

**Effects of spatiotemporal heterogeneity of
vegetation conditions on the movement of a
migratory ungulate, Mongolian gazelle**

(植生条件の時空間的不均一性が移動性有蹄類
モウコガゼルの移動に及ぼす影響)

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Chapter 1

General introduction

1.1 General objective

The general objective of this thesis is to investigate the influence of spatiotemporal heterogeneity of vegetation conditions on the movement of Mongolian gazelles (*Procapra gutturosa*). The Mongolian gazelle is one of the terrestrial species that moves the greatest distances (Berger 2004, Teitelbaum et al. 2015, Tucker et al. 2018). In addition, the habitat of the species is characterized by relatively low interannual predictability of environmental conditions (von Wehrden et al. 2012).

Interannual predictability of vegetation conditions is a key factor influencing the movement patterns of herbivores, based on its direct effects on vegetation availability, and indirectly on seasonal changes and the associated shifts in the spatial heterogeneity of vegetation availability (Mueller and Fagan 2008). Movement of Mongolian gazelles has been reported to be nomadic (Olson et al. 2010, Mueller et al. 2011, Ito et al. 2013a), which suggests that the spatial heterogeneity of environmental conditions in the Mongolian gazelles' habitat is relatively high (Mueller and Fagan 2008, Mueller et al. 2011).

However, studies on the relationship between nomadic movements and vegetation conditions have been quite limited for both the Mongolian gazelle and other ungulate species. The expansive and continuous habitat of the Mongolian gazelle (Batsaikhan et al. 2014), which is characterized by spatial heterogeneity of vegetation conditions

(Eckert et al. 2015, Vandandorj et al. 2015), would be a suitable environment for the analysis of such relationships. In the present thesis, I investigate the relationships between movements of Mongolian gazelles and spatiotemporal heterogeneity of vegetation conditions to facilitate a better understanding of animal movement ecology.

1.2 Background

1.2.1 Effects of spatiotemporal heterogeneity of food resource amounts on animal movement patterns

The reasons for long-distance movement include to seek superior food resources, (Murray 1995, Boone et al. 2006), to find mates (Avgar and Fryxell 2014), to escape from severe climate conditions (Singh et al. 2012), to minimize predation risk (Hebblewhite et al. 2009, Hopcraft et al. 2010) among other factors. Among the above-mentioned factors, food availability and its spatiotemporal variation is the major factor influencing the movement patterns of numerous animal species (Dussault et al. 2005, Milner-Gulland, Fryxell and Sinclair 2011, Avgar and Fryxell 2014).

Animal movement patterns vary inter- and intra-specifically, for example, seasonal migrations, nomadic, and sedentary (Bunnefeld et al. 2011, Mysterud et al 2011, Singh et al. 2012). In the case of large terrestrial herbivores, forage resource distribution influences movement patterns (Mueller and Fagan 2008). Forage amounts, and seasonal changes, spatial heterogeneity, and temporal predictability of forage amounts are components of forage resource distribution in the prediction. Animals would not require to move over expansive ranges in habitats with adequate forage amounts. Conversely, animals in habitats with relatively low forage amounts would require to move over

expansive ranges to seek more forage. Even in areas with adequate forage amounts, in some seasons, forage shortages due to seasonal changes force some animals to migrate to other areas.

Spatial heterogeneity in forage amounts influences animal movements within a season and between seasons (Mueller et al. 2011, van Moorter et al. 2013). Large-scale spatial heterogeneity with conspicuous seasonal changes explains the seasonal migration. Interannual predictability also influences animal movement patterns. Seasonal migrations between specific seasonal ranges are predicted in areas with high interannual predictability of environmental conditions, while nomadism and moving irregularly are predicted in areas with low seasonal and interannual predictability of environmental conditions (Mueller and Fagan 2008). Nomadic movement is generally defined as “unpredictable movements that vary among individuals for any given year (type I nomadism) or among years for any given individual (type II nomadism)” (Mueller and Fagan 2008).

There are various movement patterns in ungulate species. Seasonal migrations are observed in areas with distinct predictable seasonal changes between summer and winter or between wet and dry seasons. Some ungulates migrate over long distances (horizontal movements) while others climb up and down mountains and hills (vertical movements) seasonally to exploit superior habitats across seasons. The famous round-trip migration of wildebeests (*Connochaetes taurinus*) between wet and dry season ranges across more than 200 km in Serengeti, East Africa, is an example of horizontal movements (e.g., Boone et al. 2006, Murray 1995). Long-distance horizontal movements also occur between summer and winter ranges in cool and temperate zones (e.g., moose [*Arces arces*] in Sweden (Bunnefeld et al. 2011, Singh et al. 2012) and in

Alaska, USA (White et al. 2014)). For vertical movements, mountainous red deer (*Cervus elaphus*) in Sweden, Norway (Bischof et al. 2011) and the Swiss Alps (Zweifel-Schielly et al. 2009), and mule deer (*Odocoileus hemionus*) in USA (Sawyer et al. 2011) are examples. The deers move between winter ranges at high elevations and summer ranges at low elevations, and the differences in elevation reach approximately 800 m in some cases.

In addition to species participating in seasonal migrations, numerous sedentary species and populations of ungulates exist worldwide. For example, Japanese serows (*Capricornis crispus*), which inhabit mountainous forests in Japan have high site fidelity throughout their lifespans, and the sizes of their annual ranges in a region were lower than 30 ha (Ochiai and Susaki 2002). Guanacos (*Lama guanicoe*) in the Patagonian Steppes and moose in USA (Mueller et al. 2011) are other examples of relatively sedentary species.

Detailed information on the nomadic movements of ungulates remains limited. However, nomadic movements of Asiatic wild asses (*Equus hemionus*, Kaczensky et al. 2008, 2011) and Mongolian gazelles (Olson et al. 2010, Mueller et al. 2011, Ito et al. 2013) in Mongolia have been studied.

1.2.2 Effects of forage quality on habitat selection in herbivores

Spatiotemporal variation in forage quality is also a key driver of animal movement, in addition to forage quantity (Fryxell et al. 1998). For herbivores, nutrient concentrations and nutrient digestibility are highest in young leaves and decline as plants mature due to the accumulation of fiber (White 1983). Therefore, for herbivores, there is a trade-off between forage quality and quantity with regard to energy intake for herbivores. In

addition, energy intake would be maximized when vegetation biomass is at an intermediate level, even though the biomass associated with maximum energy intake varies based on animal body size (Fryxell 1991). The above relationship is called the forage maturation hypothesis and has been demonstrated in numerous studies (e.g., Thomson's gazelle [*Gazella thomsonii*] (Fryxell et al. 2004) and wildebeest [*Connochaetes taurinus*] (Boone et al. 2006) in Serengeti, elk [*Cervus elaphus*] in Canada (Hebblewhite et al. 2008), and mule deer [*Odocoileus hemionus*] in USA (Sawyer et al 2011)).

1.2.3 Movement strategies of ungulates

The green wave hypothesis (Drent et al. 1978, Owen 1980) proposed the concept that migratory herbivores would track waves of high forage quality to maximize energy intake. Time lags of vegetation growth along elevational or latitudinal gradients are referred to as "green waves" and some ungulates' movements are consistent with the green wave hypothesis in spring. Such a movement strategy is called "surfer" (Bischof et al. 2012). "Jumper" is another strategy, which is not consistent with the green wave hypothesis. However, "jumpers" move to the summer ranges earlier than the green wave to avoid predation risk and forage competition with other individuals along the migration route. Most migratory red deer in Sweden and Norway have been classified as "jumpers" (Bischof et al. 2012). Such movement strategies have been observed in areas with relatively high temporal predictability of environmental conditions, mainly because of high spatiotemporal predictability of green waves and suitable vegetation conditions in the seasonal ranges are required for the strategies. However, in areas with

the low temporal predictability of environmental conditions, the movement is predicted to be nomadic, and movement strategies remain unclear.

1.2.4 Challenging issues on movement ecology of ungulates

Compared to studies on animal movements in areas with high temporal predictability of environmental conditions, studies in areas with low temporal predictability remain limited. This is partly attributed to challenges in tracking animals and evaluating environmental conditions associated with nomadic movements. In the case of typical migration, seasonal locations of animals and key areas in each season can be predicted. Therefore, research on typical migration has been possible without the need for advanced technologies. In contrast to typical migration, research on nomadic movement requires advanced technologies for animal tracking, even at the basic level. In addition, evaluation of environmental conditions over wide ranges of habitats would be necessary.

1.3 Methods of addressing the challenges in studying long-distance movements of ungulates inhabiting areas with low levels of temporal predictability of environmental conditions

1.3.1 Mongolia's Gobi-Steppe Ecosystem as the study area

I selected the Gobi-Steppe Ecosystem in Mongolia as the study area (Fig. 1.1). The ecosystem is one of the largest grasslands in the world (827,000 km²). Many migratory mammal species inhabit the ecosystem (Batsaikhan et al. 2014). Interannual

predictability of climatic conditions in the ecosystem is low, which is a typical of drylands (von Wehrden et al. 2012). In addition, seasonal changes and regional differences in climatic and vegetation conditions are distinct. The wide area over which ungulate species are distributed includes various environmental conditions, ranging from desert to forest steppe. Such situations are suitable for investigating long-distance movements of mammals in relation to environmental conditions.

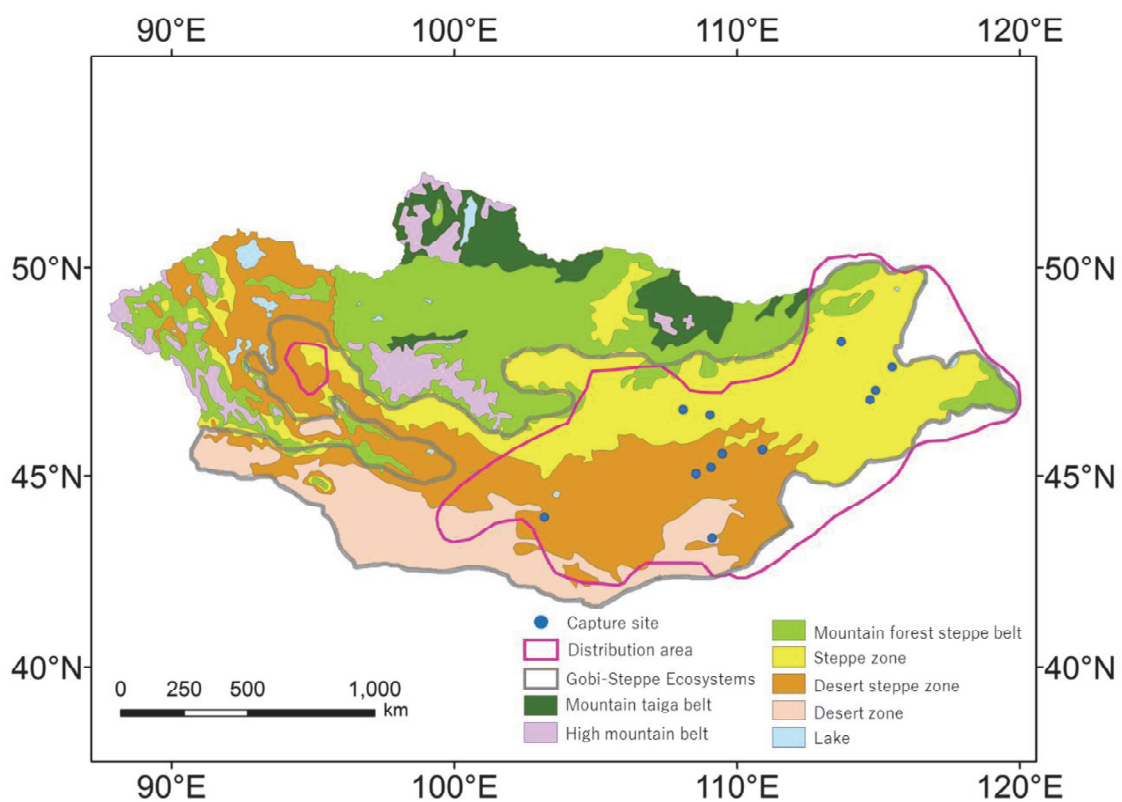


Fig 1.1 Vegetation zones in Mongolia, area of the Gobi-Steppe Ecosystem (GSE), and distribution of the Mongolian gazelle. Tracked gazelles were captured in various vegetation zones. Original vegetation and distribution maps were in Gomboluudev et al. (2018) and IUCN SSC Antelope Specialist Group (2016), respectively.

1.3.1.1 Climatic and vegetation conditions of Mongolia

Vegetation conditions in the Gobi Steppe Ecosystem have been conserved in relatively good conditions, largely due to the low human population density (Batsaikhan et al.

2014). In Mongolia, 46% of the human population is concentrated in the capital city of Ulaanbaatar; therefore, population density in other regions is relatively low (1.1 ind./km²) in 2017 (National Statistics Office of Mongolia 2018). The landscape consists mainly of flat highlands with several mountains, and elevation ranges from approximately 550 to 2700 m above sea level.

The climate is a strong continental type climate (maximum temperature exceeds 40°C in summer and minimum is below -35°C in winter). The annual mean precipitation ranges from less than 50 mm in the south to approximately 400 mm in the north (Worden and Savada 1989, Nandintsetseg and Shinoda 2011, Vandandorj et al 2015). Winter snowfall is also higher in the north (more than 30 cm in severe winters) than in the south (Nandintsetseg et al. 2017). Large interannual variations in precipitation sometimes cause severe drought in summer (Miao et al. 2016) and winter clamities called “*dzud*” (Tachiiri et al. 2008, Miao et al. 2016, Nandintsetseg et al. 2017).

The vegetation gradually changes from forest steppe in the north to desert in the south (Fig. 1.1). The dominant tree species in the forest steppe are *Larix gmelinii*, *Betula platyphylla*, *Populus davidiana*, among others (Yu et al. 2004). Grasses and forbs (e.g., *Stipa* spp., *Carex* spp., *Allium* spp., and *Artemisia* spp.) dominate the typical and dry steppe regions, while shrubs (e.g., *Caragana* spp., *Anabasis brevifolia*) dominate the desert steppe (Sasaki et al. 2008, Olson et al. 2010b).

1.3.1.2 Large migratory herbivores in Mongolia

Several wild ungulates including migratory and nomadic species inhabit Mongolia. The Mongolian gazelle (*Procapra gutturosa*) is the most numerous and widely distributed

wild ungulate species in Mongolia (Milner-Gulland and Lhagvasuren 1998), and their movement seems to be nomadism (Olson et al. 2010, Mueller et al. 2011). Their movements and seasonal distributions have been analyzed based on the spatiotemporal heterogeneity of vegetation conditions (Ito et al. 2006, 2013, Olson et al. 2010, Mueller et al. 2008, 2011).

The goitered gazelle (*Gazelle subgutturosa*), another gazelle species that has a body shape and size similar to the Mongolian gazelle, and the Asiatic wild ass inhabit the Mongolia Gobi Ecosystem. The distributions of both species overlap in the southern parts (drier regions) of the range of the Mongolian gazelle. The goitered gazelle (IUCN SSC Antelope Specialist Group 2017) and the Asiatic wild ass (Kaczensky et al. 2011) have been listed as vulnerable and near threatened species in the IUCN Red List, respectively. The Asiatic wild ass is one of the ungulates that moves the greatest distances in the world (Teitelbaum et al. 2015, Tucker et al. 2018), exhibiting nomadic movements (Kaczensky et al. 2008, 2011). Ecological studies have been restricted to both species. The Asiatic wild ass has been reported to exhibit preference to areas with high productivity and small interannual variability of vegetation, and with nearby water sources in the desert ecosystem in western Mongolia (Nandintsetseg et al. 2014). In addition, the negative impacts of human activities on habitat selection for both the species in the desert steppe in southern Mongolia (Buuveibaatar et al. 2016) have been reported.

Two critically endangered migratory ungulates, the Mongolian saiga (*Saiga tatarica mongolica*), which is distributed in western Mongolia (IUCN SSC Antelope Specialist Group 2018), and the wild Bactrian camel (*Camelus ferus*), which is distributed in southwestern Mongolia (Hare 2008), inhabit Mongolia's Gobi-Steppe

Ecosystem, although their distribution does not overlap with that of Mongolian gazelles. Mongolian saigas move seasonally and prefer areas away from towns that are closer to water sources (Buuveibaatar et al. 2014). Wild Bactrian camels have large home ranges and prefer intermediate vegetation productivity in their habitat in southwestern Mongolia (Kaczencky et al. 2014). However, information on their ranges and habitat preferences remains rather limited.

The main predator of the ungulates in the Mongolia Gobi-Steppe ecosystem is the gray wolf (*Canis lupus*). The gray wolf is widely distributed in Mongolia (Davie et al. 2014), although wolf populations have declined due to intense hunting to protect livestock (Kaczensky et al. 2008, Davie et al. 2014). Wolf density may influence habitat selection and the movements of the ungulates. However, basic information on gray wolf ecology is lacking in Mongolia.

1.3.1.3 Impacts of livestock on vegetation and wildlife

Traditional nomadic pastoralism characterized by low human and livestock density has been the major human activity in Mongolia's Gobi Steppe Ecosystem. The lifestyle has been sustained for thousands of years (Rao et al. 2015). However, livestock numbers, particularly goats, have been increasing following the transition into a market economy in 1990 (Figure 1.2, National Statistics Office of Mongolia 2018). Sheep numbers have also increased after 2000, and the total number of the five major livestock species in Mongolia—horse, cattle, camel, sheep, and goat—is approximately 66 million in 2017. Overgrazing, following increased livestock numbers, has led to changes in vegetation composition (Sasaki et al. 2008) and land degradation (Hilker et al. 2014), and could influence herbivore habitat selection. Increasing livestock numbers and decreasing

vegetation could also enhance forage resource competition between wild and domestic ungulates, as the overlaps in forage plant categories (Compos-Arceiz et al. 2004, Yoshihara et al. 2008) or species (Sugimoto et al. 2018) become greater between sympatric species with similar body sizes and close taxonomic groups has been reported in Mongolia.

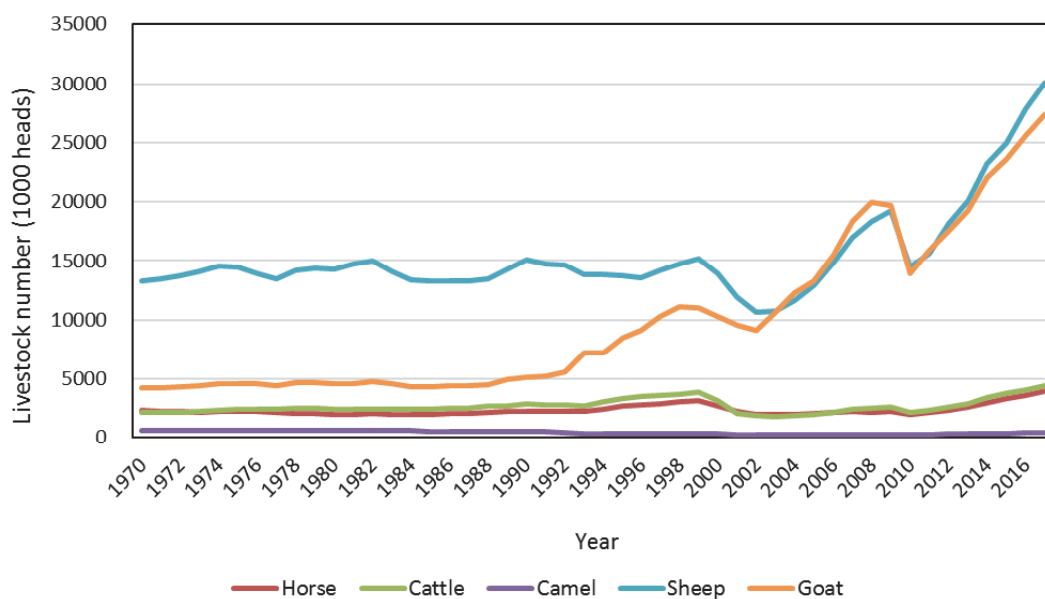


Figure 1.2 Changes in numbers of the five major livestock species in Mongolia from 1970 to 2017 (from National Statistics Office of Mongolia 2018).

1.3.1.4 The Mongolian gazelle as the study species

The Mongolian gazelle is the study species in the present thesis (Fig. 1.3). The species inhabits typical steppe and desert steppe in Mongolia, northern China, and southern Russia (IUCN SSC Antelope Specialist Group, 2016) and moves over several hundred kilometers (Ito et al. 2006, Olson et al. 2009, Teitelbaum et al. 2015). The species tends to make large herds, and herd sizes change seasonally and regionally —larger in the northeast than in the southwest (Lhagvasuren and Milner-Gulland 1997, Olson et al.

2005). In the 2007 drought year, in September, a herd consisting of more than 200,000 gazelles was reported in northeastern Mongolia (Olson et al. 2009). The body weight of a Mongolian gazelle in peak conditions is approximately 45 kg and 37 kg for males and females, respectively (Lhagvasuren and Milner-Gulland 1997). The males mature sexually at 2.5 years and bear a pair of horns. The females mature at 1.5 years and do not have horns. Mongolian gazelles seem to be polygynous; however, their community structure remains unclear (Lhagvasuren and Miler-Gullaand 1997). The Mongolian gazelle is a strong seasonal breeder and rutting season is from mid-November to the beginning of February. Females usually give birth from mid-June to mid-July (Lhagvasuren and Milner-Gulland 1997).



Figure 1.3 Mongolian gazelles in Tuv Province in central Mongolia. All gazelles are females or calves except one male that has horns. *Stipa krylovii* (short grass) and *Achnatherum splendens* (tall grass) are dominant species in the photographed area.

The current population is estimated at 400,000–2,700,000, and the current status on the IUCN Red List is least concern (IUCN SSC Antelope Specialist Group, 2016). However, the population declined from about 1,000,000 in the 1940s to about 200,000 in 1980s (Milner-Gulland and Lhagvasuren 1998). The distribution range also declined from 780,000 km² in the 1950s to 190,000 today. The eastern steppe is the current main habitat of the Mongolian gazelle in Mongolia, and a small population is distributed in western Mongolia (IUCN SSC Antelope Specialist Group, 2016).

There are several threats to the conservation of the Mongolian gazelle. An international railroad transects the gazelles' main distribution area from north to south and fences surround the railroad, which curtails the movement of the gazelles (Ito et al. 2005, 2008, 2013a, Batsaikhan et al. 2014). In addition, new railroad and mining projects that are underway in south Mongolia portend further habitat fragmentation (Ito et al. 2013a, Batsaikhan et al. 2014). Habitat degradation by overgrazing by livestock is also a key concern (Hilker et al. 2014). Mongolian gazelles have been hunted for a long time. Although the national government has brought hunting under control, illegal and unrecorded hunting activities persist. Diseases such as foot and mouth disease may negatively influence population numbers (Nyamsuren et al. 2006).

