brown bears [51, 53]. They were installed on a tree or stake at 55–152 cm above the ground, 5.8–9.0 m away from the hair trap, such that the field of view spanned from the root of the tree to 230 cm in height. In total, we used 65 cameras (one per each trap site) that were placed at multiple locations throughout the study area (Fig. 1). The recording time and intervals were set to 25 and 5 sec, respectively. These camera-trap surveys were conducted during a period of approximately 5 months from 24 May to 29 October 2019, although data from May were excluded because of a shortage of observation periods. The collection of hair and video data were conducted at approximately 2-week intervals during the study period (ten times in total). For collected hairs, after DNA was extracted, microsatellite genotyping (6 loci for individual identification, and 21 loci and one sex-marker for parentage analysis) was conducted in the same manner described in our previous studies [52, 53]. Among the 65 hair traps, two traps in the Rusha area in the Area 2 for capturing natural rubbing behavior were set on trees that were not treated with wood preservative. The presence or absence of the solvent odor may affect the frequency of bear visits; therefore, data for these two traps were excluded from the comparisons of observation frequency among areas and those among months, but were included in that of diel activity pattern. For the other animals, these data were included for both analyses. Hair/camera trap procedures were conducted in accordance with the Guidelines for Animal Care and Use of Hokkaido University, and were approved by the Animal Care and Use Committee of Hokkaido University (Permit Number: 19-0047). The installation of camera-traps was approved by the Hokkaido Regional Environmental Office (Permit Numbers: 1905131 and 1905132), the Abashiri Southern Forest Management Station (Permit Number: 26), and Konsen Eastern Forest Management Station (Permit Number: 89).

#### Analysis of camera-trap data

All videos were checked after collection from the camera-trap. When animals were found, we recorded the date, start and finish times, animal species, sex, and age class. Methods for sex-age classification were described in the next section. For bears, we recorded the area of the tree trunk on which the bear rubbed their back, which sometimes helped to identify the individual that left hairs on the tree in combination with genetic identification through DNA analysis. Additionally, for adult female bears, we recorded the presence or absence of offspring, the number of offspring, and their ages (i.e., cub-of-the-year or yearling). In the case of deer, we counted the number of deer according to sex-age class in a herd.

We classified the recorded time of each video into three time periods; day-time (from 1 hr after sunrise to 1 hr before sunset), night-time (from 1 hr after sunset to 1 hr before sunrise), and twilight (1 hr before and after sunrise and sunset), according to the previous studies [16, 17]. The average day-time-lengths of each month were 13 hr 26 min (13 hr 14 min–13 hr 28 min) in June, 13 hr 13 min (12 hr 39 min–13 hr 25 min) in July, 12 hr 01 min (11 hr 47 min–12 hr 36 min) in August, 10 hr 32 min (9 hr 48 min–11 hr 14 min) in September, 9 hr 03 min (8 hr 32 min–9 hr 45 min) in October, and 11 hr 50 min (8 hr 32 min–13 hr 25 min) throughout the study period.

distributions and abundances of animal species (Fig. 1): Area 1, Shiretoko Cape area: northern end of the peninsula (4 camera-trap sites); Area 2, northwestern part of the national park: north side of Iwaubetsu River (9 sites); Area 3, middle west part of the peninsula: the area between Iwaubetsu River and Nukamappu River (10 sites); Area 4, southwestern part of the peninsula: south side of Nukamappu River (8 sites); Area 5, northeastern part of the national park: north side of Sashirui River (7 sites); Area 6, middle east part of the peninsula: between Sashirui River and Uebetsu River (9 sites); Area 7, southeast part of the peninsula: south side of Uebetsu River (18 sites).

#### Camera-trap survey

Camera-trap surveys were conducted as a part of our research project aiming to estimate the population size of brown bears based on DNA analysis. For DNA collection, hairs were sampled using hair traps, consisting of barbed wire wrapped around a tree 30–230 cm above the ground, at 30 cm intervals [53]. To trigger tree-rubbing behavior, wood preservative (Creosote R; Yoshida refinery, Tokyo, Japan) was spread on the trunk, which emitted an organic solvent odor attractive to brown bears [46]. This odor seems

