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Wildlife responses to naturally altered and human-modified landscapes in Malaysia and Japan

(マレーシアならびに日本の自然および人為的景観における野生動物の応答解析)

Hokkaido University Graduate School of Agriculture
Frontier of Agriscience Doctor Course

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CONTENTS

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Abstract

The growing demand on forestry resources and development leads to the expanding of settlements or agricultural land that contributed to the global forest decline. Major natural forest is threatened by timber extraction and conversion into more profitable land-use such as conifer plantation forest, oil palm plantation and other agriculture plantation. Moreover, alteration on natural forest habitat give a great influence on most of the wildlife species. The response of wildlife species on habitat modification are depending on the taxa and the group they belong to i.e., generalist and specialist.

Focusing the study area on the tropical rainforest in Malaysian Borneo and boreal forest ecosystem in Northern Japan, the thesis aimed to assess the response of wildlife on the modified landscape in regard to the forestry and wildlife management system between the two regions. To achieve the general aims of the thesis, the study in Chapter 2 was designed to assess the response of terrestrial mammals and birds to the different rehabilitation practices i.e., gap-cluster planting, line planting and liberation that uses enrichment planting method to restore biodiversity on the degraded forest. The Chapter 3 of the thesis aimed to understand on the home range and habitat selection patterns of the overabundance population, the sika deer *Cervus nippon* in response to the landscape structure and geomorphic factors. Lastly, the Chapter 4 in the thesis was conducted to study the home range and habitat selection patterns of sika deer as a response to the abundance of resource availability from both natural environment and agriculture land.

The results in Chapter 2 suggest that well-managed degraded forest still holds a high conservation value with the record of 33 species of medium-to-large mammals and birds inhabit on the area. Moreover, rehabilitation methods applied in Innoprise-IKEA

(INIKEA) forest rehabilitation project area have aided the forest recovery and were able to provide habitat for the ground-dwelling mammals and birds in Sabah. There is no significant difference in term of general forest structure, species richness and species composition between the areas subjected to rehabilitation treatment and the control area. Besides, the sika deer population in the Chapter 3 and Chapter 4 shows greater core area in winter than summer revealing that sufficient resources within the habitat. The sika deer in south Hokkaido select natural grassland and closer to cropland in summer, whilst shows the important of forest edge habitat as a response to avoid hunter or human interference from the open habitat. Habitat selection in winter shows topographic factors as important selection. In east Hokkaido, sika deer selected on coniferous forest, natural grassland, closer to road, southing and flat habitat in summer, whereas selected closer to forest edge and agriculture as well as farther away from road in winter. Shifting in habitat selection were observed on migratory deer, from away to forest edge, closer to road and southing in summer to less selected in winter. Meanwhile resident deer remained their selection in both seasons except on the distance to agriculture land.

Thus, wildlife species shows a variation in responding to the modified landscape. A good quality of habitat supplies a sufficient of resources to the wildlife species i.e., high diversity of species in rehabilitated forest and small core area and home range in summer.

Chapter 1:

General introduction

1.1 Landscape heterogeneity from land development

Land development contributed to landscape modification from the conversion of natural forest to human settlement, agriculture land as well as for timber and non-timber extraction. There were at least 1,500 million ha and 2,000 million ha of forest covering the developed and developing countries respectively (Ashbindu et al. 2001). The world forest resources are increasingly under threatened effect from the natural forest conversion and overexploitation to meets the growing demands. In Asia regions, the total forested area reported by the Global Forest Assessment in 2000 is around 700 million ha in which the annual shifting in forest cover between 1990 to 2000 was estimated to be 1,000 ha (FAO, accessed 2021). Specifically in the developed country i.e., Japan, the land still covered by 66.4% of forest as of 2011 (Japan Forestry Agency 2013), whereas in developing country i.e., Malaysia, the estimated percentage of forest cover reported between 2000 to 2005 is around 72.8% (Giree et al. 2013). Sodhi et al. (2010) reported a gradual expand of agriculture land in Malaysia from 1981 to 1992 and remained constantly the highest among the Southeast Asia countries between 1993 and 2005. Hence, the implementation of forest policy plays a vital role in guiding the extraction of forest resources and proper management of forest area to ensure sustainability.

1.2 Forest policy: The case of Japan and Malaysia

Sustainable forest management (SFM) was defined as dynamic and evolving concept aiming to maintain and enhance the economic, social and environmental values of all types of forest, for present and future benefits (Food and Agriculture Organization of the United Nation, FAO). As there is a need to maintain the dynamic flows of good and services from the forest, a priority on well management should be given to ensure the sustainable use of ecosystem services. In the case of Japan and Malaysia, the SFM was practices due to the demand on the forest resources, particularly for wood production. Thus, forest management policy regulated by its own country holds a great responsibility to achieve the sustainable forest management.

In Japan, the Forestry Agency reported a changing in the ratio between natural forest and plantation forest from 1951 to 2012, where the trends for plantation forest cover was increasing from 20% to 40% and for natural forest cover decrease from 70% to 50%. This was due to the active planting of Japanese cedar *Cryptomeria japonica* D. Don and Japanese cypress *Chamaecyparis obtusa* Endl. (Shinohara et al. 2015, Japan Forestry Agency, 2013). In between 1950 to 1970, the Japanese Government encouraging forest plantation due to the high demand of timber in Japan (Iwamoto 2002, Akao 2002). As of part of the effort to manage the biodiversity, several acts were introduced such as Natural Parks Act, Nature Conservation Law and Conservation on Endangered Species of Wild Fauna and Flora Act to protect the natural parks, nature conservation area and natural habitat protection area respectively. Furthermore, the protection of wildlife and proper hunting activity to maintain biodiversity, conserving living environment and developing agriculture, forestry and fishery was regulated under the Wildlife Protection and Proper Hunting Act. The management practices in regard to the wildlife-conflicts from both sika deer *Cervus nippon* and wild boar *Sus scrofa* were also under the act (Saitoh et al. 2015).

In regard to Malaysia, most of the natural forest were threatened not only from logging activity but by the growing of oil palm *Elaeis guineensis* plantation area. The oil palm plantation in Malaysia increasing by 1.8 million ha to 4.2 million ha between 1990 to 2005, leads to the lost of 1.1 million ha of forest area (FAO, accessed 2021). Due to the less complexity in forest structure, uniform tree age structure, low canopy, sparse undergrowth and unstable microclimate (Chung et al. 2000), oil palm plantation support fewer species richness and composition (Yue et al. 2015, Bernard et al. 2014, Fayle et al. 2010) and even lower than the other forest species such as plantation of Acacia tree *Acacia mangium*, rubber *Hevea brasiliensis* and cocoa *Theobroma cacao* (Fitzherbert et al. 2008). The government strives in regulating the policies to maintain the remaining forest from further deforestation. Additionally, a policy for managing the present oil palm plantation area for a more sustainable use and wildlife friendly but at the same time could maintain or increasing the yields was introduced. Malaysian Sustainable Palm Oil (MSPO) is one of the organisations that responsible to generate the principles for a sustainable manner of palm oil production. Management of plantation can be adapted so that they were able to support a substantial proportion of forest species. Moreover, the national policy on biological diversity was formulated to conserve the biological diversity and ensure its component are utilised in a sustainable manner. The regulation on wildlife protection, conservation and management is regulated by the Wildlife Conservation Act (Peninsula, west Malaysia), Wildlife Protection Ordinance (Sarawak, southwest Borneo) and Wildlife Conservation Enactment (Sabah, north Borneo) on its own area.

1.3 Wildlife response to the landscape modification

Depending on the condition of the area i.e., biotic and abiotic factors, the response of wildlife on habitat alteration is varied among species (Meijaard et al. 2005). The reduction in food resources availability, forest structures as well as microclimate indirectly affected on the wildlife, specifically on the specialist species. On the other hand, generalist species i.e., group living animals such as ungulates and several primates might benefits habitat alteration. These species favour the fast growing of pioneer vegetation or grasses that merged after disturbance. A growing study documented on the importance of altered forest habitat or secondary forest for the conservation of wildlife habitat (Putz et al. 2012, Granados et al. 2016, Laneng et al. 2020). Thus, the conversion of altered forest to other commercial purpose such as agriculture or buildings, effects from human disturbance i.e., logging or natural disturbance i.e., forest fires or landslides should be considered as it still holds a high conservation value.

The expansion of commercial land i.e., human settlement, agriculture activity results in landscape modification and habitat fragmentation, which is the treats to global species loss (Fischer and Lindenmayer 2007). Interestingly, depending on the region, wildlife exposed a varied response on landscape modification effect from the growing industrial, human settlement and agricultural activity. In Japan, the increasing in agricultural land is facing with the human-wildlife conflicts mostly on the growing density of sika deer *Cervus nippon* and wild boar *Sus scrofa* (Honda 2009). Sika deer is the most reported species that causes damage not only on the agriculture land, but disturbance on the forestry resources including both natural (Kaji et al. 2000, Akashi and Nakashizuka 1999) and plantation forest (Akashi and Terazawa 2005) from the over grazing. This species survived from the bottleneck and expanded in distribution range throughout Japan (Kaji et al. 2000). Takatsuki (2009) reported that effect of sika deer browsing expanding to natural and alpine forest as well as marshes. To overcome the problems, various effort was implemented such as fencing of agriculture land and planted seedlings in the forest including aggressive culling program i.e., conducted by the Hokkaido Government (Sakuragi et al. 2002).

Conversely in Malaysia, most of wildlife species is negatively affected from the landscape modification. Besides of the sensitivity of some species to the extent of disturbance, illegal hunting is the major threats on the declining of some wildlife. Modified landscape, specifically from the rising of oil palm plantation and logging activity offer a chance for illegal hunting. Several wildlife such as ungulates and primates that still utilized oil palm plantation area (Bernard et al. 2014) were highly exposed to hunting pressure. Furthermore, logging activities could ease the movement of hunter into the forest through the logging roads (Meijaard et al. 2005). Though ungulate species such as sambar deer *Rusa unicolor*, bearded pig *Sus barbatus*, muntjac *Muntiacus* sp and mousedeer *Tragulus* sp are the species dominating the most compared to other medium-to-large mammals' species, intense hunting leads to drastic decline within the habitat. Azlan et al. (2006) reported no sambar deer and bearded pig recorded in the camera-trapping survey in the Lambir Hills Park due to high hunting pressure. In addition, the effect on landscape modification and habitat fragmentation also affected on the largest terrestrial mammals in Malaysia i.e., Asian elephant *Elephas maximus* and Bornean pygmy elephant *Elephas maximus borneensis*. These mammals were not hunted for bush meat but hunted to extract the tusk. Due to its large-bodied size, elephant exposed large home-range size as reported by Alfred et al. (2012), the Bornean pygmy elephant shows home-range between 11.90 km^2 to 778.62 km^2 in Malaysian Borneo. Meanwhile, in west Malaysia Aini et al. (2015) reported the home-range of Asian elephant between the range of 34 km^2 to 317 km^2. Human-elephant conflicts in Malaysia occurs from the disturbance on oil palm resources, access into private land including crossing on the road or highways which leads to car accident or traffic (Wadey et al. 2018). Thus, it is not denied that forest fragmentation affected on wildlife movement (Said et al. 2016) and increase the exposure to human.

1.4 Approaching wildlife: camera-trapping and GPS-radio collar

Camera-trapping has been long used in the survey and monitoring the occurrence of wildlife species (Jenks et al., 2011). It is useful to detect the rare and elusive species instead of direct sighting on the animals i.e., distance sampling (Kays and Slauson, 2008). There is no doubt that this method contributed to many scientific literature and wildlife management in understanding wildlife-habitat interaction especially the threatened species such as impact of logging on ungulate density (Heydon and Bulloh 1997), estimating primate density and spatial distribution (Hensen et al. 2019) and surveying on orang utan population *Pongo pygmaeus wurmbii*. It was also contributed to the management of conflict causing animals due to overabundance such as estimating population density of sika deer in Hokkaido (Uno et al. 2017) and assessing population growth (Tsujino et al. 2004) as well as estimating red deer abundance (Torres et al. 2015). However, the limitation of distance sampling to detect scarcity and cryptic behaviour animals offers a great opportunity to the application of camera-traps. The utilization of camera-traps provided the preliminary documentation of Bornean Bay cat *Catopuma badia*, that was thought to be extinct in the forest of Malaysian Borneo (Mohd-Azlan and Sanderson 2007), due to the secretive behaviour of the species. Besides mammals, the use of camera-tapping method can also be most appropriate to detect the large terrestrial birds such as cracids and pheasants (O’Brien and Kinnaird, 2008). The rising attempts to understand wildlife and habitat relationship in structuring better wildlife management and conservation applied the camera-trapping method such as to 1) documented species list, particularly endangered or elusive species (Gonzalez-Esteban and Irizar 2004, Mohd Azlan and Sanderson 2007, Bernard et al. 2013, Laneng et al. 2019), 2) monitoring or estimating population density or abundance (Royle and Nichols 2003, Rowcliff et al. 2008), 3) assessing habitat preferences (O’Brien and Kinnaird 2018, Rovero et al. 2014), 4) studying the behaviour and activity patterns of terrestrial wildlife (Lynam et al. 2013, Fonturbel et al. 2021), as well as 5) monitoring of arboreal species i.e., primates (Bowler et al. 2017, Whitworth et al. 2016, Gracanin and Mikac 2022) and birds (Dinata et al. 2008, Martyr 1997). Rovero et al. (2013) documented the growing number of camera traps application in approaching wildlife from 2006 to 2013.

Despite of its importance in the growing of wildlife studies, there is a determination to further assess on the animal’s movement, home range as well as behaviour in term of habitat selection or use in which unable to be acquired by camera-trapping method. The evolution of technologies giving the opportunity for the Global Positioning System (GPS) radio-collar to be applied on a free-ranging wildlife (Uno et al. 2010). The Very High Frequency (VHF) radio-collar were first used and gradually replaced by the GPS radio-collar to track the animal’s movement, where it allows for a less time required for monitoring and provides larger number of locations per animal than VHF radio-collar (Pellerin et al. 2008, Johnson et al. 2002). Regardless of the disadvantages in term of time consuming and small number of locations acquired, VHF radio-collar has a notable influence on wildlife ecology and management study to assess the home-range of ungulates (Dyke et al. 1995, Reinecke et al. 2014), habitat selection and space use by common palm civets (Nakashima et al. 2013), developing resource selection model of red deer (Bojarska et al. 2020), European wildcat (Klar et al. 2008) and dingoes *Canis lupus dingo* (Newsome et al. 2013) as well as seasonal migration patterns by sika deer (Agetsuma et al. 2011, Igota et al. 2004, Borkowski and Furubayashi 1998). In addition, the GPS radio-collar is being increasingly used and overcomes the limitation of VHF radio-collar. Kochanny et al. (2009) documented on the similar home-range size recorded by the utilization of VHF and GPS radio-collar, yet they missed the fine-scale movement from the VHF method especially when the animal used on the important habitat patches. Thus, GPS radio-collar provides more details information in the location of animal movement. The widely usage of GPS radio-collar in modelling the habitat selection for Asiatic black bear (Takahata et al. 2014, Takahata et al. 2017), mountain elk (Sawyer et al. 2007, Devore et al. 2016), mule deer (Coe et al. 2018) as well as wolf *Canis lupus* prey selection (Sand et al. 2016) and mountain lion *Puma concolor* (Benson et al. 2016) had improved the information for wildlife management efforts from the fine-scale data collected from the GPS radio-collar.

1.5 Aims and objectives

The general aim of this thesis is to understand the respond of wildlife on the altered landscape effects from natural disturbance and human modification. The case studies can be divided into two distinct environment of forest type i.e., the tropical rainforest ecosystem in Malaysian Borneo and boreal forest ecosystem in Hokkaido, Japan.

To achieve the aim of this thesis, in Chapter 2, the study attempted to assess on the response of terrestrial mammals and birds on rehabilitated forest that was affected from both conventional logging and natural disasters i.e., forest fire from El-nino event.

The objectives are 1) to record the species occurrence of medium-to-large mammals and birds, 2) to compare the species richness and composition among different planting techniques and natural regeneration and 3) to assessed how rehabilitation methods and natural recovery alter forest structures and subsequently wildlife diversity.

In the Chapter 3 of this thesis, the study focusing on the sika deer *Cervus nippon* population that causes on the rising of human-wildlife conflicts in Japan, particularly on the forestry and agriculture resources. This chapter, aimed to provide management implication on sika deer habitat use on the study area. The objectives of the study are 1) to investigate the home range and 2) assessed the habitat selection patterns of female sika deer in different seasons i.e., summer and winter.

The Chapter 4 of this thesis was attempted to monitor the sika deer population in the largest wetland in Japan, the Kushiro Shitsugen National Park. As the high population density of sika deer on the wetland could lead to the alteration on vegetation species, the study was designed to assess the habitat selection by sika deer to provide an insight for further management efforts. Two objectives were generated in following of the study aim i.e., 1) to assess the patterns of seasonal home-range of sika deer and 2) to describe the seasonal habitat selection by sika deer at the home-range scale.

Chapter 2:

Camera-trapping Assessment of Terrestrial mammals and Birds in Rehabilitated Forest in INIKEA Project Area, Sabah, Malaysian Borneo

2.1 Abstract

The Innoprise-IKEA (INIKEA) Forest Rehabilitation Project in Kalabakan Forest Reserve, Sabah, was established to rehabilitate degraded forest affected by conventional logging and forest fires that occurred during an El-Nino event (1982–1983). The present study aimed to investigate the responses of ground-dwelling mammals and birds to the different rehabilitation practices in INIKEA: gap-cluster planting, line planting and liberation, where enrichment planting applied in both gap-cluster and line planting. A total of 74 camera traps were deployed at random locations across reforested INIKEA plots, including plots in control areas comprising naturally regenerated forest. A total of 6534 independent photographs of medium-to-large vertebrates from 7266 camera-trap nights representing 33 species from 14 families and 7 orders were obtained. Among the detected vertebrate species, 2 are listed as Critically endangered, 5 as Endangered, 8 as Vulnerable and 6 as Near threatened on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Mousedeer was the most frequently photo-captured species, followed by muntjac, bearded pig, sambar deer, pig-tailed macaque and crested fireback. The present study demonstrates that the rehabilitation methods applied in INIKEA have aided forest recovery, providing habitat for the ground-dwelling mammals and birds in Sabah. General forest structure, species richness and species composition did not significantly differ between the areas subjected to rehabilitation treatment and the control area. The results suggest that the liberation method should be abandoned to ensure a variety of food resources for animal species. Provided major forest components remain after disturbance, disturbed forest areas should be left to undergo natural recovery.

KEYWORDS Camera traps · Enrichment planting · Forest rehabilitation · Medium-to-large vertebrates

2.2 Introduction

The tropical rainforest of Borneo is a home to at least 222 mammal species, of which 20% are endemic to the island (Myers et al. 2000; Payne et al. 2005; Rautner et al. 2005). Tropical rainforest that consists of dense vegetation can be divided into five layers: the forest floor, shrub layer, understory layer, canopy layer and the emergent layer. Its dense canopy layers provide microhabitats for various wildlife species, including rare and endemic organisms, resulting in higher species richness than found in other forest types (Meijaard et al. 2005). However, as developing countries strive to urbanize, tropical rainforest faces rapid loss and degradation due to logging activities, land conversion-township development and land conversion-agricultural activities. In Borneo, a substantial portion of its original forest cover has been converted into human-disturbed landscapes, including timber concessions, agricultural estates, grassland and human settlements (Rautner et al. 2005). The forest destruction, fragmentation and degradation are among the greatest threats to biodiversity in Borneo (Fritz et al. 2009; Sodhi et al. 2010; Cordeiro et al. 2015). In addition, logging activities alter the forest structure, jeopardizing forest biodiversity and regeneration capacity (Aerts et al. 2011).

Most of the large vertebrates in tropical East Asia are highly threatened due to habitat loss and overhunting (Kinnaird et al. 2003; Meijaard et al. 2005; Lindenmayer and Fischer 2006; Corlett 2007). Degradation of tropical rainforest is associated with reductions in the populations of most mammal species as well as alterations in species long-term survival in the habitat (Kinnaird et al. 2003). According to Gray et al. (2007), the impact of disturbance varies with body size, with larger species tending to be more affected than smaller ones under habitat degradation. Logging has pronounced negative impacts on mammalian diversity (Samejima et al. 2013), as many animals rely on forest resources for foraging, reproduction and protection, and the related resources vary with forest age (DeWalt et al. 2003). Ground-dwelling vertebrates, especially large mammals, that are highly dependent on the forest floor for foraging and shelter face limited food resources and habitat in fragmented and degraded forest.

Although the world's area of logged secondary forest is increasing, several studies have suggested that such forest is important for biodiversity rehabilitation and recovery (Smeraldo et al. 2020; Hagger et al. 2019; Samejima et al. 2013; Berry et al. 2010). Heavily degraded forest, even forest that has been repeatedly logged, holds potential value for tropical biota and conservation (Struebig et al. 2013). To better understand the effectiveness of forest rehabilitation efforts, it is important to determine biodiversity status in affected forest areas. The responses of bird communities to enrichment planting techniques used to improve degraded forest in Sabah were documented by Edwards et al. (2009) and Ansell et al. (2011), while the impacts on invertebrates were reported by Edwards et al. (2012) and Cerullo et al. (2019). The responses of mammalian communities to land-use change (Wearn et al. 2017), the effects of logging (Brodie et al.

2015; Granados et al. 2016), the development of sustainable forest management by reducing logging impacts (Samejima et al. 2012, 2013), forest fragmentation (Bernard et al. 2014) and general species surveys (Bernard et al. 2013) have been conducted in Sabah. However, no studies of the responses of terrestrial mammal and bird communities to enrichment planting methods aimed at improving degraded forest habitat have been conducted in Sabah. As mammals are good indicator taxa of forest biodiversity (Feng et al. 2020; Bosso et al. 2018; Samejima et al. 2012), the present study collected information on medium-to-large terrestrial mammals and birds to evaluate biodiversity in the study area.

