Seasonal and year-round use of the Ramsar-listed Kushiro Wetland by sika deer (*Cervus nippon yesoensis*)

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The sika deer (*Cervus nippon yesoensis*) population in the Ramsar-listed Kushiro Wetland has increased in recent years, and the Ministry of the Environment of Japan has decided to take measures to reduce the impact these sika deer are having on the ecosystem. However, their seasonal movement patterns, i.e., when and how the deer inhabit the wetland, remain unclear. Thus, we examined seasonal movement patterns and the population structure of sika deer in the Kushiro Wetland from 2013 to 2015 by analyzing GPS location data for 28 hinds captured at three sites in the wetland. Seasonal movement patterns were quantitatively classified as seasonal migration, dispersal, nomadic, resident, or atypical, and the degree of wetland utilization for each individual was estimated. The overlap areas of population-level home ranges among capture sites were calculated for both the entire year and for individual seasons. Our results showed that approximately one-third of the individuals moved into and out of the wetland during the year as either seasonal migrants or individuals with atypical movement. Some of the individuals migrated to farmland areas outside the wetland (the farthest being 64 km away). Half of the individuals inhabited the wetland all or most of the year, i.e., 81–100% of their annual home range was within the wetland area. The movement patterns of these deer were classified not only as resident but also as seasonal migration, dispersal, nomadic, and atypical. Even among individuals captured at the same site, various seasonal movement patterns were identified. Annual population-level home ranges showed little to no overlap, and seasonal population-level home ranges were completely segregated among capture sites. Individual deer used the wetland either seasonally or year-round, and some populations inhabiting the wetland had sub-populations with different seasonal movement patterns, which need to be considered to achieve more effective ecosystem management including deer management in the wetland.

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Abstract

The sika deer (*Cervus nippon yesoensis*) population in the Ramsar-listed Kushiro Wetland has increased in recent years, and the Ministry of the Environment of Japan has decided to take measures to reduce the impact these sika deer are having on the ecosystem. However, their seasonal movement patterns, i.e., when and how the deer inhabit the wetland, remain unclear. Thus, we examined seasonal movement patterns and the population structure of sika deer in the Kushiro Wetland from 2013 to 2015 by analyzing GPS location data for 28 hinds captured at three sites in the wetland. Seasonal movement patterns were quantitatively classified as seasonal migration, dispersal, nomadic, resident, or atypical, and the degree of wetland utilization for each individual was estimated. The overlap areas of population-level home ranges among capture sites were calculated for both the entire year and for individual seasons. Our results showed that approximately one-third of the individuals moved into and out of the wetland during the year as either seasonal migrants or individuals with atypical movement. Some of the individuals migrated to farmland areas outside the wetland (the farthest being 64 km away). Half of the individuals inhabited the wetland all or most of the year, i.e., 81–100% of their annual home range was within the wetland area. The movement patterns of these deer were classified not only as resident but also as seasonal migration, dispersal, nomadic, and atypical. Even among individuals captured at the same site, various seasonal movement patterns were identified. Annual population-level home ranges showed little to no overlap, and seasonal population-level home ranges were completely segregated among capture sites. Individual deer used the wetland either seasonally or year-round, and some populations inhabiting the wetland had sub-populations with different seasonal movement patterns, which need to be considered to achieve more effective ecosystem management including deer management in the wetland.

Introduction

Ungulates are known as keystone species that can cause substantial impacts to ecosystem processes and functions through the alteration of plant biomass and community composition (Rooney & Waller, 2003; Côte et al., 2004). In recent decades, numerous regions in the Northern Hemisphere have experienced increasing cervid populations and expansion of their distributions resulting in significant impacts to natural ecosystems (Côte et al., 2004). These impacts are observed not only in forest ecosystems but also wetland ecosystems such as has been seen with white-tailed deer (*Odocoileus virginianus*) in eastern North America (Pellerin, Huot & Côté, 2006), red deer (*Cervus elaphus*) in England (Welch & Scott, 1995), sika deer (*Cervus nippon*) in Japan (Takatsuki, 2009), and introduced sika deer in England (Hannaford, Pinn & Diaz, 2006). For instance, population growth of introduced sika deer in the Arne Saltmarsh, England, has decreased plant biomass and altered plant species composition ultimately resulting in the degradation of redshank (*Tringa tetanus*) habitat (Hannaford, Pinn & Diaz, 2006). Furthering our understanding of cervid ecology in wetland ecosystems is vital to conservation of these ecosystems.

In many ungulates, seasonal migratory and non-migratory individuals coexist within the same population (eg. Hebblewhite & Merrill, 2007; Bolger et al., 2008; Singh et al., 2012; White et al., 2014). While migration imposes an energy cost on individuals (Bolger et al., 2008; Chapman et al., 2011), there are also numerous benefits such as avoiding predation, gaining access to nutritious food resources, and reducing competition among individuals (Fryxell & Sinclair, 1988; Hebblewhite & Merrill, 2007; Hebblewhite, Merrill & McDermid, 2008; Mysterud et al., 2011; Bischof et al., 2012; White et al., 2014). Therefore, whether an individual migrates or not directly affects its fitness and ultimately the population (Hebblewhite & Merrill, 2011; White et al., 2014; Rolandsen et al., 2016). Ungulate migration can lead to spatiotemporal variation in population density (Nelson, 1998; Mysterud et al., 2011), and spatial variation in ungulate distribution creates spatial heterogeneity in the ecosystem through changes in plant diversity and composition, predator behavior, and nutrient cycling (via excreta and carcasses) (Bump, Peterson & Vucetich, 2009; Hurley et al., 2012; Murray, Webster & Bump, 2013). The variation of timing of ungulate browsing determines the response of plants to the browsing (Hester et al., 2006; Takafumi et al., 2015). Therefore, understanding how many individuals in a population migrate as well as the migration start and end points are valuable pieces of information not only for ungulate conservation and management (Bolger et al., 2008; Singh & Milner-Gulland, 2011; White et al., 2014), but also for better understanding of the ecosystem that they inhabit.