### Sex-age classification

Sex-age classes of brown bears were estimated according to their body size, sexual characteristics, the presence of offspring, and DNA-based parentage analysis, as shown in the flowchart (Supplementary Fig. 1). Brown bears exhibit sexual dimorphism in body size—*i.e.*, males are larger than females [49]. Based on videos, we preliminary calculated the height of adult females when they stood upright, by targeting ten identifiable adult females ( $\geq 9$  years of age; with ear-tags or characteristic chest marks) in Rusha area where continuous survey had been conducted [51]. We took snapshots of their tree-rubbing behaviors and used ImageJ version 1.52a [48] to calculate the height with reference to a visual guide at 2.0 m above the ground. Those females ranged from 1.65 to 1.86 m in height ( $1.76 \pm 0.02$  m on average). Based on this, bears over 2.0 m in height were categorized as adult males, even when their sexual characteristics were unavailable. Additionally, we calculated the height of bears with known ages, including 3 two-years-old bears (1 males and 2 females), 2 three-years-old bears (1 males and 1 females), and 2 four-years-old bears (2 females). They ranged from 1.40 to 1.48 m, from 1.50 to 1.60 m, and from 1.55 to 1.70 m, respectively. Therefore, in this study, female bears between 1.5 and 2.0 m in height were considered as adult females ( $\geq 4$  years of age), and solitary bears less than 1.5 m were categorized as sub-adults ( $\leq 3$  years of age). Sub-adults were not classified by sex. Adult females were discriminated from young males (1.5–2.0 m in height) by the presence or absence of a penis, urination behavior (*i.e.*, males excrete from the front of the hind legs, whereas females excrete near the rump), the presence of offspring, and other external characteristics (*i.e.*, loss of hair around the nipple, a sign of lactation experience). In some cases for which a bear did not stand upright, or his/her sexual characteristic was unavailable, DNA analyses (by use of hairs they rubbed on the trap) revealed that he or she had reproduced in the past. Parentage analysis using microsatellite markers has been conducted in brown bear populations in the study area [52] and was partially used as a tool for the determination of sex-age classes in this study, *e.g.*, bears with reproductive experience revealed by DNA-based parentage analysis, were categorized as adults. In addition, males  $\geq 8$  years of age [56], females  $\geq 4$  years of age [59], and bears  $\leq 3$  years of age, revealed by genetical identification and/or parentage analysis, were categorized as adult males, adult females, and sub-adults, respectively. Ultimately, bears were categorized into four sex-age classes: adult males (males  $> 2.0$  m in height, or those with reproductive experience, or  $\geq 8$  years of age), adult females (females between 1.5 and 2.0 m in height, or with offspring, or with reproductive experience, or  $\geq 4$  years of age), sub-adults (males/females  $< 1.5$  m in height, or  $\leq 3$  years of age), and status unknown/others. In this study, sex-age classes were classified mainly based on height. Adult males did not include young males ( $< 2.0$  m in height) even if they might have reached sexual maturity, and adult females might include some sexually immature females among three/four-years-old females. The “status unknown/others” included 1) male bears with 1.5–2.0 m in height (Supplementary Table 1; “young males”), 2) bears with unknown sex or bears whose height was undetermined (“sex/height undetermined young/adults”), and 3) bears whose physical characteristics were almost unavailable (*e.g.*, only part of the body was recorded; “unknown”).

Sex-age classes of sika deer were classified based on body size and antlers. Deer exhibit clear sexual dimorphism, with only males having antlers on their heads. Antlers begin to grow at the age of 1 year and become branched after the age of 2 years [13]. This information can be used to discriminate between adult ( $\geq 2$  years of age) males (branched antlers), 1-year-old males (branchless horn), females (without antlers), and fawns. When individual status could not be determined, the status was categorized as “unknown”.

### Data analysis

The diel activity patterns of brown bears and deer were estimated by the kernel density analysis, according to the previous study [17]. One individual (or a herd of deer) was followed from the appearance to the exit, and the number of animals was counted based on their individual status at 30-min intervals. For example, if a certain individual was observed again 35 min after the first observation, the individual was counted twice (two observations, one each for two 30-min periods). To distinguish among the four diel activity patterns (*i.e.*, diurnal, nocturnal, crepuscular, and cathemeral), we calculated observation frequencies per 100 trap-days for three time periods (*i.e.*, twilight, day-time and night-time) in each month, according to the previous study [17]. We defined “crepuscular” behavior as having video observations more frequently during twilight, “diurnal” as having observations more frequently during day-time, and “nocturnal” as having observations more frequently during night-time. Behavioral patterns were defined as “cathemeral” when no significant differences in observation frequencies were observed among these time periods. Since it was unclear whether the population would follow a normal distribution, to rank among the three time periods, observation frequencies were compared by the Steel-Dwass multiple comparison test which is non-parametric method. Observation frequencies throughout the study period for animals that were observed multiple times (*i.e.*, for brown bears, sika deer, red foxes, *Vulpes vulpes schrencki*, red squirrels, *Sciurus vulgaris orientis*, raccoon dogs, *Nyctereutes procyonoides albus*, and sables, *Martes zibellina brachyura*) were compared among areas by the Steel-Dwass multiple comparison test. Monthly changes in observation frequencies per areas and those by sex-age classes (for brown bears and sika deer) were compared by the Steel-Dwass multiple comparison test. For the comparisons of diel activity patterns among three sex-age classes in bears (*i.e.*, adult males, adult females and sub-adults), observation frequencies in each time period were compared by  $\chi^2$  test. Subsequently, for multiple comparisons, percentage of observations in each time period were compared among three sex-age classes by Tukey’s wholly significant difference (WSD) test [45]. Furthermore, to test how human activity influences behavioral patterns in bears and deer, we compared observation frequencies in each time period between inside (Fig. 1; 19 camera-trap sites) and outside SNP (46 sites), using  $\chi^2$  test, then percentage of observations in each time period between the areas were compared by Tukey’s WSD test. Statistical analyses were performed in R version 3.6.1 [44]. Statistical significance was assessed at  $P < 0.05$ . All values are expressed as mean  $\pm$  standard error of the mean (SEM).