As part of the effort to evaluate biodiversity in the affected area after 20 years of rehabilitation, this study focuses on the assessment of wildlife species after the severe damage due to conventional logging and the wildfires that occurred during the El-Nino drought in 1983. The data collected during this study are preliminary; no studies have yet assessed animal biodiversity in the study area in Sabah. Three hypotheses was generated in this study, i.e., (1) the frequency of animals recorded were expected to be very low due to severely degraded forest habitat; (2) species richness and composition of terrestrial mammals and birds were different according to different rehabilitation techniques and naturally regenerated forest area; and (3) the enrichment planting and liberation used to facilitate forest recovery assumed to affect forest structures and wildlife diversity differently as compared to the natural regeneration. To answer all the research questions, camera-trapping survey was used to achieve the objectives, i.e., (1) to record the species occurrence of medium-to-large terrestrial mammals and birds in the study area, (2) to compare species richness and composition of terrestrial mammals and birds among different planting techniques and natural regeneration (control), and (3) to assessed how rehabilitation methods and natural recovery alter forest structures and, subsequently, wildlife diversity.

2.3 Materials and methods

Study area

The study was conducted in Innoprise-IKEA (INIKEA) Forest Rehabilitation Project Area, in the southeast of Sabah in Kalabakan Forest Reserve (Figure 2.1). It is part of the Yayasan Sabah Concession area, which covers approximately18,500 ha. INIKEA is located between the two main virgin jungle reserves in Sabah: Danum Valley Conservation Area (DVFC) and Maliau Basin Conservation Area (MBCA) (Figure 2.1). The area suffered severe damage due to conventional logging followed by wildfires during the El- Nino Drought in 1983. Almost all of the forested area was affected by fire during the drought.

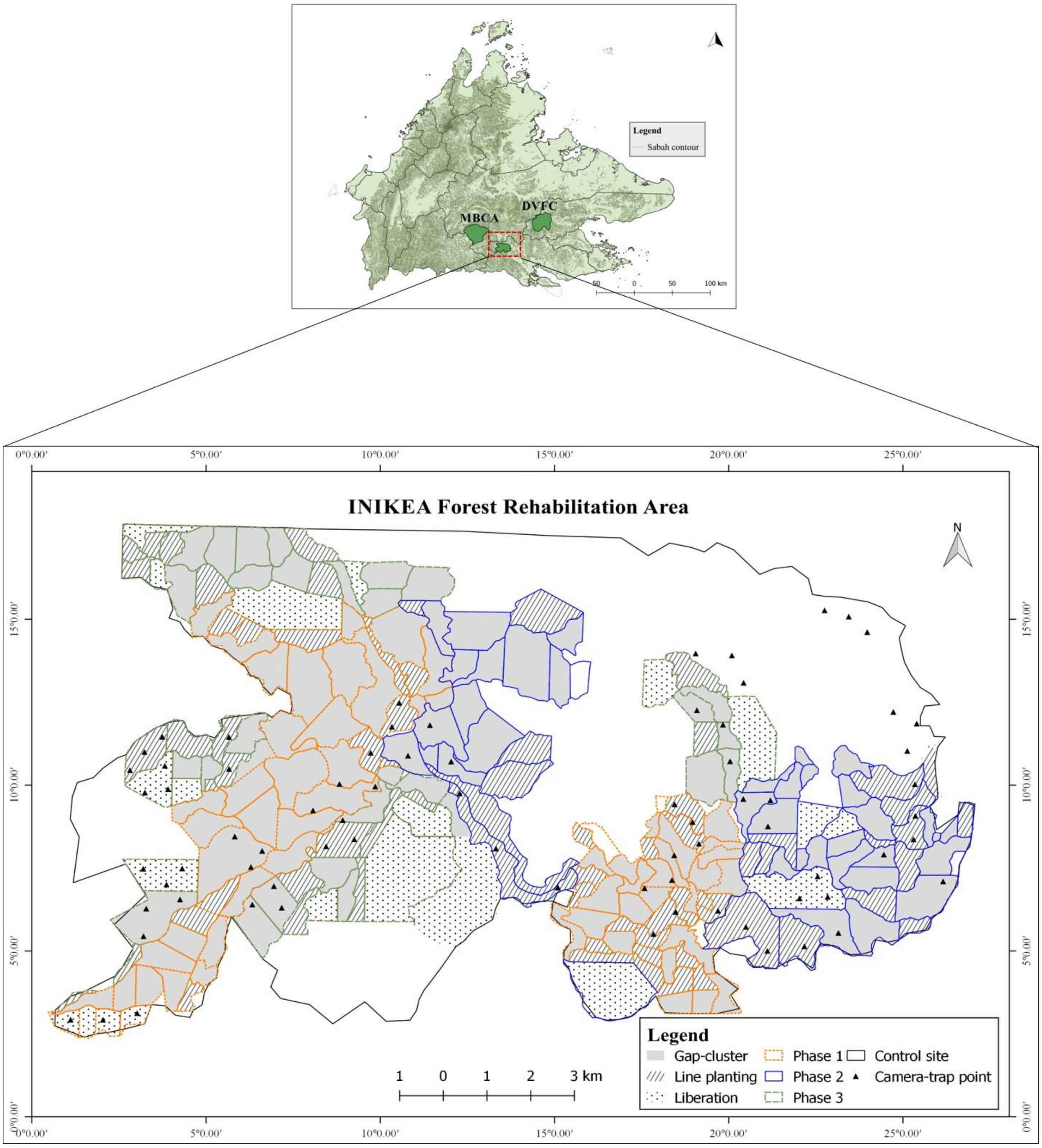

Figure 2.1: INIKEA Forest Rehabilitation Project Area in south-eastern Sabah, Malaysian Borneo, and the location of 74 camera-trapping points.

The INIKEA Forest Rehabilitation Project, also known as “Sow a Seed” Project, was established to rehabilitate degraded forest in the study area. Rehabilitation process can be divided into three phases i.e., Phase 1 of the project spanned from 1998 to 2003 and was followed by Phase 2 (2003–2008) and Phase 3 (2008–2013). The aim of the project was to improve the biodiversity of degraded forest through enrichment planting of indigenous tree species. Enrichment planting is the planting of tree comprising random mixtures of 70% dipterocarp seedlings, 25% non-dipterocarp seedlings, and 5% wild fruit tree seedlings. Tree planting from wider range of genera was to ensure the variety of food resources to dependent animal species (Reynolds et al. 2011). The reforestation efforts included the combination of different planting methods, i.e., gap-cluster and line planting (planted through enrichment practice) (Figure 2.2) and liberation to facilitate the tree growth.

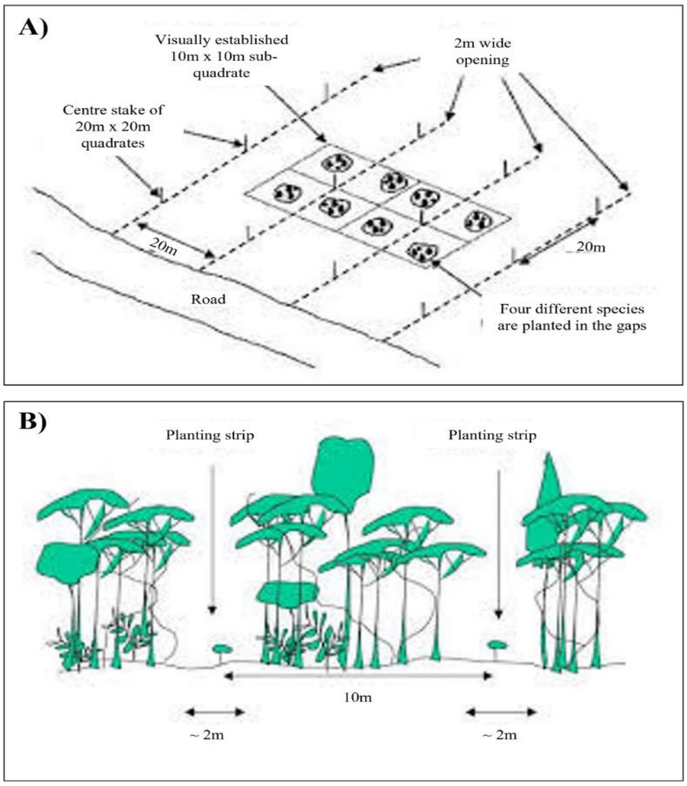

Figure 2.2: The illustration of A) gap-cluster planting (Alloysius et al. 2010) and B) line planting (Garcia and Falck, 2003) methods applied in INIKEA.

Gap-cluster planting was conducted in the area with many large climax trees remaining but dominated by pioneer species, such as *Macaranga* spp. Most of the pioneer species trees were removed, and the gap areas were planted with various dipterocarp, non-dipterocarp and wild fruit tree species. Seedlings of three different species were planted in a cluster in every gap. This method was undertaken in approximately two-thirds of the entire rehabilitation area. No planting was carried out if more than five natural dipterocarp species were present. Line planting involves the establishment of 2-m wide planting strips in areas of degraded forest, with a seedling planted every 3 m. This method was conducted only in areas with low vegetation and no large trees. In contrast to the other two methods, liberation was conducted in areas categorized as old growth forest or less damaged. With this method, selective climber cutting and ring-barking of the shade-producing *Macaranga* spp. was conducted to increase the amount of light reaching the forest floor, promoting natural regeneration. Details of all planting techniques are provided by Alloysius et al. (2010).

Camera trapping

A camera-trapping survey was conducted to document the occurrence of ground-dwelling mammals and birds in INIKEA. No bait or lure was used to attract animal species. Bushnell Trophy Cam HD camera traps with a 0.3 s trigger speed were used. Sampling was conducted for 18 months, between November 2017 and March 2019. The placement of the camera traps was divided into three sessions due to the limited number of camera traps available. The first session was conducted in Phase 1 with a total of 27 camera traps activated between November 2017 and April 2018, followed by the second session in

Phase 2, with 24 camera traps activated from May 2018 to October 2018, and the third session in Phase 3, with 23 camera traps activated from October 2018 to March 2019. This procedure yielded a total of 74 camera-trap points across the INIKEA area (Figure 2.1). There were 27 cameras in the gap-cluster planting treatment, 26 in the line planting treatment, 12 in the liberation treatment and 9 in the control treatment. Reductions in the number of camera traps used in sessions 2 and 3 occurred due to theft by poachers and camera malfunctions. All camera traps were active 24 h per day and were set to take 3 shots per trigger, with a 30-s delay between triggers. Camera traps were set up in each of the rehabilitation treatments (gap-cluster planting, line planting and liberation) and control areas, i.e., area that left for natural regeneration, without any treatment.

As this study aimed to record as many animals as possible, the camera traps were placed in area considered to be heavily frequented by animals, such as along game trails and near fruiting trees, salt licks, stream beds and logging roads. Each camera trap was mounted on a tree trunk approximately 30 cm from the ground and oriented according to the terrain, the geographic coordinates were recorded using a GPS receiver (Garmin GPSMAP62S). The distance between any two cameras was at least 0.5 km (range 0.5−21.08 km) to reduce the spatial autocorrelation, and the elevation of the camera-trap stations ranged from 90 to 545 m above sea level.

Vegetation structure

To assess the general forest structure across the four different forest areas (gap-cluster planted areas, line-planted areas, liberation-treated areas and control area), 14 microhabitat variables were recorded at each camera-trap location. These variables included (1) canopy height, measured by rangefinder; (2) canopy cover, estimated using a densiometer, with four measurements from four directions (north, east, west and south); (3) understory vegetation, defined as vegetation between 5 and 20 m above ground level; (4) low vegetation, defined as vegetation 2–5 m above the ground; (5) ground vegetation (shrub cover), defined as vegetation less than 2 m tall; (6) percentage of lianas; (7) depth of leaf litter, measured by a centimetre ruler at four random locations near the camera-trap; tree DBH (diameter at breast height), classified as (8) DBH 1 (10–20 cm), (9) DBH 2 (20–30 cm), (10) DBH 3 (30–40 cm), (11) DBH 4 (40–50 cm) and (12) DBH 5 (more than 50 cm) and measured using a diameter tape; tree species identification according to the (13) counts of climax trees of the family Dipterocarpaceae and (14) counts of pioneer species such as *Macaranga* spp. and *Mallotus* spp. (Azlan et al. 2013), which were identified by a botanist. Variables 1 through 6 were estimated by the same observer. All 14 variables were recorded within a circular plot of 0.01 ha (5.64 m radius) near the camera-trap point.

Data analysis

The photographed animals were identified based on Payne et al. (1985) and Phillipps and Phillipps (2016) to the species level where possible; animals that were difficult to distinguish and were only identified to the genus level included mousedeer (*Tragulus* sp.), muntjac (*Muntiacus* sp.), mongoose (*Herpestes* sp.) and porcupine (*Hystrix* sp.). Small mammals, such as rats and squirrels, small birds and reptiles were excluded from the analysis, as were animals that were unidentified due to low image quality.

To measure trapping success, the Relative Abundance Index (RAI) was calculated for each animal species. Trapping success (*TS*) was calculated as the number of independent photographs of a species (*N*) per 100 trap nights using the formula as below:

$$TS = (N/\Sigma\, TN) \times 100,$$

where $\Sigma\, TN$ is the total number of camera-trap nights. To be considered an independent photographic event, consecutive photographs of the same species had to have been taken more than half an hour (30 min) apart (O'Brien et al. 2003). To detect the spatial autocorrelation in the trapping records between sampling points, spatial coordinates of trapping points computed as Euclidean matrix were compared with the species abundance computed as Bray−Curtis dissimilarity matrix (Legendre and Legendre 2012). The correlation between both matrices was analyzed with Mantel test with 9999 permutations.

To determine the pattern of terrestrial mammals and bird species richness across the four different treatments, a sample-based rarefaction curve with 95% confidence interval was constructed using EstimateS software (version 9.1.0, Colwell 2013) with observations randomized 100 times. The total number of individuals recorded per treatment was used to standardize the species accumulation curve. To find out the 'true' species richness, four non-parametric species richness estimators, i.e., ACE (abundance-based coverage estimator), Chao1, Jack1 and Bootstrap, were used to estimate the most likely number of species at each sampling site (Colwell and Coddington 1994). Jaccard's similarity index was used to compare similarity in species composition among treatments. The species similarity was calculated as Jaccard's index:

$$SJ = a / (a + b + c),$$

where a is the number of species that is common to the sampling site, b is the number of species that is unique to the first sampling site and c is the number of species that is unique to the second sampling site.

Canonical Correspondence Analysis (CCA) was used to analyse the relationships between species occurrence and the 14 habitat variables recorded at each camera-trapping point and to identify the effect of enrichment method in comparisons to the natural regeneration on general forest structure in INIKEA. The CCA analysis was performed using R version 3.6.2. The relationships between species abundance and the recorded habitat variables were investigated through the Analysis of Variance (ANOVA) with 999 permutations under the reduced model.

2.4 Results

Trapping effort, animal species richness and composition

A total of 74 camera-trap points were successfully deployed in INIKEA for 18 months, from November 2017 to March 2019. Overall, the trapping effort yielded a total of 6534 independent photographs of ground-dwelling mammals and birds from 7266 camera-trap nights. Thirty-three species from 14 families and 7 orders of medium-to- large mammals and birds were represented. Among the recorded species, two are classified as Critically Endangered (CR), three as Endangered (En), eight as Vulnerable (Vul) and six as Near threatened (NT) in the IUCN Red List of Threatened Species (IUCN 2018). The remaining species are classified as Least concern (LC). The recorded species was listed as Table 2.1.

Table 2.1 Summary of the camera-trapping data collected at INIKEA Forest Rehabilitation Project Area (at Phase 1, Phase 2, Phase 3 and control sites) and the IUCN Red List status of recorded species (CR= critically endangered, En= endangered, Vul= vulnerable, NT= near threatened, LC= least concern).

Order/Family	Scientific name	Common name	No. of photographs				Total	IUCN status
			Phase 1 sites	Phase 2 sites	Phase 3 sites	Control sites		
Artiodactyla								
Bovidae	*Bos javanicus*	Bornean banteng	3	0	2	0	5	En
Cervidae	*Rusa unicolor*	Sambar deer	596	49	106	63	814	Vul
	Muntiacus sp.	Muntjac (Barking deer)	378	316	200	166	1060	NT
Tragulidae	*Tragulus* sp.	Mousedeer	413	283	313	192	1201	LC
Sulidae	*Sus barbatus*	Bearded pig	353	393	141	158	1045	Vul
Proboscidae								
Elephantidae	*Elephas maximus*	Bornean pigmy elephant	1	0	0	0	1	En
Carnivora								
Felidae	*Neofelis diardi borneensis*	Bornean clouded leopard	4	1	0	1	6	En
	Catopuma badia	Bay cat	1	2	9	1	13	En
	Pardofelis marmorata	Marbled Cat	1	1	3	3	8	NT
	Prionailurus bengalensis	Leopard cat	8	2	4	3	17	LC
	Prionailurus planiceps	Flat-headed cat	0	0	2	0	2	En
Viverridae	*Viverra tangalunga*	Malay civet	105	111	89	50	355	LC
	Paguma larvata	Masked palm civet	3	2	1	2	8	LC
	Diplogale derbyanus	Banded civet	50	28	38	56	172	NT

	Paradoxurus hermaphroditus	Common palm civet	0	0	1	0	1	LC
	Arctictis binturong	Binturong	4	5	3	2	14	Vul
	Prionodon linsang	Banded linsang	0	0	0	1	1	LC
	Herpestes sp.	Mongoose	7	6	4	3	20	NT
Mustelidae	*Martes flavigula*	Yellow-throated marten	18	4	1	5	28	LC
	Mydaus javanensis	Sunda skunk/Malay badger	14	1	0	6	21	LC
	Aonyx cinerea	Small-clawed otter	0	0	2	0	2	Vul
Ursidae	*Helarctos malayanus*	Bornean sun bear	6	26	4	19	55	Vul
Primates								
Pongidae	*Pongo pygmaeus*	Bornean Orangutan	0	0	0	2	2	CR
Cercopithecidae	*Macaca fascicularis*	Long-tailed macaque	5	0	0	1	6	LC
	Macaca nemestrina	Pig-tailed macaque	292	173	71	92	628	Vul
	Presbytis rubicunda	Red leaf monkey	0	0	0	1	1	LC
	Presbystis hosei	Hose's langur	13	0	0	3	16	Vul
Pholidota								
Manidae	*Manis javanica*	Sunda pangolin	1	2	3	3	9	CR
Rodentia								
Hystricidae	*Hystrix* sp.	Malayan porcupine	111	81	57	53	302	LC
	Trichys fasciculata	Long-tailed porcupine	0	0	13	0	13	LC
Galliformes								
Phasianidae	*Argusianus argus*	Argus pheasant	66	112	46	5	229	NT
	Lophura ignita	Crested fireback	207	105	108	56	476	NT
	Lophura bulweri	Bulwer pheasant	0	1	0	2	3	Vul
		Total	**2 660**	**1 704**	**1 220**	**949**	**6 534**	
		Camera-trap nights	**2 823**	**1 890**	**1 534**	**1 019**	**7 266**	
		Total species detected					**33**	

As a whole, the species accumulation curve (Figure 2.4A) appears to reach asymptote indicating sufficient sampling efforts to record the occurrence of terrestrial mammals and birds in the study area. The Mantel test between geographic distance and species Bray−Curtis dissimilarity was not significant (Mantel's r = 0.03; p = 0.39), indicating no spatial autocorrelation occurred in the trapping records between camera-trapping points. The trapping effort is summarized in Table 2.1.

All the families in the order Artiodactyla except Bovidae, i.e., Cervidae, Tragulidae, and Sulidae, were recorded at high frequencies, together accounting for 63% of the photographs. Mousedeer (*Tragulus* sp.) showed the highest photo-capture rate, followed by muntjac (*Muntiacus* sp.), bearded pig (*Sus barbatus*), sambar deer (*Rusa unicolor*, pig-tailed macaque (*Macaca nemestrina*) and crested fireback (*Lophura ignita*) (Figure 2.3). The species that were recorded on only one occasion included the Bornean pygmy elephant (*Elephas maximus*), banded linsang (*Prionodon linsang*), common palm civet (*Paradoxurus hermaphroditus*) and red leaf monkey (*Presbytis rubicunda*).

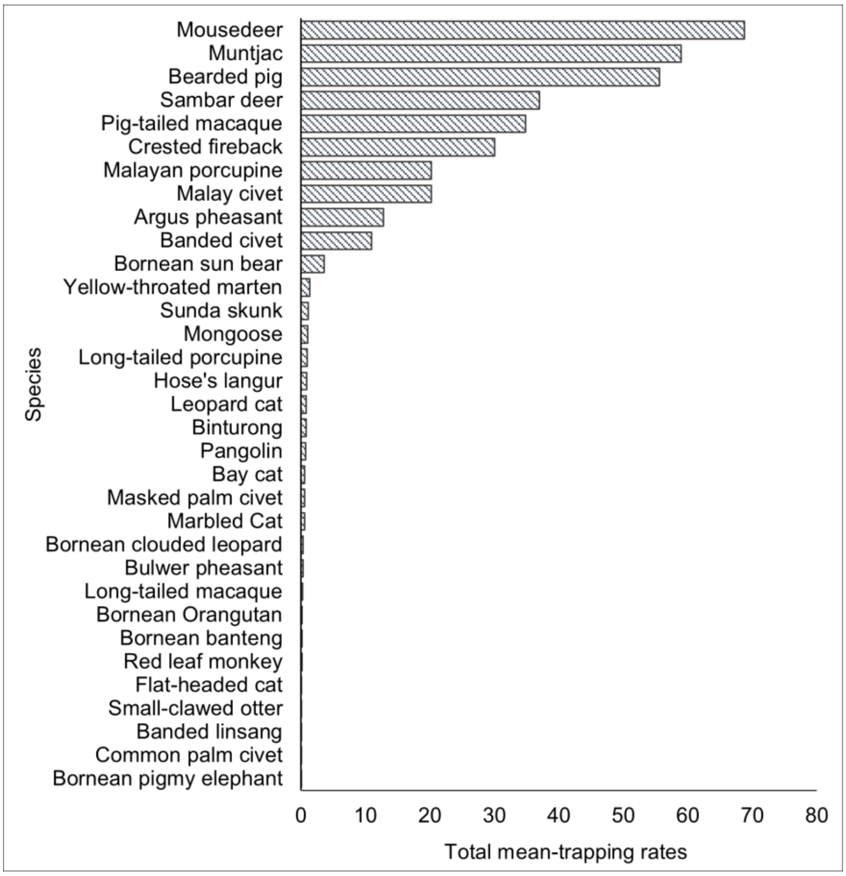

Figure 2.3: The total mean trapping rates per 7,266 camera-trap nights of each species of ground-dwelling mammals and bird recorded in INIKEA Forest Rehabilitation Project Area.

