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Habitat selection of Hokkaido brown bears changed seasonally and being influenced by human-disturbed landscape features

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Abstract

As large carnivore populations recover, identifying space and time overlap with humans becomes important to minimize the risk of human-carnivore interactions. In response to increased brown bear occurrences in Hokkaido Island, human-bear conflicts have dramatically surged, resulting in the culling of over a thousand bears. However, spatiotemporal prioritization to manage the conflict has yet been conducted due to limited knowledge of habitat selection.

We collected GPS data of female bears in northern Hokkaido and developed a habitat selection model (HSM) for four seasons with habitat covariates, including human-modified landscape features. According to our HSM, brown bears exhibited significant seasonality in habitat selection, indicating the importance of phenology of key food. Wet forests were constantly selected across seasons, whereas access to riparian zones was profoundly restricted. Positive selection for plantations during spring to early summer turned negative later, whereas secondary forests were positively selected during autumn. The distance to human-disturbed lands had a great effect on the model fit. These results indicate that the effects of human-disturbed landscape features on habitat selection were not negligible across seasons.

Wet forests, plantations, and secondary forests are commonly located in proximity to human-settled areas, indicating important factors responsible for bear occurrence. Considering the depopulated aging rural society in Japan, spatiotemporal prioritization of these landscape features is necessary to mitigate conflicts and to promote coexistence with large carnivore nearby on the small island.

Introduction

Wild animals select specific landscape features that provide resources and shelter for survival. Since humans dominate a large part of the terrestrial earth, most productive lands have been profoundly modified [1]. Considering that species inhabit areas greatly overlap with human activities, identifying landscape features that are selected or avoided is critical to understanding effects of human land use on the availability of their habitat. Bear species are known to be highly adaptable to disturbed habitats [2], enabling them to utilize areas close to humans, including agricultural land, riverside parks, and woodlands near the city center. Given the recovery of several bear populations, human-bear interactions have increased in Europe, North America, and Japan, surging human-bear conflicts through crop damages and human casualties. Meanwhile, changes in anthropogenic disturbance may affect the spatial patterns of suitable resources and shelters for bears both globally and locally. For instance, rapid habitat loss caused by a warming climate is shifting the ranges of polar bears into more terrestrial habitats close to towns and cities [3]. In contrast, depopulation due to an aging rural society has increased the number of foraging habitat in abandoned farmlands and unmanaged woodlands. In the latter case, one of the factors responsible for increased human-bear conflicts might be attributable to specific landscape features generated by reduction of human use, providing a suitable combination of food and cover that motivates bears to utilize areas near humans. Understanding how bears adaptively

select or avoid anthropogenic landscapes is essential to identify the causes and effects of land use change on the frequency of human-bear interactions. Conversely, if we do not have any knowledge about habitat selection by bears, it is almost impossible to understand the mechanism of increased bears near human-settled areas.

Brown bears in Hokkaido Island have been isolated from continents since the end of Holocene era; hence, the genetic uniqueness is known to be high [4]. Before human-initiated habitat conversion, brown bears were free to access riparian habitats to obtain the rich protein of salmon [5]. Due to overexploitation of salmons at most of river mouth and heavily modified riparian zones for human use, brown bears have become vulnerable to starving in salmon season from late summer to early autumn, shifting bears become dependent on crops e.g., maze [6–9]. From den emergence to early summer, brown bears intensively forage for fresh herbaceous plants and insects [10, 11], and then face harsh conditions in late summer [12] while nuts of Japanese stone pine support bears if alpine habitat is available [13]. According to previous dietary studies, the habitat selection of Hokkaido brown bears must be highly seasonal, driven by the phenology of key bear foods [14]. Brown bears have been one of the most frequently studied species for estimating habitat selection using GPS relocation data [14–21]. However, in the case of brown bears in Hokkaido, there is profoundly limited data available for modeling habitat selection. In the Shiretoko Peninsula, GPS data of eight female bears were obtained in 2013–2015, and this study showed that female bears selected alpine shrub during late summer when corn of Japanese stone pine is available [22]. That study was conducted for bears living in a protected area designated as a World Heritage Site; however, we have yet to know about the habitat selection of brown bears adaptably surviving in human-made landscape mosaics in other Hokkaido regions.