Currently, approximately 86% of all wetlands in Japan can be found in Hokkaido, the northern island of Japan, and the majority of wetland areas in Hokkaido are located in the eastern part of the island (Kobayashi, 2016). Sika deer (*Cervus nippon yesoensis*; from here on ‘deer’) populations in Hokkaido erupted after recovering from a population bottleneck in the 1950s and are having a serious impact on the natural vegetation, especially in eastern Hokkaido (Kaji et al., 2000; Matsuda et al., 2002). The Kushiro Wetland, located in eastern Hokkaido, is the largest wetland in Japan comprising 73 endangered plants and provides habitat for many endangered species such as the Red-crowned Crane (*Grus japonensis*) and the Japanese Huchen (*Hucho perryi*) (Ministry of the Environment, 2005). Kushiro Wetland is recognized as a valuable ecosystem and was listed as a Ramsar site in 1980. The main part of the wetland has been designated the Kushiro-shitsugen National Park and Wildlife Protection Area. Japanese law prohibits harvesting wildlife in the area, but deer hunting and pest control are permitted in surrounding areas. Previous studies have investigated deer population growth and its impact on the wetland. An aerial survey during winter here showed that the deer population had increased by approximately 2.5–2.9 times from 1994 to 2015 (Ministry of the Environment, 2017). Deer trails detected from aerial photographs in the wetland increased by 2.4 times from 1977 to 2004, and deer browsing, trampling, and mud bathing has disturbed the primary vegetation, such as the hummock and hollow, resulting in a shift to bare ground or novel plant communities (Fujita et al., 2012; Muramatsu & Fujita, 2015). On the basis of these circumstances, the Japanese Ministry of the Environment planned an ecosystem maintenance and recovery project to restore the Kushiro

Wetland ecosystem to its pre-Ramsar Site registration state, i.e., how it was in or before 1980, which was scarcely affected by deer, by reducing the impact of deer on the wetland ecosystem. Previous studies have reported the impacts of deer on vegetation in the Kushiro Wetland (Fujita et al., 2012; Muramatsu & Fujita, 2015; Inatomi et al., in press), and the deer distribution was surveyed only during the winter (Inatomi, Uno & Ueno, 2014; Ministry of the Environment, 2017). However, deer seasonal movement patterns and population structure, which are essential information for achieving more effective deer management, have not been thoroughly studied. If deer migrate outside the wetland, then the population dynamics of the deer and harvest pressure by humans around the wetland could affect the interactions between the deer and the ecosystem within the wetland. On the other hand, if the deer migrate to other areas within the boundaries of the wetland, it is reasonable to assume that the spatial distribution of the impact on the ecosystem varies seasonally. Moreover, if deer inhabiting the wetland consist of multiple populations or sub-populations with varying seasonal movement patterns, ecosystem managers must consider adapting their management strategies to correspond to each population and/or sub-population.

This study aimed to clarify the use patterns of the Kushiro wetland by deer and their population structure in the Kushiro Wetland. To this end, GPS location data for the deer were used to classify individual seasonal movement patterns, calculate overlapping home range area among the population-level home ranges, and compare degree of utilization of the wetland by individuals among capture sites and seasonal movement patterns. On the basis of these results, we discuss factors related to deer use patterns of the Kushiro wetland, how many deer populations and sub-populations inhabit the wetland, and the implications for ecosystem management and deer management in the wetland.

Methods and materials

Study area

The Kushiro Wetland (20 366 ha) is Japan's largest wetland, most of which makes up Kushiro-shitsugen National Park (Ministry of the Environment, 2005). The center of the park has been designated a Wildlife Protection Area and a Ramsar site. Kushiro Wetland is comprised of various vegetation types. The fen area of the wetland is dominated by *Phragmites australis* and *Carex* spp., and the wetland forests feature mainly *Alnus japonica*. Bogs compose the smallest part of the wetland and mainly consist of *Sphagnum* spp. Annual average temperature and precipitation between 1981 and 2010 were 5.5 °C and 1119.6 mm, respectively, and monthly mean maximum snow depth per day in February was 25.9 cm between 1985 and 2016 (at the Tsurui Weather Station, which is close to the study area; obtained from the Japan Meteorological Agency http://www.data.jma.go.jp/obd/stats/etrn/ 2017/1/15), which is shallow compared to other regions in Hokkaido.

Deer location data

A total of 28 hinds, 27 adults (i.e., over the age of three) and 1 yearling, were captured in three different designated areas (capture sites) inside Kushiro Wetland (Fig. 1) and fitted with GPS collars (IridiumTrackM2D, LOTEK). Three capture sites were selected: one in the north, one in the center, and one in the south of the wetland, all in accessible areas. We focused only on hinds, as they are key factors driving population dynamics in polygynous ungulates (Gaillard et al., 2000). The first capture site was located north of Lake Takkobu (from here on 'Takkobu'). The second site was at the Right Embankment of Kushiro Wetland, which runs through southwest of the wetland (from here on the 'embankment'). The third and last site was located in the northern part of the wetland near Prefectural Route 1060, which runs across the northern part of the wetland from Kottaro Observatory to National Route 391 (from here on 'Kottaro'). GPS collar fitting was carried out in February 2014 (one collared hind) and February–March 2015 (seven collared hinds) at Takkobu. Ten more hinds were fitted with collars at the embankment October–November 2014 and another ten were fitted in Kottaro in February 2015. Collar data were obtained at a fixed interval of every 3 h. Three individuals whose location datasets did not span a full year were omitted from all data analyses. Two of these individuals moved out of the wetland and were harvested by humans in the area, and the signal from the third individual's GPS collar was lost after it traveled 60 km away from the wetland into the nearby Japan Self-Defense Forces base in Betsukai town.

To quantitatively classify seasonal movement patterns using the net squared displacement (NSD) method (Bunnefeld et al., 2011), described below in detail, the datasets were required to include 365 time steps (i.e., one-year of data) from the start day (Bunnefeld et al., 2011); thus, we used one-year of location data for each individual in all analyses. The data collecting periods encompassed the time from when the collars were set to when their drop-off mechanisms were activated, and the start days for deer in Takkobu were February 14, 2014 (n = 1), February 14, 2015 (n = 3), March 17, 2015 (n = 1), and March 18, 2015 (n = 1). For all remaining individuals, the start day was March 1, 2015. One point/day (at noon) was selected from the movement trajectories for seasonal movement pattern classification, and all location data were used for the other analyses.

The data from Takkobu were a part of the "Capturing method evaluation of deer in Kushiro-shitsugen National Park in 2014" project of the Ministry of Environment. Permission to capture and handle wildlife was obtained from the Hokkaido government (Approval Number: 176-5 and 423-5), and permission to capture and handle wildlife in a wildlife protection area was obtained from The Ministry of Environment (Approval Number: 1409291 and 1510071). Permission for field study on government land was obtained from the Hokkaido Development Bureau (Approval Numbers: 68, 69 and 105), complying with the current laws and regulations of Japan.