The movement patterns of Mongolian gazelles have been identified as nomadic due to large annual variations in climatic conditions, low temporal predictability of environmental conditions, and coarse spatial variation in environmental conditions (Mueller and Fagan et al. 2008, Mueller et al. 2011). Interannual variation in seasonal ranges (Olson et al. 2010, Ito et al. 2013a) or uncoordinated movements of individuals have been reported (Mueller et al. 2011). Mongolian gazelles prefer areas with intermediate normalized difference vegetation index (NDVI) values in spring and autumn (Mueller et al. 2008) and avoided areas with prolonged snow-cover (Ito et al. 2018). In addition, seasonal changes in vegetation conditions between summer and winter ranges, based on NDVI, corresponded to seasonal movements (Ito et al. 2006, 2013b). However, the movement patterns and strategies of Mongolian gazelles may vary between populations, since climatic and vegetation conditions in the gazelle's distribution area vary regionally. Therefore, in the present study, I focus on movement

patterns and strategies of Mongolian gazelles across the wide distribution range of the gazelle.

1.3.2 Approaches and techniques for addressing the challenges

1.3.2.1 Regional comparison of movements

Determination of the spatial variation in vegetation conditions and the continuous distribution of Mongolian gazelles would facilitate the examination of relationships between gazelle movements and vegetation conditions. To examine the relationships, I collected data on the movements of 20 Mongolian gazelles captured over a wide range of distribution (about 222,000 km²), which included different vegetation zones, ranging from typical steppe to desert (Fig 1.1).

1.3.2.2 Satellite technology

Recent technological advances have facilitated the development of reliable tracking devices for long-distance animal movements, which had been difficult to achieve based on direct observations of individual movements. Satellite tracking technologies such as Argos system (CLS 2007) and Global Positioning System (GPS) are effective tools for the observation of long-distance animal movements of ungulates, birds, and fishes (Kays et al. 2015). The sizes of devices such as transmitters and receivers have considerably reduced while their performance has improved. Using such tracking technologies, we could obtain location information of target individuals over prolonged periods.

Remote sensing, based on satellite technologies, has also facilitated the continuous collection of environmental information over a wide range. For example, NDVI is an efficient indicator of vegetation biomass (Cihlar et al. 1991, Reed et al. 1994). Moderate Resolution Imaging Spectroradiometer (MODIS), which operates aboard both the Terra and Aqua satellites, has provided useful NDVI data for researchers. Terra was launched in 1999 while Aqua was launched in 2002. MODIS provides NDVI data at a 250-m spatial resolution and a 16-day composite. The higher spatial resolution in MODIS compared to that of a former dataset derived from satellites such as advanced very high resolution radiometer (AVHRR), operated by National Oceanic and Atmospheric Administration (NOAA) (1.09 km spatial resolution), facilitated our analysis of the vegetation conditions at a finer spatial scale. NDVI data has been analyzed as an important environmental factor in studies on animal ecology including movement ecology (Boone et al. 2006, Mueller et al. 2011, Pettorelli et al. 2011, van Moorter et al. 2013).

By combining the satellite tracking and remote sensing data on environments, we could study the relationship between long distance animal movement and environmental factors. Relationships between animal movements and satellite derived NDVI data have been studied, with discernible trends in numerous animals (for example, wildebeests in Serengeti, East Africa (Boone et al. 2006), red deer in Sweden and Norway (Bischof et al. 2012)). MODIS NDVI data have been employed to understand the movements of Mongolian gazelles (Ito et al. 2005, 2006, 2013b, 2018, Mueller et al. 2011). In the present study, I employed MODIS NDVI datasets in the same period, from 2003 to 2012, over a wide range in Mongolia, while tracking gazelle movements.

1.3.2.3 Statistical modeling approach

It had been challenging to interpret animal movement patterns and important areas based solely on location data. However, statistical modeling approaches facilitate the determination of seasonal ranges and periods of movement and stay periods based on animals' location data. In the present study, I applied two statistical models that have been developed recently including net squared displacement (NSD) modeling and Brownian bridge movement model (BBMM).

The NSD modeling approach facilitates the classification of individual movements into several movement types (migratory, dispersive, sedentary, etc.) (Bunnefeld et al. 2011). Movement pattern of Mongolian gazelles have been evaluated based on the overlap of seasonal ranges between years (Olson et al. 2009, Ito et al. 2013b) or movement coordination among individuals (Mueller et al. 2011), which were not based on individual movement patterns. To assess individual movement patterns, seasonality and regularity in annual movements are critical factors, and the NSD model approach could effectively identify the movement types of individual Mongolian gazelles and regional differences. Similarly, BBMM facilitates the identification of stay periods and stopover sites based on location data (Horne et al. 2007, Sawyer et al. 2011). In previous studies on Mongolian gazelles, seasonal ranges were defined based solely on seasons, for example, summer as from June to August (e.g., Ito et al. 2006, 2013b). However, such an approach does not reflect actual resident periods and gazelles' movement patterns. To determine the actual periods and areas of movement and residence, BBMM would be effective and could facilitate the evaluation of gains or losses based on movements.

1.3.2.4 Quantification of benefit based on movement

To understand movement strategies, benefit evaluations of individual movements are necessary, although they may be challenging to carry out. Several indices have been used in benefit evaluations of movements. For example, rump fat thickness in moose (White et al. 2014, Middleton et al. 2018), visual assessment of body condition in impala (*Aepyceros melampus*) (Gaidet and Lecomte 2013), and predation risk by wolf in elk (Hebblewhite et al. 2009) have been employed to evaluate benefits based on the movements of the species in their ranges. However, collecting such indices is challenging in the case of Mongolian gazelles because direct observation of individual gazelle conditions and collecting predator information are difficult.

In herbivores that move over long distances in grassland ecosystems, changes in the vegetation index could be a benefit index based on movements. The cumulative instantaneous rate of green-up (CIRG), which is determined using satellite derived NDVI, explained the migration of “surfer” red deer and the existence of “jumper” deer in Norway (Bischof et al. 2014). CIRG could be a suitable index in humid environments with high spatiotemporal predictability. However, CIRG would not be effective in arid environments with low spatiotemporal predictability since green-up waves are unclear, and plants do not mature adequately in some areas and years. Therefore, I firstly analyzed the preferable range of NDVI for Mongolian gazelles in the plant growing season. Subsequently, I evaluated benefit by comparing the differences between the actual NDVI values and the preferred NDVI ranges based on movements.

1.4 Thesis structure

To achieve the general objective, which is understanding the relationships between movement patterns of Mongolian gazelles and spatiotemporal heterogeneity of vegetation conditions, I categorized the movement patterns into three elements, including general movement patterns (migratory or nomadic), movement distances (annual home range size), and movement strategies, in the plant growing season (Fig. 1.4). For temporal predictability, I focused on two different temporal scales including seasonal changes and interannual variability. For spatial heterogeneity, I examined environmental gradients and heterogeneity within vegetation zones. Thereafter, I explored the relationships among the above factors and their regional differences.

In Chapter 2, I applied statistical modeling approaches to obtain the overall patterns of movement of Mongolian gazelles. In chapter 3, I compared annual range size and vegetation conditions, while in Chapter 4, I explored the movement strategies of gazelles in the plant growing season. In the General Discussion, I combined the results from Chapter 2 to 4, and discussed the relationships among gazelle movements, spatiotemporal heterogeneity, and predictability of environmental conditions.

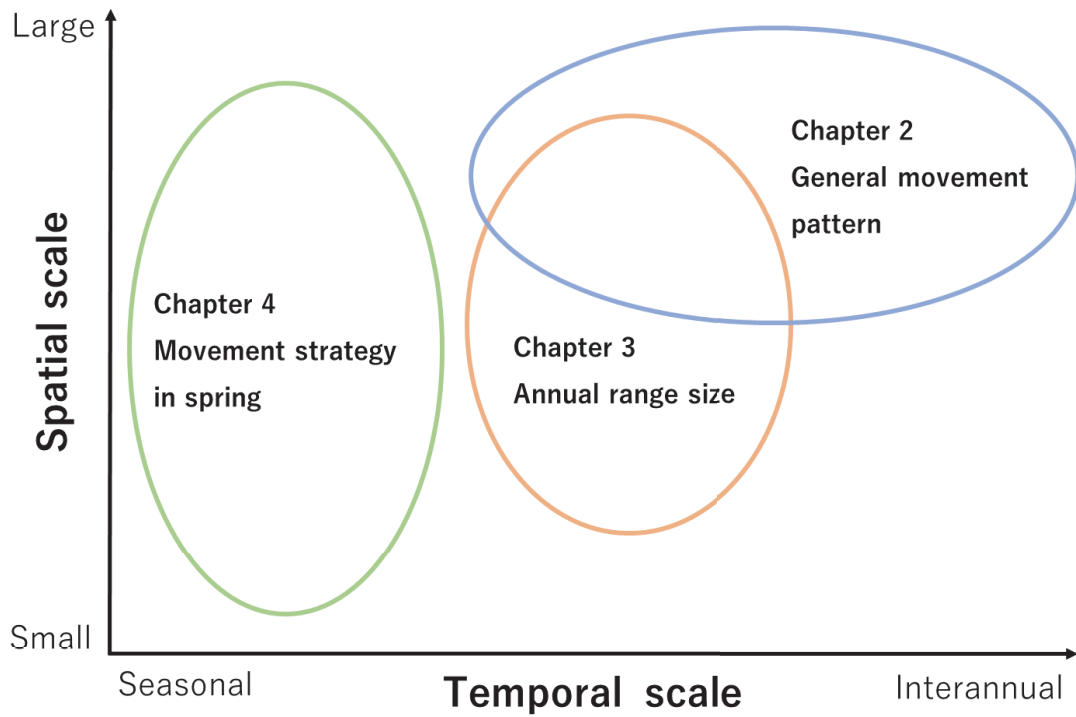


Fig 1.4 Structure of the present thesis. Different spatiotemporal scales of movement and vegetation factors are analyzed in each chapter.

Chapter 2

Nomadic movement of Mongolian gazelles identified through the net squared displacement approach

This chapter is based on: Shunsuke Imai, Takehiko Y. Ito, Toshihiko Kinugasa, Masato Shinoda, Atsushi Tsunekawa and Badamjav Lhagvasuren

Abstract

The Mongolian gazelles (*Procapra gutturosa*) that inhabit Mongolia's steppe and semi-desert travel several hundred kilometers each year, and their movement pattern has been considered to be nomadic, but the details of their movement patterns remain unclear. The aim of this study was to gain an overall perspective of the movement of Mongolian gazelles, which experience diverse environmental conditions with large interannual variations across their continuous distribution range. Based on net squared displacement (NSD) modeling approach, the mixed migration type was the most observed type in the statistical assignment among five movement types, and some movements were assigned into the migration or sedentary types. However, NSD seasonal change was irregular in the most annual movements of gazelles, suggesting the nomadic movements of individuals. Most gazelles tracked for more than a year changed their movement types annually, and the movement period differed among individuals. These results also support nomadic movement of the species, although some difficulties of modeling nomadism by using the NSD approach were revealed.

Key words: dryland, grassland, migration, net squared displacement, nomadism, *Procapra gutturosa*, satellite tracking, ungulate

2.1 Introduction

Improving understanding of the relationships between animal movement patterns and environmental conditions is a key goal in movement ecology and is necessary for the conservation of target animal species (Nathan et al. 2008; Milner-Gulland et al. 2011). Both spatial heterogeneity and temporal predictability of resources affect animal movement patterns (Mueller and Fagan 2008). Typical seasonal migrations are predictable and occur in areas with obvious seasonal change, spatial heterogeneity along the migration path, high temporal predictability of resources, and sufficient forage productivity.

In contrast to migration, nomadism is generally defined as unpredictable movements without specific seasonal changes. The unpredictable movements of nomadism consist of two irregularity—variation among individuals for any given year (type I nomadism) and variation among years for any given individual (type II nomadism). Nomadism is likely to occur in areas with low temporal predictability of environmental conditions (Mueller and Fagan 2008). However, this relationship has not been fully confirmed.

The Mongolian gazelle (*Procapra gutturosa*), which inhabits steppe and semi-desert, is an interesting species to study in terms of movement ecology; the animals move several hundred kilometers annually (Ito et al. 2006; Mueller et al. 2011; Batsaikhan et al. 2014; Teitelbaum et al. 2015; Imai et al. 2017), and their annual range size differs markedly and regionally across the species' continuous distribution range (Imai et al. 2017). The species' movement pattern has been considered as nomadic (Mueller et al. 2011; Olson et al. 2010a; Ito et al. 2013a), but co-existence of short- and long-range movement types in southern Mongolia was recently reported (Ito et al. 2018). Therefore, different movement types, other than nomadism such as migration and

sedentary types, and regional differences in proportion of movement types may exist in Mongolian gazelles. However, the detailed movement patterns of individuals and populations have not been clarified.

Net squared displacement (NSD) is an effective method for analyzing animal movement (Bunnfeld et al. 2011). This modeling approach can be used to classify animal movement types. Indeed, it has revealed the presence of partial migration (Myrsterud et al. 2011), regional differences (Singh et al. 2012), and interannual changes (Eggeman et al. 2016) in the movement types of ungulates.

However, the model for nomadism by NSD has not been developed. In the previous studies, the linear increase functions of NSD to the time series were used as the model for nomadism (e.g., Bunnfeld et al. 2011; Singh et al. 2012). The classification of movements into migration and sedentary by the NSD models would be useful in environments with relatively high predictability of seasonal and interannual changes. However, in environments with low temporal predictability where most animals move nomadic, the linear increase function of NSD would not be suitable to describe nomadism. Thus, we applied the NSD approach with careful inspection of each movement pattern for identifying details of movement of Mongolian gazelles.

To gain an overall perspective on the movement pattern of Mongolian gazelles across their broad continuous range, we classified gazelles' annual movements by using the NSD modeling approach. We also discuss the gazelles' movement pattern in relation to the environmental conditions in their habitat as well as the effectiveness and limitations of the NSD modeling approach for studying Mongolian gazelles.

2.2 Materials and methods

2.2.1 Study area

The study area was the eastern half of Mongolia (Fig. 2.1). The region is about 1000 m above sea level, and the climate is strongly continental and dry; the maximum temperature exceeds 40 °C in summer and the minimum temperature is below –35 °C in winter. Annual precipitation increases from 100 mm in the southern desert steppe to 300 mm in the northern forest steppe (Nandintsetseg et al. 2011), and winter snowfall is greater in the north (more than 30 cm in severe winters) than in the south as well (Nandintsetseg et al. 2017). Therefore, the seasonal change in environmental conditions is greater in the north. The vegetation types are typical of steppe and semi-desert. Grasses and forbs (e.g., *Stipa* spp., *Carex* spp., *Allium* spp., *Artemisia* spp.) dominate in the typical and dry steppe regions of the north, whereas shrubs (e.g., *Caragana* spp., *Anabasis brevifolia*) dominate in the desert steppe of the south (Olson et al. 2010b).

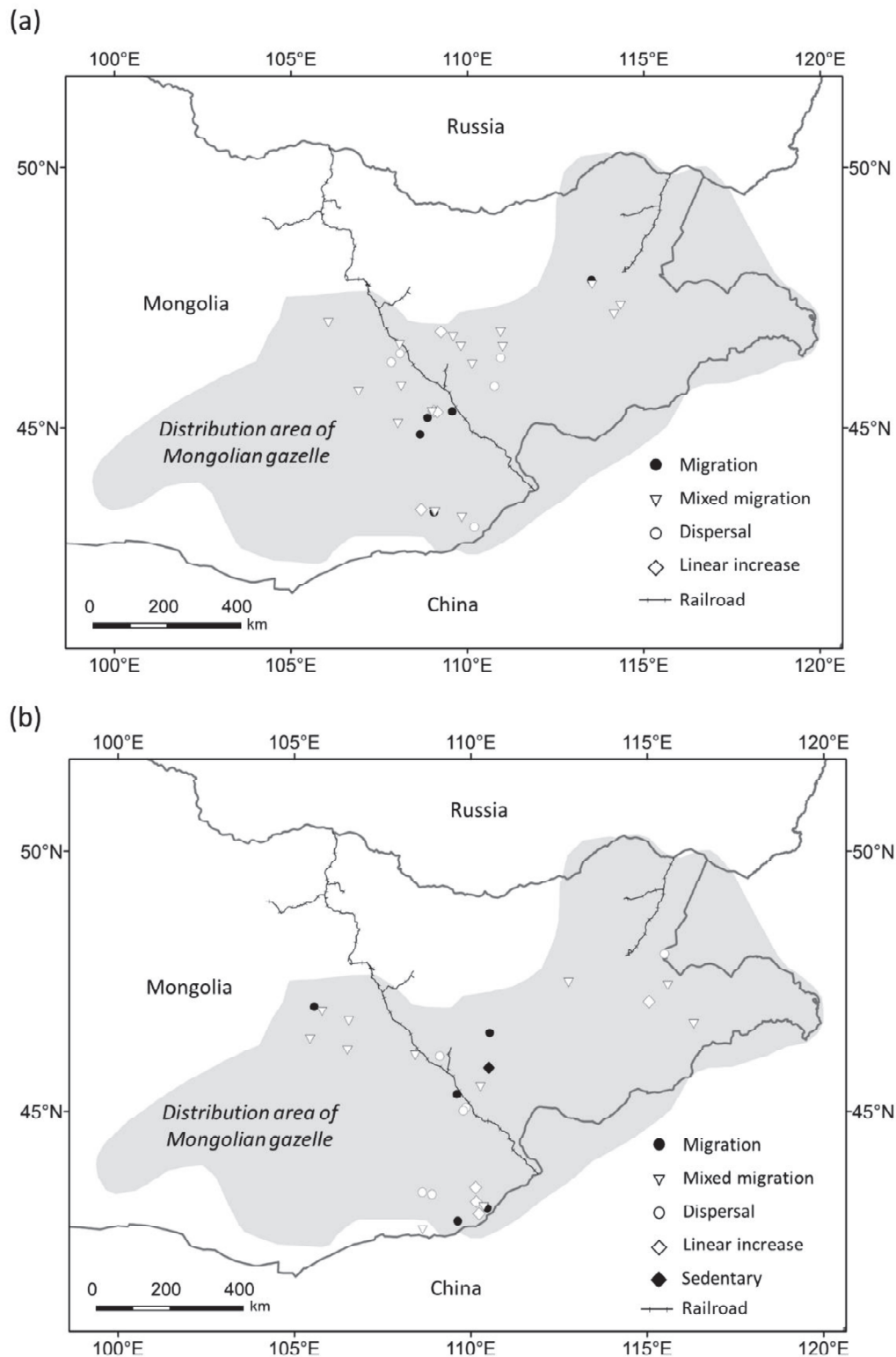


Figure 2.1. Spatial distribution of movement types of Mongolian gazelles tracked from 2002 through 2010. The symbols indicate start points for the (a) winter-start and (b) summer-start cases; gray shading indicates the distribution area of Mongolian gazelles.

2.2.2 Mongolian gazelles

The Mongolian gazelle inhabits the typical steppe to desert regions of Mongolia, northern China, and southern Russia (IUCN SSC Antelope Specialist Group 2016), and, in general, individuals move 100 to 500 km annually within these regions (Ito et al. 2006; Mueller et al. 2011; Teitelbaum et al. 2015). The total population decreased from about 1.5 million head in the 1940s to between 300 000 and 500 000 in the 1990s (Lhagvasuren and Milner-Gulland 1997; Jiang et al. 1998; Olson et al. 2005). The population in the 2000s was considered stable and was estimated to be 400 000 to 2 700 000 (IUCN SSC Antelope Specialist Group 2016). An international railroad between Russia and China runs through the distribution range of the Mongolian gazelle (Fig. 3.1), and barbed-wire fences alongside the railroad tracks prevent livestock accidents but are barriers to movements of wild ungulates, such as Mongolian gazelles and Asiatic wild asses (Ito et al. 2005, 2008, 2013b; Kaczensky et al. 2010).

2.2.3 Movement data of gazelles

We captured 20 gazelles (6 male and 14 female) from a wide range of habitats and attached a collar with a satellite transmitter (platform terminal transmitter: model ST-18, ST-20, or A3210, Telonics, Mesa, AZ, USA) (Kaczensky et al. 2010; Ito et al. 2013b; Imai et al. 2017) during each of the years 2002, 2003, and 2007. We programmed each transmitter to transmit radio signals for an 8-h period every seven or eight days and obtained location data from October 2002 through December 2010 (Table 2.1). Location data were ranked from 3 to 0 according to estimation errors: <250 m for location class (LC) 3, from 250 to <500 m for LC 2, from 500 to <1500 m for LC 1, and ≥ 1500 m for LC 0 (Collecte Localisation Satellites). Less accurate data without estimation error were

provided as LC A and B due to the difference of number of messages received per satellite pass. We selected the most accurate LC data of each day for each gazelle; when we had multiple location data for the same LC on a particular day, we chose the last location. We included the LC A (5.4%) and B (5.7%) location data in our analyses, because the ratios of such low-accuracy data to all location data were relatively large for some gazelles but still fell into the annual home ranges delineated without using data of LC A and B.

2.2.4 Movement models

We classified the movements of individual gazelles during a year by using NSD pattern modeling (Bunnefeld et al. 2011). NSD measures the straight-line distance between the starting location and subsequent points along the movement path of individual animals. NSD changes as the animal moves, and the pattern of the NSD change within a period differs between movement types (Fig. 2.2).

We classified the gazelles' annual movements into five types (migration, mixed migration, dispersal, residency, and linear NSD increase) by using NSD pattern models (Fig. 2.2). Linear increase of NSD with time was used as a model of nomadism in Bunnefeld et al. (2011) and other previous studies (e.g. Singh et al. 2012, 2016). However, nomadic movements that are generally defined as unpredictable movement (Mueller and Fagan 2008) are not demonstrate linear NSD increase with time logically. Thus, we used the word "linear increase" instead of "nomadism" for the model in the analysis in the present study.

According to NSD modeling, the migration pattern includes two movement periods (i.e., first and second movement periods) and two resident periods within a year (Fig.

2.2), and gazelles returned to the starting locations. Like the migration pattern, mixed migration is a double-sigmoid function, with two movement periods and two resident periods in a year, but the animal does not return to the starting location. In the dispersal movement type, the animal moves to a different region once during a year, and the NSD model for this pattern is a logistic curve. The linear NSD increase does not have any resident periods, and the model is a simple linear equation with a zero intercept. The residency movement type stays within the range during the year, such that the NSD does not increase during the entire term.