Differences in species richness and composition between the three rehabilitation treatment areas and the control areas

The species accumulation curves representing gap-cluster planting and line planting in Figure 2.4B show asymptotes, indicating that the sampling effort was sufficient to compare the species richness between the two types of sites. However, the curves for the liberation treatment and control show increasing trends, suggesting that the sampling effort was not sufficient for comparison and that more sampling effort is needed. Following to Carbone et al. (2001), minimum of 1000 camera-trap nights was adequate for a complete species list indicating that the sampling effort accumulated in gap-cluster planting, line planting, liberation and control that resulted in 2595 trap nights, 2576 trap nights, 936 trap nights and 1071 trap nights, respectively, was sufficient for all sites excluding liberation.

Thus, the average values of four non-parametric species richness estimators (ACE, Chao1, Jack1 and Bootstrap) were calculated using EstimateS for all treatments, i.e., gap-cluster planting, line planting, liberation and control (Table 2.2) to identify the expected species richness. Gap-cluster planted yielded the highest average of estimated species richness, followed by control, line planting and liberation. The averages of all estimators (Table 2.2) indicated the same trends in the species observed (number of species) (Figure 2.4B). After resampling the data, the patterns in the species accumulation curves (Figure 2.4B) for gap-cluster planting, control, line planting and liberation were confirmed with the four abundance-based species richness estimators (Table 2.2).

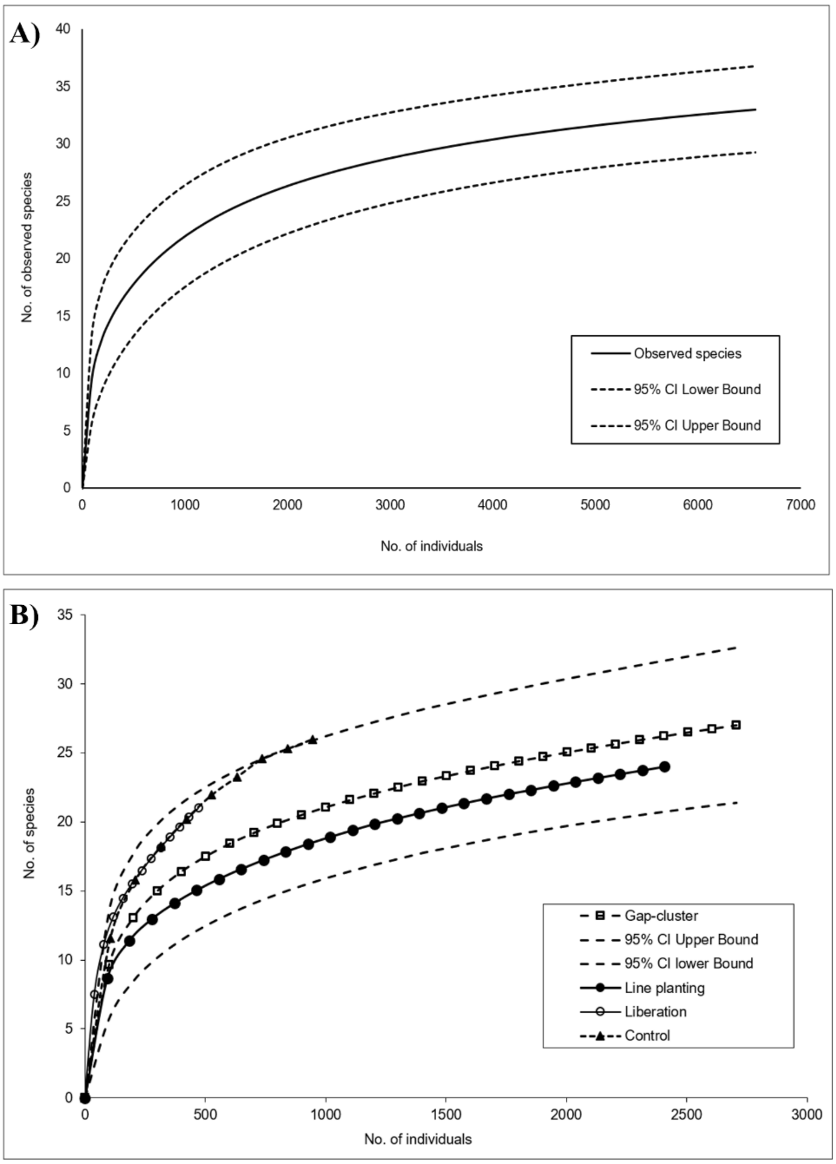

Figure 2.4: Species Accumulation curve for the A) overall species accumulated in INIKEA and B) species detected in each treatment in gap-cluster planting, line planting, liberation and control produced with 100 randomization runs in EstimateS (Colwell 2013).

Table 2.2: The observed and estimated species richness of vertebrates based on 4 non-parametric species richness estimators (ACE, Chao1, Jack1 and Bootstrap).

Treatment	Species observed	ACE	Chao1	Jack1	Bootstrap	Mean

Gap-cluster planting	27	30	28	33	30	30
Line planting	24	27	29	31	27	28
Liberation	20	24	23	28	24	25
Control	26	29	29	31	29	29

Jaccard's similarity coefficient was calculated as a measure of the similarity in species composition of terrestrial mammals and birds between pairs of the different rehabilitation treatments, i.e., gap-cluster planting, line planting, liberation and control. The species composition was very similar between the treatments. Gap-cluster planting and line planting (75.9%) and line planting and control treatment (75.9%) showed comparable percentage similarity and higher values than the other comparisons (Table 2.3).

Table 2.3: Jaccard's similarity coefficient (as a percentage) of species composition of ground-dwelling mammals and birds between pairs of rehabilitation treatments.

Treatments	Gap-cluster Planting	Line Planting	Liberation	Control
Gap-cluster Planting				
Line Planting	75.9			
Liberation	71.4	55.2		
Control	74.2	75.9	60	

General forest structure and the responses of vertebrate community to habitat features in INIKEA

Canonical Correspondence Analysis (CCA) was performed on all 14 habitat variables recorded at each of the camera-trapping points to assess the impact of different rehabilitation methods, i.e., gap-cluster planting, line planting and liberation in comparisons to natural regeneration (control) on general forest structure in INIKEA (Figure 2.5A) and the relationships between the distribution of ground-dwelling mammals and birds with specific habitat features (Figure 2.5B). The CCA results were significant ($\chi 2 = 0.64$, $F = 3.33$, $P < 0.003$), with *CCA 1* explaining a higher percentage of the variance in forest structure (30.6%) than *CCA 2* (17.3%). The arrows in Figure 2.5 indicate the direction of significance in habitat variables. The longer arrows for canopy height, climax and pioneer trees, trees with DBH1, DBH2, DBH4 and DBH5, leaf litter, understory, lower and ground vegetation indicate that these variables have greater importance than the other variables.

Generally, *CCA 1* and *2* reveal no distinction in terms of general vegetation structure among the gap-cluster planting, line planting, liberation and control sites (Figure 2.5A). *CCA 1* shows an increasing prevalence of lianas and medium-to-large sized trees (DBH between 40 and 50 cm) and decreasing ground vegetation cover, reflecting the characteristics of disturbed forest habitat. CCA 2 shows increases in tall canopy cover and the abundances of large trees and small trees (DBH > 50 cm and DBH 10–20 cm, respectively) and climax tree species and decreases in leaf litter depth, small-to-medium sized trees (DBH between 20 and 30 cm), pioneer tree species, and the density of understory and lower vegetation. CCA 2 appears to reflect the characteristics of less disturbed forest habitat. The results clearly show that all three enrichment treatments show similarity to the control treatment in terms of general forest structure, which formed a cluster reflecting the characteristics of undisturbed forest habitat (Figure 2.5A).

Out of the 33 species of ground-dwelling mammals and birds recorded in the study area, the 10 most abundant species were analysed to identify their preferences for selected habitat features (Figure 2.5B). The abundance of sambar deer *Rusa unicolor* was strongly associated with the presence of dense ground vegetation. The two species of large ground-dwelling birds, Argus pheasant (*Argusianus argus*) and Crested fireback (*Lophura ignita*), and the Malayan porcupine (*Hystrix* sp.) preferred areas with tall and dense canopy cover and an abundance of large and climax tree species. The muntjac (*Muntiacus* sp.) and bearded pig (*Sus barbatus*) were most abundant in areas with dense understory vegetation, abundant pioneer tree species and medium-sized trees (DBH 20–30 cm) and thick leaf litter. Mousedeer (*Tragulus* sp.), Malay civet (*Viverra tangalunga*), banded civet (*Diplogale derbyanus*) and pig-tailed macaque (*Macaca nemestrina*) preferred habitats with abundant lianas and medium-to-large trees (DBH 30–50 cm).

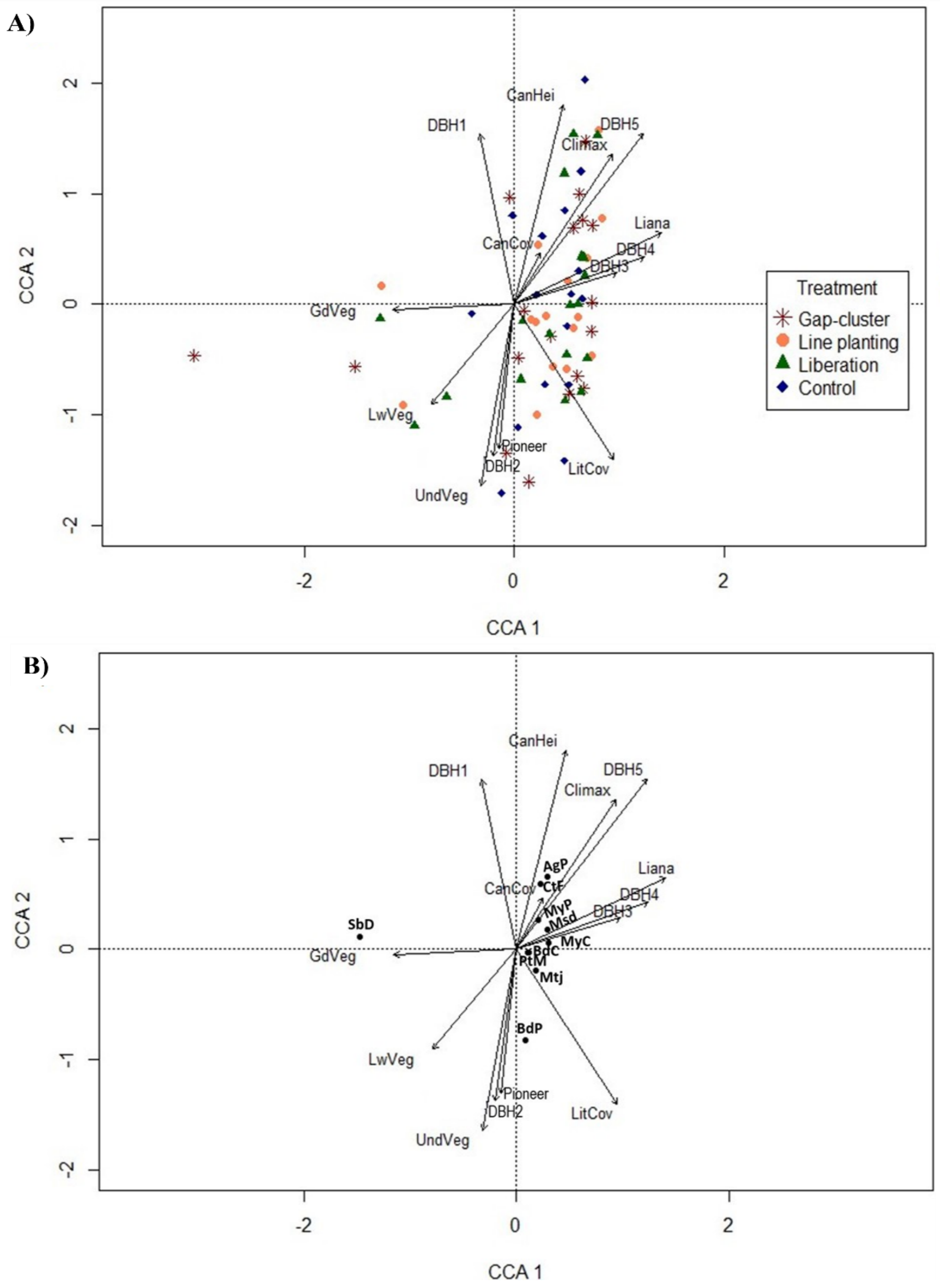

Figure 2.5: CCA plots showing the A) characteristics of general forest structure in gap-cluster planting, line planting, liberation and control treatments in INIKEA (‘CanHei’ (canopy height); ‘CanCov’ (canopy cover) ‘UndVeg’ (understory vegetation); ‘LwVeg’ (low vegetation); ‘GdVeg’ (ground vegetation); ‘LitCov’ (leaf litter); ‘DBH1’ (DBH 10–20 cm); ‘DBH2’ (20–30 cm); ‘DBH3’ (30–40 cm); ‘DBH4’ (40–50 cm); ‘DBH5’ (DBH

≥50 cm); ‘Climax’ (climax tree); ‘Pioneer’ (pioneer tree); ‘Liana’ (coverage of lianas)) and the B) relationship between environmental variables with species abundance. The solid rectangle indicates the distribution of the 10 most frequently detected species: ‘Msd’ (mousedeer, *Tragulus* sp.); ‘Mtj’ (muntjac, *Muntiacus* sp.); ‘BdP’ (bearded pig, *Sus barbatus*); ‘SbD’ (sambar deer, *Rusa unicolor*); ‘PtM’ (pig-tailed macaque, *Macaca nemestrina*); ‘CtF’ (crested fireback, *Lophura ignita*); ‘MyP’ (Malayan porcupine, *Hystrix* sp.); ‘MyC’ (Malay civet, *Viverra tangalunga*); ‘AgP’ (Argus pheasant, *Argusianus argus*); ‘BdC’ (banded civet, *Diplogale derbyanus*)

2.5 Discussion

The overall sampling effort in the present study was sufficiently large to document the occurrence of rare and elusive species in INIKEA. Carbone et al. (2001) suggested a minimum of 1000 camera-trap nights was necessary to reliably estimate the occurrence of cryptic species in a dense vegetation area, whereas Giman et al. (2007) suggested more than 1000 camera-trap nights were needed to conduct a comprehensive survey. According to these suggestions, the number of camera-trap nights included in this study was sufficient to obtain adequate information on the diversity of ground-dwelling mammals and birds in INIKEA. Thirty-three species of ground-dwelling mammals and birds were detected in this study, more than the 27 species detected by Bernard et al. (2013) over 1436 trap nights in primary forest of Imbak Canyon Conservation Area. However, the number is lower than those reported by Samejima et al. (2012, 2013) in the well-managed commercial forest of Deramakot Forest Reserve, who recorded 36 species from 34,386 trap nights and 39 species from 15,400 trap nights, respectively. The study differences in the number of species recorded is likely due to the differences in sampling effort among the studies.

The results of this study demonstrate high diversity of ground-dwelling mammals and birds occurred in INIKEA Forest Rehabilitation Area after 20 years of rehabilitation efforts. The documentation of three of the largest mammals in Borneo, i.e., the critically endangered (EN) Orangutan, the endangered (E) Borneo pygmy elephant and the Borneo banteng, as well as the three endangered species of wild felids, i.e., clouded leopard, bay cat and flat-headed cat (IUCN 2018), suggests that this area plays an important role in the conservation of these threatened species, which will indirectly protect the habitat for other animal species as well. Habitat generalists and group-living animals, such as sambar deer, mousedeer, muntjac, bearded pig, pig-tailed macaque and crested fireback, were the most frequently detected species in this study. The high detection rates of most ungulate species in this study support the suggestion by Meijaard et al. (2005) that some species such as herbivores, benefit from the increase in grass abundance after logging or fires. In contrast, in Lambir Hill National Park, Sarawak, Azlan and Engkamat (2006) detected only one occasion of bearded-pig and no sambar deer species; the absence of these species was due to illegal hunting activities in the area. This difference is evidence that the legal enforcement of the hunting ban in the present study area has successfully limited illegal hunting. In addition, the present findings suggest that these species are tolerant to habitat disturbance but not hunting pressure.

The estimated species richness of terrestrial mammals and birds in the sampling sites did not differ greatly from the observed species richness, suggesting that only a few species went undetected during the study period. Some of the arboreal or true canopy species, such as primates, went undetected in the study due to the bias of sampling method that focusing more on ground-dwelling vertebrates. In addition, some species might have gone undetected due to the dense vegetation at some of the camera-trapping sites, with limited visibility. The inability to differentiate some morphospecies during the species identification process due to poor image quality and unidentified small animals could cause sampling imperfect in this study.

The gap-cluster planting area was associated with the highest species richness of ground-dwelling mammals and birds, followed by control and line planting areas; the lowest was recorded for the liberation area. The removal of fruit-producing pioneer tree species and climbers reduces the availability of fruits to frugivores and omnivores, resulting in low species richness in the liberation area. This finding is consistent with a previous study demonstrating that the species richness and abundance of birds was positively related to the prevalence of lianas (Ansell et al. 2011). As compared to the other two rehabilitation methods, liberation was operated on less degraded forest area in INIKEA or the area categorized as old growth forest. Liberation was performed by eliminating climbers and pioneer tree species *Macaranga* spp. that colonized after disturbance, to promote the growth of existed natural trees. This method, however, alters the variety of food resources from both climbers and pioneer trees that produces fruits continuously to the wildlife species, along with the microhabitat for some specific animal species, i.e., protection from predators and Orangutan using woody climbers as a ladder (Lagan et al. 2007). Moreover, liberation resulted in fewer trees, shrub seedlings and lianas or climbers, creating a more open understory (Ansell et al. 2011). On the other hand, the high species richness recorded in both gap-cluster and line planting could be explained due to the inclusion of planting wild fruit trees to provide variety of food resources to wildlife species. Gap was created through the removal of only pioneer tree species, *Macaranga* spp. and replanted with random mixtures of Dipterocarps, non-Dipterocarps and wild fruit trees. At least 25 species of seedlings per planting blocks to fulfill the biodiversity criteria (Alloysius et al. 2010). It is suggested that enrichment planting applied in both gap-cluster and line planting were able to provide variety of food resources to wildlife species. The high species richness in the control area compared to the liberation area indicates that climber cutting negatively affected the community of ground-dwelling mammals and birds in INIKEA. In contrast to the liberation area, the untreated disturbed forest (control) area supplied a variety of food resources from the rapidly growing vegetation that appeared after disturbance. In the region’s primary forest, most climax tree species produce fruit only once a year or less, while understory and gap tree species, such as species of Rubiaceae and Moraceae, produce fruit several times a year due to the abundant light (Whitmore 1998). Thus, pioneer tree species and lianas could be important habitat features in addition to climax tree species, providing resources for the mammals and birds. The presence of a variety of food resources is crucial for maintaining forest biodiversity.

Though gap-cluster planting, line planting, liberation treatment and control areas in INIKEA were connected to one another and not isolated (Fig. 1), the results revealed no significant of spatial autocorrelation between geographical distance and species Bray–Curtis dissimilarity. At species level, it is almost impossible to discard spatial autocorrelation especially for the larger-sized animal species with greater home range. However, the finding indicates there is no occurrence of spatial autocorrelation detected in the recorded animal species among sites. Thus, in the present study, camera traps were established at least 0.5 km apart to reduce the probability of detection of the same individuals. Yet, high similarity in the species composition of the ground-dwelling mammal and bird community was observed among the study areas; it is possible that there are no large differences in forest habitat among the gap-cluster planting, line planting, liberation and control area, which could explain this finding. Moreover, the similarity in species richness between adjacent areas is due to the response of different species group towards the environmental factors (Diniz-Filho et al. 2003). Thus, most of the wildlife species were able to utilize different treatment types of the habitat area in INIKEA.

Generally, an undisturbed forest is characterized by dense canopy cover and understory vegetation, an abundance of medium-to-large trees with a tall canopy and thick leaf litter on the forest floor. The present study suggests that the different rehabilitation techniques, i.e., gap-cluster planting, line planting, and liberation, did not yield significant differences from naturally regenerated disturbed forest in terms of the general forest structure. However, enrichment methods, i.e., combining the random mixture of plant species applied to facilitate forest regeneration have affected forest structure in INIKEA. After 20 years of rehabilitation efforts, the gap-cluster planting, line planting, liberation and control sites exhibit characteristics of less disturbed forest habitat. Most forest in INIKEA shows a tall canopy, dense canopy coverage, a prevalence of climax tree species (*Dipterocarpaceae* spp.), abundant medium-to-large trees, thick leaf litter on the forest floor and the presence of lianas. These observations suggest that the rehabilitation efforts have enhanced the recovery of forest habitat in INIKEA. The similarity in forest structure between the rehabilitation treatments and control site could be because many climax tree species able to undergo natural regeneration persisted in the control sites, while most of the planted area was severely degraded and dominated primarily by pioneer tree species, such as *Macaranga* sp. However, whether the forest habitat in INIKEA has improved to the point of resembling primary forest cannot be inferred from this study as no comparisons with undisturbed or mature forest habitat were performed and no data are available for the region of INIKEA severely affected by logging and wildfires.