Classification of seasonal movement patterns

Following the recommendations of Cagnacci et al. (2016), we used a combination of two methods to classify the seasonal movement patterns of deer: analysis of NSD (NSD method) and analysis of overlapping individual winter and summer home ranges (overlap method). First, movement patterns were classified using the NSD method and then the overlap method was used to confirm the seasonal migration pattern. Utilizing this combination enabled us to discriminate between 'true' seasonal migrants and individuals that only make minor seasonal movements from their home range (Cagnacci et al., 2016).

NSD is a measure of movement that can be used to infer seasonal home ranges and the duration of time individuals occupy them. In an NSD analysis, the squared distance between each location and the location where an individual was on the start day is calculated and indicates how far an individual is on a given day from where it was no the start day.

By fitting different theoretical seasonal movement patterns models based on the pattern of the NSD time series (Fig. 2), such as seasonal migration and dispersal, the NSD method quantitatively classifies individual seasonal movement patterns and estimates the timing of migration initiation and duration of time spent in the seasonal home range for seasonal migration individuals (Bunnefeld et al., 2011).To identify seasonal movement patterns using the NSD method, we calculated NSD values for the location at noon every day for each individual using the adehabitatLT package (ver. 0.3.21) (Calenge, 2006) in R (ver. 3.2.4, R development Core Team 2016). By selecting the best fit theoretical movement models, the results were classified according to Bunnefeld et al. (2011) into seasonal migration, mixed (seasonal movement away from a home range, like with seasonal migration, but without returning to the home range of the preceding year), dispersal, nomadic (random movements), and resident (lacking long distance movement, no difference in home range area between seasons). Model selection was based on the concordance criterion (Börger & Fryxell, 2012), and evaluation was performed using the nls.lm function of the minipack.lm package (ver 1.2-0) in R. Next, the overlap method was applied for the individuals with movement classified as seasonal migration by the NSD method. The overlap method distinguishes whether an individual is or is not a seasonal migrant by evaluating whether or not the degree of overlap of the home range before and after seasonal movement is smaller than the threshold values (Cagnacci et al. 2016). For applying overlap method, we arranged the location data of the individuals. The location data recorded during the migratory movement period, which was estimated based on the results of the NSD analysis, were removed and the remaining location data were classified as occurring during one of three periods: first winter, summer, and second winter. Home ranges were estimated for each period using kernel density estimation in the adehabitatHR package (ver. 0.4.14) (Calenge 2006), and the degree of home range overlap was evaluated using Bhattacharyya's affinity index

(Bhattachayya, 1943). Movement patterns were classified as seasonal migration when the degree of overlap of first winter *vs.* summer and that of summer *vs.* second winter did not exceed 15% (threshold) and when first winter *vs*. second winter the degree of home range overlap exceeded 50% (threshold) (Cagnacci et al., 2016). Trajectories that met neither of the conditions were classified as atypical (short and/or multiple trips between home ranges) (Cagnacci et al., 2016). Finally, the movement patterns for all individuals were classified as seasonal migration, dispersal, nomadic, resident, or atypical. No individuals were classified as mixed.

To investigate where home range centers were during summer and both winter periods, we calculated centers of activity (COAs) by averaging the locations for each deer in every season (Hayne, 1949), as has been done in previous studies (e.g. Igota et al., 2004), and mapped the results. Each COA period was defined by applying the estimated parameters calculated with the NSD method according to seasonal movement patterns. For migrant individuals, the estimated period for each individual was used directly. For the other individuals, all or a part of the periods were defined as follows: the duration of time that all migrant individuals remained in their seasonal home ranges because periods were not uniquely defined for non-seasonal migrants as they did not move with the seasons (Fig. 2). For dispersing individuals, the estimated period for each individual during first winter, which is the season occurring before dispersal, was determined by the NSD analysis, and the periods in which individuals remained in their summer and second winter home ranges were used to define the summer and second winter. For nomadic, resident, and atypical individuals, the periods in which all migrant individuals remained in their winter and summer home ranges were used to define the periods. Additionally, to compare migration distances observed in this study with those determined in previous studies, the distance between summer and winter COAs was calculated for each migrant.

Home range overlap among capture sites and degree of wetland utilization

To determine the amount of overlap of the home ranges of deer from the same capture site (termed 'population-level home range') with those of deer from different capture sites, annual and seasonal population-level home ranges were estimated using the adehabitatHR package in R and mapped by creating a 95% local convex hull (LoCoH) (Getz & Wilmers, 2004; Getz et al., 2007) from the pooled location points (as collected by the GPS collars) for all deer at a given capture site. Seasonal population-level home ranges were estimated by excluding seasonal movement periods of all migrant individuals (as estimated by the NSD method). The ratio of the area of overlap of a given population-level home range with other population-level home ranges to the total population-level home range area (termed 'ratio of overlap area') was calculated annually and seasonally, i.e., for first winter, summer, and second winter. For example, the ratio of overlap area for the Takkobu capture site home range was calculated as follows: (overlap area of the Takkobu and embankment capture site home ranges + overlap area of the Takkobu and Kottaro capture site home ranges) / Takkobu capture site home range. Moreover, to compare the degree of wetland utilization among individuals from the different capture sites and seasonal movement patterns, the wetland area per annual home range for each individual was calculated by dividing the total area of wetland in a given home range by the annual home range area. To statistically examine whether the degree of wetland utilization differed among capture sites and/or seasonal movement patterns, we constructed a normally distributed generalized linear model to explain the degree of utilization. The model used the amount of wetland area in the home range of each individual as the response variable, capture sites and seasonal movement patterns as explanatory variables, and annual home range size of each deer as an offset variable. The contribution of the explanatory variables was evaluated with a likelihood ratio test. Estimations for home ranges and statistical analyses were performed with R (ver. 3.2.4, R development Core Team, 2016). Home range sizes, the area of home range overlap among population-level home range at capture sites, and the area of overlap of home ranges and wetland area use were calculated with ArcGIS (ver. 10.3.1).

Seasonal migration timing and distance

Snow depth has been reported to affect the migration behavior of cervids (Mysterud et al. 2011), and the timing of migration initiation has been shown to be related to the timing of snow melt in eastern Hokkaido (Uno & Kaji, 2000). To examine the relationship between snow depth and the timing of migration initiation, we compared the state of snow accumulation and migration initiation. The date of loss of snow cover (defined as the first day snow depth fell below 1 cm) and the date of first snow cover (defined as the first day snow accumulation exceeded 1 cm) were obtained from the Japan Meteorological Agency data for the Tsurui Meteorological Weather Station (N43°14′, E144°20′) in a nearby study area. We compared the date of loss of snow cover and the date of first snow cover with the timing of migration initiation for spring and autumn, respectively, which were estimated by the NSD method.