In recent years, human-bear conflicts have sharply surged in Hokkaido and Honshu Islands in Japan, owing to the unprecedented number of bears lingering around human-settled areas, even near city centers [23]. In response to frequent bear presence nearby, local authorities blame wildlife managers for increased population size of bears as the cause of problems. Therefore, lethal population control has been the major management action, leading to a high mortality rate; for example, the number of culled brown bears was 1422 in 2023 and 2037 in 2025 [24]. In these circumstances, there is still limited understanding of the reason why bears select such human-induced risky areas because of limited studies on habitat selection of brown bears around human settlements. Coupled with the prevalent culling of bears and uncertainty in population size estimates [25], it is an urgent need to investigate other factors for frequent bear occurrence, including changes in the available habitat other than population increase, to evaluate effectiveness of culling bears in terms of mitigating human-bear conflicts. Furthermore, identifying landscape features selected or avoided by bears improves our ability to focus on management period and areas adjusted with animal behavior as a long-term solution for both conflict mitigation and bear conservation.

To acquire movement data necessary to estimate habitat selection of brown bears, we captured bears to equip a GPS collar in a university research forest. Using GPS data from female brown bears, we built habitat selection model (HSM) based on resource selection functions (RSFs). Focusing on bear

response to human-modified landscape features, we included plantations, agricultural lands, and distances to open roads and residential areas. To confirm seasonality in the habitat selection of brown bears, we developed HSMs for four seasons based on bear diet [26]. As the first study to reveal habitat selection of brown bears in Hokkaido, we explored the relationship between human land use and habitat selection in a region of multiple-use lands to address potential landscape features of human-bear interactions, which is essential to prioritize time and space for conflict mitigation to promote long-term human-bear coexistence for a long term.

Results

Movement data and vegetation use of brown bears

We used a total of 9,098 satellite relocations of five female brown bears from 15 bears (six females and nine males) during 2020-2022 because the other captured bears were juveniles unsuitable for equipping a GPS collar. The movement range of the bears was sedentary within the Nakagawa Experimental Forest (NEF) of Hokkaido University, whereas three bears had a short-term excursion outside the protected NEF (Figure 1). The mean annual home range size was 97.6 (SD=135.7) km2 (Table 1). The mean elevation used by the bears was 176.3 (SD = 111.9) m. The mean distance from rivers (374.9m) and forest roads (365.9m) was much shorter than the mean distance from both open roads (791.7m) and national roads (3360.4m). Manly's standardized selection ratio indicated that vegetation types selected by bears differed remarkably among seasons (Figure 2). During spring, the female bears used wet forests, plantations, and deciduous-dominated mixed forest. In early summer, bears selected both mixed forest types, followed by plantation and wet forest. Vegetation selected in late summer was subalpine forest, whereas other vegetation types were less selected. In autumn, the bears used secondary forest and deciduous-dominated mixed forest followed by conifer-dominated mixed forest and wet forest. Overall, female brown bears were less selective for agricultural lands in this study area.

Selected variables for each seasonal model

Table. 3 shows modeling process to determine the best combination of variables for seasonal habitat selection. For spring model, we started with 6 vegetation types according to univariate logistic regression. We could keep all vegetations significant after adding two aspects: South and West. Terrain Ruggedness was also an important variable that improved spring model. Distance variables which contributed model fit were Stream, Forest roads, Open roads and Human-dominated lands. For early summer model, we first added North and Northwest aspects to 5 vegetations with significant effects on model fit. Distance to Forest edge contributed to model improvement. Furthermore, we included quadratic terms of distance to Rivers and Human-dominated lands to refer non-linear effects. For the late summer model, based on 4 vegetation types, addition of Northeast and Solar radiation improved the model. Distance variables included in the late summer model were Forest Edge, Ridges and Stream. Anthropogenic features such as distance to Open roads and Residential areas with exponential decay form also included because of their great influence on the model fit. In the process of autumn modeling,

after addition of South and West aspects to initially selected 6 vegetation types, we added terrain Ruggedness and Solar radiation. We found distance to Forest roads and Forest Edge were important variables in autumn model as well as distance to Human-dominated areas with non-linear form.

Seasonal habitat selection by brown bears in Hokkaido

According to selection coefficients (Table 4), habitat selected by Hokkaido brown bears changed remarkably along with seasonal shifts.