## RESULTS

### *Species identified*

From 1 June to 29 October 2019, a total of 7,530 observations were recorded. Eight species of mammals were identified using the camera-trap surveys. Lists of the mammals identified and total number of observations (Supplementary Table 2) and percentages of observation were as follows; brown bears (1,485 observations, 19.7%; 1,360 observations, except the two sites in the Rusha area), sika deer (5,570 observations, 74.0%), red foxes (403 observations, 5.4%), raccoon dogs (91 observations, 1.2%), red squirrels (85 observations, 1.1%), sables (19 observations, 0.2%), a raccoon (*Procyon lotor*) (1 observation, 0.01%), and an American mink (*Neovison vison*) (1 observation, 0.01%). In addition, we found flying mammals (e.g., bats and flying squirrels) and rodents (e.g., voles and mice), but we were unable to identify species due to poor images taken at night. Detailed results on observations of each species in each area were presented in Supplementary Table 2.

### *Distribution and sex-age classification of brown bears*

Throughout the study period, bears were observed one or more times at all traps. Steel-Dwass multiple comparison tests revealed that average number of observations were significantly higher in the western area of SNP (Area 2) than in either the northeastern (Area 5) or southeastern areas of the peninsula (Area 7) (Supplementary Table 2;  $P < 0.05$ ).

Total number of observations by sex-age classes were shown in Supplementary Table 1. DNA-based parentage analysis identified their sex-age classes for 9 cases (3.9% of total observations) in adult males and 59 cases (27.1% of observations in solitary adult female) in adult females. In addition, we identified 56 cases as solitary adult females, due to the presence of ear-tags and GPS-collars for bears previously captured for research purposes [51], or to consorting behavior with adult males in the mating season [49]. In total, 115 out of 217 (53%) observations in solitary adult females were classified based on definitive information, in addition to their physical/sexual characteristics. Average number of observations per trap site during the study period (Jun–Oct) were  $3.2 \pm 0.5$  for adult males,  $5.8 \pm 1.0$  for adult females,  $4.1 \pm 0.7$  for sub-adults,  $8.5 \pm 1.1$  for status unknown/others, and  $21.6 \pm 2.5$  for all bears. Average number of observations per trap site for adult females with offspring and solitary females were  $3.2 \pm 0.6$  and  $2.6 \pm 0.2$ , respectively.

### *Monthly differences in observation frequencies and diel activity pattern in brown bears*

Observation frequencies exhibited monthly changes, as values were significantly higher in September than in July (Supplementary Fig. 2) ( $P < 0.05$ ). This tendency was prominent in Area 2, where frequencies were significantly higher in September and October than in June and July. Monthly differences were not significant in the other areas. Monthly observation frequency in each sex-age class was presented in Supplementary Fig. 3. No significant differences in monthly observation frequencies were found for either adult males or sub-adults. For adult females, observation frequencies were higher in September than in July–August ( $P < 0.05$ ).

The activity patterns of all bears were categorized as diurnal/crepuscular from June to September and as cathemeral in October (Supplementary Table 3). The pattern of adult females and sub-adults were categorized as diurnal or diurnal/crepuscular from June to September, and as cathemeral in October. Adult males were categorized as diurnal/crepuscular in June and as cathemeral from July to October.

### *Differences in diel activity pattern by sex-age classes in brown bears*

The average observation frequencies per 100 trap-days among the three time periods throughout the study period are shown in Table 1. The Steel-Dwass multiple comparison test revealed that all bears and all of sex-age classes, including adult females, adult males, and sub-adults, exhibited diurnal/crepuscular patterns (Table 1 and Fig. 2). There was a significant difference in observation frequency in each time period among adult males, adult females and sub-adults (Supplementary Table 1;  $\chi^2$  test,  $P < 0.05$ ). Tukey's WSD test revealed that percentage of observations in day-time was significantly higher in adult females and sub-adults than adult males ( $P < 0.05$ ). In contrast, percentage of observations in night-time and in twilight were significantly higher in adult males than adult females and sub-adults ( $P < 0.05$ ). There were no significant differences in any time periods between adult females and sub-adults. According to reproductive status in females, the activity pattern of females with offspring was categorized as diurnal/crepuscular, but solitary females were as cathemeral (Table 2 and Supplementary Fig. 4). Observation frequencies in each time period did not differ significantly between these two types of females (Supplementary Table 1;  $\chi^2$  test,  $P > 0.05$ ).