Additionally, for the sake of comparing migration distance determined in this study with that of previous studies, the distances between summer and winter COAs were calculated for each migrant individual.

Results

All capture sites contained multiple individuals with differing movement patterns (Table 1). More than half of the individuals from Takkobu were classified as migrant individuals along with two deer from the embankment. Takkobu migrants spread over a large area to agricultural areas in the towns of Shibetsu, Betsukai, and Shibecha, as well as to Tsurui Village (Fig. 3). One individual from the embankment migrated to an urban area in the town of Kushiro and to a forested area close to a quarry. Another migrant from the embankment had its COAs in different areas within the wetland. Regarding the atypical movements of Takkobu individuals, two individuals did not return from their wintering ranges with one moving 16 km northwest of the wetland and establishing a home range outside the wetland during the second winter. Approximately half of all individuals had COAs within the wetland year-round regardless of their movement patterns (Fig. 4).

A small ratio of overlap area of annual population-level home range was found (Fig. 5): 1.1% of Takkobu home ranges (0.5% with the embankment, 0.6% with Kottaro), 5.6% of embankment home ranges (5.6% with Takkobu and 0% with the Kottaro), and 5.8% of Kottaro home ranges (0% overlap with embankment and 5.8% overlap with Takkobu) overlapped with those of other population-level home ranges. There were no overlapping seasonal population-level home ranges among capture sites for any season (Fig. S1).

The degree of wetland utilization differed substantially among individuals and ranged from 2.7 to 100.0% (Table 2). Eleven individuals had home ranges that consisted largely of wetland with two of these deer using wetland exclusively (i.e., 100% utilization) and the other nine individuals with 81%–96% of their home range comprised of wetland. The degree of wetland utilization did not differ among movement patterns ($P = 0.966$). However, Takkobu individuals utilized the wetland less than deer from the other capture sites (Takkobu: 21.2%, the embankment: 76.8%, and Kottaro: 75.9%); the effect of capture site on the degree of wetland utilization was statistically marginal ($P = 0.075$).

Regarding the timing of migration initiation, most individuals exhibited substantial variation in when they started migrating with as much as a one-month delay between individuals (Table S1) although one individual captured in 2015 in Takkobu initiated migration six days after the loss of snow cover.

Individuals from Takkobu migrated up to four times farther than embankment individuals did. Average spring migration distances were 31.8 ± 9.1 km (mean ± SE) (range 6.8–69.9 km) for all migrants, 40.8 ± 10.1 km for Takkobu migrants, and 9.3 ± 0.5 km for embankment migrants. Average autumn migration distances were 31.2 ± 8.6 km (range 6.7–63.9 km) for all migrants, 40.2 ± 9.1 km for Takkobu migrants, and 8.7 ± 0.7 km for embankment migrants.

Discussion

Individuals from all capture sites exhibited a variety of movement patterns, e.g., resident and seasonal migration, even though they inhabited the same area at one point during the year. Thus, the individuals from the different capture sites may belong to different sub-populations that inhabit the areas sympatrically in a particular season, but which are in separate areas in another season. In addition, population-level home ranges of the three capture sites exhibited little to no overlap in their annual home ranges and no overlap in their seasonal home ranges. Thus, individuals from different capture sites were likely from different populations, although we could not strictly examine this since the individuals at the embankment site were captured in autumn despite the others being captured in winter.

Approximately one-fourth of all individuals exhibited a high degree of wetland utilization meaning they inhabited the wetland exclusively or to a large extent year-round. The individuals may inhabit the wetland to avoid hunting risk (Lone et al., 2015) as the majority of this area is a Wildlife Protection Area, which could allow these individuals to continue to increase until reaching the carrying capacity of the wetland. After the extinction of the gray wolf, *Canis lupus*, around 1890 (Inukai, 1995) in Hokkaido, the main cause of deer mortality in eastern Hokkaido has primarily been harvest by hunters with adult female mortality rates estimated at 0.118 (harvest) and 0.053 (natural) (Uno & Kaji, 2006). Furthermore, movements of some Takkobu individuals that exhibited atypical movements, such as leaving the wetland for surrounding areas and establishing new home ranges there, indicated that Kushiro Wetland may be a population source in eastern Hokkaido.

Our results showed that six deer seasonally migrated into the wetland. Previous studies have highlighted factors for seasonal migration, such as predation risk avoidance (Hebblewhite & Merrill, 2007; White et al., 2014), access to nutritional resources (Fryxell & Sinclair, 1988; Hebblewhite, Merrill & McDermid, 2008; Bischof et al., 2012), and social interaction avoidance due to density (Mysterud et al., 2011). The predation risk avoidance and nutritional resources hypotheses may be supported by the migration data observed in the present study; we cannot examine the avoidance of social interactions hypothesis since accurate information about summer deer density are limited. Takkobu migrant individuals moved into the Kushiro Wetland in winter, and they moved out of the wetland in summer. Sport hunting and pest control are conducted outside of the wetland with the open season spanning from October to March, and pest control is conducted year-round. However, harvests are prohibited in the wetland and deer, therefore, can avoid predation risk here, especially during the open season. In fact, hunters harvested two individuals moving out of the wetland during winter, but no tracked deer died in the wetland. The summer habitats of Takkobu migrant individuals were agricultural areas in places such as Shibecha Town. These individuals can browse highly nutritional crops grown in the summer. The movement patterns of Takkobu migrant individuals suggested that they move into the wetland to avoid predation risk in the winter and out of the wetland into agricultural areas in summer because the benefit of foraging on these high nutritional resources exceeds the predation risk. On the other hand, one of the migrant individuals from the embankment moved out of the wetland in winter and back into the wetland in summer. The winter habitat of this individual was forestland near urban areas and developed land where hunting pressure is thought to be slightly lower due to legal constraints imposed by the Japanese Firearms and Swords Control Law. In summer, many embankment deer have been observed feeding on pasture grasses planted on the slopes of the embankment to prevent erosion (Ministry of the Environment, 2017). Pasture grasses have higher nutritional value compared to naturally growing plants, e.g., *Phragmites australis*, and are often foraged by sika deer (Takatsuki, 2001; Tsukada, Fukasawa & Kosako, 2008). It seems, therefore, that migrant deer move to the embankment during summer to access nutritional food resources. Another migrant individual migrated from the embankment to another area of the wetland in winter, i.e., it migrated within the wetland. This individual may have used the embankment in the summer for the sake of accessing high nutritional food resources, but the reasons for the individuals leaving the embankment in winter is uncertain

The results of the present study showed that the proportions of movement patterns differed among individuals from different capture sites, even though the capture sites themselves were geographically near one another. The factors for determining the proportion of migrants in an ungulate population have been debated (Bolger et al., 2008; Chapman et al., 2011). By comparing populations living in close proximity but consisting of different proportions of individuals exhibiting different movement patterns, like the populations in our study, we can develop an understanding of these factors (Bolger et al., 2008; Chapman et al., 2011). Taking into account the environmental factors, deer survival rates, and nutritional status of individual deer (White et al., 2014) in future studies of Kushiro Wetland's deer populations would contribute to identifying the factors determining the proportion of the migrants in the populations.