In spring, brown bears strongly selected forests that succeeded under wet conditions, as well as areas closer to streams. The probability of bear selection of plantation was higher than that of subalpine forest. Rugged slope with a southern aspect near the ridge was also preferred habitat during spring. Bear responses to both forest roads and open roads were negative, whereas distance to all human-dominated areas indicated a positive response. In early summer, natural forests, such as mixed forest dominated by both coniferous and deciduous trees and wet forest were positively selected by bears. Plantation was positively associated with bear selection, whereas agricultural land was strongly avoided by bears during early summer. Bears negatively responded to areas near forest edges, rivers, and human activities; however, the responses were not linear. The late-summer model indicated positive selection for alpine and subalpine zones. The bear selection for wet forest was constantly positive whereas the selection for plantation became negative during late summer and autumn. Bears selected slopes facing northeast with less sunlight and areas near streams and forest edges that were away from ridges. In terms of response to human-modified habitat, the probability of bear selection was high in areas close to open roads, proximity to residential area. In autumn, brown bears in this study region strongly avoided anthropogenic landscapes such as plantation and agricultural land. The forests selected by bears were mixed, wet, and secondary forests. Rugged terrain with sufficient sunlight was also a preferred habitat. Bears selected areas near forest roads and edges, as well as proximity to residential areas during autumn.

Discussion

Seasonal changes in habitat selection

Brown bears in Northern Hokkaido had a significant seasonality in their habitat selection, which is concordant with previous studies in Japan [7,13,26] and in other countries [14,27–30] The seasonality indicates that habitat selection of Hokkaido brown bears is driven by the phenology of key food [13,14,31]. For instance, the higher probability of selection for wet forest and proximity to stream during spring indicates the importance of those conditions for foraging several herbaceous plants; *Araceae* spp. such as *Symplocarpus renifolius* and *Lysichiton camtschatcensis Schott* [10] grown well in moist conditions. The south or southwest slope and forest edges have better light condition, and snow melting occurs much earlier in rugged slopes than in other places. These terrain conditions are beneficial for spring ephemeral herbs, which are critical for recovering body conditions exhausted during hibernation [17,32]. The positive response to plantation from spring to early summer partly indicates the foraging

behavior of insects, including cicada nymphs [33]. Tomita and Hiura (2021a) found that digging for cicada nymphs by bears only occurred in conifer plantations on the Shiretoko Peninsula, where cicada densities were higher than in other forest types. In cool temperate forests in this study region, the forest floor is commonly covered by dense dwarf bamboo (*Sasa* spp.), which suppresses the growth of herbaceous plants. In plantations, dwarf bamboo is thought to be a barrier to timber production; therefore, soil scarification to remove dwarf bamboo is a common practice to promote tree regeneration [34]. In addition, this forestry practice has been found to be beneficial for diverse understory species [35] including bear foods. In early summer, the distance to forest edges and rivers influenced bear selection, but the effect was not linear. Stewart et al. (2013) showed that grizzly bears had different responses to edges between different vegetation types, including anthropogenic edges [5]. In this study, we treated forest edges as one variable; therefore, we are not certain whether bear response to multiple edges differ between cover-open combinations. However, edge selection can be attributed to the importance of herbaceous plants under good light conditions. The selection of two types of mixed forest indicates that these natural forests have heterogeneous structures, beneficial diverse plants [36] and insects (particularly ants) [31,37] during early summer.

Late summer is known to be famine season for Hokkaido brown bears [6,38] due to the elimination of salmon intake caused by overexploitation at river mouth, and the profoundly restricted accessibility to rivers by large-scale encroachment [5]. Instead of feeding on high-calorie salmon during the transitional period of diet from soft mast to hard mast [7], most Hokkaido brown bears have become dependent on crops such as corn *Zea mays* [8–10]. In this study region, the availability of fish is very limited in some somall branch rivers, whereas corn becomes available in late summer. In our model, female brown bears strongly avoided agricultural lands during early summer and autumn, whereas the avoidance was not clear during late summer. This may be partly due to the use of agricultural land by some bears. On the other hand, the alpine and subalpine zones were positively selected habitats, which is consistent with studies on the Shiretoko Peninsula, if abundant nuts of Japanese stone pine *Pinus pumila* are available in late summer [13]. However, foraging stone pine sites are very limited in the NEF; consequently, most bears may have to search for other foraging sites, including agricultural lands. A positive response to forest edges was apparent during late summer and autumn, probably because bears foraged on berries provided by liana species (e.g., *Actinidia arguta, Actinidia polygama, Vitis coignetiae*), which are more abundant at edges [39]. In contrast, the selection of plantation changed from positive to negative in late summer and autumn. This may indicate a diet shift from insects and soft herbaceous plants to berries and hard mast, which are more abundant in naturally grown forests. Since food volume is small and scattered in space, whatever that occurs naturally or artificially, it is reasonable to assume that disturbances such as floods, landslides and logging are critical factors that increase diverse foraging patches to survive through this harsh season. During autumn, we found that Hokkaido brown bears selected secondary forest. Secondary forests have naturally grown after the cessation of firewood use (around the 1950s) and are currently dominated by deciduous trees such as *Quercus crispula* which provide high-caloric acorns, a critical hyperphagic food to prepare for hibernation. In addition, the