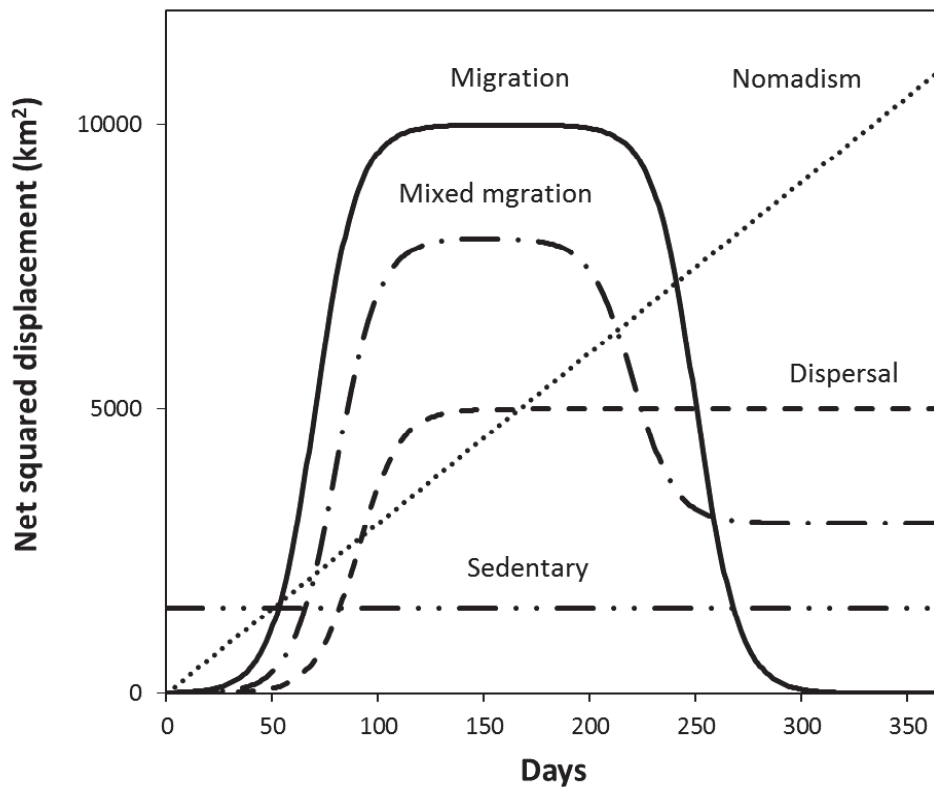


Figure 2.2. Examples of net squared displacement plots of the five movement types (modified from Bunnefeld et al. 2011).

2.2.5 Classification of movement types and statistical analysis

The start point of an NSD pattern should be set in the resident period (Bunnefeld et al. 2011), but the primary time of the starting movement of the tracked Mongolian gazelles was unclear. We considered the cases in which gazelles had resident periods in both summer and winter or in either season and analyzed their NSD patterns over a year in two different periods, that is, from 1 June (summer-start case) and from 1 December (winter-start case), because previous studies on Mongolian gazelles have suggested the importance of winter and summer ranges (Leimgruber et al. 2001, Ito et al. 2006). When gazelles were tracked for at least two years, we analyzed separately for each year.

We classified the movement type of each movement by following Bunnefeld et al. (2011). We fitted each annual movement to nonlinear least squares models (*nls* function in R) of the five movement types and calculated the Akaike information criterion (AIC) of each model by using the statistical software package R (R Development core Team 2015). We assigned the movement type with the smallest AIC for each movement.

2.3 Results

2.3.1 Movement patterns of Mongolian gazelles

We obtained 27 and 31 annual movements for winter- and summer-start cases, respectively. The tracked gazelles demonstrated all five types of movement for both summer- and winter-start cases except sedentary type for the summer-start cases (Table 2.1, Figs. 2.3 and 2.4), although several annual movements had closely high values of Akaike weight for two movement types. Mixed migration was the most frequent movement type in both the winter-start (40.7%) (two males and nine females) and

summer-start (54.8%) (three males and 14 females) cases, which occurred widely throughout the study area (Fig. 2.1). Migration type comprised 18.5% (five females) of the winter-start case and 16.1% (five females) of the summer-start case (Table 2.2). Dispersal type was observed in both sexes (two males and three females) in the summer-start case and various ages (Table 2.1). Only one movement was assigned to sedentary type.

NSD patterns of movements assigned as mixed migration, dispersal, and linear increase showed irregular movement without fixed seasonal ranges (Figs. 2.3 and 2.4). The timing of mixed migration and dispersal movements was not concentrated within specific periods. A gazelle assigned to the sedentary type moved to 126 km from the start site, which was not shorter than all movements assigned into other movement types, and showed irregular movement.

Some gazelles assigned to the migration type moved more than 300 km stayed in the winter range for more than six months and returned to the start site (Figs. 2.3 and 2.4). For individual animals that were classified as the migration type in a year and tracked for at least two years were assigned into different movement types in other years (Table 2.3). When all movement types were counted, nine of the ten summer-start cases and seven of the eight winter-start cases changed the movement type between years (Table 2.3).

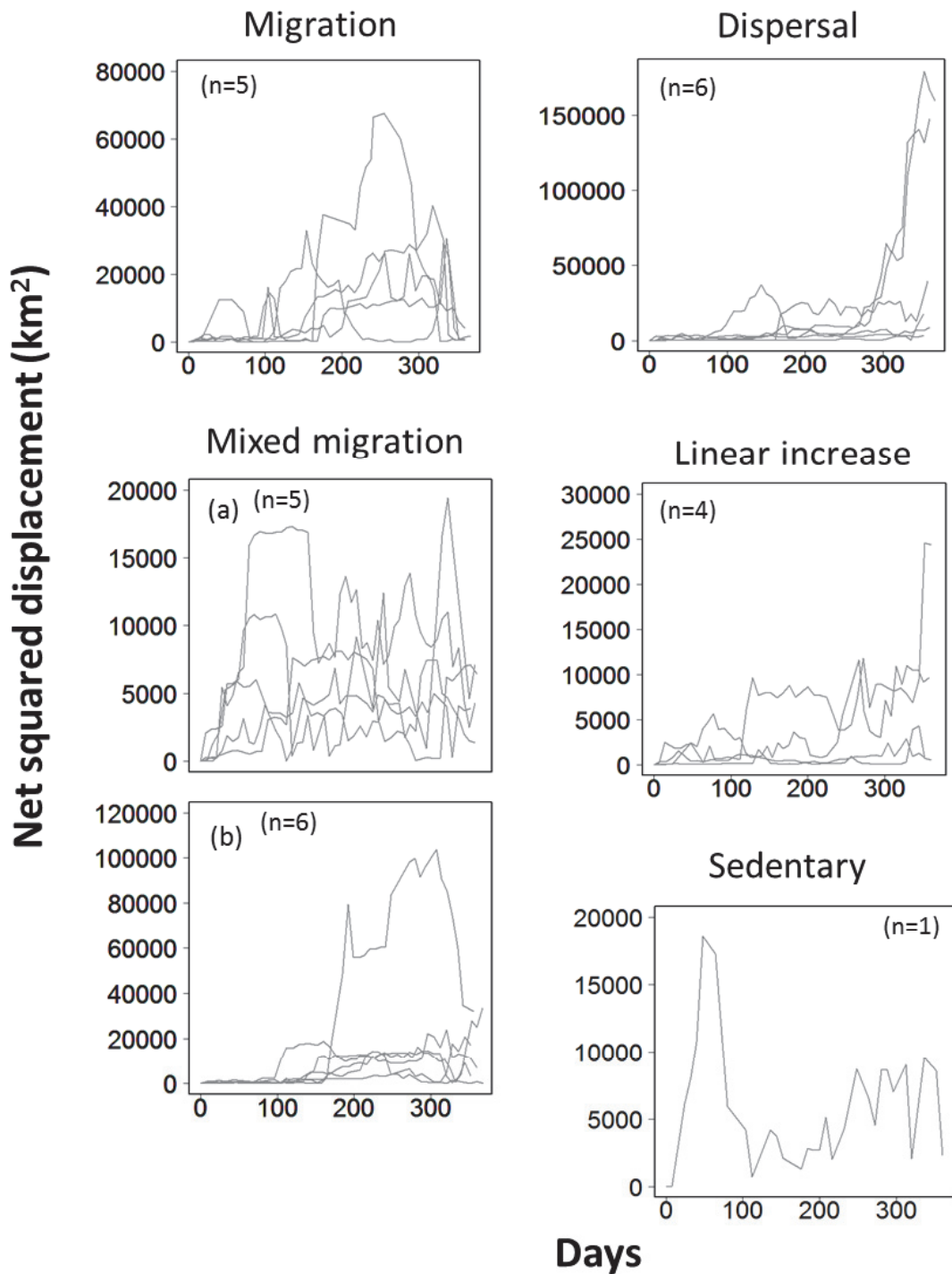


Figure 2.3. Observed net squared displacement plots of summer-start cases of Mongolian gazelles tracked from 2002 to 2010. The plots were assigned to each movement type. The mixed-migration plots were separated into two types: a, start movement before 100 day, and b, start movement after 100 day. Days indicates the cumulative number of days since 1 June is indicated.

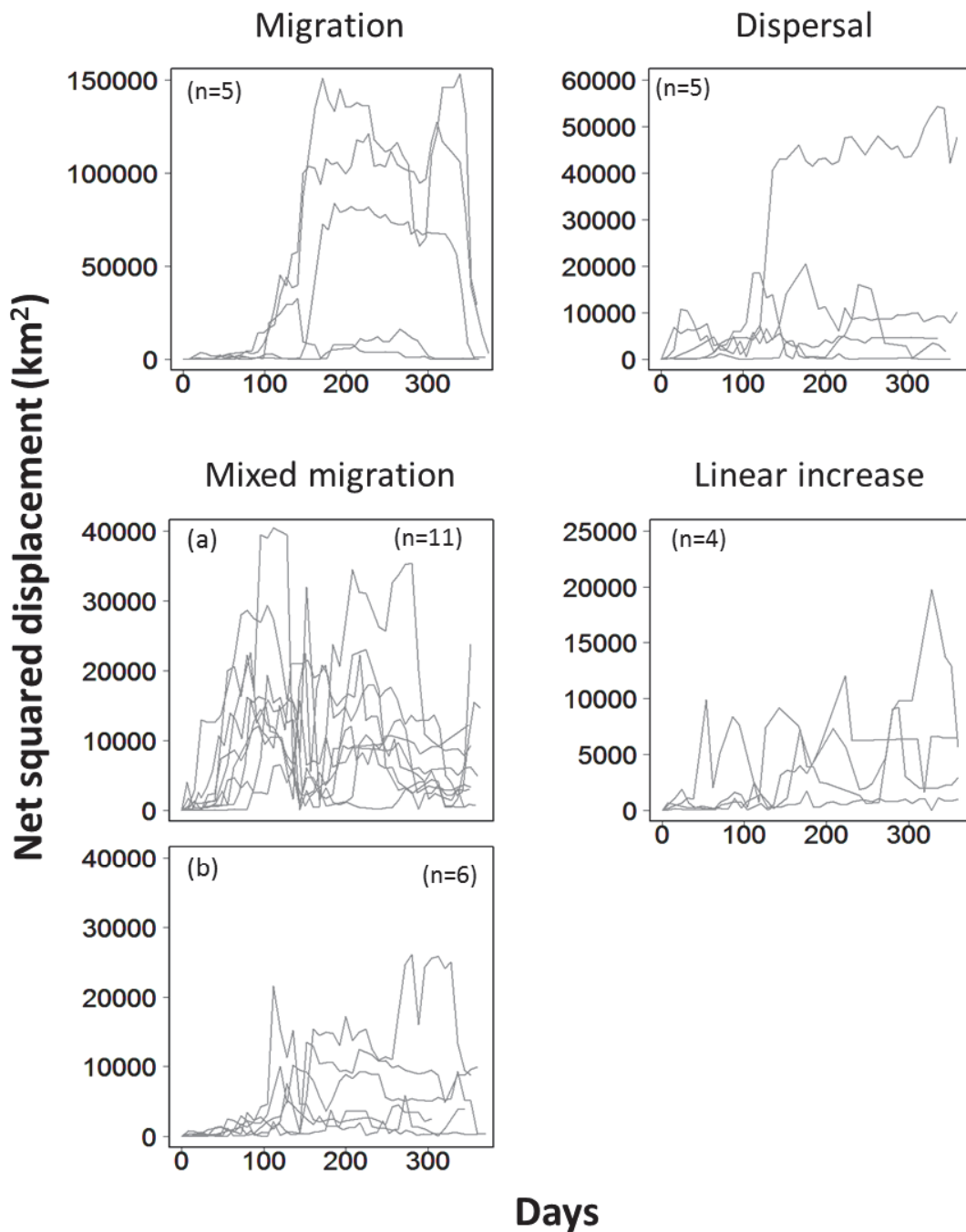


Figure 2.4. Observed net squared displacement plots of the winter-start cases of Mongolia gazelles tracked from 2002 to 2010. The plots were assigned to each movement type. The mixed-migration plots were separated into two types: a, start movement before 100 day, and b, start movement after 100 day. Days indicates the cumulative number of days since 1 December.

Table 2.1. The start season, year, and AIC weight of each movement type of Mongolian gazelles. s; summer-start case. w; winter-start case, F; female. M; male, *, models did not converge.

ID	Start point	Year	Sex	Age (Years)	Migration	Mixed migration	Dispersal	Linear increase	Sedentary
25363	S	2004	F	3-4	0.006	0.938	0.057	0.000	0.000
	S	2005		4-5	0.000	1.000	0.000	0.000	0.000
	W	2003		2-3	0.000	1.000	0.000	0.000	0.000
	W	2004		3-4	0.000	*	0.000	1.000	0.000
25448	W	2004	M	3	0.000	0.797	0.181	0.001	0.021
37571	S	2003	F	2-3	0.000	0.961	0.038	0.000	0.000
	S	2004		3-4	0.902	0.097	0.000	0.000	0.000
	W	2002		1-2	1.000	0.000	0.000	0.000	0.000
	W	2003		2-3	0.000	*	1.000	0.000	0.000
	W	2004		3-4	0.644	0.356	0.000	0.000	0.000
37572	S	2003	F	adult	0.999	0.001	0.000	0.000	0.000
	W	2002		*	0.948	0.049	0.003	0.000	
41243	S	2004	F	3-4	0.947	0.053	0.000	0.000	0.000
	S	2005		4-5	*	1.000	0.000	0.000	0.000
	W	2003		2-3	0.000	0.000	1.000	0.000	0.000
	W	2004		3-4	0.000	1.000	0.000	0.000	0.000
42645	S	2003	F	adult	1.000	*	0.000	0.000	0.000
	S	2004			0.269	0.727	0.004	0.000	0.000
	W	2003			0.000	*	1.000	0.000	0.000
	W	2004			0.132	0.867	0.001	0.000	0.000
67920	S	2007	F	1	*	*	*	0.986	0.014
67921	S	2007	F	2	0.000	0.882	0.118	0.000	0.000
	S	2008		3	0.072	0.927	0.000	0.000	0.000
	S	2009		4	*	*	0.997	0.000	0.002
	W	2007		2	*	*	0.996	0.004	0.000
	W	2008		3	0.000	1.000	0.000	0.000	0.000
67923	S	2007	M	1	0.000	*	0.712	0.113	0.176
	W	2007		1	0.000	0.000	0.000	0.002	0.998
67925	S	2007	F	1	0.000	*	0.002	0.998	0.000
67926	S	2007	M	1	0.000	*	0.071	0.915	0.014
67927	S	2007	M	2	0.000	*	1.000	0.000	0.000
	S	2008		3	0.000	1.000	0.000	0.000	0.000
	W	2007		2	0.455	0.543	0.001	0.000	0.000
67928	S	2007	F	adult	0.000	*	0.983	0.009	0.008
	S	2008			0.321	0.679	0.000	0.000	0.000
	W	2007			0.000	0.967	0.033	0.000	0.000
	W	2008			0.003	0.997	0.000	0.000	0.000
67929	S	2007	M	1-2	0.015	0.985	0.000	0.000	0.000
67931	S	2007	F	1	0.011	0.989	0.000	0.000	0.000
	S	2008		2	0.000	1.000	0.000	0.000	0.000
	W	2007		1	0.757	0.243	0.000	0.000	0.000
67932	S	2007	F	adult	0.000	0.995	0.005	0.000	0.000
67933	S	2007	F	adult	0.061	0.939	0.000	0.000	0.000
78510	S	2008	F	3-4	0.002	0.686	0.309	0.003	0.001
	S	2009		4-5	0.000	1.000	0.000	0.000	0.000
	S	2010		5-6	*	*	0.622	0.318	0.060
	W	2007		2-3	0.131	0.869	0.000	0.000	0.000
	W	2008		3-4	0.603	0.397	0.000	0.000	0.000
	W	2009		4-5	*	*	0.000	0.955	0.045
	W	2010		5-6	*	*	0.010	0.769	0.221
	S	2008		3-4	1.000	*	0.000	0.000	0.000
78511	S	2009	F	4-5	0.000	0.999	0.001	0.000	0.000
	S	2010		5-6	*	*	0.005	0.995	0.000
	W	2007		2-3	0.000	*	0.115	0.885	0.000
	W	2008		3-4	0.001	0.980	0.009	0.003	0.007
	W	2009		4-5	0.667	0.333	0.000	0.000	0.000
	W	2010		5-6	*	*	1.000	0.000	0.000
78513	W	2007	M	1	*	*	1.000	0.000	0.000

Table 2.2. Incidence (number of cases) of each movement type among Mongolian gazelles tracked from 2002 to 2010.

Start season	Migration	Mixed migration	Dispersal	Linear increase	Sedentary
Winter	5	11	6	4	1
Summer	5	17	5	4	0

Table 2.3. Mongolian gazelles that changed movement type during the years tracked. D, dispersal; M, migration; MM, mixed migration; L, Linear increase.

Start season	ID	1st year	2nd year	3rd year	4th year
Summer	78510	MM	MM	D	
	78511	M	MM	N	
	67921	MM	MM	MM	
	25363	MM	MM		
	37571	MM	M		
	41243	M	MM		
	42645	MM	M		
	67927	D	MM		
	67928	D	MM		
	67931	MM	M		
Winter	78510	M	MM	N	N
	78511	N	MM	M	D
	37571	M	D	M	
	25363	MM	N		
	41243	D	MM		
	42645	D	MM		
	67921	D	MM		
	67928	MM	MM		

2.4 Discussion

Annual movements of the tracked gazelles were assigned into the all five movement types and there was no obvious difference in frequency among the movement type between in the winter and summer start cases. These suggest that there is no common movement pattern and no season when regularly come back to specific areas for most individuals. In addition, NSD seasonal change in most movements, especially those assigned to the mixed migration, linear NSD increase, and dispersal types (The three movement types accounted for 78 % of winter-starts and 84 % of summer-start cases), were much irregular than the typical seasonal change of NSD in the movement models (Figs. 2.3, 2.4), which indicate the characteristic of nomadic movement in the general concept. No noticeable bias to young male in the movements assigned to the dispersal type suggests that the movements in the dispersal type were rather nomadic than natal dispersal movement, although the limited sample size cannot give a clear conclusion. The timing of movement was also not synchronized among the gazelles, even in gazelles assigned in the same movement type. These results correspond to the general definition of nomadism: “unpredictable movements that vary among individuals for any given year (type I nomadism) or among years for any given individual (type II nomadism)” (Mueller and fagan 2008).

The movement type changed among years in the same individuals (Table 2.3) is another characteristic of the general definition of nomadic movement: type II nomadism described as “unpredictable movements that vary among years for any given individual” (Mueller and Fagan 2008). The movement of Mongolian gazelles likely satisfies the conditions of both types I and II, and therefore we concluded that the general movement pattern of Mongolian gazelle is nomadic.

Despite the nomadic movement of Mongolian gazelles, the linear increase type, which was originally used a model of nomadism (Bunnefeld et al. 2011), was low (14% of all movements). As we expected, it suggests the difficulty of modeling nomadism and the use of increasing linear function of NSD as the model of nomadism failed to express actual nomadic movement. However, the NSD approach remains useful for species in which most individuals in a population move nomadically, because it reveals irregular movements.

The nomadic movements of Mongolian gazelles likely are due to the large spatiotemporal variation in the environmental conditions of their habitat (Yu et al. 2004, Vandandorj et al. 2015, Ito et al. 2018). This pattern is quite different from typical migrations between two particular seasonal ranges (e.g., wildebeests, *Connochaetes taurinus*, in the Serengeti (Boone et al. 2006); moose, *Alces alces* (Singh et al. 2012); red deer, *Cervus elaphus*, in Sweden and Norway (Bischof et al. 2012) and from the annual gathering of many individuals in calving grounds (e.g., moose, White et al. (2014); Tibetan antelope, *Pantholops hodgsoni*, Schaller et al. (2006) or winter ranges (e.g., mule deer, *Odocoileus hemionus*, Sawyer et al. (2009)). Comparing the interannual variability of rainfall and vegetation biomass worldwide revealed that variability in the Mongolian gazelle habitat is high (von Wehrden et al. 2012), and this is likely the main factor underlying the nomadic movements, including interannual change of movement types in the same individuals, of Mongolian gazelles, which have pointed out in the previous studies (Mueller and Fagan 2008, Mueller et al. 2011, Ito et al. 2013a). Interannual change of spatial distribution of snow cover would also affect interannual change of movement types in the same individuals of Mongolian gazelles (Ito et al. 2018). It would be an interesting feature of animals inhabiting highly

unpredictable environments. To understand movement of Mongolian gazelles and other animals inhabiting habitat with large spatiotemporal variation of environmental conditions, analysis and accumulation of long-term tracking data at least two years of individuals and environmental conditions are needed.

Chapter 3

Effects of spatiotemporal heterogeneity of forage availability on annual range size of Mongolian gazelles

This chapter is based on: Shunsuke Imai, Takehiko Y. Ito, Toshihiko Kinugasa, Masato Shinoda, Atsushi Tsunekawa and Badamjav Lhagvasuren

Abstract

We analyzed the effects of forage amount and its spatiotemporal heterogeneity on the annual range size of Mongolian gazelles by tracking 20 gazelles over a wide range of their distribution in Mongolia and by applying the normalized difference vegetation index (NDVI). Annual ranges were separated into four regions. The maximum individual annual range size was more than 40 times the minimum (range: 900 to 37,000 km²). Annual range size was increased with increasing forage amount and spatial heterogeneity and seasonal change in forage amount. Many tracked gazelles changed their range locations between summer and winter, and these ranges occupied only small parts of their annual ranges. The smaller annual range size in the areas with smaller forage amount was explained by the smaller seasonal change and spatial heterogeneity of forage amount. Knowledge of such variations of movements and environments in a continuous distribution can improve our understanding of movement ecology.