### *Observation frequencies and diel activity pattern in sika deer*

Throughout the study period, sika deer were observed one or more times at all traps, with the exception of one trap in the Area 7. Average number of observations were significantly higher in the northwestern (Area 2) and northeastern parts of the national park (Area 5) than in the southeast part of the peninsula (Area 7) ( $P < 0.05$ ; Supplementary Table 2). In terms of sex-age classes, average number of observations per trap site were  $14.8 \pm 2.3$  for  $\geq 2$ -year-old males,  $46.0 \pm 5.3$  for adult females,  $3.4 \pm 0.5$  for 1-year-old males,  $11.3 \pm 1.3$  for fawns, and  $87.9 \pm 11.8$  for all deer. Monthly observation frequency in each sex-age class was presented in Supplementary Fig. 5. No significant differences in monthly observation frequencies were found for adult females, 1-year-old males, or fawns. For adult males, observation frequencies were higher in October than in June–September ( $P < 0.05$ ).

Average observation frequencies per 100 trap-days among the three time periods throughout the study period are presented in Table 3. The Steel-Dwass multiple comparison test revealed that the activity pattern of adult sika deer (i.e., males  $\geq$  two years old and females  $\geq$  one-year-old) could be categorized as crepuscular, whereas those of one-year-old males and fawns were categorized as cathemeral and diurnal/crepuscular, respectively (Table 3 and Fig. 3).

**Table 1.** Diel activity patterns of brown bears by sex-age class

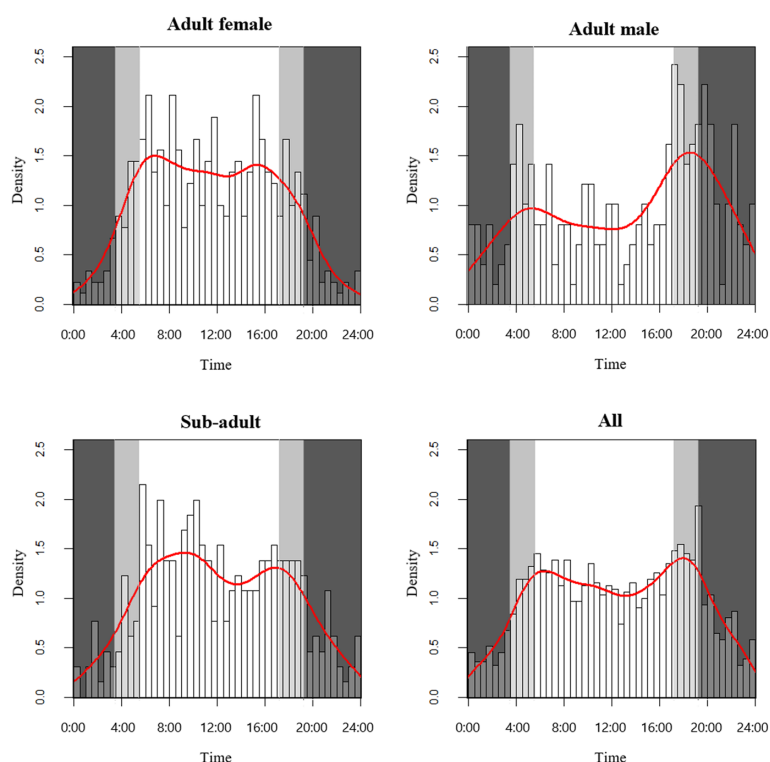
Sex-age class	Twilight	Day-time	Night-time	Category
Adult female	5.6 ± 1.0 <sup>a</sup>	6.4 ± 1.2 <sup>b</sup>	2.3 ± 0.6 <sup>a, b</sup>	D/Cr
Adult male	4.2 ± 0.7 <sup>a</sup>	2.0 ± 0.4	2.2 ± 0.5 <sup>a</sup>	Cr/D
Sub-adult	3.7 ± 0.7 <sup>a</sup>	3.8 ± 0.7 <sup>b</sup>	2.3 ± 0.8 <sup>a, b</sup>	D/Cr
Status unknown/ Others	9.8 ± 1.5 <sup>a</sup>	6.3 ± 1.0	5.8 ± 1.1 <sup>a</sup>	Cr/D
All	23.5 ± 2.7 <sup>a</sup>	18.5 ± 2.7 <sup>b</sup>	12.7 ± 2.3 <sup>a, b</sup>	Cr/D

Values indicate the average observation frequencies (mean ± SEM) per 100 trap-days. D and Cr indicate diurnal/crepuscular activity, respectively. When no significant differences among time periods were observed, the categories are listed in descending order of observation frequency. The same letter indicated significant differences among time periods ( $P < 0.05$ , Steel-Dwass multiple comparison tests).

### Differences in diel activity pattern between inside and outside the national park

The Steel-Dwass multiple comparison test revealed that both of brown bears live inside and outside SNP exhibited diurnal/crepuscular patterns (Supplementary Table 4 and Fig. 4). There was a significant difference in observation frequencies in each time period between inside and outside SNP (Supplementary Table 5;  $\chi^2$  test,  $P < 0.05$ ). Tukey's WSD test revealed that percentage of observations in day-time was significantly higher in bears inside SNP than those outside SNP ( $P < 0.05$ ), whereas percentage of observations in night-time was significantly higher in bears outside SNP than those inside SNP ( $P < 0.05$ ). There were no significant differences in twilight between the areas.