Habitat features play important roles in providing wildlife with shelter and food. The present study revealed that the sambar deer *Rusa unicolor* prefers area with dense ground vegetation. As a generalist grazer that feeds on grasses and other plants, this species benefits from the ground vegetation that grows rapidly after forest disturbance. Heydon (1994) reported a high density of sambar deer in disturbed forest relative to that in primary forest, which was associated with the grass vegetation in disturbed forest. In addition, the present study documented that two species of ground-dwelling birds, Argus pheasant (*Argusianus argus*) and Crested fireback (*Lophura ignita*), preferred areas with tall canopy, dense canopy coverage and numerous Dipterocarp tree species, characteristics of a less disturbed forest or primary forest. These species require dense canopy cover for their breeding sites and, in the case of Argus pheasant, dancing grounds. Due to its sensitivity to habitat degradation, Argus pheasant is more common in primary forest than in secondary forest (Davidson 1981; Nijman 1998; Johnsgard 1999). The associations of muntjac (*Muntiacus* sp.) and bearded pig (*Sus barbatus*) with dense understory vegetation, thick leaf litter, and a dominance of pioneer and medium-sized trees suggest that these species prefer disturbed forest habitat. The abundance of fruits produced frequently by pioneer tree species and the generalist behaviours of muntjac and bearded pig make these species tolerant to disturbed forest habitat. Furthermore, the fruits of lianas or climber species benefit omnivorous species, such as mousedeer (*Tragulus* sp.), Malay civet (*Viverra tangalunga*) and pig-tailed macaque (*Macaca nemestrina*). The high abundance of small mammals, such as rats, in the areas with high liana coverage might explain the preference of the banded civet (*Diplogale derbyanus*) for such habitat.

Rehabilitation can be the best way to improve the forest quality and biodiversity of degraded forest habitat at the stage where natural regeneration is almost impossible. This management strategy can help reverse the negative consequences of forest alteration (Brown and Lugo 1990). As tropical forest continues to be cleared, secondary forest habitat has become more important for forest conservation (Chazdon et al. 2009). The present study suggests that degraded forest habitat can retain high conservation value, supporting wildlife species diversity, if it is properly managed. The high species richness and abundance of ground-dwelling mammals and birds detected in INIKEA suggest that this area is crucial for the conservation of many vulnerable species, including charismatic species such as the Borneo sun bear, Borneo orangutan, Borneo pygmy elephant and the five species of wild felids; these species serve as keystone species that are crucial in maintaining the organization and diversity of their ecological communities (Mills et al. 1993; Wilting et al. 2006). However, the presence of some species may not reflect that they are permanent residents of the forest area (Bernard et al. 2014). Long-term monitoring of wildlife populations in the area is recommended to reduce the effects of hunting, which is facilitated by the ease of access from the roads near the forest edge. In addition, the sensitivities of specific species to different rehabilitation methods should be studied to evaluate the long-term persistence of these species in the area.

2.6 Conclusion

INIKEA has a rich diversity of ground-dwelling mammals and birds. The total number of species recorded in this study is consistent with that reported in a previous study in primary forest in Sabah. Degraded secondary forest can provide suitable habitat to many medium-to-large vertebrates as long as it is well managed, especially in terms of restricting hunting activities. The present study confirmed the presence of the two charismatic species Borneo banteng and orangutan and the five species of Bornean Felidae, i.e., clouded leopard, bay cat, leopard cat, flat-headed cat and marbled cat, in INIKEA. Regarding the different rehabilitation methods and species richness, most of the wildlife species were found to be well adapted in the gap-cluster planting, line planting, liberation and control habitat conditions. To enhance biodiversity in the study area, liberation treatment should be reduced to increase the abundance of food resources. The general forest structure in INIKEA exhibited characteristics of less disturbed forest habitat, suggesting that the rehabilitation methods that includes the enrichment planting to facilitate forest recovery in INIKEA have been successful. Moreover, the application of different rehabilitation methods (gap-cluster planting, line planting and liberation) did not result in a forest structure distinct from that of naturally regenerated degraded forest. This finding is consistent with the lack of difference in species richness between the treatment and control conditions. Nevertheless, the observation that the control sites had similar forest structure and species diversity to those of the treated sites (gap-cluster planting, line planting, and liberation sites) suggests that if major components of forest structure that cannot recover within 20 years, such as large, climax trees, remain after disturbance, disturbed forest should be left to undergo natural recovery. Therefore, the establishment of rehabilitation forest and proper management is crucial to protect wildlife habitat, especially the habitat of specialist taxa.

Chapter 3:

Seasonal home range and habitat selection patterns of sika deer in southern Hokkaido, Japan

3.1 Abstract

In 1980 and 1981, eight and nine individuals of sika deer *Cervus nippon* were reintroduced in southern Hokkaido, Japan, to cope with population decline in a few decades ago. As recent population growth has led to human–wildlife conflicts, this study investigated the responses of sika deer to resource availability and geomorphic factors during the summer and winter seasons in southern Hokkaido. Global positioning system data collected from 2016 to 2018 were used to assess the home range patterns and habitat selection of 14 female sika deer located in Mount Esan and Shiriuchi. The core home range size was defined using a 50% kernel density estimation that indicated a larger home range in winter than summer for all deer. Habitat selection was assessed using a generalized linear mixed model. The results showed variation in habitat selection between resident deer of Mount Esan and Shiriuchi, as well as migratory deer in Shiriuchi during summer. Resident deer in Mount Esan and migratory deer in Shiriuchi preferred coniferous forest and forest edge habitats in summer, and both resident deer in Mount Esan and Shiriuchi selected habitats closer to croplands in the summer. Interaction effects revealed that sika deer in Mount Esan preferred cropland and grassland away from the forest edge, whereas both resident and migratory deer in Shiriuchi selected cropland closer to the forest edge, and migratory deer selected grassland habitats closer to the forest edge and croplands, which reveals a tactic to avoid humans. In winter, forest edge habitat, southing, low elevation, and being away from the river were important habitat features for all deer across the study area. Thus, sika deer habitat selection depends on human interference in summer and topographic factors in the winter.

KEY WORDS GPS-collar, habitat selection, home range, sika deer, summer, winter

3.2 Introduction

Large herbivores, an important component of forest ecosystems (Forbes et al. 2018), have been linked to the alteration in the forest structure (Persson et al. 2000, Yokoyama et al. 2001), composition (Synnove et al. 2016), and forest regeneration process (Fuller and Gill 2001, Wilson et al. 2006, Tremblay et al. 2007), particularly when a herbivore population is overabundant. In Japan, the current population of sika deer (*Cervus nippon*) has exceeded the capacity of the local ecosystem, such that the forest and agricultural resources of the region have sustained severe damage (Kaji et al. 2004). The sika deer population, once a threatened species, has expanded by 70% over the last three decades (Takatsuki 2009, Nakajima 2007). Comparing specific areas in Japan, the distribution expansion was highest in Hokkaido (73%), as observed between 1978 to 1991, with continued spread from the east (Kaji et al. 2000, Takatsuki 2009). Moreover, the development of urban areas and agricultural and farmland activities have contributed to an increase in landscape heterogeneity. Herbivores favour habitat heterogeneity (Kie et al. 2002) due to the abundance of resources available (Anderson et al. 1998), such as the areas between forested and agricultural land. In fact, studies have indicated that the carrying capacity for deer increases with the fragmentation of forests into small patches of wooded areas surrounded by highly nutritious cropland (e.g., Iijma and Ueno 2016).

However, this gives rise to human–wildlife conflicts, particularly during non-winter seasons. The absence of predator such as wolves *Canis lupus* as part of the factors that once regulated deer population had led to more difficulties in managing the population. By contrast, during winter, food resources are scarce, and mobility is restricted due to the deep snow cover. Schmitz (1990) observed an increase in the deer's consumption of coniferous twigs over the winter season, due to the smaller amount of deciduous twigs available, whereas in a mild winter, deer consumed more deciduous twigs than coniferous twigs (Dumont et al. 2005). Sika deer in Hokkaido depend on both bamboo grasses (*Sasa*) and leafy/woody plants in winter, and the deer have adapted to severe winters by relying on the latter when bamboo grasses are inaccessible (Yokoyama et al. 2000). Moreover, in deep snow, deer tend to increase their home range, to find shelter from fluctuating weather conditions and to find more food (Borkowski and Furubayashi 1998, Said et al. 2009).

Telemetry or global positioning system (GPS)-collar studies have focused on forest ungulates to examine their behavioural changes in response to habitat heterogeneity. For example, studies have investigated the distribution of mule deer in California (Kie et al. 2002); the effects of resource availability, forest cover, and threats on sika deer habitat selection in southwest England (Uzal et al. 2013); and the pattern of resource selection by sika deer introduced to central North Island, New Zealand (Latham et al. 2015). An understanding of habitat selection behaviour is crucial for controlling population expansion and conserving declining populations. In Japan, the rapid expansion of the sika deer population has been detrimental to agricultural crops and forestry plantations.

However, most studies of wildlife conflicts in Hokkaido have focused on the eastern region. For example, Takafumi et al. (2017) examined the movement patterns and area used by sika deer in the Kushiro Wetland. Estimations of the population density (Uno et al. 2017), seasonal distributions and habitat selections (Sakuragi et al. 2003), and seasonal migration patterns (Igota et al. 2004) of female sika deer in eastern Hokkaido have been well documented. Notably, the eastern part of Hokkaido consists mostly of flat terrain and open habitat, e.g., pastures, cropland, and natural grasslands. Snow cover is relatively low, compared to other regions of Hokkaido.

There have been estimations of the sika deer population in some other specific areas. Ikeda et al. (2013) documented the population on Nakanoshima Island, located within a lake in southwest Hokkaido. However, little is known regarding the factors that affect regional and seasonal differences in sika deer habitat selection in southern Hokkaido. Compared to the relatively flat, open areas of eastern Hokkaido, southern Hokkaido is located close to the Pacific Ocean and is covered mostly by rugged, forested terrain, with fewer agricultural areas. Notably, this region experiences more snowfall in the winter. Thus, due to the differences in the geomorphic and climatic conditions between eastern and southern Hokkaido, southern Hokkaido is of particular interest to study. In addition, few studies have been conducted in southern Hokkaido. Moreover, the sika deer population there was part of an experimental reintroduction in 1980 and 1981 (Kaji et al. 2000), and many questions remain regarding the home range patterns and habitat selection of sika deer in this area.

Hence, in this study, we used GPS radio-collared data to monitor female sika deer in this region. We investigated their home ranges and assessed their habitat selection in different seasons.

3.3 Materials and Methods

Study area

The GPS-collar study was conducted in Mount Esan and Shiriuchi; both areas are located in the southern part of Hokkaido, Japan (Figure 1). Mount Esan is an active volcano with the highest elevation of 618 m a.s.l. Located in the eastern part of Hakodate (Figure 3.1A), Mount Esan is surrounded by natural grass cover, and deciduous and coniferous forest. At lower to mid-elevation (200–400 m), 75% of the area is composed of deciduous forest and 25% is coniferous forest. It is also part of the Prefectural Natural Park (Hokkaido Government, access date: January 4th, 2022).

Shiriuchi is situated southwest of Hakodate (Figure 3.1B) and consists mostly of deciduous and coniferous forest, with crops and paddy plantations and human settlement towards the coastal area. At elevations higher than 200 m a.s.l, the area is covered by mixed forest (40% coniferous and 60% deciduous). The southern part of Hokkaido has a rugged terrain and cliffs that fall towards the sealine. Most of towns and agricultural activities, i.e., crops and paddies, cover the area at elevations of less than 100 m a.s.l. The area receives an average annual precipitation of 1,318 mm and an average maximum snow accumulation of 105 cm (Meteorological Agency of Japan). The overall characteristics of the land cover types are summarized in Table 3.1.

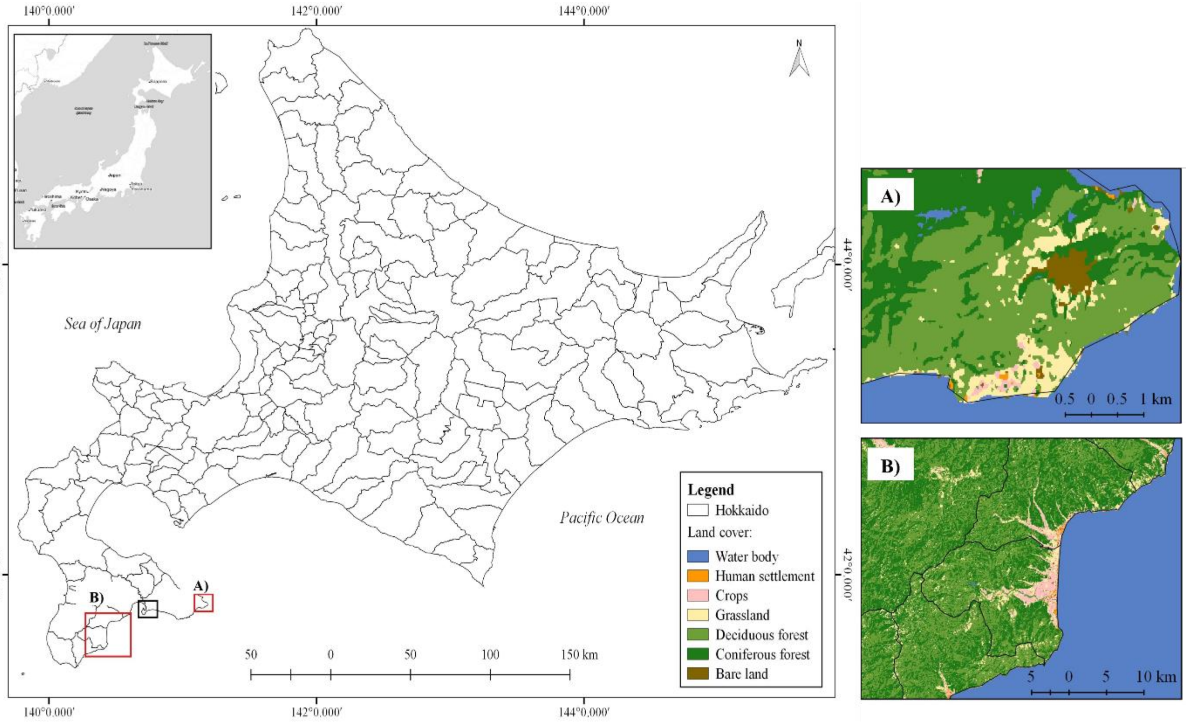

Figure 3.1: Global positioning system-collar study area located in eastern Hakodate (in black rectangle) in A) Mount Esan and southwest in B) Shiriuchi located in the southern part of Hokkaido, Japan.

Table 3.1: Summary of the proportion of land cover within the global positioning system (GPS)-collar study areas in Mount Esan and Shiriuchi, Southern Hokkaido, Japan.

	Proportion of land cover (%)	
Land cover	**Mount Esan**	**Shiriuchi**
Deciduous forest	57.53	45.18
Coniferous forest	22.64	42.78
Grassland	13.63	6.14

Crop & paddy	1.27	5.07
Human settlement	0.34	0.57
Bare land	4.58	0.26

Global positioning system (GPS) radio-collared data

The habitat model was built using a GPS-collar (IridiumTrackM2D, LOTEK) database provided by the Hokkaido Prefectural Government, containing 77,766 locations of 14 female sika deer: 5 individuals (n = 27,356) in Mount Esan and 9 individuals in Shiriuchi (n = 87,385). The GPS data fix success rate was calculated as the numbers of successful fix divided by the number of attempts. All collared sika deer were monitored between 2016 to 2018. Data were classified into summer (June–October) and winter (January–March) according to the seasonal separation by Uno et al. (2010). Individuals showing overlap in their core home range in summer and winter were classified as resident deer, whereas individuals that travelled outside of their winter home range during summer were classified as migratory deer (Takafumi et al. 2017). In the present data, all five deer in Mount Esan were resident deer. In Shiriuchi, three deer were resident, and six deer were migratory.

Landscape variables

To identify the habitats of the deer, we recorded 11 variables, including the characteristics of the land cover, topography, and distance to covariates (Table 3.2). Land use data were collected from the High-Resolution Land Use and Land Cover map from the Japan Aerospace Exploration Agency (JAXA, Ver.18.03 and Ver.21.03) at 30 m^2 resolution.

Land cover was classified into five cover types: deciduous forest, coniferous forest, natural grassland, cropland (including paddy fields), and human settlement. The distance of sika deer GPS points from crops, human settlement, forest edge, rivers, and roads were measured using Euclidean distance in the Spatial Analyst tool set.

Topographic variables such as elevation, slope angle, and south aspect were derived from a digital elevation model provided by JAXA. These variables were selected to determine their importance in habitat selection during the winter season (Sawyer et al. 2006, Shanley et al. 2021). All raster extent was standardized to 10 m^2 resolution. Geographic information system analysis was conducted in ArcMap (ver. 10.7.1). Recorded candidate variables are summarized in Table 3.2.

Table 3.2: Eleven candidate variables recorded from individual sika deer according to the GPS point.

Variables	**Code**	**Type**	**Unit**
Land cover:			
Coniferous forest	conif	Binary	NA
Deciduous forest	decid		
Natural grassland	grass		
Distance to crops	d_crop	Continuous	Metre (m)
Distance to human settlement	d_human		
Distance to forest edge	d_foredge		
Distance to river	d_river		
Distance to road	d_road		

Topography:			
Elevation a.s.l	Elev		
Slope angle	slope		Degree (°)
Aspect-south	south	Binary	NA

Data analysis

To define the study area for analysis, a 100% minimum convex polygon (MCP) was calculated for all locations of sika deer in Mount Esan and Shiriuchi. The 95% bivariate kernel density (KDE) was calculated to generate the area in which the deer spent the most time, restricting the infrequently used areas; in addition, a 50% KDE was calculated to define the core home range area of individual sika deer. Home range analysis was conducted with the "*adehabitHR*" package in R statistical software (ver. 4.0.3, R Core Team 2020). To compare the differences in home range size between summer and winter, a *t*-test analysis was conducted for seasonal comparisons of Mount Esan and Shiriuchi, whereas two-way analysis of variance was used to test the differences between the study areas and seasons. The analysis was separated into resident deer and migratory deer, as both showed differences in home range behaviour in the summer and winter seasons.

To quantify the habitat selection of sika deer using the home range scale, resource selection function (RSF) models were applied to compare the proportions of observed GPS points of deer individuals to a random location (Manly et al. 2002). The observed GPS points were derived as "used" and random locations as "available" points. The "available" points for each deer were generated within the 100% MCP of each sika deer. The evaluation of the RSF framework for sika deer was followed by a third-order selection process (Johnson 1980), in which the variation in logistic regression was used to approximate the relative probability of deer selection at the home range scale (Manly et al. 2002). The probability of selection of sika deer is given by the following:

$$w(x) = exp\ (\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + ... + \beta_m x_m + \beta_p x_1 x_2), \qquad (1)$$

where w(x) is the RSF probability, x_i are the predictor variables, and β_i are the corresponding coefficients (Manley et al. 2002).

RSF was fitted using logistic regression, specifically, the Generalized Linear Mixed Model with logit link (GLMM). A random effect was assigned for individual deer. Prior to the building of the model, the collinearity between variables was tested using Pearson's correlation test to exclude paired variables with $|r| > 0.60$ from being in the same model. Candidate models were designed for summer and winter seasons based on the following hypotheses.

(1) Sika deer select areas with various food resource availability, e.g., active croplands, grasslands, and the forest edge during summer.

(2) In response to snow cover and harsh winter conditions, sika deer prefer coniferous forest and specific topographic features, such as a lower elevation, a steep slope, and aspect facing to the south.

To explore how sika deer use the landscape with respect to variation in the habitat type and resources, interaction effects were tested during the summer season, as opposed to the winter season. The reason for this was that the selection regarding land cover and topographic factors were related more to the snow depth (Borkowski et al. 1996, Gilbert et al. 2017), thus limiting the scope of the data in the analysis. At first, the general model (without interaction) was constructed and selected based on the lowest Akaike information criterion (AIC) values. Then the interaction effect was added to the selected model if it improved the model fit. The interaction effects allowed for assessing the influence of certain habitat types and resource availability on the habitat selection of the deer. The interaction effects on deer habitat selection in summer included a) the selection of grassland and distance to the forest edge, b) distance to the forest edge and distance to crop land, and c) the selection of grassland and distance to crop land. The best model was selected by the lowest AIC value. The parameter estimates and confidence interval (CI, 95% confidence limit) were used to explain the variables of the best model, in which a significant influence occurred when zero was excluded between the confidence intervals. GLMM was performed with the "*lme4*" package using R statistical software (ver. 4.0.3, R Core Team 2020).

3.4 Results

Home range size in summer and winter

A total of 50,479 locations of 14 female sika deer were used to assess the home range patterns and habitat selections in southern Hokkaido in Mount Esan and Shiriuchi. The analysis was separated into resident and migratory deer for summer and winter. The overall fix success rate was 99.4%. Figure 3.2 shows the comparisons for 50% KDE and 95% KDE between the summer home range and winter home range for migratory and resident deer in Shiriuchi, as well as the resident deer in Mount Esan. Overall, the results showed that the mean home range of sika deer was smaller during the summer compared to the winter season for both core area (Figure 3.2A) and home-range (Figure 3.2B). The seasonal difference in core area and home range for resident deer in Mount Esan was significant (Core area: $t = -3.344$, $df = 8$, $p\text{-value} = 0.010$; home range: $t = -5.240$, $df =$

8, p-value = 0.001); however, in Shiriuchi, the home range was not significant for resident deer (Core area: *t = –0.932; df = 4; p-value = 0.404*; home range: *t = –0.825; df = 4; p-value = 0.456*) or migratory deer (Core area: *t = –1.278; df = 10; p-value = 0.230*; home range: *t = –1.110; df = 10; p-value = 0.293*). Across the study sites, the core area and home range size of migratory deer in Shiriuchi was larger, followed by resident deer in Shiriuchi, and resident deer in Mount Esan; however, the differences were not significant (Core area: *F = 1.659; df = 2; p = 0.21*; home range: *F = 1.831; df = 2; p = 0.182*), including the differences between seasons (Core area: *F = 3.820; df = 1; p = 0.083*; home range: *F = 2.339; df = 1; p = 0.139*).