A study conducted in Akan, located approximately 40 km northwest of Kushiro Wetland, found that the timing of spring migration is closely related to the timing of snow melt in May (Uno & Kaji, 2000). However, in the present study, no clear relationship was found between snow melting and migration initiation, except for in individuals captured in 2015 in Takkobu. This could possibly be due to the short snow cover period and shallow snow depth in Kushiro Wetland compared to Akan. Uno & Kaji (2000) reported a total of 121 days with a snow depth over 50 cm during the study period (1993–1996) with snow melting in mid-May. On the other hand, in Kushiro Wetland, snow depth was only 20 cm in February 2015 (Ministry of the Environment, 2016), and the snow melted in early April.

In the present study, the average migration distance during spring for deer was 31.8 ± 9.1 km, and it was 31.4 ± 8.6 km during autumn. These distances were similar to those observed for deer in Shiranuka located approximately 50 km west of Kushiro Wetland (35.1 km) (Igota et al., 2004) and in Akan (19.9 km, spring migration; 24.3 km, autumn migration) (Uno & Kaji, 2000), but longer than those for deer in Okuchichibu (15.9 km) (Takii et al., 2012) and Kirigamine (9.9 km) (Takii, Izumiyama & Taguehi, 2012) on the main island of Japan, south of Hokkaido. This trend is in accordance with a previous study that indicated that moose (*Alces alces*) have longer migration distances at northern latitudes (Singh et al., 2012).

Conclusions & management implications

This study clarified that there were at least three populations with sub-populations in Kushiro Wetland, and one-fourth of deer observed used the wetland as their main habitat year around. Furthermore, large numbers of deer moved in and out of the wetland, and the degree of wetland utilization differed among capture sites and individuals. Therefore, ecosystem maintenance and recovery projects in Kushiro Wetland must consider the population structure of deer to effectively manage these animals in the wetland. In particular, many seasonal migrant individuals spend the winter in the wetland as a strategy to avoid hunting predation and browse on highly nutritional crops in surrounding agricultural areas during summer. Thus, to manage these individuals, both ecosystem management in the wetland as well as agricultural countermeasures in the surrounding areas need to be considered together. Furthermore, in terms of pasture grasses on the embankment, ecosystem managers should recognize that growing these grasses on the embankment is a conservation issue not only because they are exotic and planted in the core area of the wetland, but also because they would provide favorable habitats for migrant and resident deer.

Land-use development in and around Kushiro Wetland has caused marked vegetation modification due to sediments and nutrients being carried and deposited from upstream watersheds (Nakamura, Kameyama & Mizugaki, 2004) and is one of the major conservation issues of the wetland. Ungulates transfer nitrogen and phosphorous from farmlands to forests through their movement (Seagle, 2003; Abbas et al., 2012). In our study, deer migrated from farmland areas to the wetland; thus, the deer likely provided cross-ecosystem nutrient subsidies from the farms to the wetland through their excreta and carcasses. Although an overwhelming amount of nutrients flow from upstream watersheds to the wetland (Nakamura, Kameyama & Mizugaki, 2004), ungulate excreta and carcasses change the spatial distribution of soil nutrients, ultimately leading to changes in plant nutrient contents and plant community composition (Bump, Peterson & Vucetich, 2009; Murray, Webster & Bump, 2013). Therefore, both biological interactions, such as browsing, and biogeochemical ecosystem processes, such as subsidies from farmlands, should be considered when evaluating the impacts of deer on wetland ecosystems.

Before the Japanese extensively settled Hokkaido in the Meiji period (beginning in 1868), deer were distributed across the entire island (Tawara, 1979). In areas with native ungulate populations, moderate ungulate browsing lead to high plant diversity, and browsing occurring in a mosaic across the landscape would have promoted high plant diversity at a landscape scale through the spatial heterogeneity of the plant community affected by the ungulates (Royo et al., 2010). Our results suggested that deer densities in the wetland are spatiotemporally variable because ungulate migration is known to exhibit this type of variation (Nelson 1998; Mysterud et al. 2011). Therefore, for the ecosystem maintenance and recovery project in Kushiro wetland, not only is there a need to manage deer population size itself, but also to fully understand the interaction between the spatiotemporal variation of deer impacts and vegetation at the landscape level. The combination of more detailed information on the spatiotemporal distribution of deer density caused by the seasonal movements of individuals and different responses to deer browsing among vegetation types (Inatomi et al., in press) would provide essential information for ecosystem management at a landscape level in Kushiro Wetland.

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Figure 1(on next page)

Locations (n = 3) where tracked sika deer (*Cervus nippon yesoensis*; n= 28) were captured in Kushiro Wetland.

The boundary of the wetland was obtained from the Kushiro Wetland Restoration Project Shitsugen Data Center (http://kushiro.env.gr.jp/index.html).