The Steel-Dwass multiple comparison test revealed that both of sika deer live inside and outside SNP exhibited crepuscular patterns (Supplementary Table 4 and Fig. 4). There was a significant difference in observation frequencies in each time period between inside and outside SNP (Supplementary Table 5;  $\chi^2$  test,  $P < 0.05$ ). Tukey's WSD test revealed that percentage of observations in night-time was significantly higher in deer inside SNP than those outside SNP ( $P < 0.05$ ), whereas percentage of observations in day-time was significantly higher in deer outside SNP than inside SNP ( $P < 0.05$ ). There were no significant differences in twilight between the areas.



**Fig. 2.** Diel activity patterns of brown bears throughout the study period. Red line and open bars areas indicated kernel density estimates and daily observation frequency, respectively. Dark grey shaded area, light grey shaded areas, and white areas indicated night-time, twilight, and day-time, respectively.

## DISCUSSION

### Species and their distributions

The camera-trap surveys confirmed the existence of eight mammal species on the Shiretoko Peninsula. Brown bears and sika deer were predominantly distributed inside SNP, which suggests that the central to northern part of the peninsula, *i.e.*, SNP, is preferable habitat, particularly for brown bear and sika deer. In contrast, other small- to medium-sized mammals did not exhibit similar patterns. This may be partly due to the territorial features in some species, such as red foxes [50], which are less likely to share the same area with conspecifics. Also, even though they are not strictly territorial, small home ranges, *e.g.*, in raccoon dogs [32], limit the number of individuals that are potentially observed at one camera-trap site. Therefore, it is necessary to bear in mind that observation frequencies do not always reflect population density. Future studies should determine the correlation between observation frequencies and population densities in this area.

The current survey confirmed the existence of two alien species, the raccoon and American mink, although only one individual of each species was observed in the southeast part of the peninsula (Area 7). On the Shiretoko Peninsula, a raccoon carcass was first discovered in 2001 [37] and they have since been reported in the southern part of the peninsula [40]. In addition, their invasion was confirmed using camera-trap surveys in 2009, although the traps were not placed in the central to northernmost areas of the peninsula (Ministry of the Environment, unpublished). The current and previous studies suggest that raccoons are distributed on the peninsula, but their settlement area has been limited to the southern region and may not include SNP. By contrast, the presence of American mink has been confirmed since the 1980s, and this species has been reported in all areas of the peninsula, including SNP [38]. Limited

**Table 2.** Diel activity patterns of female brown bears by reproductive status

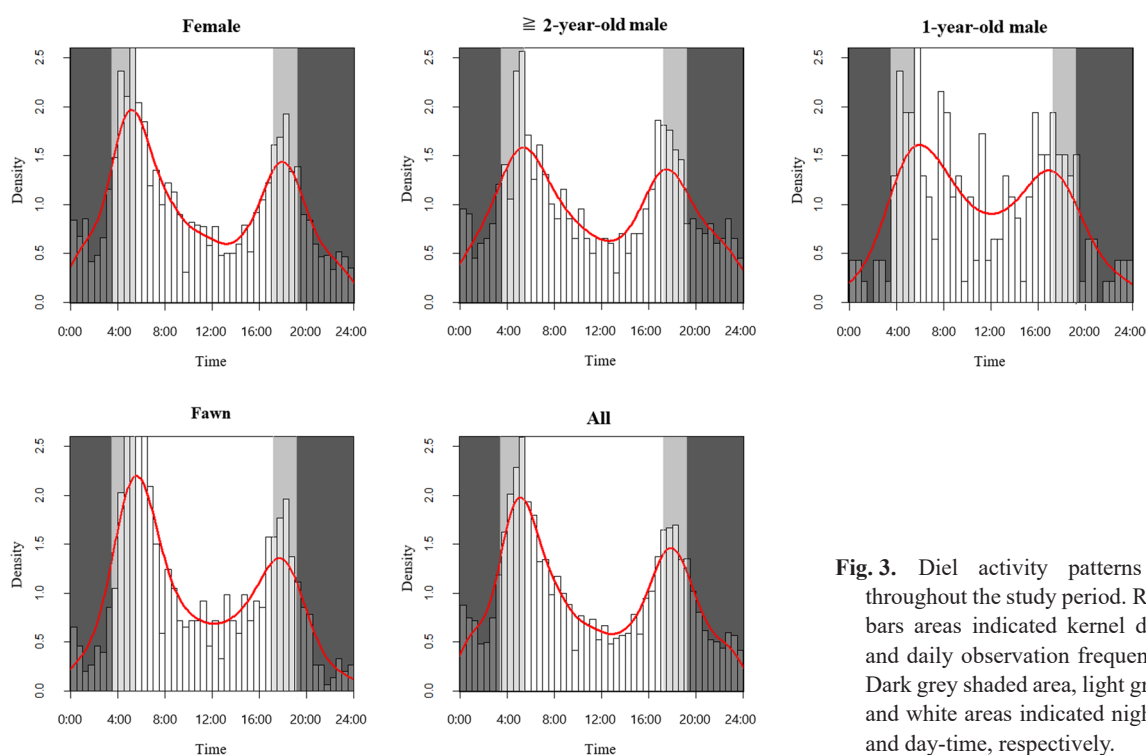
Reproductive status	Twilight	Day-time	Night-time	Category
With offspring	2.5 ± 0.6	3.4 ± 0.7 <sup>a</sup>	1.3 ± 0.4 <sup>a</sup>	D/Cr
Solitary female	2.7 ± 0.6	2.5 ± 0.7	0.9 ± 0.3	Ca