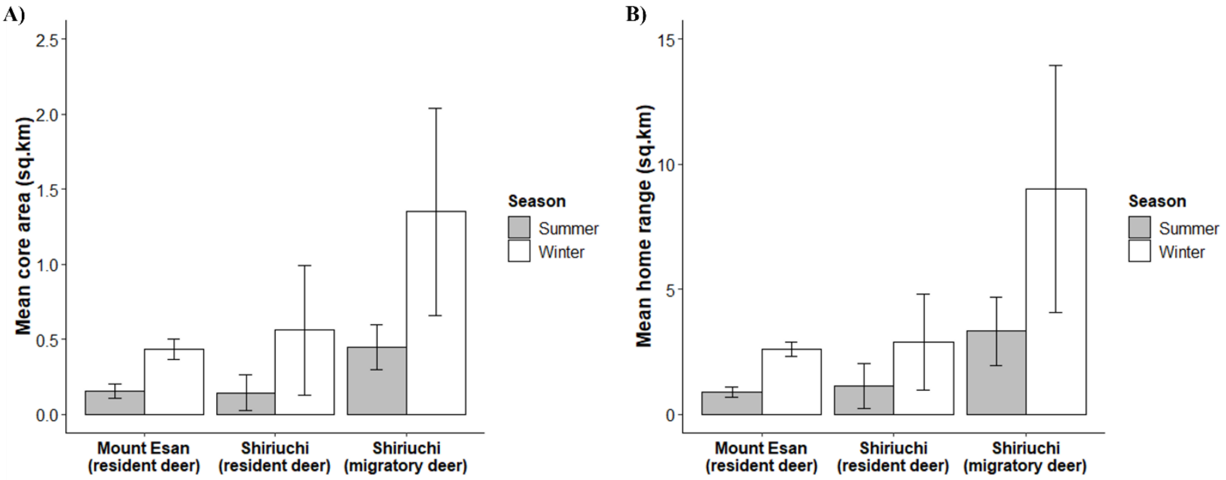

Figure 3.2: Mean ± SE differences home range size in summer and winter estimated using A) the 50% of kernel density (KDE) and B) the 95% KDE in Mount Esan and Shiriuchi, Southern Hokkaido, Japan.

Habitat selection of sika deer in summer and winter

The model development for sika deer habitat selection is summarized in the appendices Table 3.5. Overall, coniferous forest, distance to forest edge, grassland, distance to river and cropland, as well as the interaction effects, e.g., d*_foredge* × *d_crop*, *d_foredge* × *grass* and *grass* × *d_crop*, were included in all top-ranked models for summer habitat selection. In the winter top-ranked model, coniferous forest, distance to forest edge, southern exposure, slope, elevation, and distance to a river were included in all top-ranked models.

Table 3.3 shows the top-ranking models in Mount Esan (resident deer) and Shiriuchi (resident and migratory deer). The final model for summer in Mount Esan indicated that deer selected coniferous forest, grassland, habitats closer to the forest edge and croplands, and areas away from riverine. The interaction effects further revealed how deer selection of certain habitats was affected by the distance to the covariates. The interaction terms between forest edge and grassland (*d_foredge* × *grass*; $\beta = 0.223$; Figure 3.3A) showed that deer selection of grassland increased with the distance to the forest edge, in contrast to highly selected grassland closer to cropland (*grassland* × *d_crop*; $\beta = –0.344$; Figure 3.4A). As the distance to the forest edge increased, the deer tended to select habitats closer to cropland (*d_foredge* × *d_crop*; $\beta = –0.145$; Figure 3.5A). In Shiriuchi, the top-ranked model for resident deer showed that deer selected areas closer to crops and the river, away from the forest edge and coniferous forest (Table 3.4). The interaction effects showed a reduction in the selection of cropland with increasing distance from the forest edge (*d_foredge* × *d_crop*; $\beta = 1.126$; Figure 3.5B). The final model for migratory deer indicated coniferous forest, forest edge habitat, and road proximity as important habitats, with fewer deer selecting grassland and being away from crops. Sika deer tended to select grassland less as the distance to the forest edge (*foredge* × *grass*; β=–1.903; Figure 3.3B) and the distance to croplands (*grass* × *d_crop*; β=–0.171; Figure 3.4B) increased. Sika deer were also less likely to select habitats closer to cropland with increasing distance to the forest edge (*d_foredge* × *d_crop*; β= 0.224; Figure 3.5C).

The winter top-ranked models in Mount Esan and Shiriuchi are shown in Table 3.4. Resident deer in Mount Esan selected both deciduous and coniferous forest, forest edge habitats, a south-facing aspect, steep slope, and low elevation for their winter habitat, notably away from the riverine. In Shiriuchi, the final model showed that resident deer selected forest edge habitats, a south-facing aspect, less of a steep slope, a low elevation, and being closer to the road, while away from the river and coniferous forest. In the final model for migratory deer, coniferous forest, grassland, forest edge habitat, south-facing aspect, steep slope, lower elevation, and being away from a riverine habitat were the important parameters in winter.

Table 3.3. Parameter estimates of the top-ranking GLMM model for habitat selection of female sika deer in Mount Esan (resident deer) and Shiriuchi (resident and migratory deer) during summer. Each variable is presented with the estimated coefficient and 95% confidence interval (CI).

		Mount Esan			Shiriuchi					
		Resident deer			Resident deer			Migratory deer		
No		Estimate	Upper CI	Lower CI	Estimate	Upper CI	Lower CI	Estimate	Upper CI	Lower CI
	Intercept	-0.907	-0.479	-1.335	-0.812	0.527	-2.150	-0.507	1.395	-2.409
1.	Coniferous forest	0.235	0.284	0.186	-0.299	-0.240	-0.358	0.160	0.187	0.133
2.	Distance to forest edge (m)	-0.102	-0.083	-0.120	0.709	0.747	0.671	-0.321	-0.306	-0.336
3.	Grassland	0.191	0.249	0.133	0.407	1.023	-0.210	-2.132	-1.811	-2.452
4.	Distance to river (m)	0.071	0.116	0.026	-0.497	-0.470	-0.523			
5.	Distance to crop (m)	-1.505	-1.473	-1.538	-3.005	-2.924	-3.087	0.202	0.221	0.183
6.	Distance to road (m)							-6.114	-5.977	-6.251
Interaction terms:										
7.	Distance to forest edge × grassland	0.223	0.293	0.153	-0.285	0.241	-0.811	-1.903	-1.571	-2.235
8.	Distance to forest edge × distance to crop	-0.145	-0.118	-0.172	1.126	1.156	1.095	0.224	0.240	0.208
9.	Grassland × distance to crop	-0.344	-0.300	-0.389	1.237	1.535	0.938	-0.171	-0.121	-0.221

Table 3.4. Parameter estimates of the top-ranking GLMM model for habitat selection of female sika deer in Mount Esan (resident deer) and Shiriuchi (resident and migratory deer) during winter. Each variable is presented with the estimated coefficient and 95% confidence interval (CI).

		Mount Esan			Shiriuchi					
		Resident deer			Resident deer			Migratory deer		
No		Estimate	Upper CI	Lower CI	Estimate	Upper CI	Lower CI	Estimate	Upper CI	Lower CI
	Intercept	-0.898	-0.698	-1.097	-0.810	0.517	-2.138	-0.989	-0.816	-1.161
1.	Deciduous forest	0.163	0.200	0.126						
2.	Coniferous forest	0.110	0.173	0.047	-0.458	-0.401	-0.514	0.057	0.091	0.022
3.	Grassland				-0.064	0.018	-0.146	0.166	0.226	0.106
4.	Distance to forest edge (m)	-0.241	-0.223	-0.259	-0.075	-0.054	-0.097	-0.539	-0.518	-0.559
5.	South	0.140	0.173	0.107	0.837	0.881	0.792	0.030	0.064	-0.003
6.	Slope (°)	0.134	0.152	0.116	-0.209	-0.187	-0.232	0.186	0.202	0.169
7.	Elevation (m)	-0.486	-0.468	-0.504	-0.717	-0.693	-0.741	-0.787	-0.768	-0.806
8.	Distance to river (m)	0.449	0.477	0.420	0.569	0.648	0.490	1.049	1.073	1.025
9.	Distance to road (m)				-2.388	-2.099	-2.677			

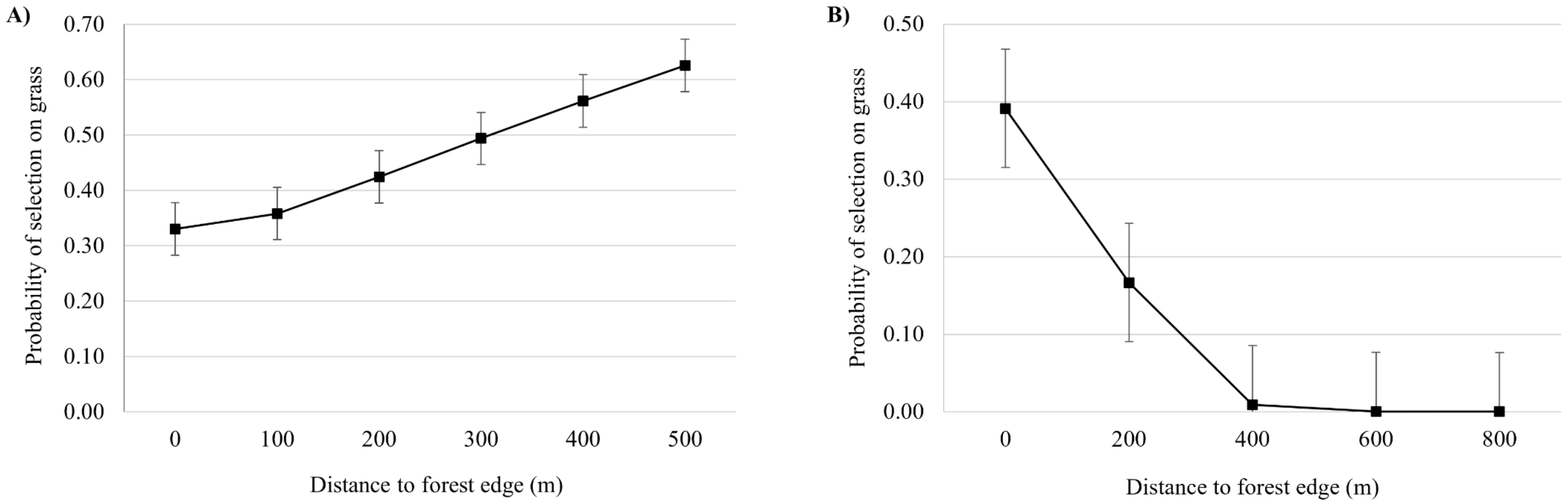

Figure 3.3: Interactive effects of forest edge on sika deer selection on grassland for A) resident deer in Mount Esan and B) migratory deer in Shiriuchi in Southern Hokkaido, Japan. Selection probability was calculated by changing the values for distance to forest edge with all other variables held at their mean values. The dots represent the mean probability of the distance.

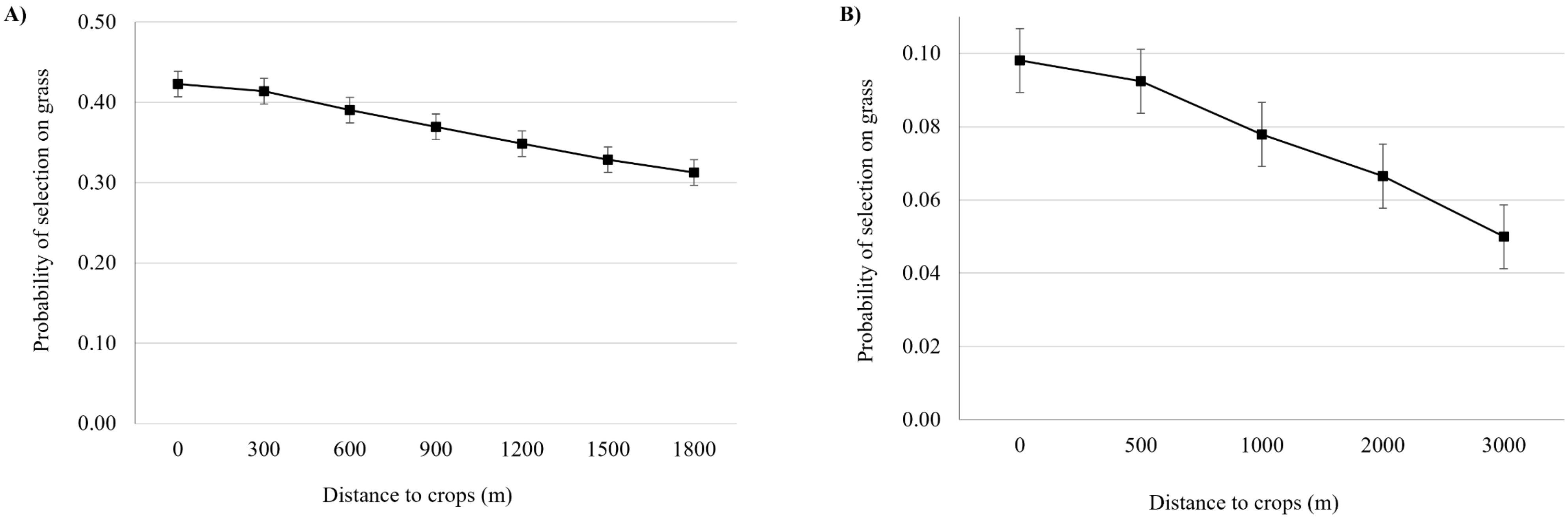

Figure 3.4: Interactive effects of distance to crops on sika deer selection for grass for A) resident deer in Mount. Esan and B) migratory deer in Shiriuchi in Southern Hokkaido, Japan Selection probability was calculated by changing the distance to crops with all other variables held at their mean values. The dots represent the mean probability of the distance.

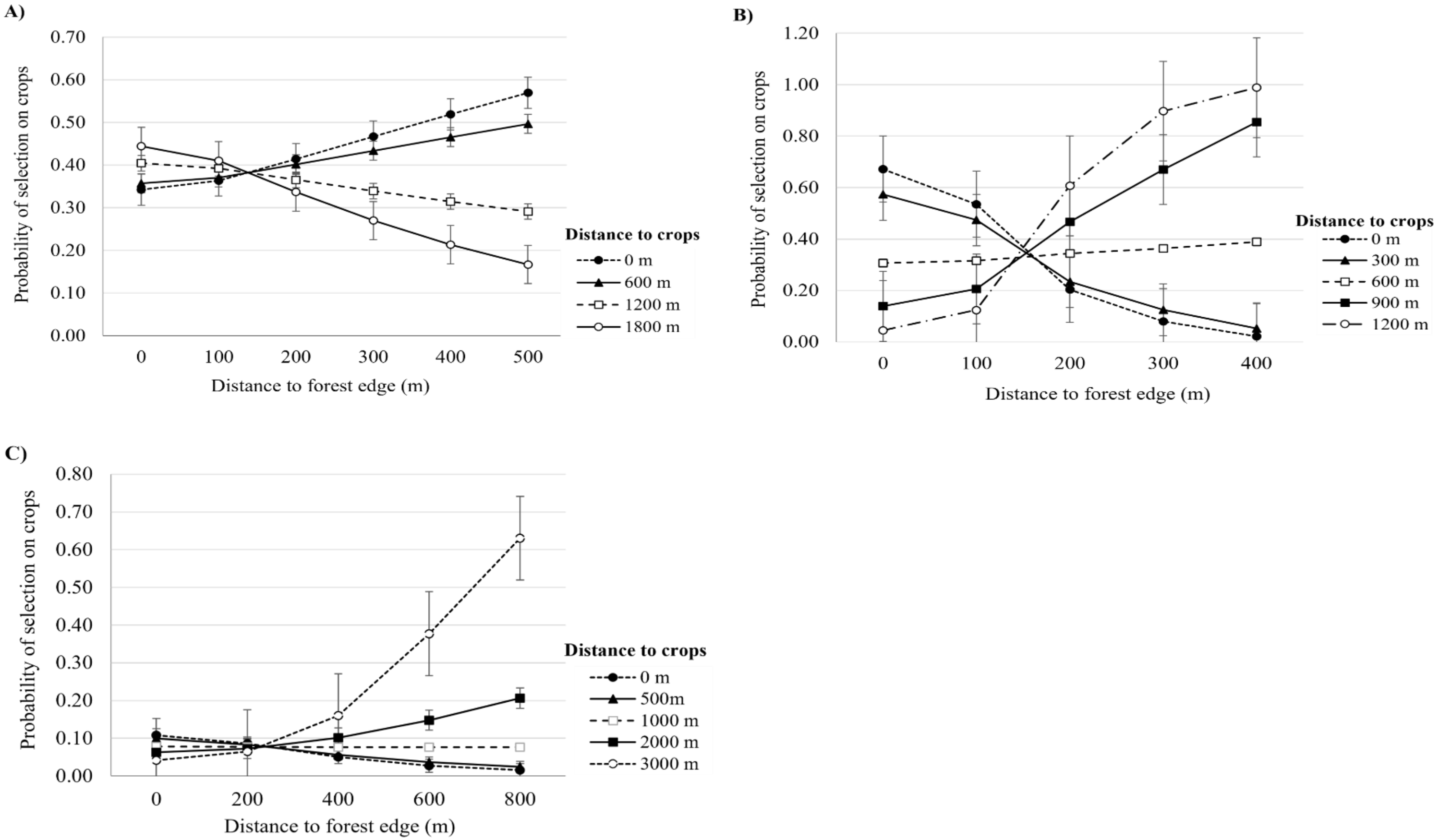

Figure 3.5: Interactive effects of forest edge on sika deer selection for distance to cropland for A) resident deer in Mount Esan, B) resident deer in Shiriuchi and C) migratory deer in Shiriuchi in Southern Hokkaido, Japan. Selection probability was calculated by changing the values for distance to forest edge with all other variables held at their mean values. The dots represent the mean probability of the distance.

3.5 Discussion

The sika deer in the present study come from deer reintroduced in 1980 (six females and two males) and 1981 (six females and three males) (Kaji et al. 2004). The findings document the preliminary habitat selection in southern Hokkaido after reintroduction. Overall, our results suggest that resident sika deer in Mount Esan and both resident and migratory sika deer in Shiriuchi have a smaller home range in summer than in winter. This finding is similar to that of a previous study in the Tanzawa Mountains of Japan (Borkowski and Furubayashi 1998), which reported that female sika deer exhibit a larger home range in winter than in summer. Said et al. (2009) suggested that the number of patches of different land cover types within a habitat influences the home range size of female deer. The availability of various resources grown within the home range in summer could also lead to a smaller home range. This is due to the patches of habitat, i.e., forest, grassland, and cropland, that cover the terrain, providing sufficient resources for ungulates (Borkowski and Furubayashi 1998, Viana et al. 2018). Although we did not analyse the calving state of female sika deer in the present study, there is the possibility that a smaller home range size in summer is influenced by calving, as female deer exhibit a smaller home range during the reproductive stage (Ciuti et al. 2005). During winter, increasing locomotion may increase energy consumption, particularly in heavy snowfall. The female sika deer in our study exhibited a large winter home range; this may be due to the need to find a suitable habitat given the fluctuating weather/climatic conditions. This pattern was also reported in white-tailed deer by Brinkman et al. (2005), who found that snow depth and temperature influenced deer migration in winter. In addition, sika deer may need to expand the home range in winter in response to limited food resources, where deer are forced to travel in search of food.

The selection of habitat with respect to season could influence the home range of ungulates. Generally, we found that there is variation in the important habitat selected by resident deer in Mount Esan and Shiriuchi, as well as migratory deer in Shiriuchi. Resident deer in Mount Esan and migratory deer in Shiriuchi selected coniferous forest and forest edge as important habitats in summer, but not the Shiriuchi resident deer. Furthermore, resident deer in both Mount Esan and Shiricuhi selected a habitat closer to crops in summer, but this habitat was avoided by the migratory deer in Shiriuchi. The findings for Mount Esan correspond to those cited by Honda (2009) that suggest that sika deer prefer areas closer to both farmland and the forest edge. The active crop land in summer benefits provides sika deer a variety of food resources. Agricultural crops attract ungulate species (Yokoyama et al. 2000, Honda 2009, Devore et al. 2016) and provide more diverse grazing. At the same time, proximity from the forest edge is important as a tactic to avoid hunters. Previous studies observed similar selections by ungulates species to both forest cover and open habitats (Uzal et al. 2013, Latham et al. 2015), in which the forest edge acts as not only a resting area or protection from hunters but also as a grazing site for sika deer consuming the browse that grows rapidly at the forest edge during summer. Many studies have also reported intense deer browsing in forest edge habitat (Takatsuki 1989, Cadenasso and Pickett 2000, Allombert et al. 2005, Ruzicka et al. 2009). In addition, Sakuragi et al. (2003) reported high avoidance of cropland by sika deer in eastern Hokkaido, which was related to hunting pressure. This behaviour was also observed in Shiriuchi migratory deer in the current study.

In addition, we observed variation in the habitat selection tactics between sika deer in Mount Esan and resident and migratory deer in Shiriuchi, with respect to the landscape characteristics within the home range. Sika deer in Mount Esan tended towards cropland and grassland at some proximity away from the forest edge, while avoiding grasslands away from crops. These selection patterns reflect a preference for open areas. By contrast, both resident and migratory deer in Shiriuchi selected cropland closer to the forest edge; furthermore, migratory deer selected grassland habitats closer to the forest edge and cropland, probably as a tactic to avoid humans. Compared to the deer in Mount Esan, sika deer in Shiriuchi showed a preference for open foraging areas near to forest edge. As Mount Esan is part of the Prefectural Natural Park, hunting is banned in the proximity of this area; thus, lower hunting pressure could be the best explanation to the less utilization to the forest edge habitat that closer to open habitat such as grassland and cropland area. Moreover, Shiriuchi consists of larger cropland areas and human settlements/towns, which tends to lead to more hunting pressure and human interference.

The differences in land cover features between Mount Esan and Shiriuchi may also affect the behaviour of sika deer in selecting a habitat. Within the home range of sika deer in Mount Esan, most of the patches of cropland are surrounded by grassland, which forces the deer to travel away from the forest edge. Meanwhile, in Shiriuchi, the large cropland covers are located adjacent to the forest, such that the deer can use both the open habitat and forest cover.