selection of areas proximate to forest edge, forest road and residential areas may also indicate that bears need more disturbed lands that provide berries in autumn.

Overall, understory conditions associated with dense dwarf bamboo are probably one of notable factors affecting habitat selection by brown bears in Hokkaido. In this study area, a great percentage of forest floor is covered by dwarf bamboo, called “Sasa” in Japanese (Figure 5). Sasa is a significant understory species that dominantly covers the forest floor regardless of overstory stands across Eastern Asia [35]. The distribution of Sasa is determined by soil fertility; therefore, the steep slope and wet condition have a negative influence on abundance [40]. The diversity of herbaceous plants is essential for maintaining the availability of bear food. Sasa abundance has negative effects on plant diversity; therefore, forests with less Sasa would be better habitat particularly during the grass feeding season; from spring to summer. We recommend that future research untangles the relationships between Sasa density and bear food. Expectably, it would clarify the effects of disturbance regime that provide important insight into the habitat selection of brown bears at a fine scale.

Bear response to human-disturbed landscape

Our model selection process revealed that the distance to human-disturbed land had a profound effect on habitat selection by bears. For example, addition of distance to both agricultural land and road networks improved the model fit in spring and early summer models (Table 3). Instead of the peak season of crop damage in Hokkaido, bears showed strong avoidance of residential areas during late summer. This indicates that bears need to avoid people because they are aware of the risk in using areas close to agricultural lands. In addition, bears selected areas near open roads in late summer and autumn, likely because of their selection of disturbed open lands including abandoned farmlands. We confirmed different responses to open and forest roads, as shown in previous studies [41,42] . This suggests that Hokkaido brown bears are highly adaptable to artificial linear landscapes, as bears are in other regions.

One possible cause of the selection of areas near human-dominated lands has been interpreted as a potential-realized habitat theory [43]. According to this theory, bears prefer to select productive land in the absence of humans. Based on this hypothesis, large watershed areas in Hokkaido have historically been irrigated for agriculture and settlement and are currently extremely limited in their availability for wildlife, including brown bears. Since poorly drained lands tend to be abandoned and become more available to wildlife [44], it is highly likely that these lands have become suitable bear habitats in recent decades. In this context, it is not surprising that bears positively selected abandoned pastures and cultivated lands in regions where human activities decreased due to an aging and depopulated local society. Overall, the probability of wet forest selection by brown bears was consistently high, regardless of the season. Spring habitat selection for wetlands may be attributable to killing of neonate ungulates occurring more frequently at wetland edges [16], However, there are not enough reports of the predatory

behavior of bears on sika deer in Hokkaido. Foraging soft herbaceous plants is probably a greater explanation for the strong selection of wet forests in this region. Such riparian forests also provide a variety of insects that support bears during the summer. However, most wetlands have been irrigated and converted into agricultural lands, remaining only as fragmented small patches (less than 10% in the study area). Within home ranges, riparian forests available in the mountains are narrow space but provide bears a corridor connecting from the mountains to flat open areas; as a result, this linear habitat drives bears to move down to human-disturbed lands. Another important finding was the positive selection of secondary forest during autumn. Before the 1950s in Hokkaido, clear-cut forests for firewood to withstand the severe winter were ubiquitous around villages and towns. After switching the energy source from local firewood to fossil fuels, secondary forests have naturally grown. Secondary forests grown after large-scale clear-cutting are also reported as the novel habitat for other bear species [45]. Positive selection of human-disturbed lands by Hokkaido brown bears may be attributable to positive selection to secondary forests which are located nearby villages and towns.