Values indicate the average observation frequencies (mean ± SEM) per 100 trap-days. D, Cr and Ca indicate diurnal, crepuscular, and cathemeral activity, respectively. When no significant differences among time periods were observed, the categories are listed in descending order of observation frequency. The same letter indicated significant differences among time periods ( $P < 0.05$ , Steel-Dwass multiple comparison tests).

**Table 3.** Diel activity patterns of sika deer by sex-age class

Sex-age class	Twilight	Day-time	Night-time	Category
Female	63.5 ± 10.2 <sup>a, b</sup>	31.0 ± 4.4 <sup>a, c</sup>	18.5 ± 4.6 <sup>b, c</sup>	Cr
Fawn	17.9 ± 3.2 <sup>a</sup>	8.5 ± 1.2 <sup>b</sup>	3.0 ± 0.7 <sup>a, b</sup>	Cr/D
1-year-old male	4.3 ± 1.0	3.0 ± 0.5	1.2 ± 0.3	Ca
≥2-year-old male	21.9 ± 3.9 <sup>a, b</sup>	9.1 ± 1.4 <sup>a</sup>	11.1 ± 2.5 <sup>b</sup>	Cr
All	124.3 ± 19.0 <sup>a, b</sup>	57.8 ± 7.2 <sup>a, c</sup>	42.7 ± 9.8 <sup>b, c</sup>	Cr

Values indicate the average observation frequencies (mean ± SEM) per 100 trap-days. D, Cr and Ca indicate diurnal, crepuscular and cathemeral activity, respectively. When no significant differences among time periods were observed, the categories are listed in descending order of observation frequency. The same letter indicated significant differences among time periods ( $P < 0.05$ , Steel-Dwass multiple comparison tests).

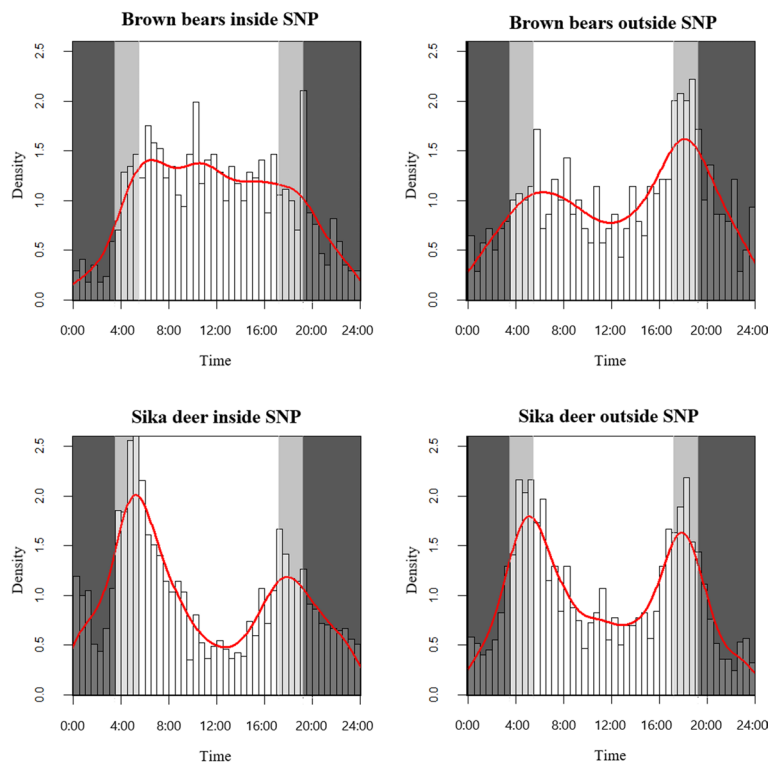


**Fig. 3.** Diel activity patterns of sika deer throughout the study period. Red line and open bars indicated kernel density estimates and daily observation frequency, respectively. Dark grey shaded area, light grey shaded areas, and white areas indicated night-time, twilight, and day-time, respectively.

observations of American mink, as well as other small- to medium-sized mammals, in the current survey were presumably due to the camera-trap survey method, *i.e.*, the current method was optimized for the observation of brown bears. To obtain detailed information on these small- and medium-sized mammals, including alien species, the methods (*e.g.*, the height and the angle of the camera) and locations for camera traps should be tailored to capture species-specific behavior and ecology.