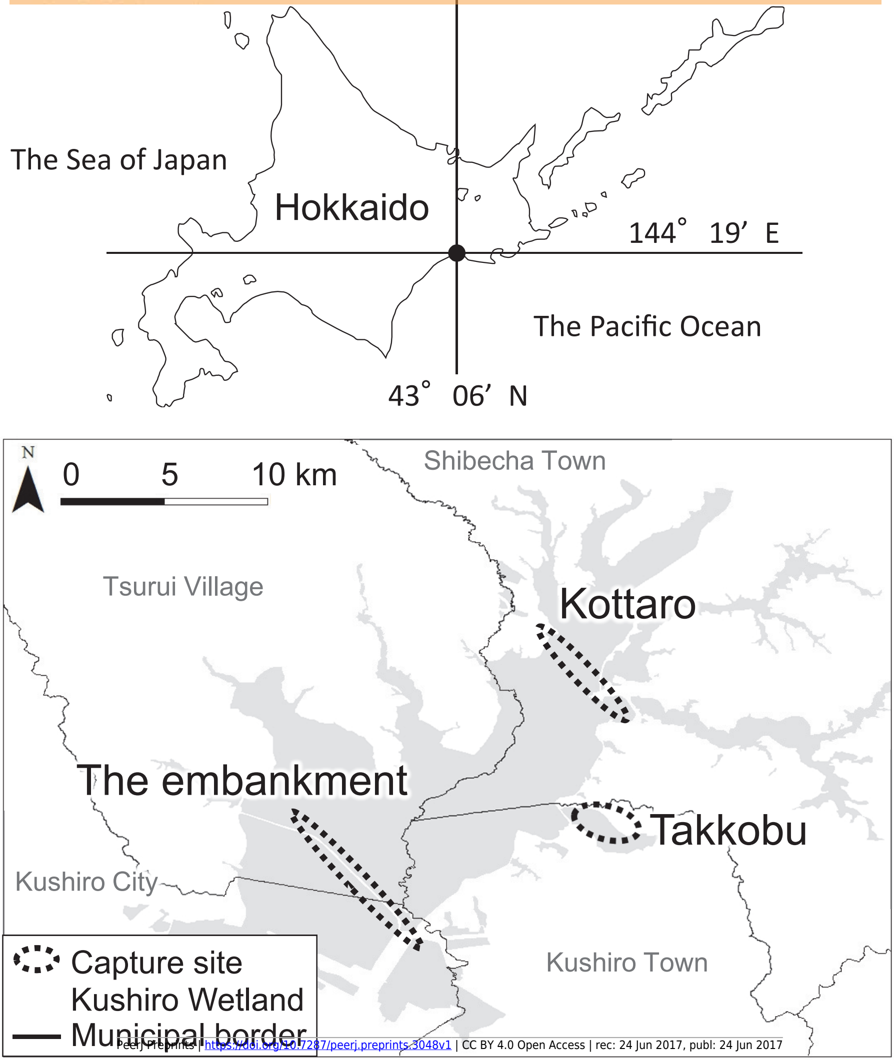
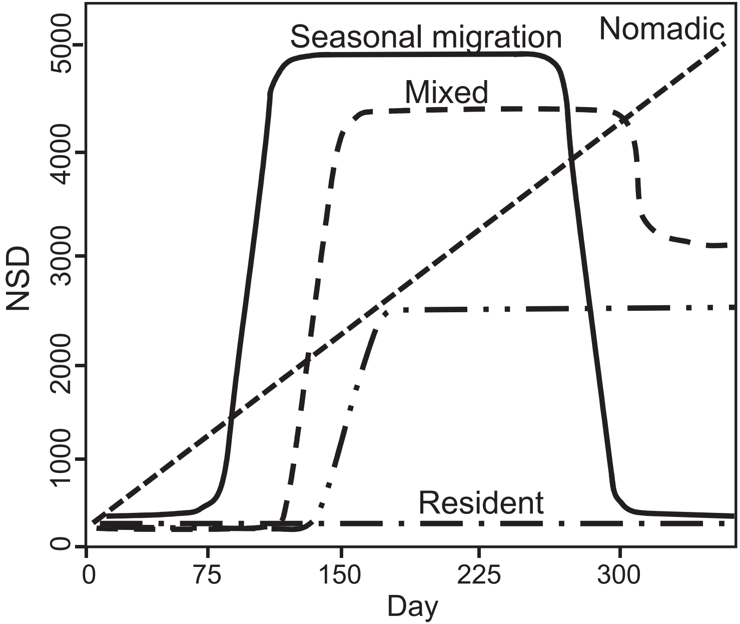

The Sea of Japan
Hokkaido
144° 19' E
The Pacific Ocean
43° 06' N
N
0 5 10 km
Shibecha Town
Tsurui Village
Kottaro
The embankment
Takkobu
Kushiro City
Kushiro Town
Capture site
Kushiro Wetland
Municipal border

Figure 2(on next page)

Models of seasonal movement patterns based on the net squared displacement (NSD) method and expected NSD plots for different seasonal movement patterns.

Solid line, seasonal migration; long dashed line, mixed; two dot-and-dash line, dispersal; short dashed line, nomadic; dot-and-dash line, resident. Model functions and plots are modified from Bunnefeld et al. (2011).



◆ **Seasonal migration**

$$NSD = \frac{\delta}{1+\exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta}{1+\exp\left(\frac{\theta_a - t}{\varphi_a}\right)}$$

◆ **Mixed**

$$NSD = \frac{\delta_s}{1+\exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta_a}{1+\exp\left(\frac{\theta_a - t}{\varphi_a}\right)}$$