Hokkaido receives greater snowfall than other regions of Japan. Sika deer have adapted accordingly. Compared to Shiriuchi, the deepest mean snowfall in Mount Esan in 2016, 2017, and 2018 was 43, 26, and 71 cm, respectively (Hakodate Meteorological Weather, Japan Meteorological Agency Station), whereas Shiriuchi received totals of 112, 90, and 155 cm (Senken Meteorological Weather Station, Japan Meteorological Agency). Thus, sika deer in Shiriuchi were exposed to deeper snow than those in Mount Esan. In general, during winter, the habitat selection of sika deer in southern Hokkaido suggests that forest edge with an aspect facing the south, a low elevation, and away from riverine areas is important during winter in both Mount Esan and Shiriuchi. Although sika deer showed less selection closer to the river, the importance of water resources in winter could be a factor. However, limitations in the resolution of river distribution data prevented identification of small streams in the study area. The selection of steeper slopes was observed in Mount Esan resident deer and Shiriuchi migratory deer. The selection of south-facing aspects, lower elevations, and steep slopes by ungulates may be related to less snow cover (Poole and Mowat 2005). In studies of sika deer in eastern Hokkaido (Igota et al. 2004) and sitka blacked-tailed deer in southern Alaska, United States (Pepin et al. 2008), both a low elevation and south aspect were selected for wintering. Southing behaviour by ungulate species, particularly in temperate regions, is a thermoregulation response in winter (Schmidt 1993). Other studies have suggested that southern slopes are more suitable wintering grounds for deer as they tend to have less snow cover than northern slopes, due to the greater amount of sunlight received (Borkowski et al. 1996, Sakuragi et al. 2003, Gilbert et al. 2017, Bojarska et al. 2020). Furthermore, less snow cover allows easier access to food. Habitats with steep slopes also play an important role in habitat selection, as snow tends to accumulate more on flat areas. For example, mule deer (Serrouya and D’Eon 2008) and mountain goat *Oreamnos americanus* (Lowrey et al. 2018) tend to select steeper slopes during winter in mountainous ecosystems. In eastern Hokkaido, sika deer select coniferous forest in winter (Sakuragi et al. 2003), which corresponds to the resident deer in Mount Esan and migratory deer in Shiriuchi in the present study. By contrast, coniferous forest was less important to resident deer in Shiriuchi. Overall, the predominant effects of snow cover are mediated by vegetation in eastern Hokkaido, which is mainly flat, whereas they are more influenced by topographic factors (elevation, slope, and south-facing aspect) in southern Hokkaido. The selection of all deer closer to the forest edge during winter may be related to the forest edge being closer to coastal cliffs, where the habitat is more exposed to the ocean. We documented new findings on the habitat selection of sika deer for wintering closer to coastal cliff environments.

Our results emphasize that the winter home range of sika deer in Mount Esan and Shiriuchi is centred on mountains closer to coastal areas. Coastal cliffs with steep slopes that face towards the south may be covered by less snow than is intact forest. Furthermore, the strong sea breeze on the coastal side reduces snow cover, setting up conditions preferred by sika deer for wintering. Kaji et al. (2004) reported similar findings in Cape Shiretoko in north-eastern Hokkaido. Therefore, the current study confirms that sika deer in southern Hokkaido select habitats depending on the landscape features in both summer and winter, but the presence of hunting or human interference also plays a role.

3.6 Management implications

Our study demonstrates that female sika deer in southern Hokkaido modify their preferred habitat by season, mainly due to resource availability in summer and topographic factors in winter. All studied deer had a smaller home range in summer than in winter, due to sufficient resources in summer but increased searching for resources in winter. Moreover, active croplands and natural grasslands offer a variety of resources to sika deer in summer. Hunting may lead to deer selecting habitats close to the forest edge. It is recommended that management efforts to control the sika deer population, such as regulated hunting activity, focus on areas closer to forest edges and open areas such as crop lands and natural grasslands. Further well-planned, regulated hunting in the proximity of the boundary of

Prefectural National Park is also suggested, as sika deer may travel outside the protection area when seeking various resources. In contrast, during winter, when food is limited, topographic factors such as low elevation, steep slope, and a south-facing aspect should be emphasized. Such features are located closer to forest edges near coastal cliffs. Hence, we recommend management efforts in coastal cliff regions.

Appendices

Table 3.5. Candidate models for resident and migratory deer to predict habitat selection in summer and winter in Mount Esan and Shiriuchi.

No	Candidate models	AIC	Weight
	Mount Esan–Resident deer		
	Summer:		
1.	Conif + grass + d_foredge + d_crop + river + *d_foredge* × *grass* + *d_foredge* × *d_crop* + *grass* × *d_crop*	29,706.0	1
2.	Conif + grass + d_foredge + crop + river + *grass* × *d_crop*	29,755.0	0
3.	Conif + grass + d_foredge + d_crop + river + *d_foredge* × *grass*	29,782.8	0
4.	Conif + grass + d_foredge + d_crop + river + *grass* × *d_crop*	29,786.5	0
5.	Conif + grass + d_foredge + crop + river	29,809.6	0
	Winter:		
1.	decid + conif + d_foredge + south + slope + elev + d_river	26,942.3	1
2.	decid + conif + d_foredge	28,114.9	0
3.	south + slope + elev	27,491.5	0
4.	decid + conif + d_foredge + south + slope + elev	27,188.7	0
	Shiriuchi–Resident deer		
	Summer:		
1.	Conif + grass + d_foredge + crop + river + *d_foredge* × *grass* + *d_foredge* × *d_crop* + *grass* × *d_crop*	17,003.1	1
2.	Conif + grass + d_foredge + crop + river + *d_foredge* × *d_crop*	17,015.1	0
3.	Conif + grass + d_foredge + crop + river + *d_foredge* × *grass*	18,632.6	0
4.	Conif + grass + d_foredge + crop + river	18,633.4	0
5.	Conif + grass + d_foredge + crop + river + *grass* × *d_crop*	18,635.1	0
	Winter:		
1.	Conif + grass + d_foredge + river + road + south + slope + elev	15,365.5	1
2.	Conif + grass + d_foredge	17,241.2	0
3.	south + slope + elev	15,522.7	0
4.	Conif + grass + d_foredge + south + slope + elev	15,428.3	0

	Shiriuchi–Migratory deer		
	Summer:		
1.	Conif + grass + d_foredge + crop + road + *d_foredge* × *grass* + *d_foredge* × *d_crop* + *grass* × *d_crop*	41,548.9	1
2.	Conif + grass + d_foredge + crop + road + *d_foredge* × *d_crop*	41,583.9	0
3.	Conif + grass + d_foredge + crop + road + *grass* × *d_crop*	41,781.2	0
4.	Conif + grass + d_foredge + crop + road + *d_foredge* × *grass*	41,782.6	0
5.	Conif + grass + d_foredge + crop + road	41,804.7	0
	Winter:		
1.	Conif + grass + d_foredge + river + south + slope + elev	28,564.4	1
2.	Conif + grass + d_foredge	33,868.8	0
3.	south + slope + elev	33,179.9	0
4.	Conif + grass + d_foredge + south + slope + elev	31,413.8	0

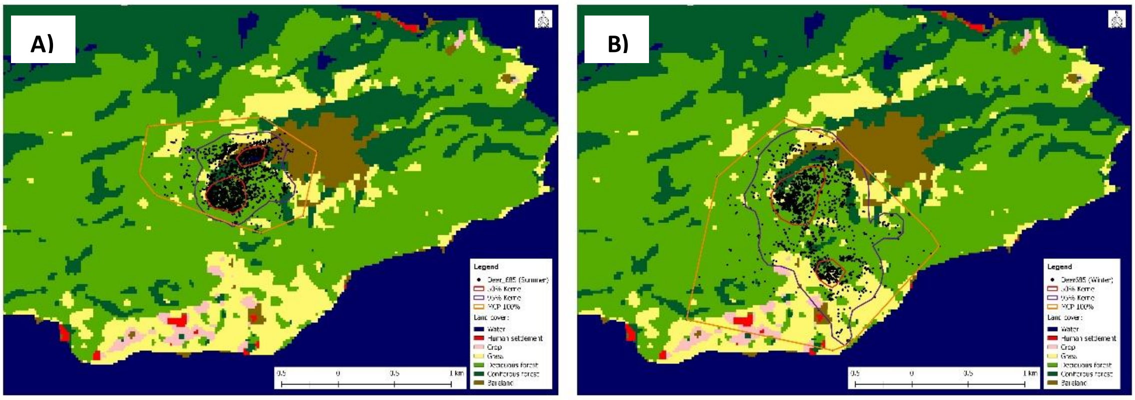

Figure 3.6. Distribution of GPS-collared resident sika deer in **A)** summer and **B)** winter in Mount Esan.

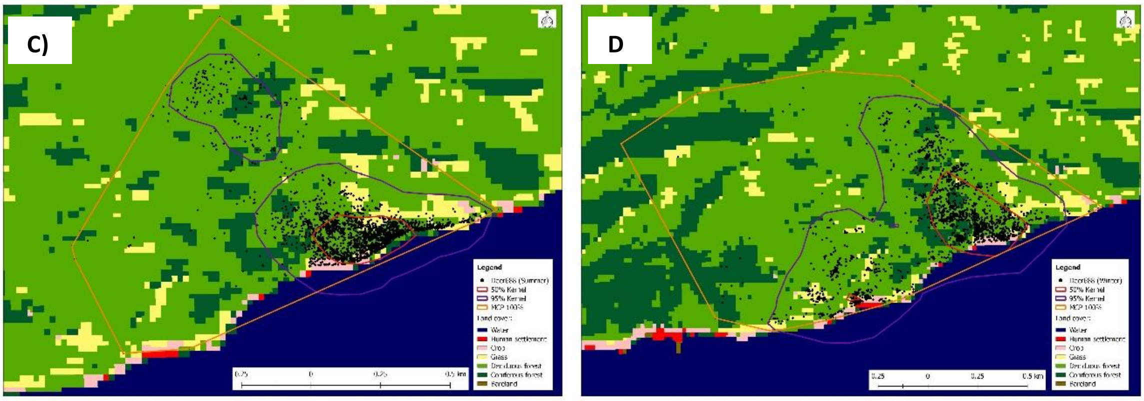

Figure 3.7. Distribution of GPS-collared resident deer in **C)** summer and **D)** winter in Shiriuchi.

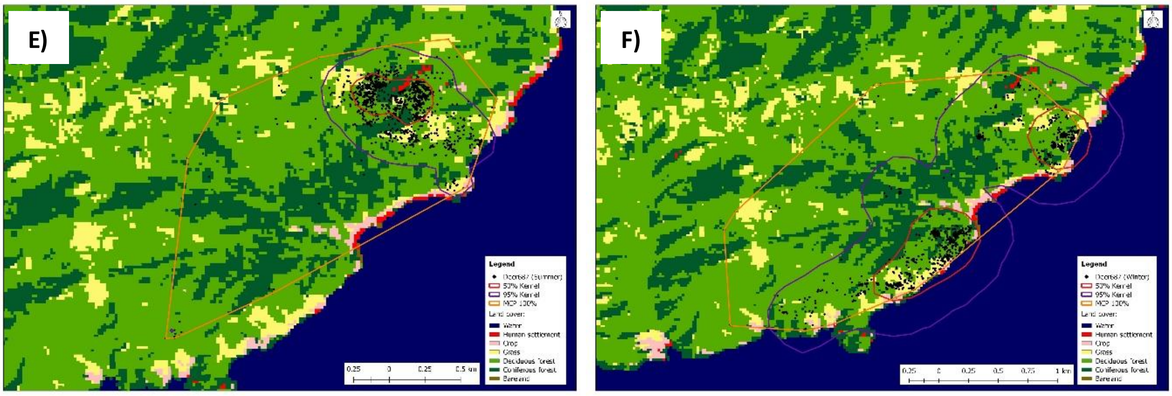

Figure 3.8. Distribution of GPS-collared migratory deer in **E)** summer and **F)** winter in Shiriuchi.

Chapter 4

Patterns of seasonal habitat selection of sika deer *Cervus nippon* on the largest wetland in Japan, Kushiro-Shitsugen National Park, Hokkaido

4.1 Abstract

Our study presented the first study on habitat selection by sika deer on the largest wetland in Japan, Kushiro Shitsugen National Park located in Hokkaido. The population was the results of population expansion from Shiranuka Hills. At least 30 individuals of female sika deer were monitored by using GPS-collared between 2014 to 2017. We aimed in assessing on the home range and core area as well as investigated on the seasonal habitat selection by sika deer population within the wetland. Kernel density (KDE) results that both resident and migratory deer shows smaller core area as well as home range size in summer compared to winter. However, only seasonal difference in core area and home range of resident deer was significant. The habitat selection was analysed by using generalized linear mixed model (GLMM) with logit link function. Results revealed that both migratory and resident deer selected on coniferous forest, grassland, closer to road, southing and flat habitat in summer. In winter, closer to forest edge and agriculture as well as farther from road were the important habitat selected by both migratory and resident deer. We also observed on shifting in habitat selection from away to forest edge, closer to road and southing in summer to less selected in winter by migratory deer, while resident deer remained their selection in both seasons except on the distance to agriculture land. We suggested on the replacement of pasture grass species planted along side of the embankment within the wetland to unfavourable natural plant to sika deer.

KEYWORDS sika deer, seasonal, home range, habitat selection, wetland

4.2 Introduction

Kushiro Wetland is the largest wetland in Japan. It is the protected basin area that inhabited by diverse of wetland vegetation including the endemic and endangered plant species. Dense population of deer within the wetland leads to disturbance on natural vegetation especially the vegetation species that only occurred in the wetland, effect from overgrazing and trampling on the vegetation. Moreover, gravel road that served as an embankment constructed within the wetland area were planted with artificial grass i.e., pasture grass species along the roadside which attracted the deer for grazing. Both summer and winter home-range of all collared deer in the study was centred in the wetland area, while only migratory deer travel outside from the wetland to the open pasture area at the east of the wetland. Kaji et al. (2004) reported the alteration of vegetation species in Shiretoko National Park due to over-grazing by sika deer, where the assessable browse species in winter decline from 13 species in 1987 to only 3 species in 1999. Thus, effective management on the abundance sika deer act as an important role to prevent further decline that leads to extinction of the vegetation species.

Sika deer in eastern Hokkaido was originated from the expansion Akan subpopulation (Kaji et al. 2000). In response towards the increasing human-wildlife conflicts related to disturbance in forestry resources i.e., national parks as well as agricultural activities i.e., crops and pasture, various study was attempted to find out an effective management dealing with those conflicts occurring in eastern Hokkaido. The eastern part of Hokkaido is not only an important conservation area of wetland, yet it is also the important area for the largest agricultural activity in regard to pasture for farming. Previous study conducted at eastern Hokkaido focusing on the sika deer population in Shiranuka Hills such as documentation of habitat selection (Sakuragi et al. 2003), dietary quality (Sakuragi et al. 2003), seasonal migration patterns (Igota et al. 2004) and describing the sika deer food habits (Campos-Arceiz and Takatsuki, 2005). The food habit and nutritional status of sika deer in Ashoro and Onbetsu (Uno et al, 2006) as well as evaluating the relative density indices in 40 municipalities in eastern Hokkaido to aids on population management were also well documented. Though there is various study focusing on sika deer population in eastern Hokkaido, no studies have yet assessed on the habitat selection by sika deer within the Kushiro Wetland. The recent study on sika deer population within the wetland was conducted by Takafumi et al. (2017) on the seasonal migration patterns.

Hence, our study was designed to assess the habitat selection by sika deer in Kushiro Wetland. Two objectives were generated in following of the study aim i.e., 1) to assess the patterns of seasonal home-range of sika deer and 2) to describe the seasonal habitat selection by sika deer at the home-range scale.

4.3 Methodology

Study Area

The GPS-collar study was conducted in Kushiro Wetland located in the east part of Hokkaido, Japan (Figure 4.1). Kushiro wetland is the largest wetland in Japan covering approximately 190 km^2, which the watershed encompasses of 2,500 km^2. The area was registered as a Ramsar site in 1980 and designated as national park few years later (Ministry of Environment, 2019). The wetland area was covered by Japanese Alder *Alnus japonica*, reeds *Phragmites australis*, bogs *Sphagnum*, sedge i.e., *Carex angustinowiczii* and *C. caespitosa*, *Fraxinus mandshurica* var. *japonica* including *Spiraea salicifolia* (Nakamura et al. 2002, Tsuji et al. 1991). An embankment for flood prevention was constructed along the Shin-Kushiro River within the wetland and planted with pasture grass species alongside. At the south area of the wetland located Kushiro town towards coastal side. Towards the eastern area of Kushiro wetland was the open large agricultural activities planting on pastures, with the Japanese Larch *Larix leptolepsis* forest plantation. Some of the Japanese Larch trees planted between the pastureland that also serve as a shelter belt for the sea breeze from the Pacific Ocean and winter blizzard. The mean total precipitation was 1,290 mm, mean daily average temperature was 6°C and mean daily total maximum snowfall was 30.5 cm between 2014 to 2017.

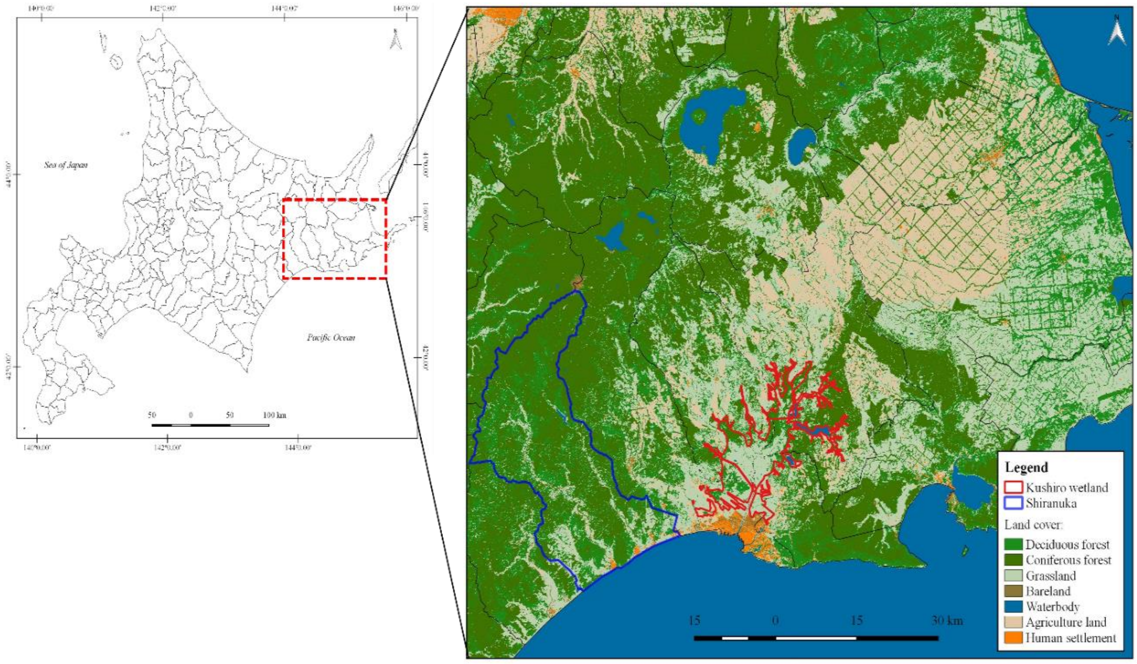

Figure 4.1: The location of GPS-study area in Kushiro Wetland located in the east part of Hokkaido, Japan.

Global positioning system (GPS) – radio collars

The habitat model was built using GPS-collar (IridiumTrackM2D, LOTEK) database provided by the Ministry of Environment (MOE) and EnVision Group, containing 118,937 locations of 30 female sika deer. Capturing sites in Kushiro wetland includes three area i.e., Kottaro (north), Takkobu (east) and right embankment (Ugan) in the southwest of the wetland area (Figure 4.2). Deer captured in Takkobu Lake (Figure 4.2B) were monitored between 2014 – 2016 while deer captured in both Kottaro (Figure 4.2C) and the right embankment (Ugan) (Figure 4.2A) were monitored between 2015 – 2017. GPS points were programmed to record eight locations with 3 hours of interval.

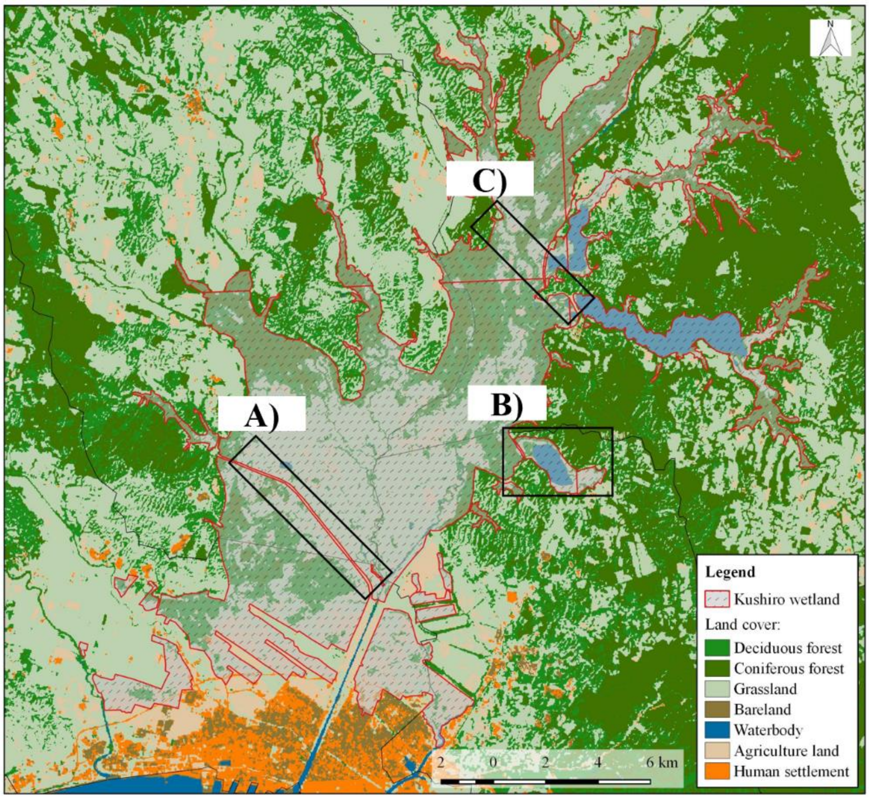

Figure 4.2: The location of deer capturing area A) the embankment, B) Takkobu and C) Kottaro that located in the Kushiro wetland.