Keywords: dryland, grassland, migration, movement pattern, NDVI, satellite tracking, Mongolian gazelle

3.1 Introduction

Animal home-range size varies both interspecifically (McNab, 1963; Harestad and Bunnell, 1979) and intraspecifically (Anderson et al. 2005, Börger et al. 2006, van Beest et al. 2011, Morellet et al. 2013). Forage availability is an important determinant of home range size (Tufto, Andersen and Linnell 1996, Anderson et al. 2005, Börger, Dalziel and Fryxell 2008). Theoretically, forage availability, which also affects animal movement patterns, consists of forage amount and the spatial heterogeneity and seasonal (temporal) change of this amount (Mueller and Fagan 2008, Mueller et al. 2011). Forage amount and its spatial heterogeneity affect home-range size in the short term (e.g., monthly or seasonally) (van Beest et al. 2011), and temporal heterogeneity of forage amount affects home-range size through seasonal changes in movement patterns (Avgar, Street and Fryxell 2014). Therefore, both spatial and temporal heterogeneities affect annual home-range size. However, the numbers of published analyses of the relationships between actual animal movements and spatiotemporal heterogeneity are limited. To understand the general relationships between animal home-range size and environmental conditions, studies in various environments are needed, because the relationships between spatial heterogeneity and its seasonal change vary among regions (Mueller et al. 2011).

The Mongolian gazelle (*Procapra gutturosa*) inhabits mainly the steppes of Mongolia (Milner-Gulland and Lhagvasuren, 1998, Jiang et al. 1998) and changes its range seasonally (Ito et al. 2006, 2013b, Olson et al. 2010). In all previous studies, only those gazelles in parts of the animal's main and widely continuous distribution area have been tracked (Olson et al. 2010, Mueller et al. 2011, Ito et al. 2013a); this area includes a vegetation gradient from typical steppe to desert (Milner-Gulland and

Lhagvasuren 1998) and appears to contain several populations (Ito et al. 2013a). Differences in the movement patterns of Mongolian gazelles among regions and among individuals have not yet been revealed because of the limited nature of the available animal tracking data. Tracking data showing the movement of gazelles over a wide distribution area would be invaluable for studying the relationship between forage availability and animal home-range size.

Here, we focused on the Mongolian gazelle's annual range size as an indicator of the effects of spatiotemporal heterogeneity of forage amount, and we tested three hypotheses regarding the effects of forage (vegetation) conditions on the animal's annual range. Under hypothesis 1), on the basis of the habitat productivity hypothesis (Harestad and Bunnell 1979), the annual range size of the Mongolian gazelle is smaller in areas with greater forage amounts. Under hypothesis 2), on the basis of the resource dispersion hypothesis (Macdonald, 1983), annual range size is greater where the spatial heterogeneity of forage amount is larger. Under hypothesis 3), annual range size is greater where seasonal change in forage amount is larger, because seasonal change of resource availability is a major driver of seasonal migration (Milner-Gulland et al. 2011).

In the distribution of Mongolian gazelles in Mongolia, vegetation amount and its seasonal change are larger on the northern steppe (Yu et al. 2004), and vegetation is scarce on the dry steppe and in the desert in the south. The gazelles' annual range size would be larger in the south, supporting hypothesis 1, if vegetation amount itself were the most important determinant of range size. However, it would be larger in the north, supporting hypothesis 3, if the seasonal change in vegetation amount were the most

important. Tests of these hypotheses, therefore, would give important information on the movement ecology of animals inhabiting dry, cold, and seasonal environments.

Our objective here was to determine the effects of forage amount and its spatiotemporal heterogeneity on the annual range size of Mongolian gazelles by testing our above-described hypotheses. Specifically, by using gazelle movement data collected over a wide area, we examined 1) individual differences in annual range size; 2) the relationships between annual range size and regional environmental conditions; 3) the importance of forage amount and its spatiotemporal heterogeneity to annual range size; and 4) the relationships between annual range size and the configuration of the gazelles' seasonal ranges.

3.2 Materials and Methods

3.2.1 Study area

The study area covered the eastern half of Mongolia (Fig. 3.1). The region is characterized by high elevation (about 1000 m above sea level) and vegetation change from forest steppe and typical steppe in the north to dry steppe and desert steppe in the south. Grasses and forbs (*Stipa* spp., *Allium* spp., and *Artemisia* spp.) dominate on the typical and dry steppe, and shrubs (*Caragana* spp.) dominate on the desert steppe (Olson, Murray and Fuller, 2010). The climate is strongly continental and arid, with hot summers (maximum temperatures above 40 °C) and severe winters (minimum temperatures below -35 °C). Annual precipitation increases from 100 to 300 mm from the southern desert to the northern forest steppe (Nandintsetseg and Shinoda, 2011). Temperatures are lower, with more snow, in the northern part (Morinaga, Tian and Shinoda 2003). Seminomadic pastoralists live over the whole study area, with a density

of 0.79 people/km² (National Statistical Office of Mongolia, 2010). The international railroad between Russia and China bisects the gazelle's habitat, and barbed-wire fences have been built alongside the railroad to prevent livestock accidents. The fences are barriers to wild ungulates such as Mongolian gazelles and Asiatic wild asses (Ito et al. 2005, 2008, 2013a).

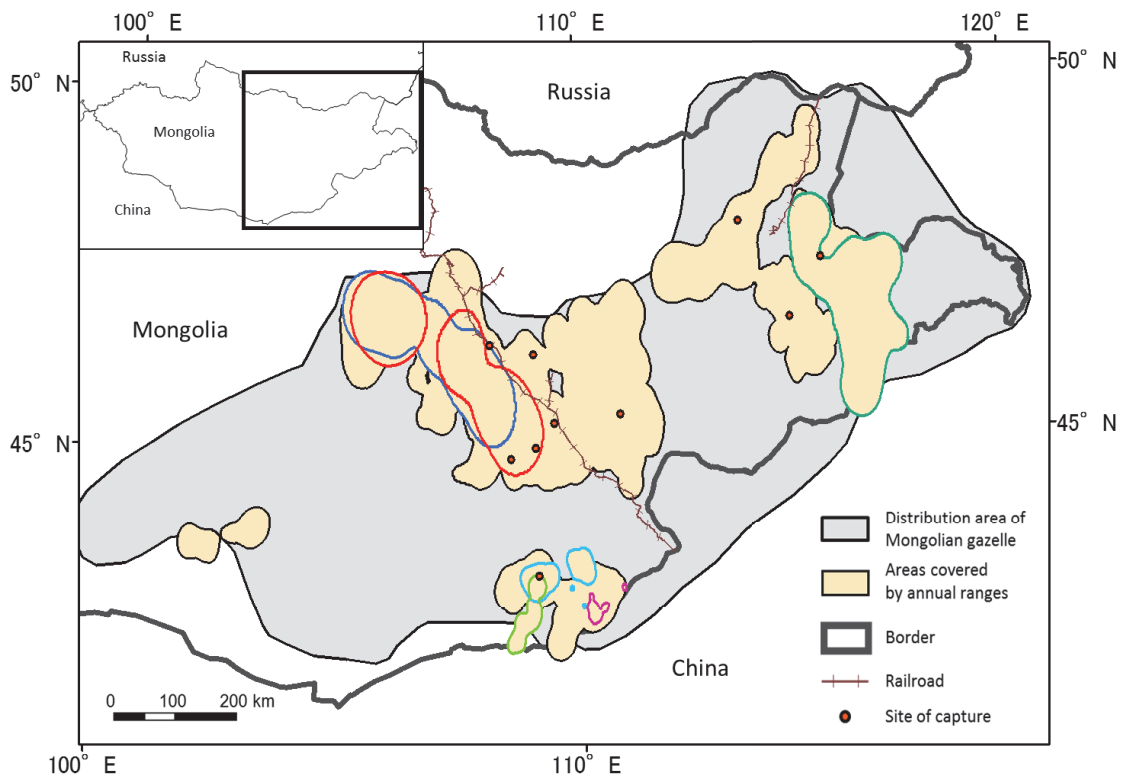


Figure 3.1. Study area and annual ranges of the tracked Mongolian gazelles. Distribution area of the Mongolian gazelle is derived from the work of Mallon (2008). Dark gray indicates merged areas of 35 annual ranges from 20 gazelles. Areas surrounded by dashed lines are the largest three and single bar lines are smallest three annual ranges of individuals (95% fixed-kernel range). Different style and thickness of the lines indicate different individuals and the thickest lines are the largest and the smallest annual ranges; the fixed-kernel ranges of two of these individuals are each separated into two areas because of the nature of the distribution patterns of the location data.

3.2.2 Mongolian gazelle population and home ranges

Mongolian gazelles (*P. gutturosa*) inhabit the steppe of Mongolia, northern China, and southern Russia and travel long distances (Ito et al. 2006 Mueller et al. 2011, Teitelbaum et al. 2015). The total population decreased from about 1.5 million in the 1940s to between 300 000 and 500 000 in the 1990s (Lhagvasuren and Milner-Gulland 1997, Jiang et al., 1998; Olson et al., 2005). However, the population in the 2000s was estimated at 400 000 to 2 700 000 and is now considered stable; the animal's current status on the IUCN red list is Least Concern (Mallon, 2008).

We captured gazelles in a wide range of habitats in 2002, 2003 and 2007. To each one we attached a collar with a satellite transmitter (platform terminal transmitter: model ST-18 [used in 2002], ST-20 [2003], or A3210 [2007], Telonics Inc., Mesa, AZ, USA) (Kaczensky et al. 2010, Ito et al. 2013a). We programmed each transmitter to transmit radio signals for an 8-h period every 7 or 8 days and obtained location data for the period from October 2002 to December 2010 (Table S1). Location data were ranked from 3 to 0 in accordance with the estimation error: <250 m for location class (LC) 3; from 250 to < 500 m for LC 2; from 500 to < 1500 m for LC 1; and ≥ 1500 m for LC 0 (Collecte Localisation Satellites, 2007). Less accurate data without estimation errors were provided as LCs A and B. We selected the best LC data on each day for each gazelle; if we had many location data of the same LC in a day, we chose the last location. We used the LC A (5.4% of all location data) and B (5.7%) location data in our analyses because the proportions of data of these low levels of accuracy were relatively large in the case of some gazelles; nevertheless, these locations fell into the gazelle ranges delineated without using the LC A and B data.

We calculated the annual home range of each gazelle by separating the animal's

location data into 1-year periods from the capture date onward (Table S1). We defined the summer range as that from June to August and the winter range as that from December to February (Table S2). Annual and seasonal ranges were calculated by using a 95% fixed-kernel home range (Worton 1989) with Arc GIS 3.2 (Environmental System Research Institute, Inc. Redlands, CA, USA.) and Animal Movement Extension (Hooge and Eichenlaub, 2000). We calculated the centroid coordinates of each home range, the distances between the centroids of the summer and winter ranges, and the overlaps between the summer and winter ranges.

3.2.3 NDVI analysis of gazelle home ranges

We downloaded MODIS Aqua normalized difference vegetation index (NDVI) products (MYD13Q1, 16-day composite and 250-m spatial resolution) from NASA (<http://modis-land.gsfc.nasa.gov/vi.html>) from 8 October 2002 to 9 January 2011 as an index of plant amount contributing to gazelle distribution. We calculated mean NDVI as a vegetation amount index, and its standard deviation (SD), and coefficient of variation (CV) as indices of the spatial heterogeneity of vegetation amount in each annual range. Annual means were calculated from 23 images of 16-day composites. We defined summer as when the mean NDVI was at a maximum and winter as when it was at a minimum in each annual range. We defined spring and autumn as the middle dates between the defined summer and winter. NDVI CV in winter could not be calculated, because in many cases the mean NDVI value for the annual range was negative. We also calculated the seasonal change in NDVI by NDVI in summer minus NDVI in winter. These processes were calculated by using Arc GIS 9.3 (Environmental System Research Institute, Inc. Redlands, CA, USA.)

3.2.4 Statistical analysis

We analyzed single linear regressions between annual range size and the coordinates of the annual range, each NDVI value in the range (annual mean and each season), and the distance between summer and winter ranges. We tested for differences in home-range size among annual, summer, and winter ranges by using ANOVA and the Tukey-Kramer test.

Generalized linear mixed models were used to estimate the relationships between annual range size and the mean, SD, CV, and seasonal change of NDVI and centroid coordinates of annual home ranges. We used gazelle ID as a random effect. We calculated the variance inflation factor (VIF) for each NDVI variable and the coordinates of annual range to estimate multicollinearity, and we eliminated factors with $VIF > 10$ from the models. Models were calculated by using the R package in the *nlme* library (R Core Team 2015). Models were selected by using Akaike's information criterion (AIC), and final models were selected on the basis of $\Delta AIC < 2$.

3.3 Results

3.3.1 Relationships between annual range size, geographical factors, and vegetation factors

We estimated 35 annual ranges of 20 gazelles; in total they covered about 230,000 km²—about 33% of the total distribution area (about 715,000 km²; Mallon 2008) (Fig. 3.1). Annual range size of the tracked gazelles was $16\,502 \pm 1672$ km² (mean \pm SE); the maximum range size (37,377 km²) was more than 40 times the minimum (908 km²) (Table S3.1).

Annual range size was positively correlated with latitude ($r = 0.52$, $P = 0.001$), but

it was not significantly correlated with longitude ($r = 0.07$, $P = 0.69$; Table S3.3). Annual range size also increased significantly with mean annual NDVI ($r = 0.48$, $P = 0.003$) and with mean autumn NDVI ($r = 0.45$, $P = 0.007$) (Table S2.3, Fig. 3.2). Hypothesis 1 was therefore rejected. Annual range size increased significantly with vegetation spatial heterogeneity (NDVI SD and CV) (except in winter for SD and in autumn for CV) (Table S3.3, Fig.3.2), supporting hypothesis 2. Annual range size increased with increasing seasonal change in vegetation amount (Table S3.3, Fig. 3.2), supporting hypothesis 3.

3.3.2 Relationships among environmental factors

Latitudinally, vegetation amount and its seasonal change increased from south to north, except in winter (Table S3.3). NDVI SD and CV also increased from south to north, except in winter for SD and in spring and autumn for CV (Table S3.3). Longitudinally, annual mean vegetation amount, mean spring and summer vegetation amounts, and seasonal change in vegetation amount increased from west to east. NDVI SD and CV were not significantly correlated with longitude, except in the case of the annual mean and summer values for NDVI CV (Table S3.3). NDVI SD increased in areas with increased mean annual NDVI ($r \geq 0.48$, $P < 0.01$; Table S3.3), except in winter. Seasonal change in vegetation amount increased in areas with increased vegetation amount (annual mean, spring, and summer; $r \geq 0.63$, $P < 0.001$; Table S3.3). NDVI SD increased with increasing seasonal change in vegetation amount, except in winter ($r > 0.49$, $P < 0.01$; Table S3.3).

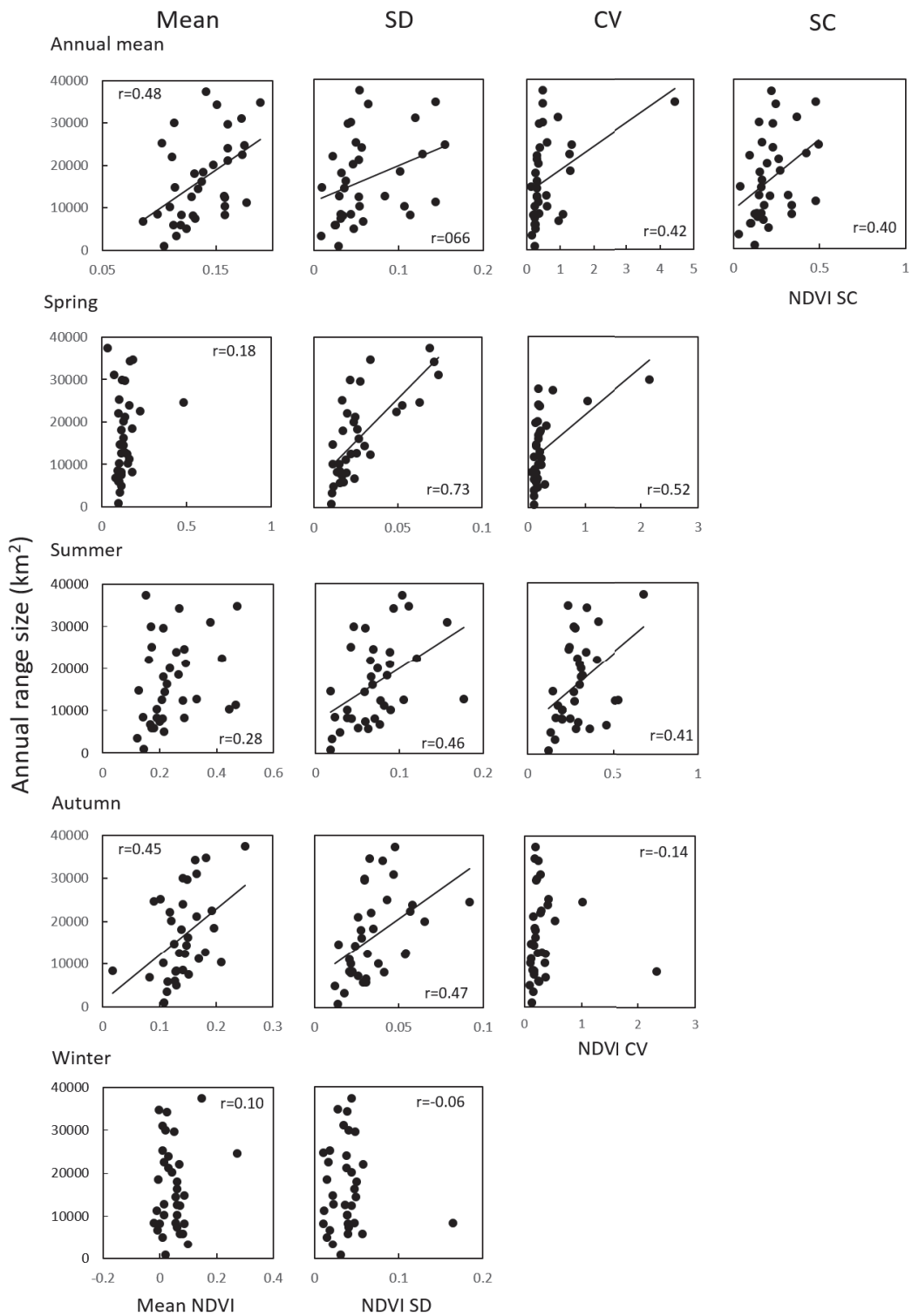


Figure 3.2 Relationships between annual range size of Mongolian gazelles and normalized difference vegetation index (NDVI) value for annual range. SD, standard deviation; CV, coefficient of variation; SC, seasonal change. Lines are plotted only for statistically significant regressions ($P < 0.05$)

3.3.3 Effects of multiple variables on annual range size

The best model for predicting annual range size included NDVI CV for annual mean, mean NDVI in spring and winter, NDVI SD in spring and winter, and latitude (Table 3.1), and the most effective parameter was NDVI SD in spring (Table 3.2).

Table 3.1. Factors included in top-ranked models (Akaike's information criterion (AIC) < 2.0) predicting annual range size of Mongolian gazelles. CV: coefficient of variation of NDVI, Mean: mean NDVI, SD: standard deviation of NDVI; Lat; latitude of annual-range centroid, an: annual mean of NDVI, sp: spring, w: winter, au: autumn.

Model	Model parameters	AIC	Δ AIC
1	$CV_{an} + Mean_{sp} + Mean_w + SD_{sp} + SD_w + Lat$	716.77	0
2	$CV_{an} + Mean_{sp} + Mean_{au} + Mean_w + SD_{sp} + SD_w + Lat$	717.78	1.01

Table 3.2. Parameter estimates, standard errors (SE), and statistical significance under model 1 in Table 3.1. Refer to Table 3.1 for variables.

Parameter	Estimate	SE	T-value	P-value
(intercept)	-126276	54835.90	-230	0.03
CV_{an}	4757	1818.53	2.62	0.03
$Mean_{sp}$	-59244	20265.90	2.92	0.02
$Mean_w$	59182	21208.46	2.79	0.02
SD_{sp}	218130	56393.39	3.87	0.004
SD_w	50432	30891.08	1.63	0.14
Lat	2989	1218.01	2.45	0.04

3.3.4 Configuration of annual and seasonal ranges

Both the summer and winter ranges were significantly smaller than the annual ranges ($F_{2,102} = 3.09, P < 0.001$; Fig. 3.3). The mean distance between centroids of the summer and winter ranges was 93.0 ± 11.7 km (mean \pm SE); the maximum and minimum distances were 304 and 10 km, respectively (Table S3.2). Annual range size increased with increasing distance between the centroids of the summer and winter ranges ($r = 0.67, P < 0.001$; Fig. 3.4). Overlap between summer and winter ranges was observed in 14 of 35 areas; the maximum overlap ratio was 0.24 (Table S3.3, Fig. 3.5). In no overlap was the distance between centroids of the seasonal ranges > 80 km (Fig. 3.5). Overlap ratio was negatively correlated with distance when the distance was < 80 km ($n = 19, r = 0.58, P = 0.009$).

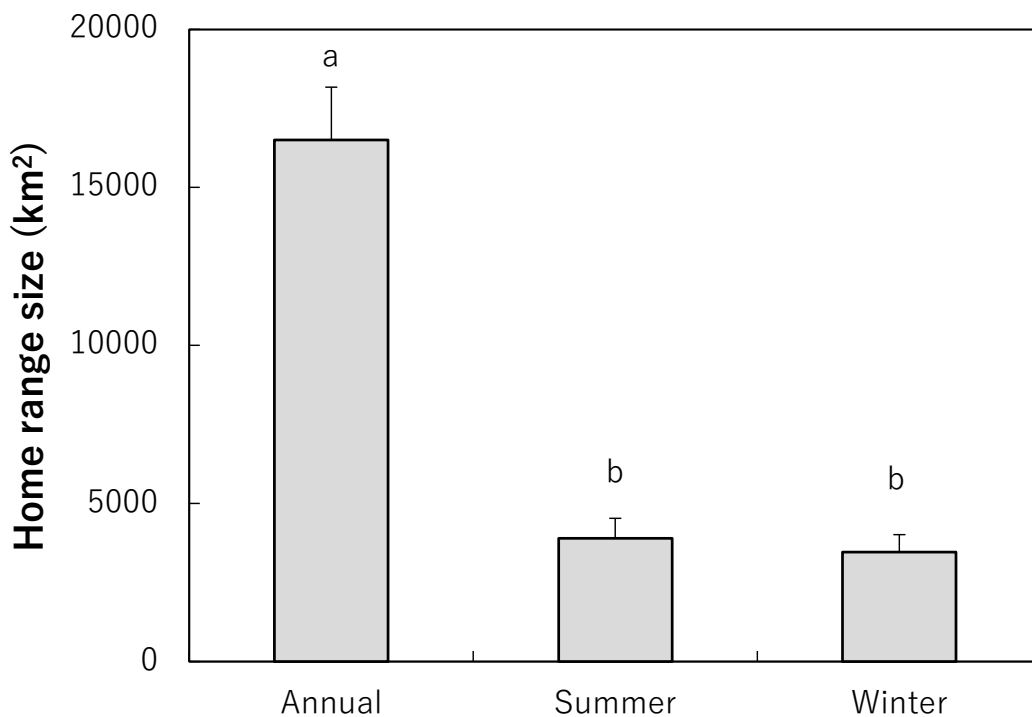


Figure 3.3 Comparison of annual, summer, and winter range sizes of Mongolian gazelles. Values with different letters differ significantly. Tukey-Kramer test: $P < 0.001$.