### Brown bear activity patterns

The observation frequencies of bears decreased in summer and increased in autumnal hyperphagia phase, which supported our first hypothesis. Previous studies of Asian black bears (*Ursus thibetanus*) using GPS radio collars have shown that they reduce summer activity to avoid energy depletion and become more active during the hyperphagia season to intercept more food [11, 25]. In addition, adult brown bears in some populations have been reported to increase their nocturnal activity in autumn [20, 39]. The current study also demonstrated that adult bears shifted their diel pattern from crepuscular and/or diurnal to cathemeral in September and October,



**Fig. 4.** Diel activity patterns of brown bears and sika deer inside and outside the Shiretoko national park (SNP). Red line and open bars areas indicated kernel density estimates and daily observation frequency, respectively. Dark grey shaded area, light grey shaded areas, and white areas indicated night-time, twilight, and day-time, respectively.

predominantly exhibit nocturnal/crepuscular patterns [42, 43]. In previous camera-trap surveys conducted in central Hokkaido, the activity pattern of Hokkaido brown bears was categorized as cathemeral, presumably due to the limited number of observations [17]. High densities of brown bears on the Shiretoko Peninsula enabled the first accurate classification of activity patterns in Hokkaido in the present study. In terms of sex-age classes, adult males exhibited the tendency of crepuscular pattern, with peak activity around sunset, whereas sub-adults tended to be diurnal, with peak activity in the late morning. These results partially supported our second hypothesis and were consistent with previous reports for several bear species, including brown bears [18] and American black bears (*Ursus americanus*) [27]. In fact, sub-adults were more active in the day-time compared to adult males, suggesting that sub-adults may prefer day-time, due to avoidance behavior from adult males that are a potential threat to their survival [61], or due to lower wariness over human activity [35].

A similar difference was found between adult males and adult females. It has been reported that females with offspring become diurnal to decrease the chance of male encounters and the risk of infanticide [3, 20, 43]. In some populations, infanticide by adult males was the major cause of death for cubs-of-the-year [2, 59]. The shift in diel pattern can be considered a counterstrategy for females to protect their cubs. However, in contrast to our original prediction, the presence or absence of offspring did not influence the diel pattern of adult females, and they were more diurnal than adult males, regardless of their reproductive status. Furthermore, infanticide by adult males appeared to occur less frequently on the Shiretoko Peninsula [51], which suggests that avoidance of infanticide is less likely to be a main factor to cause sexual differences in diel patterns. Another possible factor is social dominance. For example, large adult males dominate the most productive area and time (night-time and twilight) for catching salmon [20], which may make females and sub-adults more diurnal. Also, there may be males' matter, e.g., larger males may receive more heat stress than females and sub-adults do in hot weather, which makes adult males more nocturnal/crepuscular.

We cannot deny the possibility that different diel patterns between adult females and adult males was partially due to procedural problems, such as misclassification of sex-age classes, or poor night-time visibility. In the former case, some sub-adult females (around 3 years of age) might have been classified as adult females, because a limited number of young bears with known ages were available for height calculation to determine the threshold (i.e., 1.5 m). However, more than three-quarters of adult females (329 out of 431 observations) were classified with definitive information (e.g., presence of cubs, ear-tags, etc), which suggested that this had less of an impact on the current results. In the latter situation, differentiation between adult females and young males becomes difficult at night, which might have reduced the night-time observation frequency in adult females. To test this possibility, we compared observation frequencies in males with those of "potential" adult females (i.e., combined data between adult females and sex/height undetermined

suggesting that they extended their activity time to consume a high-calorie diet, including salmon and acorns. Thus, it is possible that the increase in daily activity was reflected in the increase in observation frequencies during the autumnal hyperphagia phase.

Another possible factor affecting changes in the observation frequencies of bears is seasonal changes in feeding location. Increase in daily activity during autumn was clear, especially in the western part of SNP (Area 2), including the Rusha area, a special wildlife protection area. A previous study conducted in the Rusha area revealed that bears consume drupes (e.g., Sargent's cherry, *Cerasus sargentii*) in July and seeds of Japanese stone pines (*Pinus pumila*), a sub-alpine plant from late July to August [55], suggesting that they use mountainous areas in midsummer. Subsequently, from late August to October, bears consume pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), which contributes to a rapid increase in body weight over a short period [55]. To obtain salmon, the number of bears increased in September in the Rusha area, which contains the mouths of three rivers where spawning migration of large numbers of salmon occurs [51]. In this study, most camera-traps were installed in readily accessible locations for field researchers, e.g., areas close to the coast. Seasonal changes in habitat use associated with changes in food items are reflected in the increased observation frequencies of brown bears in autumn.

The present study revealed that the overall activity pattern in brown bears is diurnal/crepuscular, similar to previous studies on brown bear populations in North America [36], whereas European populations



young/adults), which brought the same tendency (Supplementary Table 1). This suggests that diel activity patterns determined by camera-traps were less likely to be affected by different visibility among time periods, or by the current classification methods for sex-age classes.