The fix success rate of GPS-collar data was calculated as the number successful fix divided by the number of attempts. To assess the seasonal home-range and habitat selection, summer data were classified between June to September and winter data between January to March by referring to the seasonal classification by Uno et al. (2010). Deer was analysed separately according to migration and resident deer as both deer exposed the differences in home-range behaviour. The individuals exposed overlapping core home-range in summer and winter were classified as resident deer, while deer travelling out-side from winter home-range in summer were classified as migratory deer (Takafumi et al. 2017). For the present dataset, 18 deer are resident and 12 are migratory.

Landscape variables

To access the habitat selection by sika deer, 11 variables were recorded which includes the characteristics of land cover, topography and distance to covariates (Table 4.1). Land use data were collected from the High-Resolution Land Used and Land Cover map (HRLULC) from the Japan Aerospace Exploration Agency (JAXA, Ver.18.03 and Ver.21.03) at 30m^2 resolution. Land cover classes were classified into five cover types: deciduous forest, coniferous forest, natural grassland (included bare land or abandoned land), agriculture land (including pasture, crops, paddy field) and human settlement. The distance of sika deer GPS points from agriculture, human settlement, forest edge, river and road were measured by using Euclidean distance, analysed in the Spatial Analyst tools.

Topographic variables such as elevation and slope angle and south aspect were derived from digital elevation model (DEM) provided by Japan Aerospace Exploration Agency (JAXA). These variables were selected to find out their importance in habitat selection during winter (Sawyer et al. 2006, Shanley et al. 2021). All raster extent were standardized to 10m^2 resolution. Geographic Information System (GIS) analysis were conducted in ArcMap (Ver. 10.7.1). Recorded candidate variables were summarized as Table 4.1.

Table 4.1: Variable recorded from each sika deer individual according to the GPS points.

Variables	Code	Type	Unit
Land cover:		Binary	NA
Deciduous forest	decid		

Coniferous forest	conif		
Natural grassland	grass		
Distance to crop	d_crop	Continuous	Metre (m)
Distance to human settlement	d_human		
Distance to forest edge	d_foredge		
Distance to river	d_river		
Distance to road	d_road		
Topography:			
Elevation a.s.l	elev		
Slope angle	slope		Degree (°)
Aspect-south	south	Binary	NA

Data analysis

To define the study area prior to analysis, 100% of minimum convex polygon (MCP) was analysed for all deer locations. The 95% of bivariate kernel density (KDE) was calculated to generate the area frequently used by deer, while 50% KDE was calculated to define the core home-range habitat used by sika deer. The home-range analysis was conducted with "*adehabitHR*" package in R statistical software (Ver.4.0.3, R Core Team 2020). Since the data did not meet the assumptions of normality, the Wilcoxon's signed ranked test was used to compare the paired values of summer and winter core area as well as home range size of sika deer (resident and migration).

The evaluation of resource selection function (RSF) framework was followed by the third-order of selection (Johnson 1980), where variation of logistic regression was used to approximate the relative probability of deer selection at the home-range scale (Manley et al. 2002). To quantify the habitat selection of sika deer at home-range scale, RSF models were built by comparing the proportions of observed GPS point of deer individual to the random location (Manly et al. 2002). The observed GPS points was derived as "*used*" and random location as "*available*" points. The "*available*" points for each deer were generated within the 100% of minimum convex polygon (MCP). The probability of selection by sika deer was calculated as:

$$\boldsymbol{w(x)} = exp\ (\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + ... + \beta_{[} x_p)$$

where w(x) is the probability of RSF, x_1 are the predictor variables and β_1 are the corresponding coefficients (Manley et al. 2002).

Generalized Linear Mixed Model (GLMM) with logit link was used to fit the value of RSF. Random effect was assigned for each deer individual. Prior to the model building, collinearity between variables were tested with Pearson's correlation test to exclude paired variables with $|r|>0.60$ from being in the same model. Candidate models were designed for summer and winter seasons based on generated hypothesis that:

(1) sika deer selected area with various food resources availability i.e., active agriculture lands, natural grassland and forest edge during summer,

(2) while in order to respond towards snow cover in harsh winter condition coniferous forest is the important habitat features including topographic factors i.e., lower elevation, steep slope and aspect facing to south areas.

The best model was selected by the lowest AIC value, where parameter estimates and confidence interval (CI, 95% confidence limit) were used to explain the variables from best model. The significant influence occurred when zero was excluded between the confidence intervals. GLMM was performed with the "*lme4*" package using R statistical software (Ver.4.0.3, R Core Team, 2020).

4.4 Results

Sika deer home-range size

A total of 81,762 locations of 30 female sika deer were used to access the home-range and habitat selection patterns in Kushiro Wetland. Analysis was separated seasonally into resident and migratory deer. The total GPS-collar fix success rate for all deer was 97.7%. Figure 4.3 shows the comparisons of summer and winter core area and home-range between resident and migratory deer. Compared to winter, resident deer shows significantly smaller core area ($Z = -3.68, n=18, p=0.0002$) and home range ($Z= -3.68, n=18, p=0.0002$) in summer. Migration deer also shows the similar patterns of smaller core area ($Z = -1.412, n=12, p=0.1579$) and home range ($Z = -1.33, n=12, p=0.1823$) in summer compared to winter but the results was insignificant.

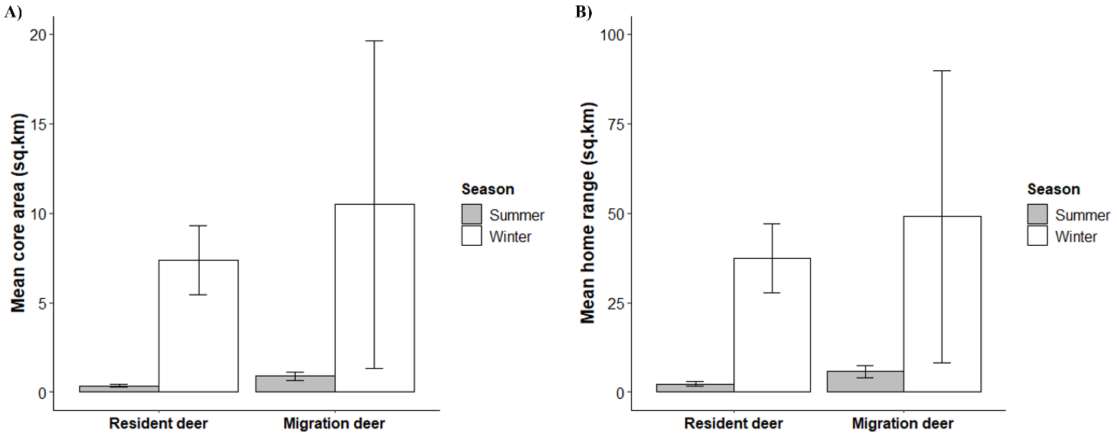

Figure 4.3: The comparisons of seasonal mean ± SE home-range size (km^2) of resident and migratory sika deer with A) 50% core area and B) 95% home-range estimated by Kernel density.

Sika deer habitat selection

The habitat selection model was built for 30 individuals of sika deer in Kushiro Wetland for migratory (Table 4.2) and resident deer (Table 4.3) in summer and winter. Overall, distance to human parameters was excluded in all models due to collinearity between parameters. In the resident deer final model for both summer and winter, deciduous forest was excluded, while elevation and slope were excluded from the summer and winter model respectively. On the other hand, elevation was excluded from migration deer summer model, whereas both deciduous and coniferous forest and slope were excluded in the migration deer winter model.

The final model for both resident and migratory deer in summer indicates the selection on coniferous forest, natural grassland, closer to road, south aspect and lower slope angle. The result also indicates that migratory deer selected more on habitat away from forest edge and river and closer to agriculture compared to resident deer in summer. In winter, resident and migratory deer selected closer distance to forest edge and agriculture as well as high elevation as important habitat. Migratory deer increase selection away from river and road while less selected on south aspect compared to resident deer during winter.

Figure 4.4 and Figure 4.5 shows the seasonal probability selection by resident deer and migratory deer respectively to the distance from A) forest edge, B) agriculture, C) river and D) road. In resident deer, probability of selection at distance to covariates was varied. Selection probability on the distance to agriculture, river and road (Figure 4.4B, Figure 4.4C, Figure 4.4D) appears to shift at distance 1,200m≤. The probability of selection on forest edge habitat by resident deer on summer and winter decrease at 200m≤ distance (Figure 4.4A). On the other hand, selection probability of migratory deer in summer to the distance to forest edge, agriculture, river and road was higher than winter (Figure 4.5) There are no obvious differences in the probability of selection on slope across all angles for both resident (Figure 4.6A) and migratory (Figure 4.6B) deer in summer. Both deer increases the selection on high elevation in winter up to only 100m a.s.l (Figure 4.7).

Table 4.2: Parameter estimates of the top-ranking GLMM model for habitat selection of female resident deer during summer and winter in Kushiro Wetland. Each variable is presented with the estimated coefficient and 95% confidence interval (CI).

			Summer			**Winter**	
No.		**Estimate**	**Upper CI**	**Lower CI**	**Estimate**	**Upper CI**	**Lower CI**
	Intercept	-0.669	-0.404	-0.934	-1.095	-0.943	-1.247
1.	Deciduous forest						
2.	Coniferous forest	0.068	0.106	0.030	0.313	0.343	0.284
3.	Grass	0.176	0.200	0.153	0.097	0.118	0.076
4.	Distance to forest edge	-0.212	-0.202	-0.223	-0.171	-0.162	-0.180
5.	Distance to agriculture	0.121	0.144	0.099	-0.115	-0.101	-0.129
6.	Distance to river	-0.540	-0.513	-0.566	-0.044	-0.034	-0.055
7.	Distance to road	-1.097	-1.065	-1.128	-0.493	-0.478	-0.508
8.	Elevation				0.219	0.229	0.209
9.	Aspect – south	0.056	0.074	0.038	0.101	0.119	0.084
10.	Slope	-0.039	-0.030	-0.049			

Table 4.3: Parameter estimates of the top-ranking GLMM model for habitat selection of female migratory deer during summer and winter in Kushiro Wetland. Each variable is presented with the estimated coefficient and 95% confidence interval (CI).

			Summer			**Winter**	
No.		**Estimate**	**Upper CI**	**Lower CI**	**Estimate**	**Upper CI**	**Lower CI**
	Intercept	-1.728	-1.435	-2.021	-1.112	-0.910	-1.313
1.	Deciduous forest	0.983	1.030	0.936			
2.	Coniferous forest	1.238	1.283	1.193			
3.	Grass	0.925	0.969	0.880	-0.031	-0.008	-0.055
4.	Distance to forest edge	0.100	0.112	0.088	-0.668	-0.652	-0.684
5.	Distance to agriculture	-0.192	-0.168	-0.216	-0.196	-0.177	-0.216
6.	Distance to river	0.520	0.555	0.484	0.077	0.094	0.061
7.	Distance to road	-1.186	-1.160	-1.213	0.113	0.126	0.101
8.	Elevation				0.831	0.863	0.799
9.	Aspect – south	0.143	0.167	0.120	-0.016	-0.015	-0.017
10.	Slope	-0.063	-0.050	-0.076			

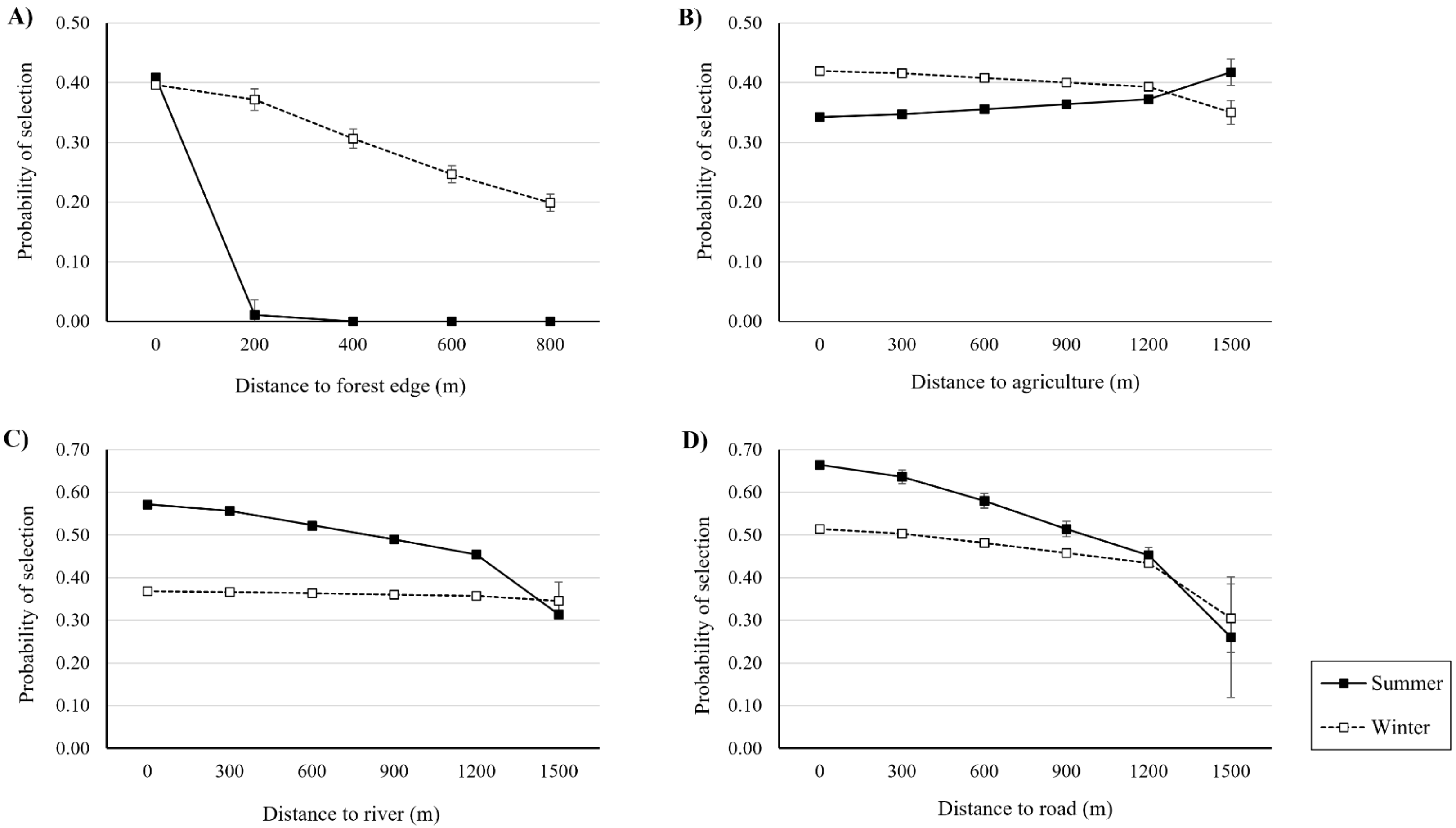

Figure 4.4: The changes in probability of selection by resident deer in summer and winter with the increasing distance to A) forest edge, B) agriculture, C) river and D) road. Dots representing the mean probability at distance (mean ± SE). Selection probability was calculated by changing the distance values with all other variables held at the mean values.

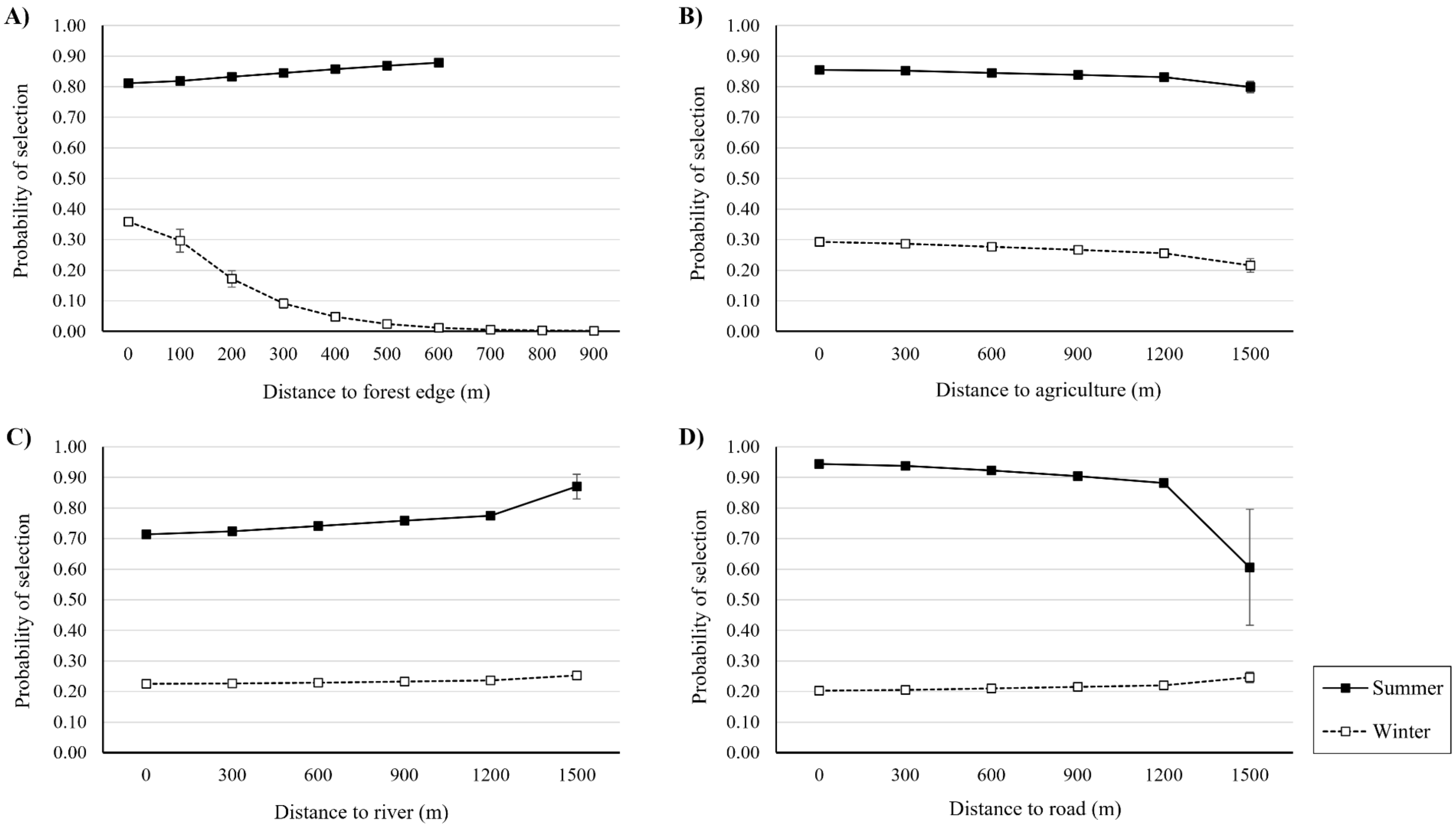

Figure 4.5: The changes in probability of selection by migratory deer in summer and winter with the increasing distance to A) forest edge, B) agriculture, C) river and D) road. Dots representing the mean probability at distance (mean ± SE). Selection probability was calculated by changing the distance values with all other variables held at the mean values.

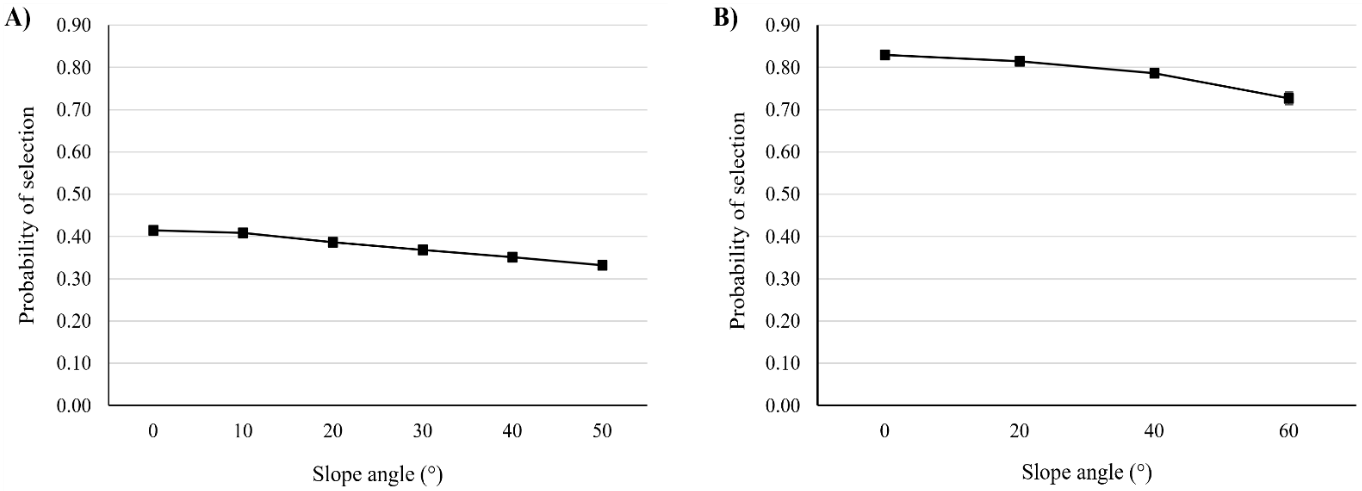

Figure 4.6: The changes in probability of selection by A) resident deer and B) migratory deer in summer with the increasing slope angle. Dots representing the mean probability of slope angle (mean ± SE). Selection probability was calculated by changing the angle values with all other variables held at the mean values.