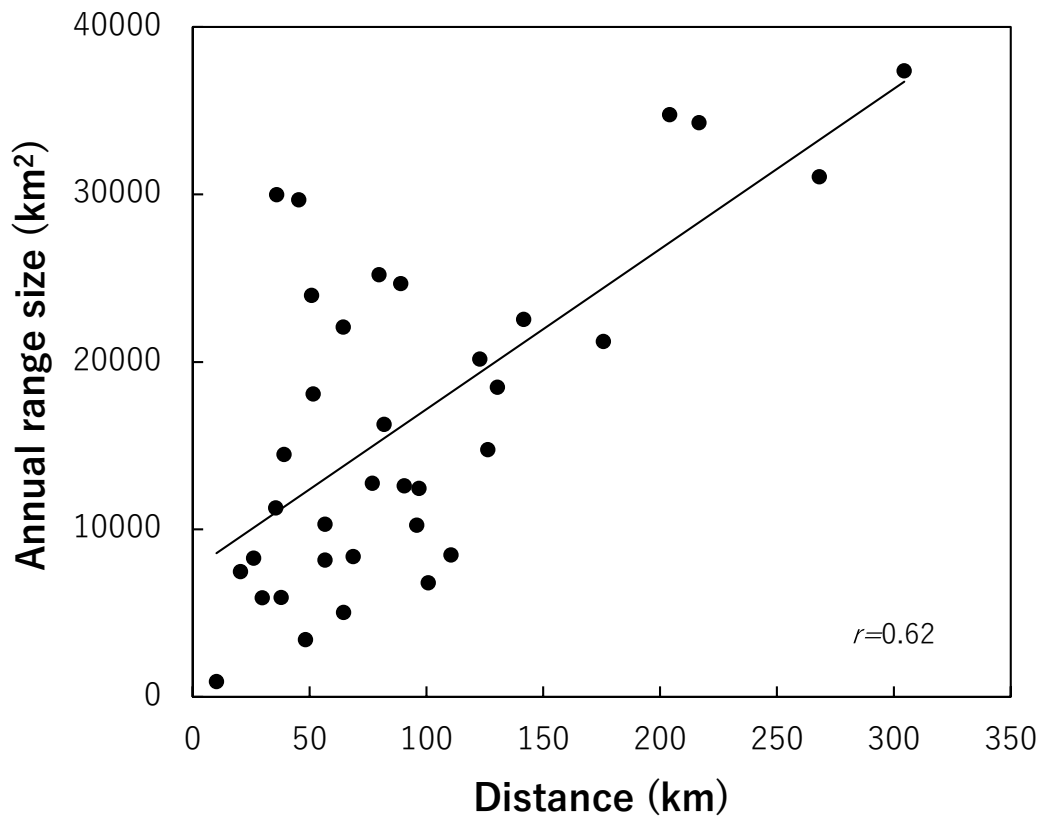


Figure 3.4. Relationship between annual range size and distance between centroids of summer and winter ranges of Mongolian gazelles. Regression analysis: $P < 0.05$.

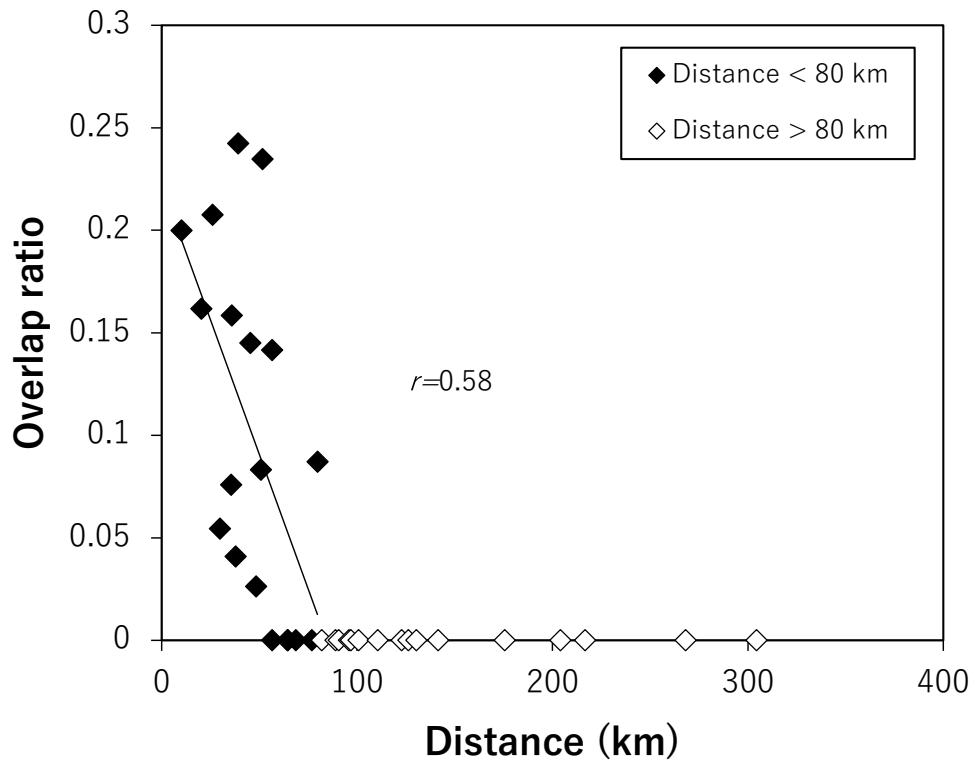


Figure 3.5. Relationship between overlap ratio and distance between summer and winter ranges of Mongolian gazelles.

3.4 Discussion

3.4.1 Size and distribution of annual ranges of Mongolian gazelles

Annual range size differed by up to more than 40 times (from 900 to 37,000 km²) among individuals, and each tracked gazelle used only part of the main and continuous gazelle distribution (Fig. 3.1, Ito et al. 2013a). The gazelles' annual ranges were separated into four regions: eastern and western parts to the east of the Ulaanbaatar–Beijing Railroad, and northern and southern parts to the west of the railroad (see Ito et al. 2013a). The railroad has a barrier effect on Mongolian gazelle movements (Ito et al. 2005, 2008, 2013a), and the limited range use within the separated regions on the eastern side of the railroad (Fig. 3.1) corresponds with other results for

Mongolian gazelles in eastern Mongolia (Olson et al. 2010, Mueller et al. 2011). To the west of the railroad, the tracking data indicate some degree of population division (Fig. 3.1, Ito et al. 2013b), despite the absence of conspicuous anthropogenic barriers. Although no regional genetic differences have been reported in this species (Okada et al. 2015), some genetic differences may exist among regions if there are in fact such separated populations.

3.4.2 Annual range size and spatiotemporal heterogeneity of forage amount

Annual range size increased with latitude, increasing forage amount, spatial heterogeneity of forage amount, and seasonal change in forage amount. These results support hypothesis 2 (increasing range size with increasing spatial heterogeneity) and hypothesis 3 (increasing range size with increasing seasonal change) but reject hypothesis 1 (increasing range size with decreasing vegetation amount). Our findings that spatial heterogeneity and seasonal change in forage amount increased with increasing forage amount (Table 3.1) are likely the main reason for the rejection of hypothesis 1.

A gradient of forage distribution, rather than a patchy one, was likely the main cause of increasing spatial heterogeneity in forage amount over the annual ranges, because in the study area forage amount generally increases with latitude in the growing season (Yu et al. 2004). The latitudinal gradient (i.e., spatial heterogeneity) of forage availability also changed seasonally: it was large from spring to autumn and small in winter (Table S3.3). The increased snowfall in the north (Morinaga, Tian and Shinoda 2003) would have decreased the gradient in forage availability during winter, because at this time the vegetation is covered with snow. Therefore, the north was characterized by

greater amounts of forage than the south from spring to autumn and greater seasonal changes in forage availability. In contrast, the forage availability was smaller year-round in the southern, dry area (Table S3). Transition of the vegetation types along the north-south gradient may cause the geographical difference of forage quality. The Mongolian gazelle is suggested as a browser (Yoshihara et al. 2008), and therefore, the geographical differences of forage quality reflecting differences of plant species composition may also affect their habitat selection.

The large variation in annual range size of the gazelles was likely caused mainly by differences in movement patterns and environmental conditions among regions. The larger seasonal change in forage amount in the north would have driven the gazelles there to move to distant areas; the gradient of forage amount in this region would have made it possible for the gazelles to find suitable areas when forage conditions deteriorated in the areas the animals had been using. Seasonal and regional shifts in vegetation amount are considered to be the main drivers of gazelle movement (Mueller et al. 2008, 2011, Ito et al. 2006, 2013b). Our results suggest that regional differences in spatiotemporal heterogeneity of forage amount exist over the gazelle's distribution; these differences likely cause regional differences in gazelle movement. The larger annual range in the north than in the south is explained by the larger seasonal change in forage amount and by the vegetation gradient across the region. The smaller annual range size in the south, where the vegetation includes desert or desert steppe, was an unintuitive result because it contradicted the habitat productivity hypothesis. However, we consider this result understandable because of the smaller seasonal change and smaller spatial heterogeneity of forage amount in the south. Smaller gazelle density in the dryer areas (Malon 2008) would be another possible explanation.

We used both SD and CV as indices of spatial heterogeneity of forage amount, and both of these indices were included in the top-ranked models (Table 2). Regional differences in forage amount would be reflected more by SD than by CV in the north, where the amount of forage and the gradient of this amount were larger. In contrast, CV would be a better index of forage amount in the south, where the forage amount was small. Therefore, both indices combined would be useful for analyzing areas with large environmental gradients and with low forage amounts in some parts.

3.4.3 Mongolia's ecosystem in relation to the movement ecology of ungulates

Amount, spatial heterogeneity, seasonal change, and predictability of forage resources are important determinants of animal movement patterns (Mueller and Fagan 2008), and these factors contribute to both intraspecific and interspecific differences in movement patterns (Mueller et al. 2011, Teitelbaum et al. 2015). In an interspecific comparative study, unlike in the case of the caribou (*Rangifer tarandus granti*), guanaco (*Lama guanicoe*), and moose (*Alces alces*), the movement of the Mongolian gazelle was evaluated as nomadic (Mueller et al. 2011). However, our results suggest that the Mongolian gazelle may have a variety of movement patterns—from residency to seasonal migration. If Mongolian gazelles have various movement patterns in the continuous distribution, it would provide a marked difference to the famous round-trip migrations—over the same routes and with the same timings—made by most ungulate populations in the Serengeti ecosystems (Boone, Thirgood and Hopcraft 2006). Intraspecific differences in annual movement distances have been reported in many species, including moose in Sweden (Singh et al. 2012) and roe deer in Europe (Cagnacci et al. 2011). The intraspecific differences in movement distances of

Mongolian gazelles are greater than those of these other ungulate species, and the Mongolian environment is dry, cold, and unpredictable. Mongolia's Gobi Steppe ecosystem is the largest intact grassland in the world (Batsaikhan et al. 2014) therefore, such variations in movements and environments in a continuous distribution have the potential to improve our understanding of movement ecology. However, the fragmentation and degradation of ungulate habitats through the construction of railroads and the development of mining projects are serious ecosystem threats (Ito *et al.*, 2013a; Batsaikhan et al. 2014). Conservation of the ecosystem is therefore crucial, not only for conservation but also for science.

Although we concentrated here on analyzing the effects of vegetation factors on annual range size in Mongolian gazelles, other factors, such as individual movement-pattern differences (Cagnacci et al. 2011, Chapman et al. 2011, Singh et al. 2012) and the effects of forage quality (e.g., Wilmshurst et al. 1999, Hebblewhite, Merrill and McDermid 2008), gazelle density, and human activities, likely affect gazelle movements. To enable us to better understand ungulate movements and habitat selection, further research into these other factors would be useful. Comparative studies analyzing multiple factors among animals that inhabit various environments are challenging, but would be important for future development of movement ecology and wildlife conservation.

Table S3.1. Data on the tracked gazelles and their annual ranges (kernel method; 95% area). Latitudes and longitudes of annual range are centroid coordinates. Gazelles tracked for several years have multiple annual ranges. F: female, M: male, Ad: Adult.

ID	Sex	Age	Captured date	Site of capture		Annual range				
				Lat (°N)	Long (°E)	Year	Term	Size (km ²)	Lat (°N)	Long (°E)
25363	F	2-3	2003/8/13	46.89	114.70	1	2003/8/13-2004/8/7	8293	47.106	114.779
						2	2004/8/7-2005/8/27	11293	46.903	114.936
						3	2005/8/27-2006/12/2	10313	46.667	114.964
25381	M	1-2	2003/11/12	47.12	114.90	1	2003/11/15-2004/11/13	18489	48.332	115.339
25448	M	3	2004/7/28	47.68	115.49	1	2004/7/31-2005/7/30	34767	47.079	116.079
37571	F	1.5	2002/10/18	45.55	109.47	1	2002/10/18-2003/10/13	25217	45.371	108.708
						2	2003/10/13-2004/10/14	29992	45.671	108.653
						3	2004/10/14-2005/10/9	34279	46.596	106.828
37572	F	Ad	2002/10/18	45.55	109.47	1	2002/10/18-2003/10/13	10259	45.576	108.850
						2	2003/10/13-2004/10/14	31061	46.313	108.017
37573	F	3-5(Ad)	2002/10/26	43.96	103.18	1	2002/10/25-2003/10/20	6808	43.871	102.535
41243	F	2-3	2003/7/24	45.06	108.54	1	2003/7/24-2004/7/18	8375	45.120	109.141
						2	2004/7/18-2005/7/27	37377	46.379	107.210
42645	F	Ad	2003/8/18	48.28	113.68	1	2003/8/18-2004/8/14	22533	48.388	114.530
						2	2004/8/14-2005/8/27	24673	47.456	113.515
67921	F	2	2007/5/18	46.52	109.04	1	2007/5/18-2008/5/14	16266	46.165	109.594
						2	2008/5/14-2009/5/17	20174	46.132	110.191
						3	2009/5/30-2010/5/17	12748	46.188	110.604
67923	M	1	2007/5/22	45.66	110.90	1	2007/5/29-2008/5/14	18079	45.621	110.708
67925	F	1	2007/5/29	45.21	109.07	1	2007/5/29-2008/5/30	22077	45.532	108.903
67926	M	1	2007/5/29	45.21	109.07	1	2007/5/29-2008/6/15	5943	45.220	109.604
67927	M	2	2007/5/31	46.65	108.08	1	2007/5/31-2008/5/30	21217	46.800	106.426
67928	F	Ad	2007/5/31	46.65	108.08	1	2007/5/31-2008/5/22	12598	46.323	107.048
						2	2008/5/22-2009/5/17	12439	46.418	106.887
67929	M	1-2	2007/6/1	46.65	108.08	1	2007/6/1-2008/5/30	7491	46.431	107.621
67931	F	1	2007/5/22	45.66	110.90	1	2007/6/21-2008/6/15	29671	46.210	110.609
						2	2008/6/23-2009/6/18	23972	46.015	110.958
67932	F	Ad	2007/5/22	45.66	110.90	1	2007/5/29-2008/5/22	14479	46.225	110.352
67933	F	Ad	2007/5/29	45.21	109.07	1	2007/5/29-2008/5/22	5914	45.367	109.196
78510	F	2.5	2007/11/1	43.42	109.11	1	2007/11/1-2008/10/29	8171	43.163	109.960
						2	2008/10/29-2009/10/24	14766	43.239	109.558
						3	2009/10/24-2010/12/30	909	42.951	110.288
78511	F	2.5	2007/11/1	43.42	109.11	1	2007/11/1-2008/10/29	5038	43.447	109.473
						2	2008/10/29-2009/10/24	3420	42.875	108.864
						3	2009/10/24-2010/10/27	8478	42.993	109.146
Average								16502		

Table S3.2. Sizes and locations of 95% fixed-kernel summer (June to August) and winter (December to February) ranges, distances between centroids, and overlap ratios of seasonal ranges of the tracked Mongolian gazelles.

ID	Year	Summer range			Winter range			Distance (km)	Overlap rate
		size (km ²)	Lat (°N)	Long (°E)	size (km ²)	Lat (°N)	Long (°E)		
25363	1	2475	47.04	114.59	9408	47.07	114.93	26.1	0.21
	2	6290	46.93	114.64	2449	46.76	115.04	35.6	0.08
	3	12584	46.95	114.80	4897	46.48	115.08	56.6	0.14
25381	1	2158	48.84	115.06	4408	47.81	115.92	130.5	0
	2	8004	47.90	115.26	3846	46.19	116.22	204.1	0
	3	12282	45.13	108.74	2338	45.26	109.73	79.7	0.09
37571	1	3700	45.33	109.09	2862	45.36	109.54	36.0	0.16
	2	6156	45.94	108.03	1835	47.06	105.71	216.7	0
	3	1578	45.27	109.14	864	46.03	108.55	95.9	0
37572	1	3332	45.31	108.91	549	47.45	107.31	268.1	0
	2	188	44.04	103.17	1032	43.74	101.98	100.8	0
	3	864	44.94	108.59	5124	45.14	109.41	68.6	0
41243	1	2839	45.15	108.60	840	47.04	105.76	304.4	0
	2	1640	47.81	113.57	680	48.03	115.44	141.6	0
	3	1447	47.77	113.49	2457	47.61	112.33	89.0	0
42645	1	1040	46.59	109.70	478	45.99	109.08	81.9	0
	2	4977	46.42	109.79	2316	45.44	110.53	122.9	0
	3	4632	46.16	110.82	779	46.79	110.39	76.9	0
67923	1	7235	45.63	110.49	14139	45.31	110.97	51.6	0.23
	2	3246	45.32	108.94	5107	45.31	109.76	64.4	0
	3	937	45.36	109.19	2294	45.31	109.67	37.8	0.04
67926	1	2939	46.85	107.61	1298	46.58	105.35	175.7	0
	2	5051	46.63	107.34	3849	45.90	106.83	90.6	0
	3	2118	45.93	107.04	878	46.77	106.71	96.9	0
67928	1	2288	46.54	107.81	10606	46.43	107.59	20.4	0.16
	2	15154	46.50	110.59	9925	46.09	110.52	45.4	0.14
	3	9723	45.82	111.00	6014	46.17	110.59	50.8	0.08
67929	1	3614	45.99	110.28	3275	46.34	110.21	39.1	0.24
	2	1154	45.41	108.92	6918	45.56	109.23	29.8	0.05
	3	581	43.11	109.72	2351	43.04	110.41	56.6	0
78510	1	2752	43.31	108.82	2273	43.14	110.36	126.3	0
	2	991	42.85	110.17	245	42.92	110.24	10.2	0.20
	3	752	43.35	109.18	3170	43.42	109.97	64.6	0
78511	1	1121	43.07	109.02	731	42.68	108.74	48.3	0.03
	2	663	43.31	108.63	877	42.60	109.56	110.6	0
	3	3900			3460			93.0	
Average									

Table S3.3. Correlation matrix of annual range size of tracked Mongolian gazelles and geographical and environmental variables in their annual ranges. Values are correlation coefficients; asterisks indicate significant differences in regression analysis. S–W dist.: distance between centroids of summer and winter ranges of each gazelle. Lat and Long indicate centroid coordinates of annual ranges.

Variables	Season	Annual range size (km ²)		Lat (°N)	Long (°E)	Mean NDVI				NDVI SD				NDVI CV						
		Summer	Winter			Annual	Spring	Summer	Autumn	Winter	Annual	Spring	Summer	Autumn	Winter	Annual	Spring	Summer		
S–W dist		0.67***																		
Lat		0.52**	0.27																	
Long		0.07	-0.17	0.45**																
NDVI SC		0.40*	0.28	0.68***	0.60***															
Mean NDVI	Annual	0.48**	0.29	0.72***	0.56***	0.83***														
	Spring	0.18	-0.10	0.48**	0.52**	0.63***	0.53***													
	Summer	0.28	0.21	0.65***	0.62***	0.88***	0.84***	0.41*												
	Autumn	0.45**	0.50**	0.37*	0.15	0.28	0.40*	-0.13	0.40*											
NDVI SD	Winter	0.10	0.04	0.04	-0.03	-0.04	0.10	0.48**	-0.02											
	Annual	0.66***	0.57***	0.69***	0.15	0.69***	0.70***	0.29	0.62***	0.47**	-0.05									
	Spring	0.73***	0.67***	0.49**	-0.04	0.49**	0.55***	0.32	0.32	0.37*	0.27	0.78***								
	Summer	0.46**	0.50**	0.65***	0.14	0.62***	0.66***	0.14	0.66***	0.49**	-0.12	0.91***	0.59***							
NDVI CV	Autumn	0.47**	0.28	0.56***	0.14	0.50**	0.48**	0.61***	0.27	-0.01	0.39*	0.68***	0.65***	0.50**						
	Winter	-0.06	0.06	-0.30	-0.23	-0.32	-0.32	-0.31	-0.32	0.09	-0.11	-0.17	-0.11	-0.24	-0.20					
	Annual	0.42**	0.35*	0.41*	0.46**	0.61***	0.47**	0.36*	0.54***	0.12	-0.13	0.43**	0.28	0.37*	0.26	-0.28				
	Spring	0.52**	0.71***	0.14	-0.27	0.09	0.14	-0.30	-0.05	0.49**	0.22	0.44**	0.65***	0.37*	0.23	0.05	0.02			
NDVI CV	Summer	0.41*	0.50**	0.35*	-0.36*	0.05	0.10	-0.21	-0.02	0.36*	0.12	0.59***	0.50**	0.68***	0.39*	-0.03	0.03	0.66***		
	Autumn	-0.02	-0.14	0.27	0.26	0.30	0.21	0.40*	0.09	-0.61***	0.09	0.12	0.11	0.07	0.44**	-0.25	0.18	-0.07	0.01	

* P < 0.05; ** P < 0.01; *** P < 0.001

Chapter 4

Spring movement strategy of Mongolian gazelles and an evaluation of the benefits

Abstract

Animal movement patterns change depending on the spatiotemporal heterogeneity of forage conditions. Animal movement is predicted to be nomadic in areas with low temporal predictability of environmental conditions, but it remains unclear whether the costs of nomadic movement outweigh the benefits received. To examine the spring movement strategy of Mongolian gazelles (*Procapra gutturosa*) in Mongolia, where predictability of vegetation conditions is relatively low, we identified the type of each movement, evaluated the preferred vegetation conditions for gazelles, and quantified the benefit achieved through each spring movement. The surveyed gazelles continuously preferred areas with intermediate normalized difference vegetation index (NDVI) values from May to July, and spatial and temporal shifts of the distribution of preferred areas explain the long-distance movements of many gazelles in spring. Three movement types were identified: the sedentary type (12.5% of cases), linear movement type (50.0%), and nomadic movement type (37.5%). The period when benefit varied most greatly among individuals differed between the linear and nomadic movement types. During the spring movement period the variance of benefit was larger for the nomadic movement type, whereas during the summer it was larger for the linear movement type, suggesting the existence of different movement strategies in the Mongolian gazelle. Linear long-distance movements over a short period in the linear movement type suggest the so-called jumper strategy, whereas other movement patterns might represent the searcher strategy. Benefit loss through movements of individuals in both strategies indicate low interannual predictability of vegetation conditions in the study area, and it would explain the co-existence of multiple movement types or strategies used by Mongolian gazelles in spring. These findings help to improve our understanding of animal movement ecology, and the species' use of multiple movement strategies has conservation implications in habitat with low temporal predictability of vegetation conditions.