It is still unknown whether the diel activity pattern observed in the Shiretoko Peninsula applies to other brown bear habitats within and outside Hokkaido, Japan. Some of the factors are specific to the study area, such as the large bear population, existence of a protected area, and salmon running in autumn, especially within SNP. We revealed that diel patterns of brown bears differ inside and outside SNP; bears outside SNP were less diurnal. There were no significant differences in the proportions of adult males (the least diurnal bears among sex-age classes) between inside and outside SNP (inside SNP: 16.5%, 126/763; outside SNP: 14.1%, 102/722;  $\chi^2$  test,  $P>0.05$ ). This suggests that different diel activity patterns were not due to differences in distributions of each sex-age class, but due to other factors, e.g., the effects of human activity. During the study period, bears outside SNP experience human-caused mortality, especially in areas near human developments and farmland. By contrast, human-caused mortality is very rare within SNP. In addition, some bears within SNP have become habituated due to repeated harmless encounters with humans [54]. This suggests that differences in vigilance towards humans affect diel patterns in the Shiretoko Peninsula. It is conceivable that diel activity patterns in other bear habitats in Hokkaido may be closer to those outside SNP.

### Sika deer activity patterns

As expected, differences in daily activity and diel activity pattern among months or among different sex-age classes were less clear in deer as compared to those in brown bears. However, we found a significant increase in observation frequencies of adult males in the autumn. This pattern was not observed in the other sex-age classes, suggesting that this behavioral shift is specific to adult males. In contrast to bears, which aggregate in coastal areas to feed on salmon in autumn [51], it seems less likely that food was the motivating factor causing the shift in habitat in adult male deer to the low-altitude areas where most camera-traps were placed. Instead, reproductive motivation is the more likely factor underlying this phenomenon, as autumn is a breeding season for sika deer [60]. Their mating system is generally categorized as polygamy with the formation of harems, in which a dominant male defends a group of females [10]. During the rutting season, dominant males establish and keep their own home ranges to guard harem females, whereas subordinate males have larger home ranges to search for mating opportunities [9]. Previous studies using GPS-collars have reported that male white-tailed deer (*Odocoileus virginianus*) expanded their home ranges and increased their behavioral activities in rutting season [62, 63]. These behavioral changes during the mating season would help to explain the increased observation frequencies in adult males in the current study.

The diel activity patterns for adult deer were categorized as crepuscular. The same results were observed in other sika deer populations on Hokkaido [16]. In addition, crepuscular activity patterns have been reported in other deer species, including elk (*Cervus canadensis*) [1], mule deer (*Odocoileus hemionus*) [1], white-tailed deer [62], and moose (*Alces alces*) [5]. These findings suggest that activity patterns in cervids are consistent regardless of region and species. However, deer outside SNP were more diurnal than those within SNP, although both diel patterns were still categorized as crepuscular. This was contrary to our prediction, because deer outside SNP are more vulnerable to human-caused mortality. Generally, human disturbance, including culling and hunting, has a profound effect on the diel activity of deer, resulting in a more nocturnal pattern [19]. Outside SNP, deer culling for management purposes was permitted throughout the study period in some regions. However, such culling activity existed only on areas around farmland and human settlements. Therefore, capture pressure during the study period was very limited compared to the hunting season (middle Oct–Mar). This may mitigate the influence of human disturbance on deer behavior in the study period. Another important factor may be predator–prey interaction. Brown bears are potential predators of sika deer, and predation risk can alter the diel activity patterns of prey animals. For example, white-tailed deer with a fawn concentrated diel activity during diurnal periods when coyotes (*Canis latrans*), their major predators, are least active [4]. In this study, there were more brown bears within SNP, and those bears showed a diurnal tendency, which may reduce the diurnal activity of deer. This may affect the diel activity patterns of deer inside and outside SNP. However, the overall activity patterns were similar (i.e., crepuscular) in both species. Therefore, it is not clear that deer avoid exposure during time when bears are most active. Further studies are needed to clarify how human activity and predator–prey interactions influence the diel activity patterns of brown bears and sika deer.

In conclusion, this study provided detailed information on the distributions of mammals and diel activity patterns of brown bears and sika deer on the Shiretoko Peninsula. The camera-trap surveys revealed the existence of six native species (i.e., brown bears, sika deer, red squirrels, red foxes, raccoon dogs, and sables) and two alien species (raccoons and American minks). These results suggest that camera-trap surveys can be beneficial for the conservation and management of domestic species and the monitoring of invasive alien species. The high density of brown bears on the Shiretoko Peninsula enabled the first documentation of the diel activity patterns (i.e., diurnal/crepuscular) in Hokkaido brown bears. Differences in activity patterns in three time periods between adult males and adult females/sub-adults suggested that competitive interactions between different sex-age classes are a potential factor shaping the activity patterns of brown bears. By contrast, the diel activity patterns of deer appeared to be less influenced by social factors. In addition, the present findings suggest that season-related behavioral changes, i.e., appetite and reproductive motivation, affect activity patterns of bears and deer, respectively. Furthermore, human activity may also affect diel activity patterns in brown bears. The current findings will contribute not only to understanding of the behavioral ecology of these species, but also to wildlife conservation and management (e.g., by promoting the avoidance of dangerous encounters and more efficient deer culling).

CONFLICT OF INTEREST. We declare no competing interests.

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