◆ **Dispersal**

$$NSD = \frac{\delta}{1+\exp\left(\frac{\theta - t}{\varphi}\right)}$$

◆ **Nomadic**

$$NSD = \beta \times t$$

◆ **Resident**

$$NSD = c$$

s, a: Summer migration, autumn migration

δ: NSD at destination of seasonal migration

θ: Day at which migration reaches half of NSD

φ: Elapsed time from half to $\cong$ 3/4 of migration

t: The number of days since the starting day

β, c: Constant

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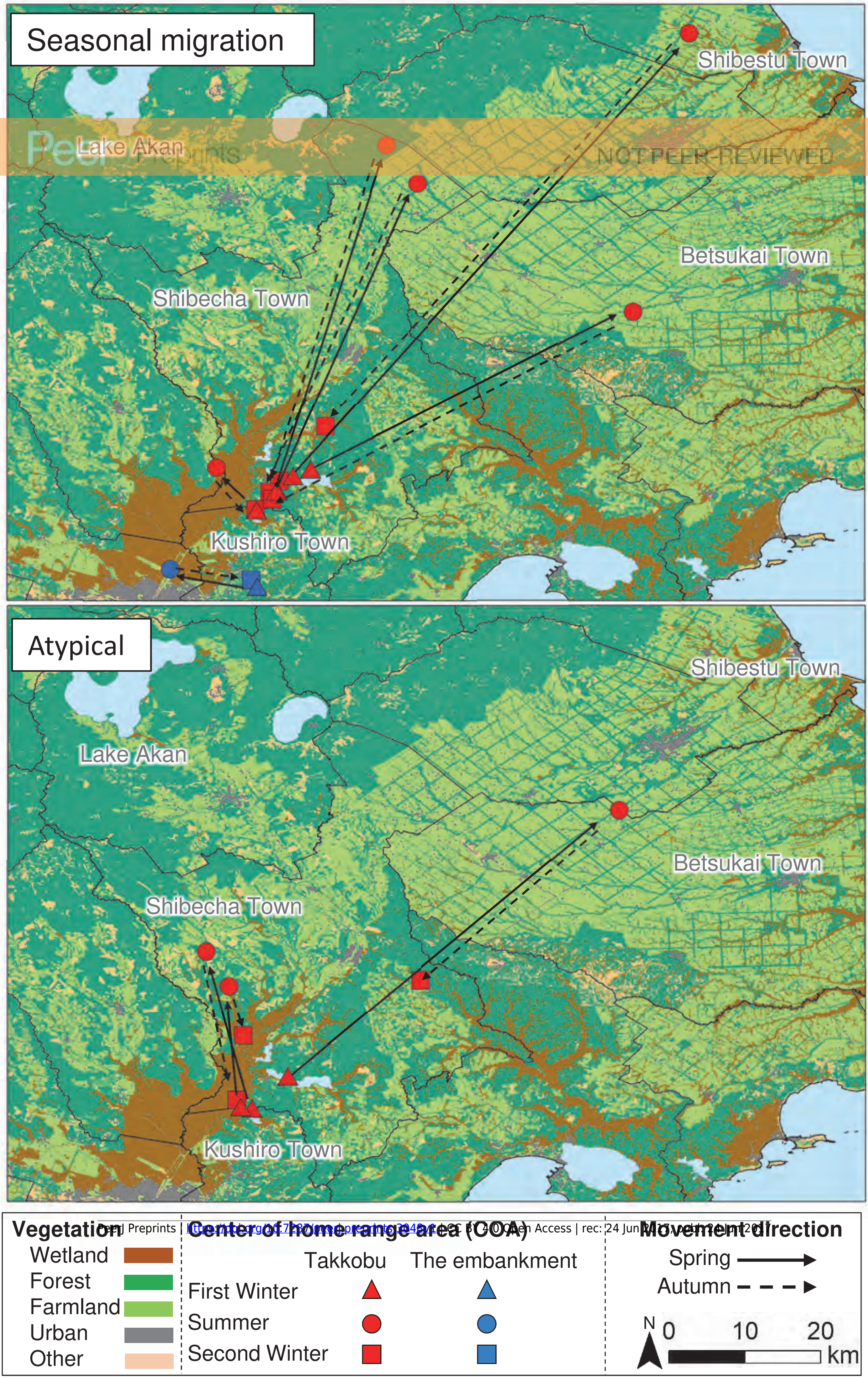
Figure 3(on next page)

Movement patterns ofsika deer (*Cervus nippon yesoensis*) with seasonal centers of activity (COAs) occurring outside Kushiro Wetland atsome point during the year.

Movements of sesonal migration (upper panel) and atypical individuals (lower panel) are shown. Dots indicate COAs for winter and summer for each individual. Lines connect individual COAs, and arrows show spring or autumn movement direction. All deer captured at Takkobu (n = 8) and one deer captured at the embankment are shown, but deer captured at Kottaro are not because their COAs were entirely within the wetland.



Seasonal migration
Shibestu Town
Lake Akan
Betsukai Town
Shibecha Town
Kushiro Town
Atypical
Shibestu Town
Lake Akan
Betsukai Town
Shibecha Town
Kushiro Town
Vegetation
Wetland
Forest
Farmland
Urban
Other
Center of home range area (COA)
Takkobu
The embankment
First Winter
Summer
Second Winter
Movement direction
Spring
Autumn
N
0
10
20
km

Figure 4

(on next page)

Movement patterns of sika deer (*Cervus nippon yesoensis*) that remained within the wetland all year.

Sika deer captured at the embankment (n = 7) and Kottaro (n = 9) sites are shown, but deer captured at Takkobu are not because all Takkobu individuals had at least one seasonal center of activity (COA) outside the wetland. Dots indicate COAs for winter and summer for each individual. Lines connect individual COAs, and arrows show spring or autumn movement direction, except for those of residents.