Key words: Brownian bridge movement model, dryland, grassland, migration, Mongolia, NDVI, nomadic movement, temporal predictability, ungulate.

4.1 Introduction

Long-distance animal movement is the consequence of evolution to adapt to spatial and temporal variation of environmental conditions (Alerstam et al. 2003). Migratory animals mainly benefit from long-distance movement by obtaining improved forage resources, finding mates, and escaping from severe climate conditions (van Beest et al. 2011, Avgar et al. 2014), as well as reducing predation risk (Hebblewhite and Merrill 2009, Hopcraft et al. 2010). Forage conditions are a particularly important factor affecting animal movement patterns (Dussault et al. 2005, Milner-Gulland et al. 2011, Avgar et al. 2014).

Animal movement patterns change depending on the spatiotemporal heterogeneity of forage conditions (Mueller and Fagan 2008). For example, seasonal migration occurs in areas with clear seasonal change and high interannual predictability of environmental conditions (Mueller and Fagan 2008), because animals are highly likely to obtain benefit through long-distance movement in such environments. The green-wave hypothesis proposes that migratory herbivores follow plant growth (the wave of green-up) across the landscape (Drent et al. 1978). Animals following this so-called surfer strategy efficiently obtain energetic benefit through the migration (Boone et al. 2006, Sawyer and Kauffman 2011, Bischof et al. 2012, Fryxell and Avgar 2012). In contrast, in areas with low temporal predictability of environmental conditions, animal movement is expected to be nomadic (Mueller and Fagan 2008), and a worldwide comparative study found the movement pattern in these conditions actually was

nomadic (Mueller et al. 2011). However, obtaining benefit through long-distance movement may not be guaranteed in environments with low predictability. Because of the difficulty of gathering data on such animal movements and quantitatively evaluating the benefit obtained through movement under environmental conditions with large spatiotemporal heterogeneity, it remains unclear whether the costs of nomadic movement outweigh the benefits received.

The Mongolian gazelle (*Procapra gutturosa*) is an interesting species for animal movement ecology studies. Many members of this species move several hundred kilometers in a year (Ito et al. 2006, Mueller et al. 2011, Teitelbaum et al. 2015), and their movements are considered nomadic (Olson et al. 2010a, Mueller et al. 2011, Ito et al. 2013a) due to the low seasonal and interannual predictability of environmental conditions in the ecosystem (Mueller et al. 2011, Ito et al. 2018). However, their annual range size varies by about 40-fold across different regions of the continuous distribution range, which is mainly related to the latitudinal gradient of vegetation conditions (Imai et al. 2017). Long-distance movement of Mongolian gazelle in Mongolia, where environmental conditions have relatively low predictability (Mueller et al. 2011, von Wehrden et al. 2012), is an appropriate research target to analyze movement strategy.

Even in migratory species in areas with relatively high temporal predictability of environmental conditions, different movement strategies coexist. In red deer (*Cervus elaphus*) in Norway, in addition to the surfer strategy, some individuals use the jumper strategy, moving toward the summer range ahead of the green-wave to avoid the high predation risk and food competition with other individuals on the migration route (Bischof et al. 2012). Thus, there may be several movement types or strategies used by Mongolian gazelles during the spring vegetation growing period.

To identify the movement patterns, in this study we statistically separated movement periods and stay periods using a Brownian bridge movement model (BBMM) used in recent ungulate movement research (e.g., Sawyer et al. 2009, Bischof et al. 2012) and compared the ratio of cumulative distance to linear distance between winter and summer ranges of each spring movement.

To evaluate the benefit obtained via movement from the perspective of improving forage conditions, we must first specify the range of preferred vegetation conditions. The forage maturation hypothesis predicts the optimal vegetation biomass for an herbivore species (Fryxell et al. 1988). Due to the trade-off between forage plant quantity and quality, this hypothesis predicts that areas with intermediate vegetation biomass are optimal for energy intake efficiency. As reported in other ungulate species (Fryxell et al. 2004, Hebblewhite et al. 2008, Sawyer et al. 2011), Mongolian gazelles use areas with intermediate normalized difference vegetation index (NDVI) values in spring and autumn (Mueller et al. 2008) and in summer (Olson et al. 2011, Ito et al. 2013a). In those studies, however, information was obtained in limited areas, seasons, and individuals. In the present study, we examined whether preferred vegetation conditions for Mongolian gazelles exist across a wide range throughout the plant growing period, and we quantified the benefit obtained by accessing improved vegetation conditions during the spring movement.

If a species uses different movement types in spring, the periods and areas that allow individuals to obtain the most benefit would be key factors. Even with low spatiotemporal predictability of vegetation conditions, nomadic movement may result in much benefit through access to improved forage conditions during the movement period. However, if spatiotemporal predictability of vegetation conditions is quite large,

nomadic movement may have negative effects in some cases. If there are some important areas with relatively high interannual predictability of vegetation conditions, some gazelles might move directly to such areas in spring, using the jumper strategy. To examine the spring movement strategy of Mongolian gazelles in relation to vegetation conditions, we identified the type of each movement, evaluated the preferred vegetation conditions for gazelles, and quantified the benefit received through each spring movement.

4.2 Materials and methods

4.2.1 Study area

The study area was defined as the area of the minimum convex polygon in central and eastern Mongolia where 19 radio-collared gazelles were located from January to August (see below; Fig. 4.1). Elevation ranges from about 550 to 2700 m above sea level, and the climate is strong continental (maximum temperature exceeds 40 °C in summer and minimum is below -35 °C in winter). Annual precipitation increases from 100 mm in the southern desert steppe to 300 mm in the northern typical steppe (Nandintsetseg and Shinoda 2011), and winter snowfall is also greater in the north (Morinaga et al. 2003). Interannual variation of precipitation in the region is not only larger than that of humid areas worldwide but also that of other arid regions (von Wehrden et al. 2012), including the Serengeti-Mara ecosystem, which is well known for its regular seasonal migrations of ungulates (Murray 1995, Boone et al. 2006, Hopcraft et al. 2014). Large interannual variation of precipitation sometimes causes severe drought in summer (Miao et al. 2016) and heavy snow in winter (Ito et al. 2018), which results in mass mortalities of

livestock (Rao et al. 2015, Nandintsetseg et al. 2017) and wild animals (Kaczensky et al. 2011). Grasses and forbs (e.g., *Stipa* spp., *Carex* spp., *Allium* spp., *Artemisia* spp.) dominate in the typical and dry steppe regions, and shrubs (e.g., *Caragana* spp., *Anabasis brevifolia*) dominate in the desert steppe (Olson et al. 2010b), although vegetation conditions also fluctuate interannually (Yu et al. 2004, Vandandorj et al. 2015).

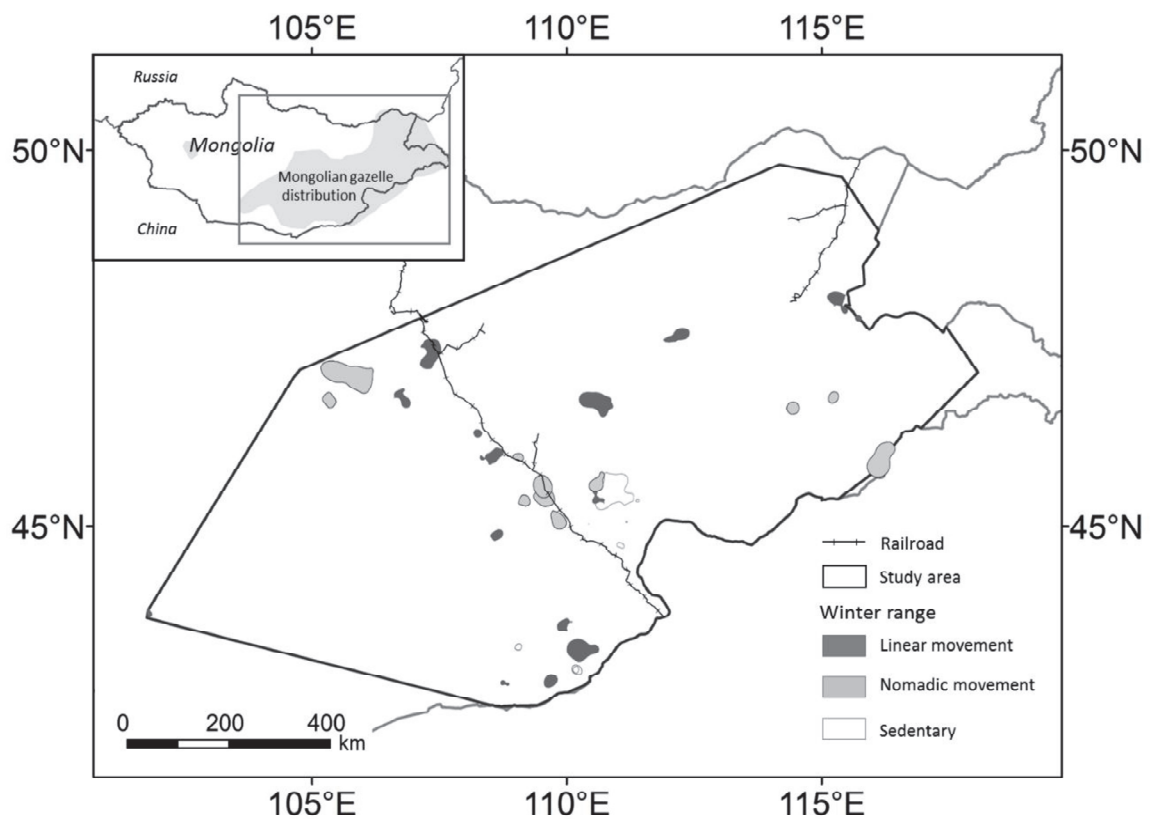


Figure 4.1. Map of the study area within the distribution of the Mongolian gazelle and locations of winter ranges of the tracked individuals. The distribution was based on information from the IUCN SSC Antelope Specialist Group (2016). The study area was the minimum convex polygon inside Mongolia of all locations of the 19 gazelles from January to August. Winter ranges were defined as areas where the gazelles stayed for more than 1 month from January to March in the highest 50% of the utilization distribution estimated by a Brownian bridge movement model.

4.2.2 Mongolian gazelles

Procapra gutturosa inhabits the typical steppe to desert regions of Mongolia, northern China, and southern Russia (IUCN SSC Antelope Specialist Group 2016). Long-distance movements of gazelles up to 500 km in linear distance were reported (Ito et al. 2006, Mueller et al. 2011, Teitelbaum et al. 2015, Imai et al. 2017), but some individuals used relatively small ranges (about 900 km²; Imai et al. 2017). The total population decreased from about 1.5 million head in the 1940s to between 300 000 to 500 000 in the 1990s (Lhagvasuren and Milner-Gulland 1997, Jiang et al. 1998, Olson et al. 2005). The population in the 2000s was considered stable and was estimated to be 400 000 to 2 700 000 (IUCN SSC Antelope Specialist Group 2016). An international railroad between Russia and China runs through the distribution range of the Mongolian gazelle (Fig. 1); barbed-wire fences alongside the railroad tracks prevent livestock accidents but serve as barriers for wild ungulates, such as Mongolian gazelles and Asiatic wild asses (Ito et al. 2005, 2008, 2013a).

4.2.3 Movement data of gazelles

During each of the years 2002, 2003, and 2007, we captured 19 gazelles from a wide range of habitats (Fig. 1) and attached a collar with a satellite transmitter (platform terminal transmitter: model ST-18, ST-20, or A3210, Telonics, Mesa, AZ, USA) (Kaczensky et al. 2010, Ito et al. 2013a, Imai et al. 2017). We programmed each transmitter to send radio signals for an 8-h period every 7 or 8 days and obtained location data from January 2003 to August 2011. We selected the data from January to August to analyze spring movement. These were essentially the same location data used by Imai et al. (2017), but some data were used only in this study because the analysis

periods were different; in Imai et al. (2017) the analysis periods were for a year from the tracking start season for each gazelle. We obtained a total of 32 spring movement patterns from 19 gazelles (14 females and 5 males), as some gazelles were tracked more than one year (Table S1). In our analyses, we used accurate data that were higher than location class (LC) 0 (CLS 2007), but we also used some less accurate data without estimation error provided as LC A (4.3%) and B (2.2%); the percentages of such low-accuracy data were relatively large for some gazelles, but the data still fell within the ranges delineated without using LC A and B data.

4.2.4 Classification of Movement types in spring

We identified winter ranges, summer ranges, and stopover sites by using BBMMs (Horne et al. 2007), which are used to analyze movement of ungulates (Sawyer et al. 2011, Bischof et al. 2012). We classified the sites as the highest 50% in the utilization distribution (UD) using the BBMM package (Nielson et al. 2013) in R (R Core Team 2015). In the 50% UD, we defined winter and summer ranges as areas where gazelles stayed for more than one month from January to March and from June to August, respectively. We defined stopover sites between the winter and summer ranges as the 50% UD where gazelles stayed for more than one week. The departure date from the winter range and the arrival date at the summer ranges were defined as the dates of the last location in the winter range and the first location in the summer range, respectively.

We assigned a movement type to each movement pattern. When a gazelle did not leave the winter range until the end of June, we assigned it as the sedentary movement type. When a gazelle left the winter range before the end of June, we calculated the ratio of linear distance to cumulative distance between the last location in the winter range

and the first location in the summer range. The ratio of cumulative distance to linear distance of all movements showed a bimodal distribution separated at the ratio of 2.0–2.5 (Fig. 4.2). Thus, we classified these movement patterns into two types: the linear movement type (< 2.0) and the nomadic movement type (> 2.5). For the sedentary movement type, we calculated the maximum linear distance between two points and cumulative distance from the first location to the last location in the winter range.

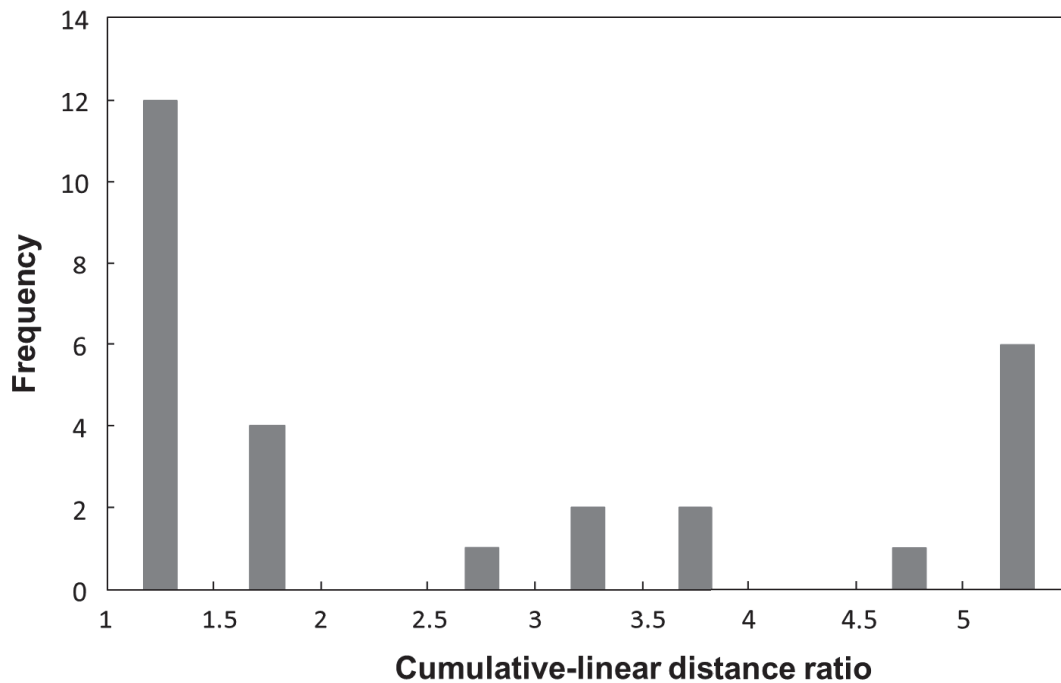


Figure 4.2. Frequency distribution of the ratio of cumulative to linear distances between the winter and summer ranges of the tracked Mongolian gazelles. The rightmost bar shows ratios that are >5 .

4.2.5 Preferred vegetation conditions for gazelles

We downloaded MODIS Aqua normalized difference vegetation index (NDVI) products (MYD13Q1, 16-day composite and 250-m spatial resolution; <http://modis-land.gsfc.nasa.gov/vi.html>) as an index of plant biomass in areas encompassing the entire ranges of all tracked gazelles from January to August in each

year from 2003 to 2011. We calculated mean NDVI values in each circular buffer zone of 7.6-km diameter, which represents the average movement distance for 7 or 8 days during the stay periods when gazelles were in the winter or summer ranges or stopover sites, at each gazelle location during the stay periods when the gazelles actually used the location. We also calculated 10-year mean monthly NDVI for 2003–2012 in the study area and the areas of each NDVI value zone at 0.05 intervals. We compared the frequency of NDVI values at gazelle locations and the relative area of NDVI value zones in the study area using Manly's selectivity index (Manly et al. 2002).

If an NDVI range was positively selected throughout the several-month vegetation growth period, we identified it as a preferred NDVI range for Mongolian gazelles. Because the NDVI range of 0.15–0.20 was positively selected from May to July (see Results, Fig. 6), we defined this range as the preferred NDVI range in the present study.

4.2.6 Benefit estimation of each movement

We estimated the benefit obtained via each spring movement by comparing the NDVI values in actual gazelle locations (L_i) and a simulated case in which the gazelle had not moved away from the winter range (W_i), where i is the order of locations after a gazelle left the winter range. We assumed that areas with the preferred NDVI range (0.15–0.20) were optimum for gazelles and that the benefit for gazelles decreased as the NDVI value at the gazelle's location deviated from the preferred NDVI range. Thus, a gazelle could benefit when it moved from the winter range to areas with the preferred NDVI range. Benefit through each spring movement (B) was calculated as the sum of differences in deviations from the preferred NDVI range between actual gazelle locations (LB_i) and

simulated locations as the gazelle stayed in the winter range (WB_i) (eq. 1), where n is the number of locations after the gazelle left the winter range.

$$B = \sum_{i=1}^n (WB_i - LB_i) \quad (\text{eq. 1})$$

$$\text{If } 0.15 \leq L_i, W_i \leq 0.20: LB_i, WB_i = 0$$

$$\text{If } L_i, W_i > 0.20: LB_i = L_i - 0.20, WB_i = W_i - 0.20$$

$$\text{If } L_i, W_i < 0.15: LB_i = 0.15 - L_i, WB_i = 0.15 - W_i$$

We used Arc GIS 10.4 (Environmental System Research Institute, Inc. Redlands, CA, USA) and R statistical software (R Core Team 2015) for the analysis.

4.2.7 Statistical analysis

To analyze the relationship between vegetation conditions of gazelle locations before and after the movement, we conducted regression analysis between mean NDVI values at the winter ranges after the movement started and the difference in average NDVI values between the actual case the gazelle experienced and a simulated case of the gazelle remaining in the winter range through August. To examine differences between the various movement types, we compared the linear and cumulative distances and the duration of movement periods by Welch's *t*-test.

We assumed the existence of different strategies underlying the spring movement. One strategy aims to maximize benefit during the movement period, and the other tries to maximize benefit in the summer range. Thus, we compared the benefit of movement in three periods: (1) the whole period from leaving the winter range to the end of the stay in the summer range, (2) the movement period (from leaving the winter range to just before arrival at the summer range), and (3) the summer period (after arrival at the

summer range). We tested the mean and variance of benefit between the linear movement type and nomadic movement type using Welch's *t*-test and *F*-test, respectively, for each period.

To reveal which movements led to gain or loss of benefit, we also analyzed the relationships between the benefit in each period and the latitude of winter range, duration of movement, linear and cumulative distances, and cumulative-to-linear distance ratio for each movement type by regression analysis.

4.3 Results

4.3.1 Movement types of Mongolian gazelles in spring

Four (one male) of the 32 movement patterns (12.5%) were the sedentary type, in which the gazelles did not move from the winter ranges until the end of June, and the remaining 28 cases (87.5%) showed movement from the winter ranges before then (Table S4.1). The frequency distribution of the ratio of cumulative distance to linear distance between the winter and summer ranges was bimodal, separated at the ratio of 2.0–2.5, and the frequency was highest for the 1.0–1.5 class (Fig. 4.2). The number of observations of a ratio less than 2.0 (linear movement type) was 16 (50.0%; 14 females, 2 males) and that of more than 2.5 (nomadic movement type) was 12 (37.5%; 10 females, 2 males).

4.3.2 Spatial distribution of movement types

The linear movement type was observed across the entire study area and was not concentrated in any particular region, whereas the nomadic movement type was concentrated in the mid-latitude (45–47°N) area (Fig. 4.3). The sedentary type was observed in the southern and central regions.