Historical land use changes have indirect effects on habitat selection by bears today through the long-term change in vegetation composition. Movement ranges of bears may also be affected by changes in landscape structures and connectivity that are determined by spatial pattern of human land use. However, studies to predict historical changes in habitat selection have still limited [46]. If we identify any specific land-use changes that affect bear habitat selection in human-dominated lands, we can more clearly unravel the mechanism of the current increase in human-bear encounters.

Management implications

Conflict management adjusted to animal behavior is acknowledged as an effective tool for achieving human-wildlife coexistence [47]. Although seasonal changes in habitat selection behavior are important for targeting a specific period for management actions, most wildlife management plans do not consider any seasonal match with bear behavior. For instance, forestry workers need to take care of brown bears from spring to early summer when the probability of selection for plantation is high. Local people must be cautious when encountering bears around forest edges and secondary forests near settlement during late summer to autumn. In this context, the probability of human-bear encounter changes depending on forest type and season; therefore, forest management aimed at mitigating the conflicts potentially have a great role in fostering long-term human-bear coexistence.

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Understanding the reason why bears have recently come down to human-settled areas is essential for managers attempting to reduce negative human-bear interactions. In the case of brown bears in Japan, most managers and experts perceive that increased human-bear conflict is caused by an increased bear population size, whereas the population estimate is commonly based on harvest numbers and has a great range (2.5-97.5 percentile: 7,854-15,601 [25] . The Hokkaido government decided to use intensive

lethal control measures associated with bounties and permission of Spring Bear Removal because they are known to be effective in reducing population size. For instance, Spring Bear Removal from 1966 to 1989 severely decreased the Hokkaido brown bear populations, particularly in the northern and western areas (Aoi 1987, 1990; Mano). To avoid putting the brown bear population at risk, further research is necessary to evaluate the effectiveness of lethal population control for the purpose of mitigating human-bear conflict. According to our results, the movement range of brown bears has probably expanded gradually because of the increase in secondary forests and abandoned farmlands around human-settled areas. If this occurs, reducing the bear population size will not be effective for reducing human-bear conflicts; rather, it will threaten bear populations. To maintain the population variability of brown bears that barely survive on this small island, non-lethal mitigation methods, such as clearing covers to reduce the number of lingering bears, restricting human activities in secondary forests during autumn, and enhancing knowledge about bear habitat and movement behavior, are all essential to recruit human-bear coexistence by promoting human behavior co-adapted with bears nearby.

Methods

Study area

We focused on brown bears in the northern part of Hokkaido Island. This local population has seriously declined due to Spring Bear Removal (SBR); hunting in hibernation dens. Mountains in this area are not steep, with a 20–716 m elevation range; therefore, hunters can access den sites easily by approaching on the snow cover. After the ban on SBR, the local population has gradually recovered since 1991 [48]. The Teshio River is the largest water flow across the northern Hokkaido region, and the watershed basin has been drained and converted into vast open lands for agriculture, settlement, and road networks. Although bears were occasionally observed foraging for salmon, most riverbanks are not accessible to wildlife because of intensive land modification, including national roads with high traffic volumes that usually run alongside large rivers.

The major forest types are boreal forests that have adapted to heavy snow with a northern climate (maximum snow depth 156 cm; mean precipitation 1277 mm; temperature range from − 16.1℃ in February to 24.4℃ in August), such as Siberian dwarf pine (*Pinus pumila*) and subalpine forests dominated by Erman's birch (*Betula ermanii*). Mixed forest is the typical naturally grown forest in Hokkaido, consisting of both deciduous trees (e.g., *Quercus mongolica var, grosseserata, Ulmus davidiana var. japonica, Acer pictum Thunb*), and coniferous trees (e.g., *Abies sachalinensis, Picea glehnii*). *Fraxinus mandschurica, Alnus hirsute and willows* typically occur in forests in wetland and riparian zones. Conspicuous shrub species, such as dwarf bamboo e.g., *Sasa kurilensis* and *Sasa veitchii* characterize forest structures by predominantly covering the forest floor. Important plant species known as bear foods were herbaceous plants from spring to late summer, including *Symplocarpus renifolius, Petasites japonicus* and *Aralia cordata*. Insects, including cicada nymphs [49] are also reported to be an important

source of protein intake during summer. The nuts of Japanese stone pine *Pinus pumila* are a preferred food during summer if the alpine zone is available [13]. Acorns *(Quercus crispula)*, berries *(Actinidia arguta Vitis coignetiae, Prunus ssiori, Actinidia polygama*) and carcasses of sika deer are critical food during hyperphagia before hibernation. Human-derived food items such as crops and edible waste are known to support bears in late summer during the transit period in foraging from herbaceous plants to nuts and berries [7, 37].