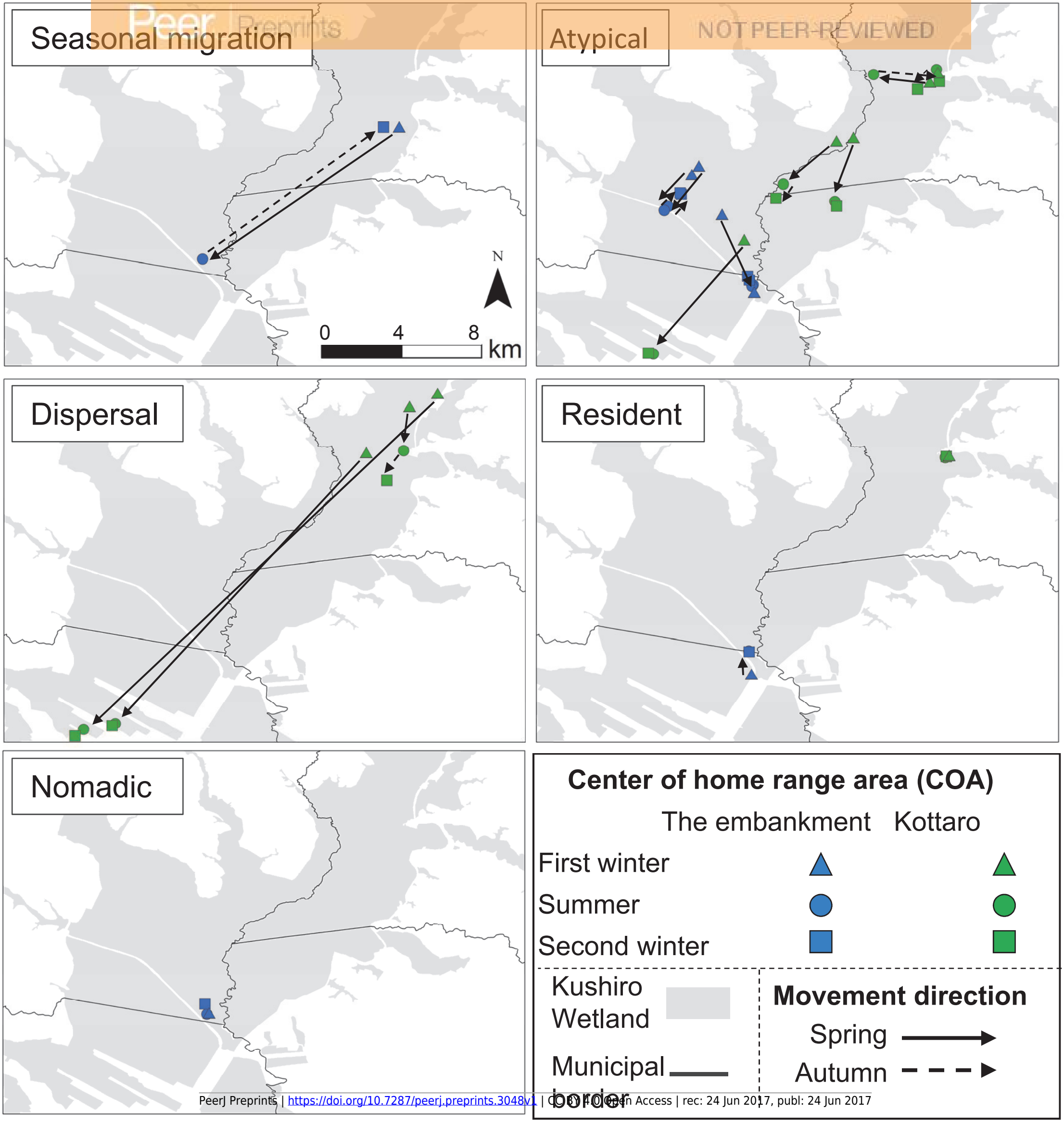


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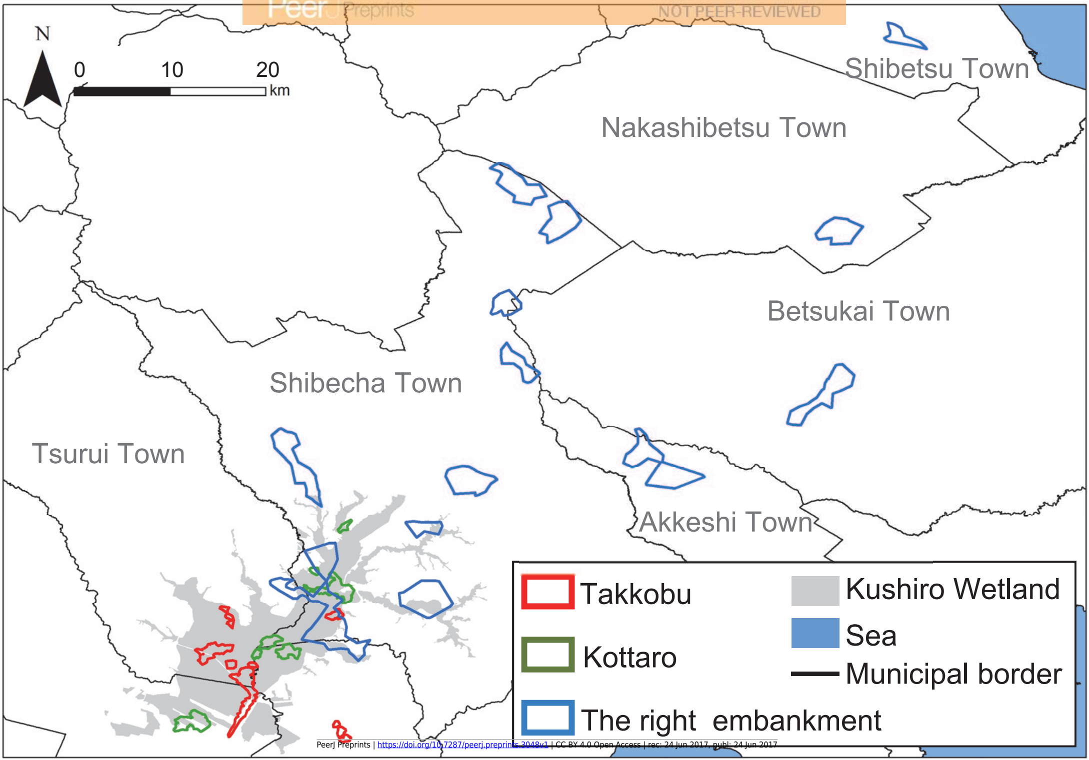
Figure 5(on next page)

Annual population-levelhome ranges of sika deer (*Cervus nippon yesoensis*) in the Kushiro Wetland per capture site.

Home ranges were estimated by a 95% local convex hull by pooling all recorded locations of deer at each capture site. Red outline, Takkobu home ranges; green outline, Kottaro home ranges; blue outline, embankment home ranges.



N
0
10
20
km
Shibetsu Town
Nakashibetsu Town
Betsukai Town
Shibecha Town
Tsurui Town
Akkeshi Town
Takkobu
Kottaro
The right embankment
Kushiro Wetland
Sea
Municipal border

Table 1(on next page)

Seasonal movement pattern classifications per sika deer (*Cervus nippon yesoensis*) capture site.

Capture site	Seasonal migration	Dispersal	Nomadic	Resident	Atypical
Takkobu (n=8)	5	0	0	0	3
The embankment (n=8)	2	0	1	1	4
Kottaro (n=9)	0	3	0	1	5

One of the seasonal migrant individuals from Takkobu was tracked from May 2014 to May 2015. The remaining individuals were tracked from May 2015 to May 2016

Table 2(on next page)

Annual home range size,amount of home range overlapping the wetland, and wetland utilization(percentage of home range overlapping wetland area).

Wetland utilization was calculated by dividing the amount of wetland in a home range by the annual home range size.

Capture site	Movement type	Annual home range size (km^2)±SE	Amount of wetland in annual home range area (km^2)±SE	Wetland utilization (%)±SE	Range of wetland utilization (%)	*n*
Takkobu	Migration	21.0 ± 4.4	3.4 ± 0.6	20.3 ± 4.4	9.9 ~ 39.0	5
(n=8)	Atypical	9.4 ± 3.5	1.2 ± 1.6	22.7 ± 8.9	2.7 ~ 40.0	3
	Mean	16.7 ± 5.9	2.6 ± 1.5	21.2 ± 4.4	2.7 ~ 40.0	
The embankment	Migration	2.7 ± 0.0	1.4 ± 1.1	51.8 ± 29.6	9.9 ~ 93.6	2
(n=8)	Nomadic	1.9	1.7	90.3	-	1
	Resident	2.5	2.0	81.3	-	1
	Atypical	2.3 ± 0.4	2.1 ± 0.8	84.8 ± 6.4	64.9 ~ 96.4	4
	Mean	2.4 ± 0.8	1.8 ± 0.8	76.8 ± 9.6	9.9 ~ 96.4	
Kottaro	Dispersal	2.5 ± 0.0	1.6 ± 0.5	63.4 ± 11.0	37.6 ~ 82.7	3
(n=9)	Resident	0.5	0.3	60.4	-	1
	Atypical	2.1 ± 0.3	1.8 ± 0.6	86.4 ± 8.0	52.1 ~ 100.0	5
	Mean	2.1 ± 0.7	1.5 ± 0.7	75.9 ± 7.0	37.6 ~ 100.0	
All		6.8 ± 1.8	2.0 ± 1.2	58.7 ± 6.6	2.7 ~ 100.0	25

SE: standard error