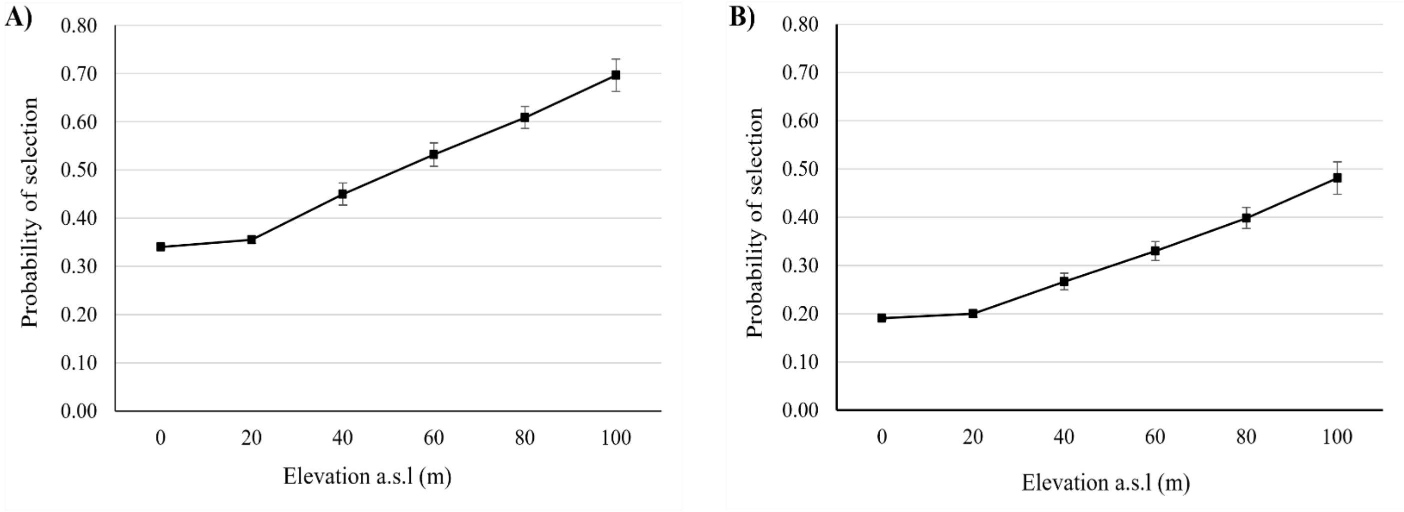

Figure 4.7: The changes in probability of selection by A) resident deer and B) migratory deer in winter with the increasing elevation. Dots representing the mean probability of elevation (mean ± SE). Selection probability was calculated by changing the elevation values with all other variables held at the mean values.

4.5 Discussion

The present study documented the home-range and habitat selection patterns of 30 radio-collared female sika deer that used Kushiro wetland for wintering, the expanded sub-population from Akan. Both resident and migratory deer show smaller summer core area and home range than in winter. The home-range patterns of resident deer in the present study were comparable to the previous study by Igota et al. (2004) that reported smaller home-range in summer than winter from deer population from the adjacent area of Shiranuka Hills. The habitat quality within the home-range can be the best explanation to the home-range size of an ungulate, as all resources needed are found within the homer-range (Van Dyke et al. 1995). The home range patterns reported by Reinecke et al. (2014) supported our findings that smaller home range of red deer in the habitat with substantial supplementary feeding, but larger home range in a fragmented habitat where supplementary feeding is scarce. Small home-range of ungulate in summer indicate sufficient of resource availability i.e., forest cover, grasses, agricultural crops (Borkowski and Furubayashi 1998), while large winter home-range indicating the adaptation to the environment to find a suitable habitat during harsh climate i.e., deep snow and low temperature as well as in searching for available graze (Brinkman et al. 2005). In the present study, the heterogeneity of land cover i.e., open natural grassland, pasture, conifer and deciduous forest could lead to the small summer home range. Meanwhile in winter, limited graze availability and weather condition i.e., snow cover, strong wind, temperature forces the deer to increase the locomotion.

We documented a variation in the habitat selection of sika deer population between seasons. In summer, coniferous forest, natural grassland, closer to road, south aspect and flat area were the important habitat for both resident and migratory deer. Selection on natural grassland habitat supported the findings by Campos-Arceiz and Takatsuki (2005) that found a high percentage of graminoids in the faecal analysis of sika deer. An open native grassland offers foraging sites for ungulate with less human interference (Jakes et al. 2020) compared to the agricultural land (Allen et al. 2014). Additionally, the selection near to road and flat area might related to the natural grassland habitat that closer to road in the study area. Within the wetland, an embankment was built for flood prevention were planted with pasture grass species alongside which attracted the deer on the area. Thus, sika deer in our study favours the grazing area as there is less human interference and hunting prohibited in the wetland compared to the agricultural pasture outside of the wetland. Moreover, we reported evidence that the grazing site within the wetland were favoured more by the resident deer than migration deer. In summer, migration deer selected the habitat much closer to the agriculture land compared to resident deer. The extensive agricultural area at the east of Kushiro wetland attracts migratory deer to travel outside of the wetland habitat for more favourable resources. Furthermore, the open and flat topographic condition towards the eastern Hokkaido eases the migration movement of deer to travel at farther distance in summer. Takafumi et al. (2017) reported on the average travel distance by migration deer from the studied population was 26.2km in spring and 24.5km in autumn, while for the Takkobu migrant could travel up to 39.4km.

Although migration deer travelled at farther distance could benefits variety of food resources from the agricultural activities, previous study by Sakuragi at al. (2003) reported that sika deer population from Shiranuka Hills that migrated to the agriculture area in the east consumed similar quality of diet to the resident deer, which was due to the hunting activities that prevent deer to spent most of the time grazing on the agriculture field, but on the plantation forest (Japanese Larch, *Larix leptolepsis*). We documented evidence that migratory deer used very close distance to forest edge with less than 600m. This tree species was planted between the agricultural plantation that not only served as boundaries but as a shelter belt from the sea breeze from Pacific Ocean and blizzard in winter. Thus, sika deer returning between agriculture area and the plantation forest of Japanese Larch to avoid human interference and hunting in the agriculture area. Though the extensive area of agriculture land offers abundance of resources to the deer, still, sika deer could not fully gain benefit from it due to the hunting activities.

Compared to the other region in Hokkaido, eastern part received less snow fall in winter. We predicted that sika deer in our study area exposed different behaviour in selecting suitable habitat for wintering. Igota et al. (2004) suggested that snow depth, good quality of bamboo grasses and coniferous forest cover are the factors of migration for Shiranuka Hills deer to the wintering area. During winter in our study, both resident and migratory deer selected habitat closer to forest edge and agriculture land as well as high elevation. Selection on the habitat closer to agriculture in winter might be due to the wintering area closer to the agriculture patches surrounding the wetland habitat in the study area. Besides, wintering on the forest edge habitat could ease the movement to the open areas to find the available browse. In addition, the present of natural spring water at the bottom-hill surrounding Kushiro Wetland causes snow melt easily at the area and allows some vegetations to merge in winter. Hence, the habitat was favoured by sika deer due to less snow depth and ease the access to available browse. In term of topography, the preference on high elevation was only up to 100m a.s.l, which was still low and suitable for wintering. The population from Shiranuka Hills were also show selection on high elevation but limited to 400m a.s.l (Sakuragi et al. 2003), which was affected by the present of coniferous forest covers. As correspond to our findings, we documented on the selection on coniferous forest in both seasons for resident deer, while only evidence on summer for migratory deer. Coniferous forest covers play an important role as a shelter for the deer as it intercepts and hold snows from accumulating on the forest floor and reducing the windspeed especially during harsh winter (Serrouya and D'Eon 2008, Crawford 1984). The patterns of utilizing high elevation by sika deer were also documented on the sika deer in central Japan that affected by coniferous forest, south aspect and steep slope (Takii et al. 2012).

We also observed on the shifting of habitat selection by migratory deer from closer to forest edge and road as well as south aspect in summer to farther from road and less on south aspect in winter. Though south aspect might offer less snow covers due to more solar radiation in winter (Borkowski et al. 1996, Takii et al. 2012, Shanley et al. 2021), it might be less important factors for the deer population in this study due to the flat topographic factors of Kushiro wetland. On the other hand, resident deer remained the selection as in summer, except for the habitat closer to agriculture in winter. As described by Igota et al. (2004), resident or non-migratory deer adopted the resident strategy where wintering are possible on the summer habitat. Additionally, as correspond to our findings, most of the habitat characteristics within summer and winter home range were comparable. In addition, we observed the home-range of resident deer was centred within the wetland habitat in both summer and winter. The high utilization of deer in the wetland habitat could lead to the alteration on the vegetation species composition in the wetland. To note, tussock grass is one of the vegetation that occupied the wetland habitat, where Latham et al (2015) also observed the utilization of sika deer on the open habitat for tussock plant in New Zealand. Therefore, our study suggested for the management to regulate sika deer population within the wetland, most probably on the resident sika deer.

4.6 Management implications

Our study demonstrates that the sika deer population in Kushiro Wetland modify their selection on habitat seasonally in order to achieve the needs to benefits from resources availability and survivorship from hunter as well as dealing with winter conditions. We noted on the successful of culling program by Hokkaido Government to regulate deer population which results in less disturbances on the agricultural source (Sakuragi et al. 2002). Though hunting is possible with the permission from the Hokkaido Government and Ministry of Environment, the method was considered dangerous due to the flat topography of the wetland area. Hence, since hunting is totally prohibited in the national park and might be difficult on the wetland, the setting of enclosure-trap was suggested within the area especially on the embankment area. We also suggest on replacing the planted pasture along the embankment with unfavourable natural plant species for sika deer.

Appendices

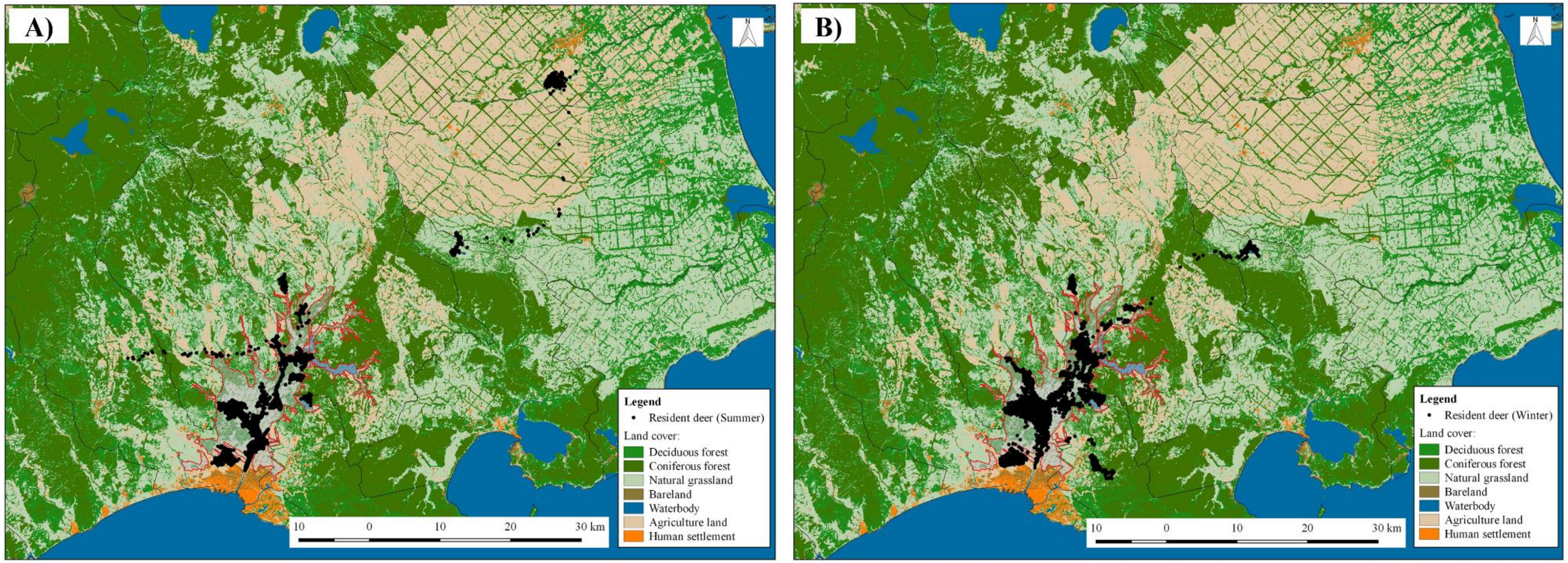

Figure 4.8: The distribution of resident deer GPS-collar in A) summer and B) winter located in eastern area of Hokkaido, Japan.

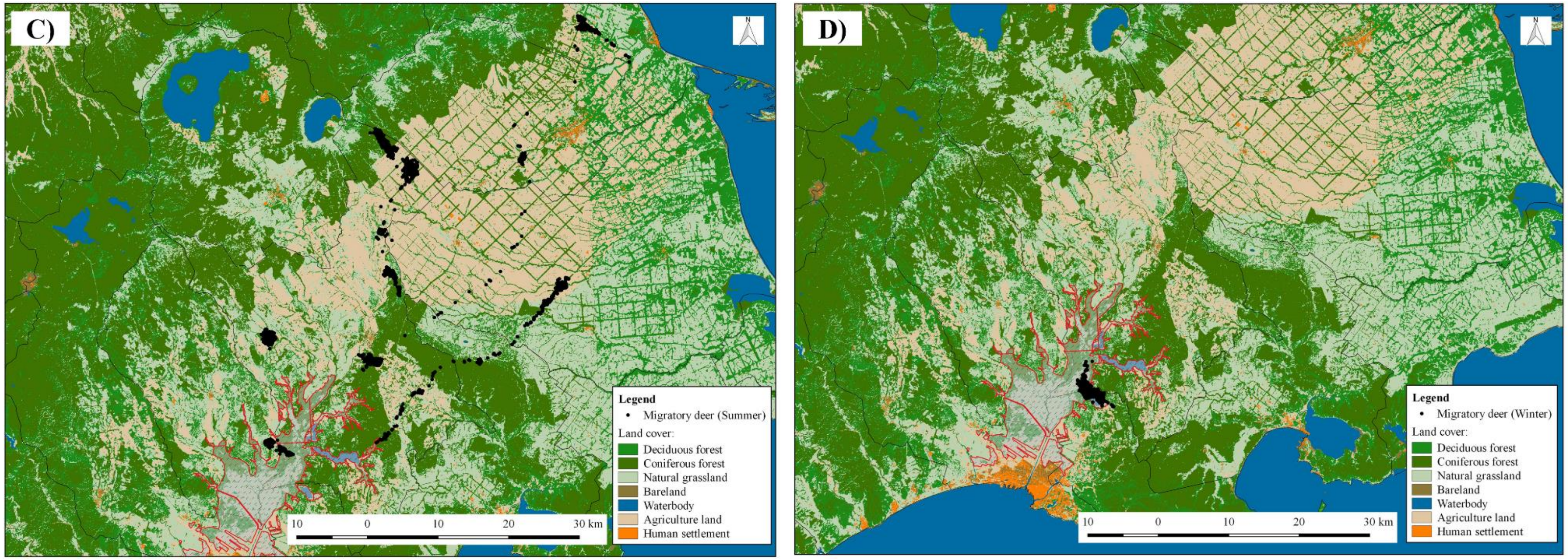

Figure 4.9: The distribution of migratory deer GPS-collar in A) summer and B) winter located in eastern area of Hokkaido, Japan.

Chapter 5:

General discussions

Overall, the thesis has answered all the objectives addressed in Chapter 2, Chapter 3 and Chapter 4. In Chapter 2, the study conducted in rehabilitated forest in the tropical rainforest of Malaysian, Borneo suggests that the forest still holds a hight conservation value of species diversity, particularly the medium-to-large mammals and birds. We had successfully documented 33 species from 14 families and 7 orders of medium-to-large mammals and birds, including 2 critically endangered, 5 endangered, 8 vulnerable and 6 near threatened species. We confirmed the presence of two charismatic species i.e., Bornean banteng *Bos javanicus* and Bornean orang utan, including 5 species of Felidae that occurred in Borneao i.e., Bornean Bay cat, clouded leopard, flat-headed cat, marbled cat and leopard cat. It was notably that the enrichment planting methods conducted in the study area have aided in the forest recovery in INIKEA. Species richness and composition shows no significant difference suggesting that most vertebrate species were able to utilize the habitat in the forest, as general forest structure are comparable between treatments and naturally recovered area. Though liberation technique could enhance the growth of the present natural tree species, we suggested to reduce the method as it reduces the food variation from the pioneer tree and climber species that grow after disturbance.

In the Chapter 3, the study focusing on the sika deer *Cervus nippon* population in southern Hokkaido. It was the first study conducted on the deer population in this district that was introduced on the area between 1980 and 1981, assessing the seasonal home range and habitat selection patterns. We found out that the core area and home range in winter was larger than the summer home range. Furthermore, the seasonal habitat selection of sika deer was varied between resident deer in Mount Esan and Shiriuchi as well as the migration deer in Shiriuchi. The variation in the preferences to open area i.e., grassland and cropland in summer was related to human interference i.e., hunting, while in winter the habitat selection was affected by topographic factors i.e., elevation, southing and slope angle in coping with the snow depth. We also reported on the new findings on the selection of habitat by sika deer closer to coastal cliff environment in winter.

In Chapter 4, the study focusing on the sika deer population located in the largest wetland in Japan, the Kushiro Shitsugen National Park in Hokkaido. The resident deer on the study area shows larger winter home range and core area than summer, while migratory deer show larger winter core area than summer but comparable winter and summer home range size. We reported that coniferous forest, natural grassland, closer to road south aspect and flat area were the important habitat selection by both resident and migratory deer in Kushiro wetland. On the other hand, in winter, both deer selected closer to forest edge and agriculture while away from road. It was also notable that migration deer shifted their habitat selection between summer and winter, whereas resident deer remained the selection seasonally except to the distance from agriculture. Most of the resident deer were noticed to utilize on the artificial grass planted along the embankment in the wetland. Hence, the study suggested to aim the management planning i.e., culling program on the embankment area.

5.1 Influence of modified habitat on wildlife

The empirical studies in the thesis have shown that wildlife species respond to habitat modification variously. It is undoubtedly that forest restoration on highly degraded forest improved the quality and biodiversity in which natural regeneration is almost impossible (Chapter 2). The enrichment planting techniques that applied to rehabilitate the degraded forest has successfully provide a suitable habitat to most of the documented wildlife in the study. Less intense rehabilitation work may retain much of the benefits in reducing the impact on remaining biodiversity (Edward et al. 2012), in the condition where major forest components still remain after disturbance (Chapter 2). Besides, the study case in Chapter 4 shows that the construction of embankment that planted with pasture grass species alongside has attracted the resident sika deer to utilize the area in both summer and winter. Thus, depending on the aim in the management of forest or wildlife, the selection of vegetation species to be planted on modified habitat should be carefully conducted as it could directly or indirectly affected on the ecosystem within the habitat.

5.2 Forestry management to enhance biodiversity conservation

A well-managed forest area is undoubtedly influence on the biodiversity composition which inhabited the forest. In the Chapter 2 we addressed on the important of rehabilitation efforts on highly degraded forest for the conservation of various endemic and endangered wildlife species that occurred in the area. Several previous study that focusing on other taxa such as birds (Ansell et al. 2011) and invertebrates (Edward et al. 2012) in rehabilitated forest reported the role of well-managed disturbed forest particularly to prevent further biodiversity loss. The sustainable forest management on commercial forest has proven the successful well-management with the records of 34 to 36 species of terrestrial vertebrates (Samejima et al. 2012, Samejima et al. 2013), which is almost correspond to the species recorded in Chapter 2 as well as other study on primary forest (Bernard et al. 2013, Bernard et al. 2014).

Besides, growing of plantation forest in Japan that replacing the natural forest cover had influence on a certain taxon. It was reported that species richness of longicorn beetles (Maeto et al. 2002) and birds (Ohno and Ishida 1997, Kawamura et al. 2021) was lower in plantation forest compared to old growth forest habitat. In contrast to the large mammals such as black bear *Ursus thibetanus* and sika deer *Cervus nippon*, both species seems to well-adapted on natural and plantation forest. Though Izumiyama and Shiraishi (2004) and Takahata et al. (2017) reported on the less use of black bear on coniferous plantation forest, decaying wood in the plantation forest supply food resources i.e., ant to the black bear (Yasue et al. 2015). The coniferous plantation forest is an important habitat for the sika deer during winter to hide from strong wind and deep snow cover (Sakuragi et al. 2002, Igota et al. 2004). In our results (Chapter 4), sika deer depends on coniferous plantation forest for shelter in winter as well as protection against hunter and human interference near to agriculture land. Thus, both remaining natural forest cover and altered or modified by human forest i.e., rehabilitated forest and plantation forest should be managed and conserve together to protect the biodiversity.

5.3 Wildlife management on threatened and overpopulation species

Throughout the chapters, it was notably that hunting pressure in Malaysia was higher compared to in Japan. The documentation of high number of species in Chapter 2 was also due to the area are fully protected forest (Class I Forest Reserve) where hunting is totally prohibited. However, Mohd. Azlan and Lading (2006) recorded a significantly low number of game animals i.e., bearded pig *Sus barbatus* and no exposure of sambar deer *Rusa unicolor* that might be due to illegal hunting as the forest area were surrounded by agriculture plantation, settlements and roads. Illegal hunting has been the major treats to most of wildlife species in Malaysia particularly the game animals such as bearded pig and sambar deer. Selective logging activity might only modestly affect the wildlife diversity (John 1992), yet the opening of some area for logging road ease the accessibility of hunter into the forest (Bennett and Robinson 2000). Thus, drastically decrease of some wildlife species in the tropical rainforest habitat was due to the high hunting pressure (Hannah et al. 1994, Bodmer et al. 1997).

A reverse scenario in Japan, regulated hunting is allowed to control the overabundance of sika deer population. This species causes severe damage on the agriculture plantation, forestry plantation as well as affected on the natural vegetation species due to over grazing (Kaji et a. 2004). In the Chapter 4 of the thesis, we noted that resident sika deer spent both of their summer and winter home range in the Kushiro Wetland, which is one of the important protected areas in Japan. The high density of deer in the wetland disturbed the vegetation species through over-grazing and trampling on the small vegetation. In term of the disturbance on agriculture land, several methods to prevent deer disturbance were applied including fencing and hunting. In Hokkaido, culling program by the government resulted in decreasing damage on agriculture resources (Sakuragi et al. 2002, Hokkaido Government 2002). Though hunting could be the most effective method in controlling population abundance, a well-regulated planning should be taken into account to prevent over hunting.

Hence, the reinforcement of hunting activity is an important measure to prevent more species to be extirpated from the habitat. Patrolling by the forest rangers in the ongoing logging concession area should be conducted frequently to prevent poaching. The policies in regard to the wildlife protection and the conservation of its habitat plays a vital role in contributing to the sustainability of biodiversity.

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