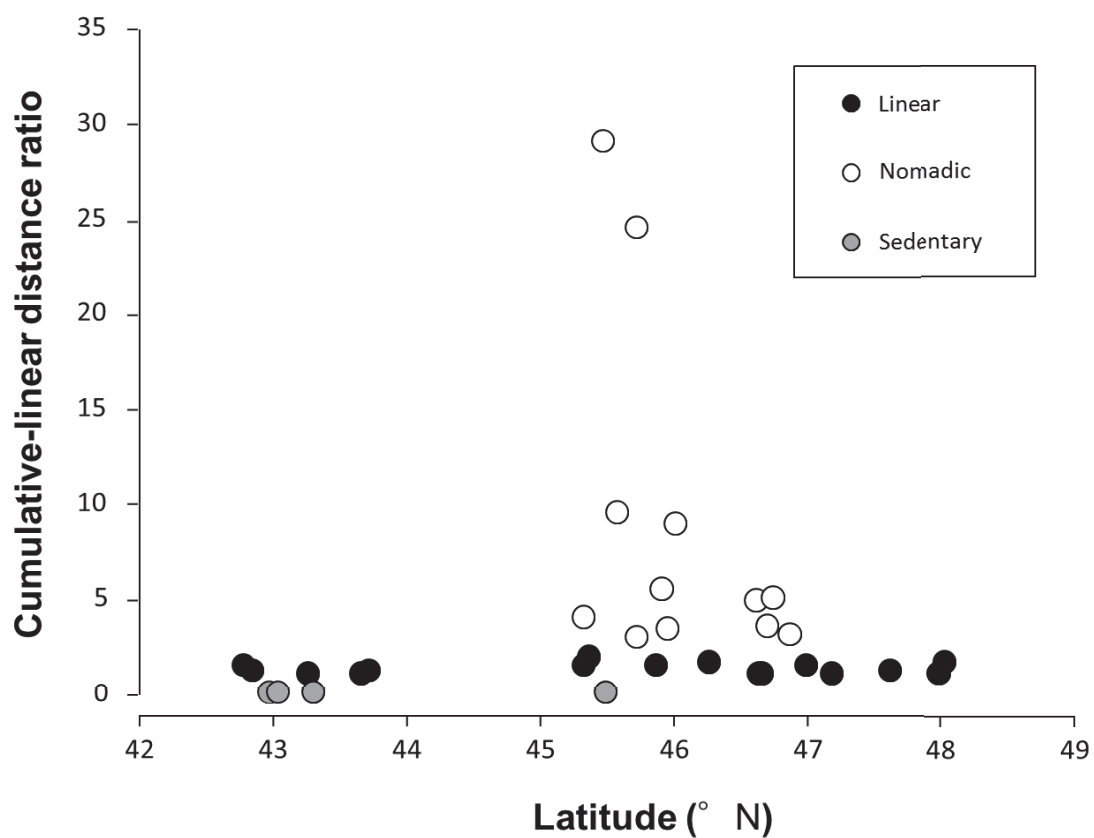


Figure 4.3. Latitudinal distribution of the linear, nomadic, and sedentary movement types and the ratio of cumulative and linear distances between the winter and summer ranges of the tracked Mongolian gazelles. Latitude of each circle indicates the location of the last point in the winter range.

4.3.3 Movement distance and movement periods

The maximum linear distance between two points and cumulative distance in the winter range of the sedentary type ranged from 8 to 56 km and from 56 to 276 km, respectively (Table S4.1). The mean linear distance between the winter and summer ranges was significantly longer in the linear movement type (109 ± 13 km, mean \pm SE) than the nomadic movement type (70 ± 13 km) ($t = 2.18$, $df = 23.88$, $P < 0.05$), and the linear distances ranged from 48 to 239 and from 16 to 152 km for the linear movement type and nomadic movement type, respectively (Fig. 4.4a). The mean cumulative distance between the winter and summer ranges was significantly longer in the nomadic movement type (410 ± 48 km) than in the linear movement type (140 ± 18 km) ($t = -5.23$, $df = 12.72$, $P < 0.01$), and the longest distance moved was 718 km (walked for 154 days) for the nomadic movement type and 342 km for the linear movement type (Fig. 4.4a).

The cumulative distance was positively correlated with linear distance between the winter and summer ranges in the linear movement type ($P < 0.001$, $R^2 = 0.80$, $n = 16$; Fig. 4.4a), but the relationship was not significant in the nomadic movement type ($P = 0.24$, $R^2 = 0.14$, $n = 12$). Cumulative distance increased with longer duration of the movement period for all movements of both movement types ($P < 0.001$, $R^2 = 0.58$, $n = 28$), but there was no significant relationship for each movement type ($P > 0.07$, $R^2 < 0.28$; Fig. 4.4b). Duration of the movement period was significantly longer in the nomadic movement type (123 ± 8 days, mean \pm SE) than in the linear movement type (38 ± 7 days) ($t = -7.80$, $df = 24.6$, $P < 0.001$). In the linear movement type, the duration was less than 64 days except two cases in which it was more than 100 days, whereas in the nomadic movement type in every case it was longer than 80 days. The

shortest period was 7 days in the linear movement type, during which the gazelle moved 114 km in linear distance.

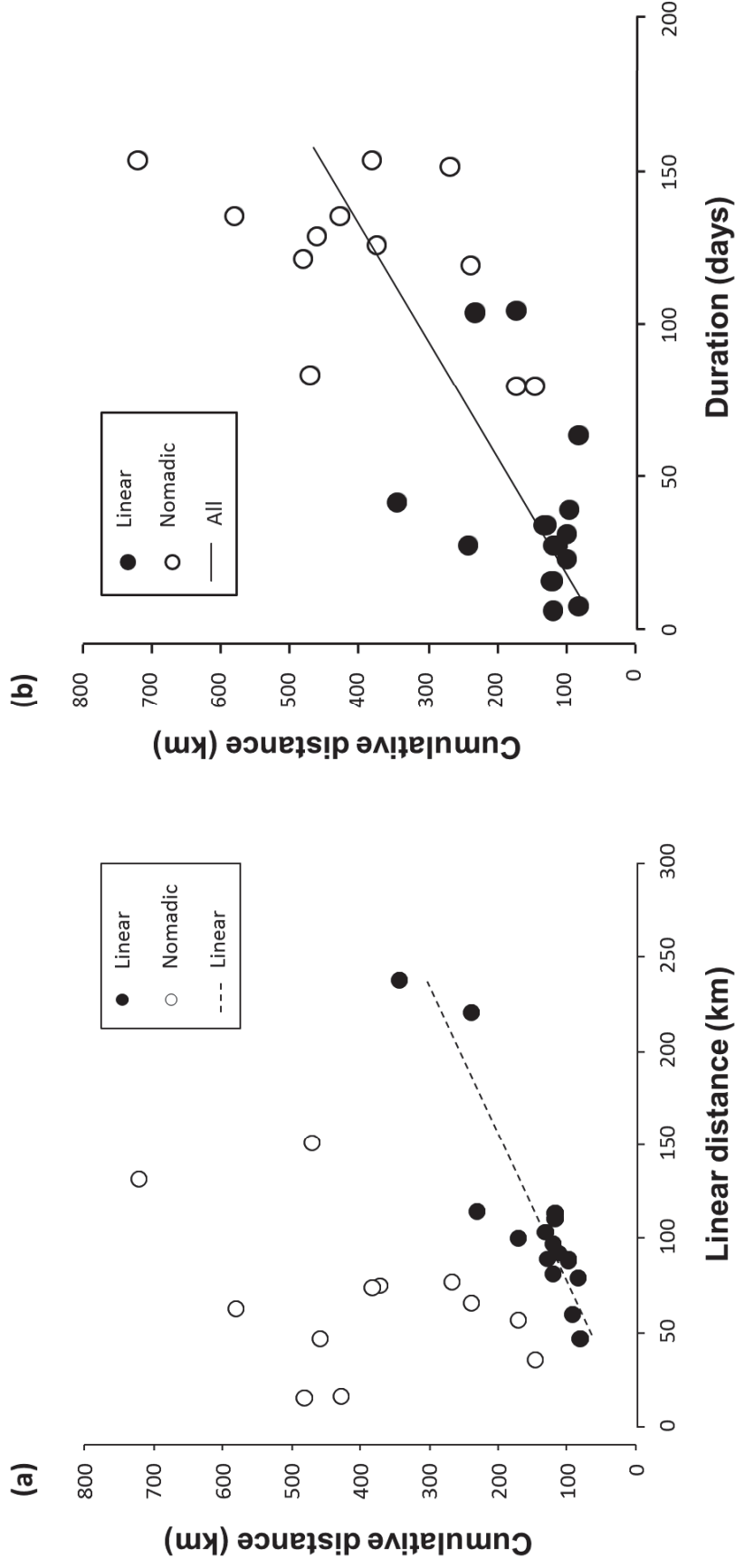


Figure 4.4. Relationships between cumulative distance and linear distance (a) and between cumulative distance and duration of movement period (b) between the winter and summer ranges of the tracked Mongolian gazelles. “Linear” and “Nomadic” refer to the movement types, and “All” indicates all data of both movement types. Regression lines are significant at the 5% level.

4.3.4 Change of vegetation conditions through movement

During spring movements, gazelles that used winter ranges with relatively low NDVI values in summer moved to areas with higher NDVI values, whereas gazelles that used winter ranges with relatively high NDVI values in summer moved to areas with lower NDVI values ($P = 0.003$, $R^2 = 0.29$, $n = 28$, Fig. 4.5). A negative relationship between the summer (after leaving the winter range) NDVI values at the winter ranges and NDVI change through movement was detected only in the linear movement type ($P = 0.012$, $R^2 = 0.37$, $n = 16$, Fig. 4.5).

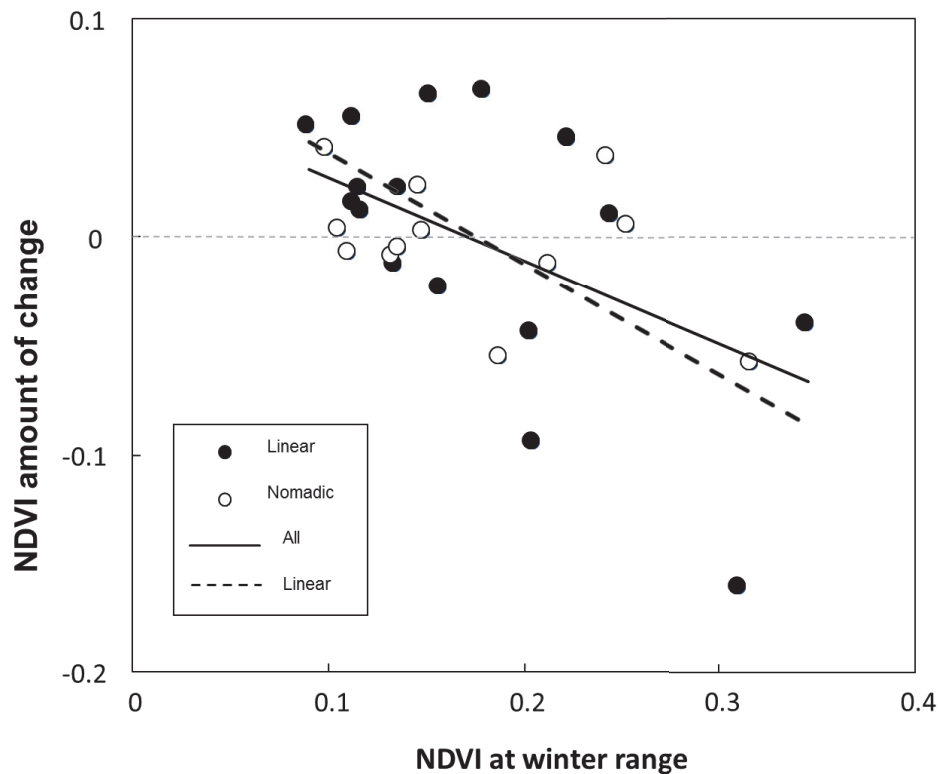


Figure 4.5. Change of normalized difference vegetation index (NDVI) values from the winter range for each movement type. Horizontal axis shows the average NDVI value in the winter range for the period from when the gazelle left the winter range to the end of August. Vertical axis shows the difference in average NDVI values between the actual case the gazelle experienced and a simulated case of the gazelle remaining in the winter range through August. “Linear” and “Nomadic” refer to the movement types, and “All” indicates all data of both movement types. Regression lines are significant at the 5% level.

4.3.5 Preferred NDVI range for Mongolian gazelles

The areas within the NDVI range of 0.15–0.2 were continuously selected, whereas those with higher or lower NDVI values were avoided or were not significantly selected by the gazelles in the growing season, that is, from May to July (Fig. 4.6). Thus, in the present study, we defined this range as the preferred NDVI range for the Mongolian gazelles in the vegetation growth season. This NDVI range was intermediate in the entire study area from April to July.

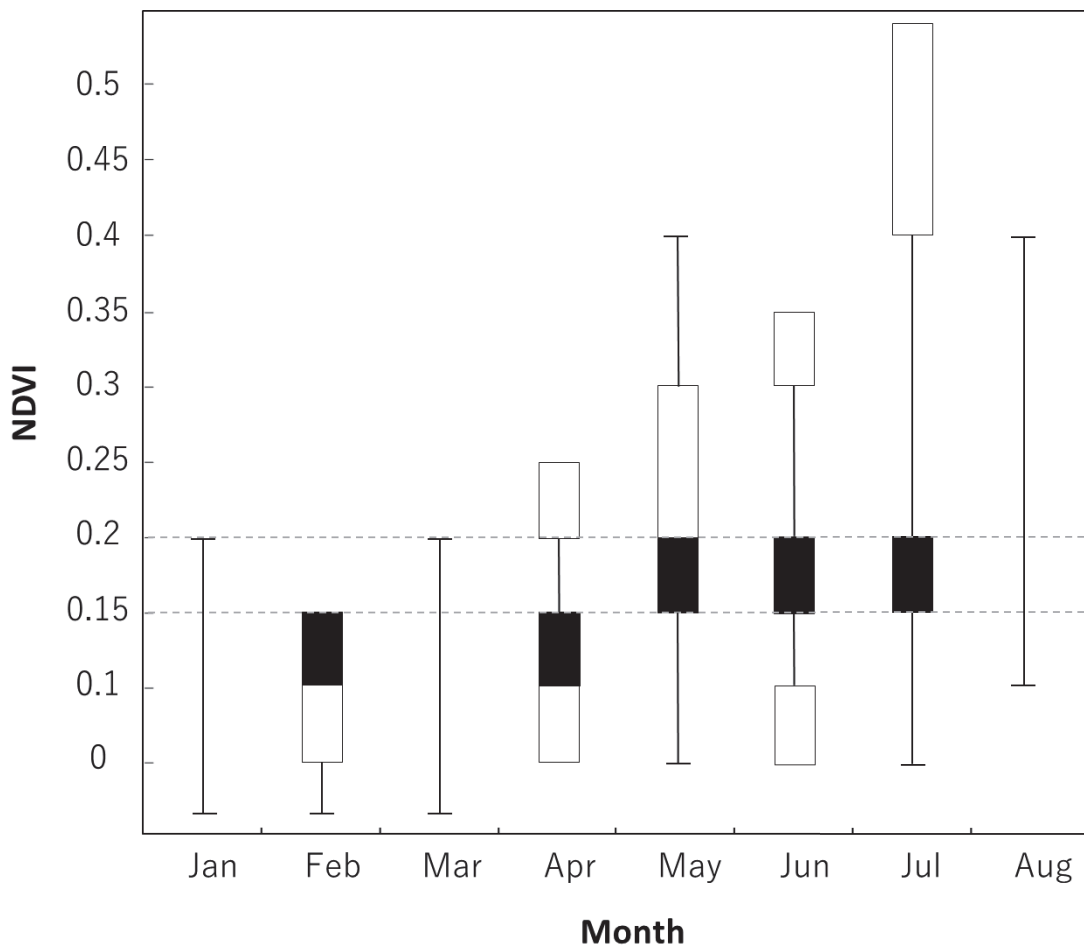


Figure 4.6. Monthly area selectivity by the tracked Mongolian gazelles, as evaluated by NDVI values. Significant positive (black bar) and negative (white bar) selection was analyzed by Manly's selectivity index. Solid lines indicate ranges without significant selectivity. The NDVI range of 0.15–0.20 (dashed lines) was positively selected throughout the vegetation growing season (from May to July).

4.3.6 Benefit of spring movement

The variance in the benefit obtained via movement differed between the movement types when the periods were separated into the movement period and summer period, and the relationship was opposite between the two periods (Fig. 4.7, Table S4.1). When we compared the benefit in the whole movement period, that is, the total of the movement and summer periods, the variance of benefit among the individuals was not different between the movement types ($F_{15,11} = 1.79$, $P = 0.33$). However, during the movement period, the variance of benefit was larger in the nomadic movement type ($F_{11,14} = 8.93$, $P < 0.001$), whereas during the summer period it was larger in the linear movement type ($F_{15,7} = 12.41$, $P = 0.003$). During the movement period the unbiased estimate of variance and interquartile range of benefit were 8.93- and 2.49-fold larger in the nomadic movement type than the linear movement type, respectively, whereas in the summer period they were 12.41- and 5.56-fold larger in the linear movement type. The highest benefit values were 0.458 in the linear movement type and 0.462 in the nomadic movement type. However, the mean benefit values were close to 0 (ranging from -0.02 to 0.07) for both movement types and did not differ significantly between the two types for all movement periods ($|t| < 1.32$, $df < 26.0$, $P > 0.21$).

To identify the movement variables that resulted in large benefit gain or loss, we analyzed their relationships with the benefit in each period (Figs. S1–S5). The only significant relationships observed were in the linear movement type, with larger benefits for shorter movement duration in the whole period ($R = 0.55$) and in the summer period ($R = 0.57$) (Fig. S4.1a) and more rectilinear movement in the summer period ($R = 0.52$, Fig. S4.2a). The gazelles that gained the first and second largest benefit in the linear movement type for the whole period moved 89 and 105 km of linear distance over 28

and 24 days, respectively, and those were the second and third largest benefits among all gazelles. The gazelle that obtained the largest benefit used the nomadic movement type. For some gazelles using the linear movement type, the benefit was small or negative even though they moved similar linear distances as others. The gazelle with the largest benefit loss used the linear movement type and moved 101 km of linear distance over 105 days. The gazelle with the second largest benefit loss used the nomadic movement type.

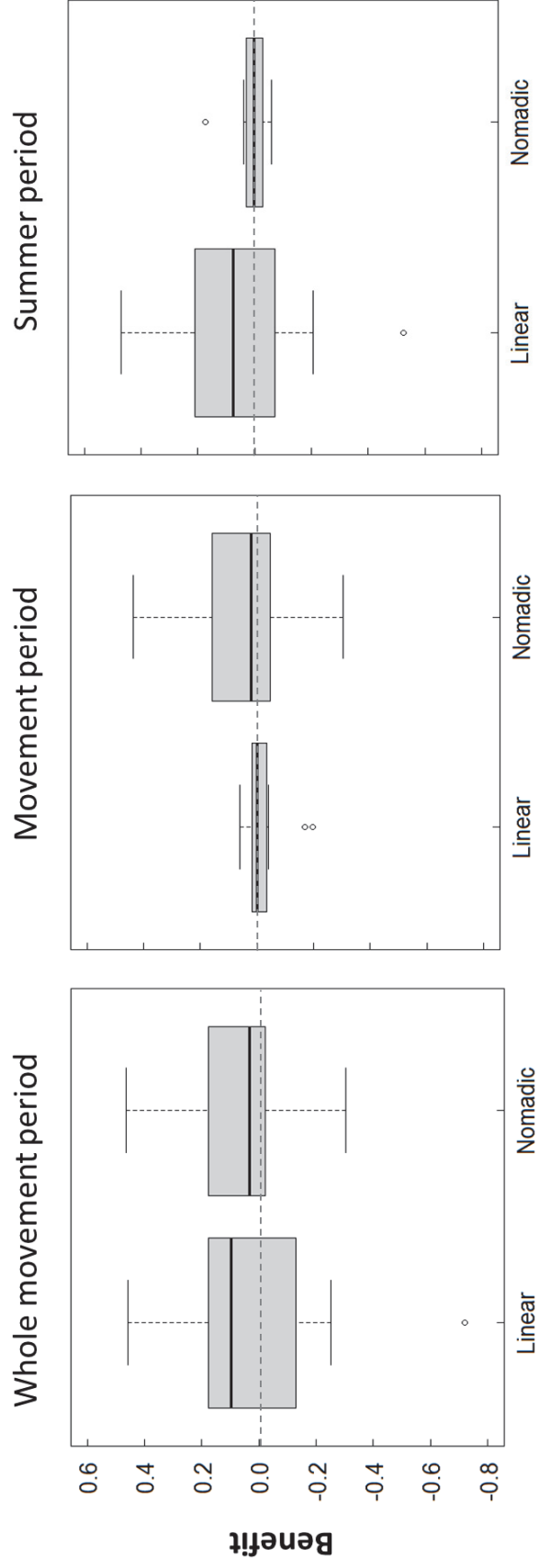


Figure 4.7. Estimated benefit obtained via movement of the linear and nomadic movement types by the tracked Mongolian gazelles. The movement period spans from when gazelles moved between the winter and summer ranges, the summer period is when gazelles remained in the estimated summer ranges, and the whole movement period is the sum of both periods.

4.4 Discussion

4.4.1 Preferred vegetation conditions for Mongolian gazelles and benefit obtained through movement

The Mongolian gazelles continuously preferred areas with an intermediate NDVI value (0.15–0.2) from May to July (Fig. 4.6). The results of this and previous studies (Mueller et al. 2008, Olson et al. 2011, Ito et al. 2013b) suggest that areas with intermediate vegetation biomass are preferred foraging sites for Mongolian gazelles from spring to autumn, as well as other ungulates such as wildebeest (*Connochaetes taurinus*, Wilmshurst et al. 1999) and Thomson's gazelle (*Eudorcas thomsonii*, Fryxell et al. 2004) in the Serengeti ecosystem of East Africa and *C. elaphus* in Canada (Hebblewhite et al. 2008), which is explained by the forage maturation hypothesis (Fryxell 1991, Wilmshurst et al. 2000). The constant NDVI values of the preferred areas during the vegetation growing season enabled us to quantify the benefit obtained via movement, although consideration of regional and interannual differences are needed to improve the evaluation method by collecting further movement data across wider ranges. The instantaneous rate of green-up was recently used to evaluate forage quality in an area (Bischof et al. 2012, Merkel et al. 2016). However, our method that simply evaluates foraging sites during long-distance movement by herbivores based on NDVI values has some merits in drylands such as Mongolia, where vegetation does not grow enough in some years and animals move across different vegetation types.

Spatial and temporal shifts in the spatial distribution of preferred areas (Fig. S6) would explain the long-distance movements of many gazelles in spring. The nomadic movement type reflects the large heterogeneity and irregular change in the spatial distribution of preferred areas. The fact that the benefit obtained via movement was

negative for about half the cases indicates the low seasonal and interannual predictability of vegetation conditions in this area.

4.4.2 Movement type and strategy of Mongolian gazelles in spring

Three movement types in spring were identified in the present study; the sedentary type represented only 12.5% of the cases, and the linear and nomadic movement types together accounted for 87.5%. Here, we mainly discuss the relationships between the movement type, movement strategy, and environmental conditions.