GPS data acquisition

We collected GPS data from individual brown bears captured in the Nakagawa Experimental Forest (NEF; 194km^2), one of the Hokkaido University research forests with capable experts in fieldwork to conduct forest management, scientific research, and outreach educational programs. In addition, it is designated as a Wildlife Protection Area, prohibiting hunting or other harmful activities. We set culvert traps to capture bears from May to November in 2020–2023. NEF staff selected capture sites where bear tracks, scats, footprints, and feeding signs were frequently observed. We remotely monitored the traps using sensor cameras connected to the mobile network to check whenever bears approached and were caught. Chemical immobilization was applied to capture bears for anesthesia by intramuscular administration using a handmade blowpipe containing a 1:1 mixture of zolazepam HCl and tiletamine HCl (3 mg/kg; Zoletil100; Virbac) and 40μg/kg medetomidine HCL (Dorbene Vet; Kyoritsu Co., Ltd.). We measured the body size and sampled blood, hair, swabs, and feces. The collected blood samples were stored at − 80°C for age estimation [50]. After blood sampling was completed, atipamezole HCl (1 mg/kg; Atipame; Kyoritsu Co., Ltd.) was intramuscularly injected to aid recovery from anesthesia after the all-handling work. We used GPS collars with iridium communication and a drop-off (VERTEX Lite; Vectronic) and set them 2 hours interval satellite locations from April to November and 6 hours interval from December to March to save battery consumption. We submitted permission to capture bears for scientific research to the Kamikawa General Promotion Bureau, a branch office of the Hokkaido government, NEF officer, and the headquarters of Forest Research Stations of Hokkaido University. All procedures for handling captured bears were in accordance with the Guidelines of the Animal Care and Use Committee of the Graduate School of Veterinary Medicine and approved by Hokkaido University (permit number: 20–0146).

Habitat covariates

To identify specific vegetation and land cover types that have a significant effect on bear selection, we reclassified the 7th National Actual Vegetation Map (downloaded from http://gis.biodic.go.jp/webgis/index.html; accessed in September 2023) into 15 land cover types according to plant and tree species known as bear food and habitat features, including agricultural lands and settlements (Table.1). Among natural forests, there are two types of mixed forest: those dominated by deciduous trees and those dominated by coniferous trees, as well as wet forests, including riparian forests and waterlogged woodlands. We assumed that bear responses may vary between agricultural lands and settlements, and agricultural lands in this study area are commonly located around settlements; therefore, we generated two types of human-disturbed land: settlements and all human-

disturbed lands (settlements + agricultural lands). To investigate how bears respond to linear landscape features, we created raster surfaces of Euclidean distance from streams, rivers, roads and forest edges. Considering that bear responses differ according to traffic volume, roads were divided into three categories: national roads, open paved roads, and forest roads. Forest edge was created by extracting lines between open land and forest cover, which were merged with all forest types. These distance variables were transformed using an exponential decay function to mitigate the excessive effect of long distances [51, 52]. In addition, we included a quadratic term for each distance variable to investigate the non-linear bear response to the seven distance variables (Table 1). We generated terrain variables that are known to be relevant to bear habitat, including elevation, ruggedness, slope, aspects, solar radiation, and soil wetness, from a 10-m digital elevation model (DEM). The original data of the linear landscape features and DEM were downloaded from the Digital Cartographic Data Standards (https://fgd.gsi.go.jp/download/ref_kihon.html; accessed in August 2023). All work on geographical information systems (GIS) was performed using spatial analysis and data management tools in ArcGIS ver7.0 (Redlands, California, USA).

Model construction

As an initial step for estimating seasonal habitat selection by brown bears, we excluded GPS data during the hibernation period and divided them into four seasons: spring (den exit-May), early summer (June-July), late summer (August-September), and autumn (October-den enter), following a previous dietary study for Hokkaido brown bears [10]. We constructed habitat selection models for brown bears using resource selection functions (RSFs). First, we outlined a polygon of year-round GPS location points of an individual bear to determine the annual home range (maximum convex polygon, MCP) and then generated random points within the MCP home range to define available sites. To confirm how brown bear responses to vegetation types varied among seasons, we estimated Manly's standardized selection ratio based on the proportion of used and available sites [53]. Next, we performed logistic regression for binary response variables (1: used sites of each season and 0: available sites of all seasons) with explanatory variables to estimate selection coefficients representing the strength and direction (positive or negative) of habitat selection. Considering the GPS data with a limited number of individual bears, we pooled all used and available data to construct population-level RSF models for each season.

For RSF model construction, we first checked collinearity among all continuous covariates using a correlation matrix to avoid overlapping effects on the estimation of logistic regression. If two covariates were correlated ($r > 0.7$), we did not include them in the same model. We then selected a set of variables using a manual step-forward procedure on univariate logistic regression with a comparison of model fit based on the likelihood ratio of chi-square test and p values. Next, we identified the best combination of land cover covariates for each season, then added terrain and distance variables from higher to lower fit according to univariate logistic regression, consecutively to develop the most parsimonious model according to AIC (Akaike's information criteria) [54]. We included only covariates with $p < 0.01$ (Wald statistics) in a model. Because the variable selection process provides important insights into habitat

selection, we reported in detail about effects of the addition and removal of variables on the model fit (Table 3). Statistical estimates were performed using STATA (SE v12.0, College Station, Texas).

Declarations

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Ethical Statement

All trapping and handling procedures were approved by the Guidelines of the Animal Care and Use Committee of the Graduate School of Veterinary Medicine, Hokkaido University (permit no. 20-0146). Wild bears were captured and released for research purposes under a permit issued by the Kamikawa General Promotion Bureau, Hokkaido Prefecture (permit no. 8, 53, 54, 113, 143)

Data availability

We cannot make GPS location data available open to the public that is necessary to consider illegal culling against the conflict prone species. However, if one wishes to use the data with proper reasons, please request the corresponding author.

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Tables

Tables 1 to 4 are available in the supplementary files section

Figures

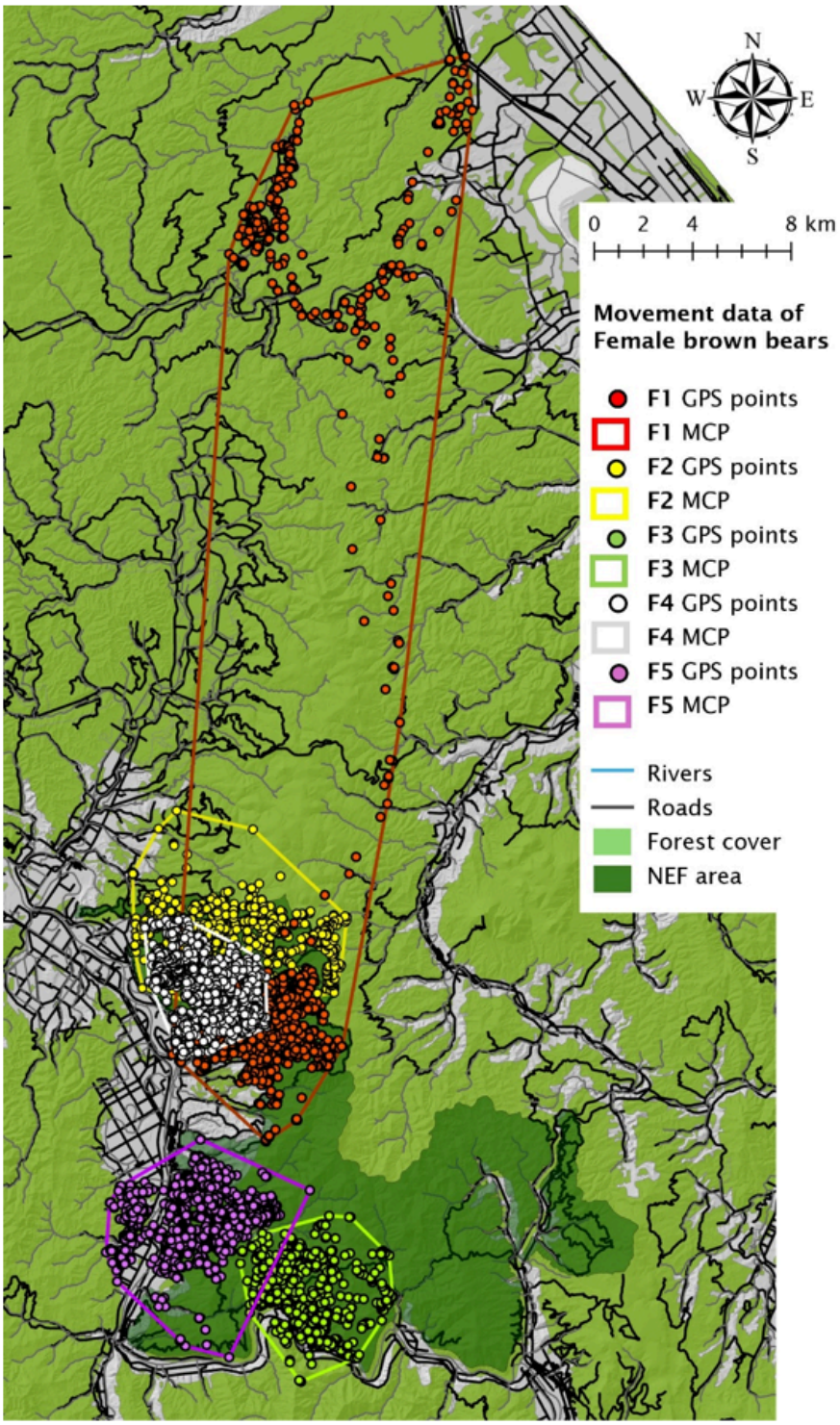


Figure 1

Study area and GPS relocation data and annual home ranges (estimated by MCP) of 5 female brown bears from 2020 to 2023 in northern Hokkaido, Japan.

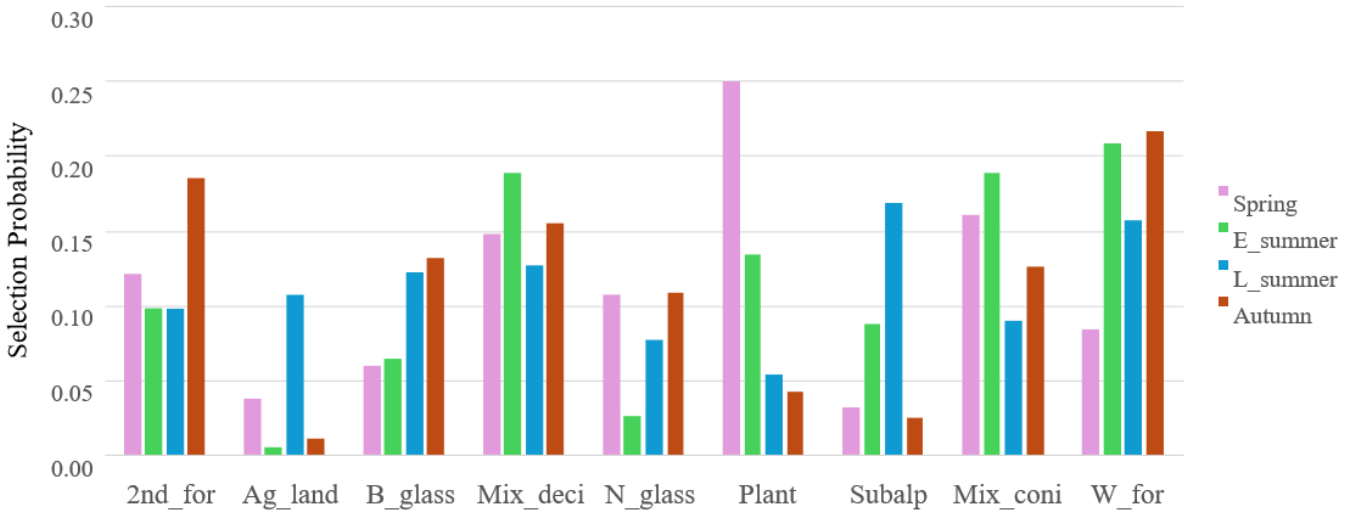


Figure 2

Seasonal changes in selection probability for vegetation types by brown bears in Northern Hokkaido.

The selection probabilities estimated based on Manly's standardized selection ratio.



Figure 3

Common forest floors dominantly covered by dwarf bamboo (*Sasa pygmaea*) in Northern Hokkaido region.

Supplementary Files

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