The period with large individual variation of benefit differed between the movement types, which suggests the existence of different movement strategies in the Mongolian gazelle. The nomadic movement type, with a large ratio of cumulative distance to linear distance between the winter and summer ranges, is a strategy used to obtain benefit during movement. Here, we call this the searcher strategy, in which the animal assesses the surrounding environmental conditions and seeks areas with better forage conditions during its movement (MacNally 2001, Zurell et al. 2010). The longer movement period in the nomadic movement type than in the linear movement type supports the assumption that the gazelles had searched for better areas. Gazelles that could find areas with better vegetation conditions obtained greater benefit during the movement period, whereas those that could not find such areas suffered a benefit loss. This difference drove the large individual variation of benefit during the movement period, and the many cases of nomadic movement that lost benefit reflects the difficulty of riding the green-wave or the absence of a clear wave of green-up in this area.

On the other hand, linear long-distance movements over a short period in the linear movement type suggest movement toward specific summer ranges, with the animals

ignoring vegetation conditions of the areas they pass through. This strategy is similar to the jumper strategy employed by other ungulate species in ecosystems with high predictability of seasonal and interannual vegetation conditions (Bischof et al. 2012). For some movement patterns classified as the linear movement type, it would be better to consider them as the searcher rather than the jumper strategy". If a gazelle searched for areas with better vegetation conditions in a linear fashion during the movement, the movement is classified as the linear movement type. In this case, the movement period would have been relatively long. Even in cases when the movement period was short, if the distance moved was short, the gazelle might find areas with good vegetation conditions by chance and stay in that area for a long time. This movement pattern may also reflect the searcher strategy.

Large-scale spatial heterogeneity of vegetation conditions is a factor that drives gazelles to move long distances in order to obtain benefit. The low temporal predictability of vegetation biomass in Mongolia's steppe means that the wave of vegetation growth phenology does not occur here. Instead of the green-wave, a clear latitudinal gradient of vegetation conditions seems to be important for spring gazelle movement. From spring to autumn, vegetation biomass is generally larger in the north than in the south of the gazelles' distributional range in Mongolia (Yu et al. 2004). Therefore, at a large spatial scale, better forage conditions (intermediate vegetation cover) for Mongolian gazelles in the mid-latitudinal zone are generally predictable (Fig. S6), and linear movement toward this zone would be effective for accessing the better vegetation conditions. The nomadic movement type would also be effective in the mid-latitudinal zone, and the sedentary type would be used in areas with good vegetation conditions.

At a smaller spatial scale, the heterogeneity of vegetation conditions would explain both movement strategies. Nomadic movements of many gazelles using the searcher strategy, which places importance on the movement period, would be caused by the patchy distribution of areas with preferred vegetation conditions in the mid-latitude zone. Use of the jumper strategy suggests the existence of some areas with relatively high temporal predictability of vegetation conditions in the study area. If there are such areas and some gazelles use these areas in usual summers, these areas would be important for the conservation of jumper populations.

The coexistence of multiple movement types or strategies including the sedentary type (or strategy) in the Mongolian gazelle is mainly explained by the large interannual variability in the spatial distribution of preferred environmental conditions. The sedentary type might experience relatively good vegetation conditions in the winter range until late spring, so moving away from the range is not necessary. The large variance in benefit values in the linear and nomadic movement types (Fig. 7) indicates that no particular strategy is clearly superior. A strategy may provide more benefit than other strategies in one year but not in others. Even within a year, some gazelles using the same strategy would be successful and others unsuccessful.

4.4.3 Future challenges and conservation implications

Our study revealed the existence of multiple movement strategies within Mongolian gazelle and the effects of spatial heterogeneity of vegetation conditions at various spatial scales on the movements of each strategy. These findings have conservation implications for managing habitat with low temporal predictability of forage conditions and can improve our understanding of animal movement ecology. The nomadic

movement type and searcher strategy of gazelles indicate low interannual predictability of vegetation conditions in the study area. Therefore, accessibility to a wide range of habitats is important for conservation of this long-distance nomadic ungulate. Use of the jumper strategy suggests the existence of some important areas where interannual predictability of environmental conditions is relatively high. Some gazelles moved linearly for long distances to some areas, but habitat fragmentation caused by new railroad construction and large mining projects in Mongolia is cause for concern (Batsaikhan et al. 2014, Ito et al. 2018). Studies focusing on important areas and the prevention of further habitat fragmentation are needed to reduce additional losses of the Mongolian gazelle population.

The benefit loss experienced by individuals using the searcher and jumper strategies also indicates low interannual predictability of vegetation conditions in the study area, but long-term research with a more rigorous definition of movement strategy is needed to better understand the strategies used by animals that move long distances. The benefit loss via movements in the vegetation growth period should not significantly affect animal survival, which may be why multiple movement types and strategies were observed in spring. However, failure to select beneficial movement directions and locations during the period when forage is decreasing can have critical effects on survival, fitness, and evolution of the movement strategy, although estimating the benefit obtained via movement during the season of forage decline is challenging. In addition, it is possible that animals inhabiting regions with low temporal predictability of environmental conditions change their movement strategy between years and within a season. For example, an animal may use the jumper strategy to move to an area that has good forage conditions in a usual year, but if after arriving the animal discovers

poor conditions, it might switch to the searcher strategy. Therefore, we need more studies of the plasticity of movement strategies within individuals and populations from both genetic and environmental perspectives.

Although the effects of multiple scales of spatial heterogeneity of environmental conditions on animal home range size (Kie et al. 2002) and movement routes (MacNally 2001) have been reported, such spatial heterogeneity is also likely to affect the movement strategy. The magnitude of interannual variability and multiple scales of spatial heterogeneity of environmental conditions also drive the coexistence of several movement strategies as represented by partial migration, in which both migratory and resident populations of a species exist within a region (Chapman et al. 2011), as well as factors such as population density (Hopcraft et al. 2014), predation risk (Bischof et al. 2012), and anthropogenic disturbance (Wilson et al. 2016). Additional tracking data and more detailed surveys of vegetation cover are needed to better understand what drives the movement strategies of animals that move long distances across areas with low predictability of environmental conditions.

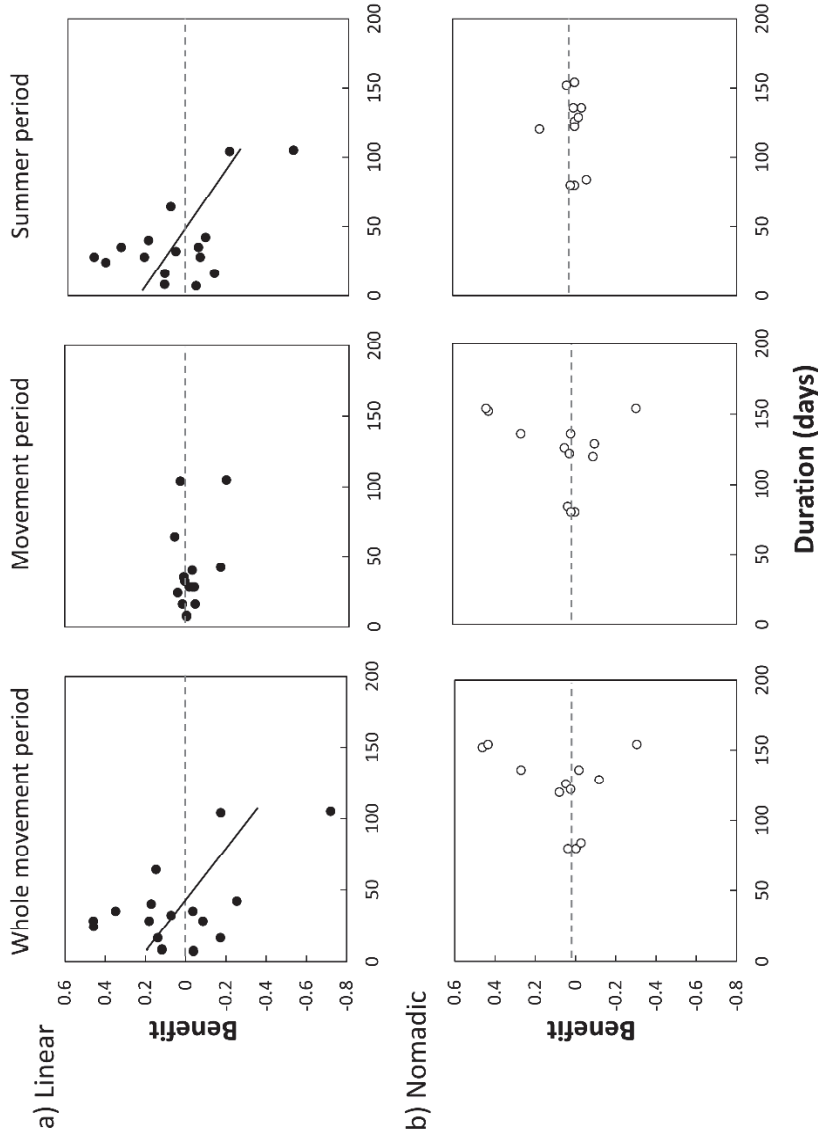


Figure S4.1. The relationships between duration of movement period and estimated benefit in each period for the linear movement type (a) and the nomadic movement type (b) of Mongolian gazelles. The movement period spans from when gazelles moved between the winter and summer ranges, the summer period is when gazelles remained in the estimated summer ranges, and the whole movement period is the sum of both periods. Regression lines are significant at the 5% level.

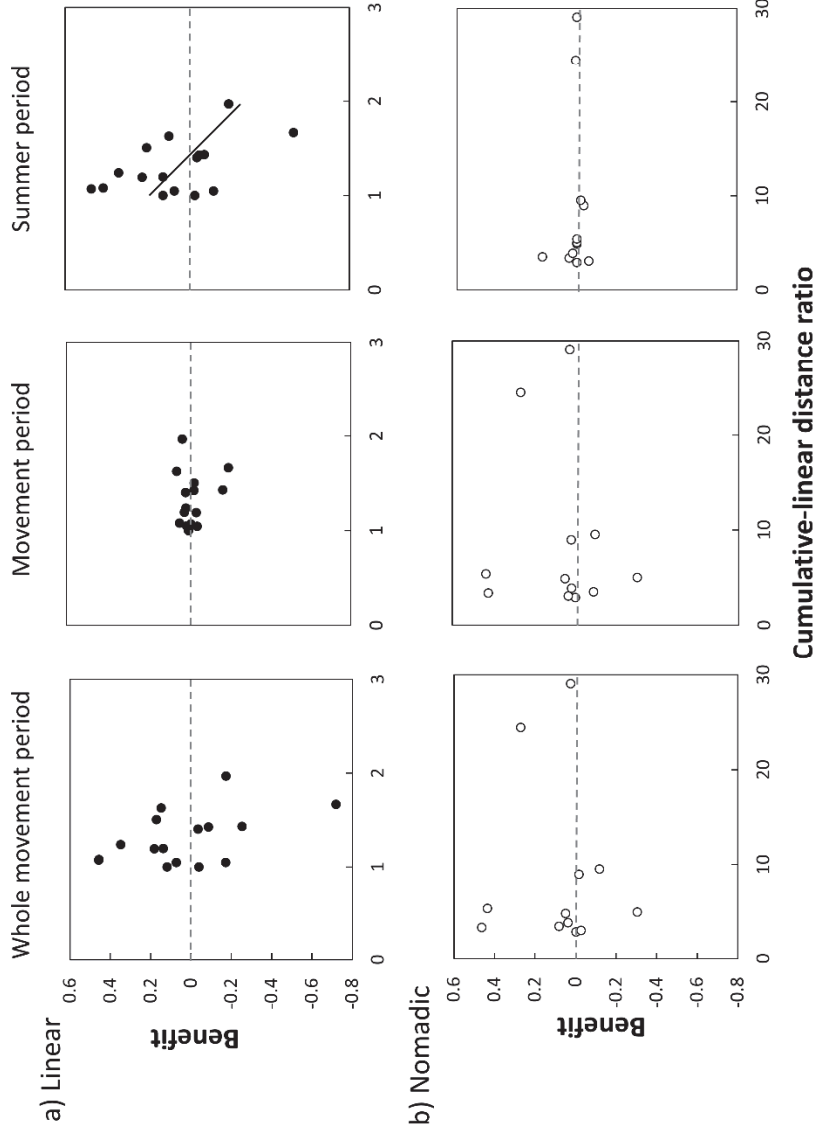


Figure S4.2. The relationships between cumulative-to-linear distance ratio and estimated benefit in each period for the linear movement type (a) and the nomadic movement type (b) of Mongolian gazelles. The movement period spans from when gazelles moved between the winter and summer ranges, the summer period is when gazelles remained in the estimated summer ranges, and the whole movement period is the sum of both periods. Regression lines are significant at the 5% level.

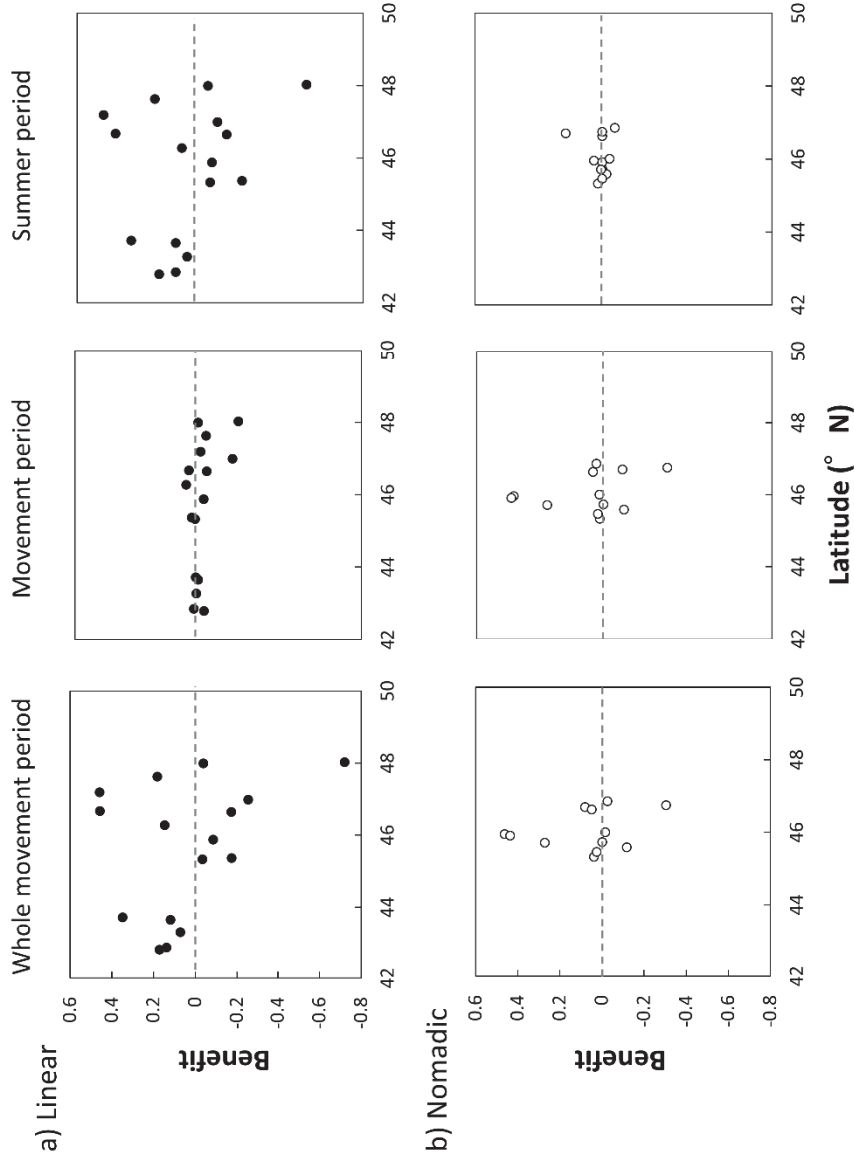


Figure S4.3. The relationships between latitude and estimated benefit in each period for the linear movement type (a) and the nomadic movement type (b) of Mongolian gazelles. The movement period spans from when gazelles moved between the winter and summer ranges, the summer period is when gazelles remained in the estimated summer ranges, and the whole movement period is the sum of

both periods.

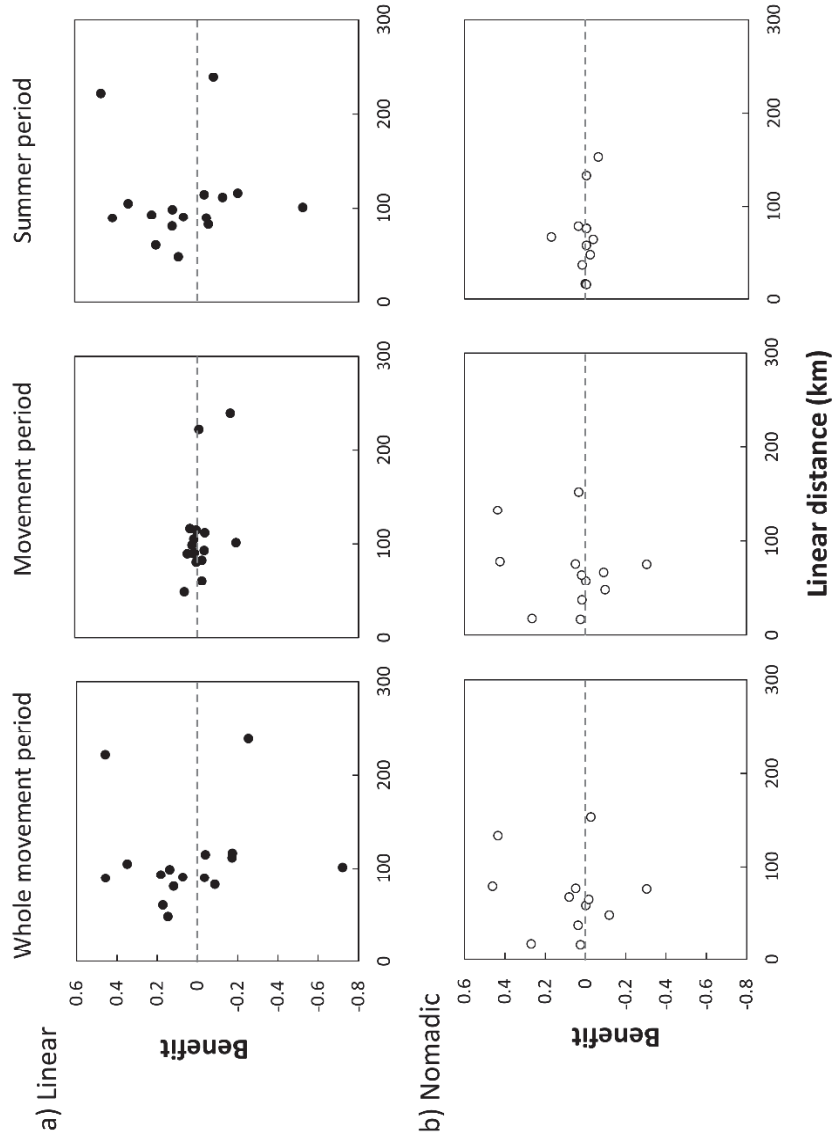


Figure S4.4. The relationships between linear distance and estimated benefit in each period for the linear movement type (a) and the nomadic movement type (b) of Mongolian gazelles. The movement period spans from when gazelles moved between the winter and summer ranges, the summer period is when gazelles remained in the estimated summer ranges, and the whole movement period is the

sum of both periods.

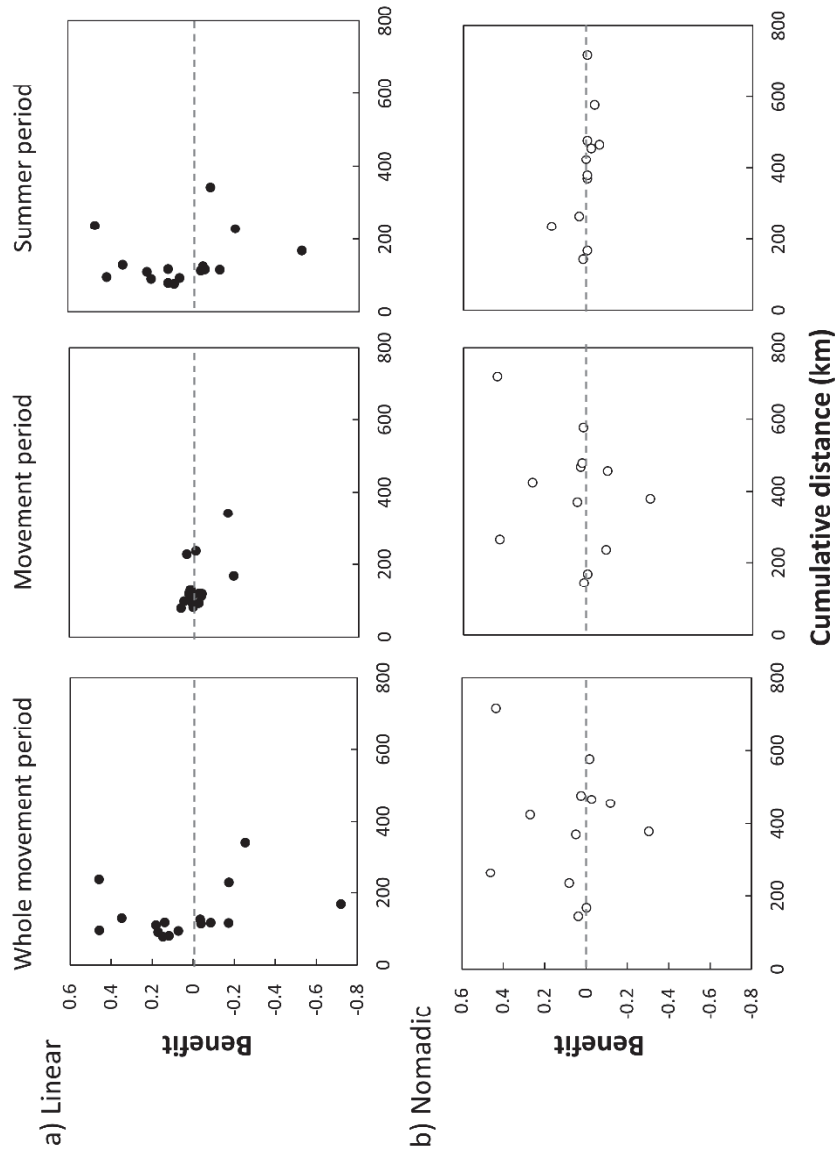


Figure S4.5. The relationships between cumulative distance and estimated benefit in each period for the linear movement type (a) and the nomadic movement type (b) of Mongolian gazelles. The movement period spans from when gazelles moved between the winter and summer ranges, the summer period is when gazelles remained in the estimated summer ranges, and the whole movement period is

the sum of both periods.

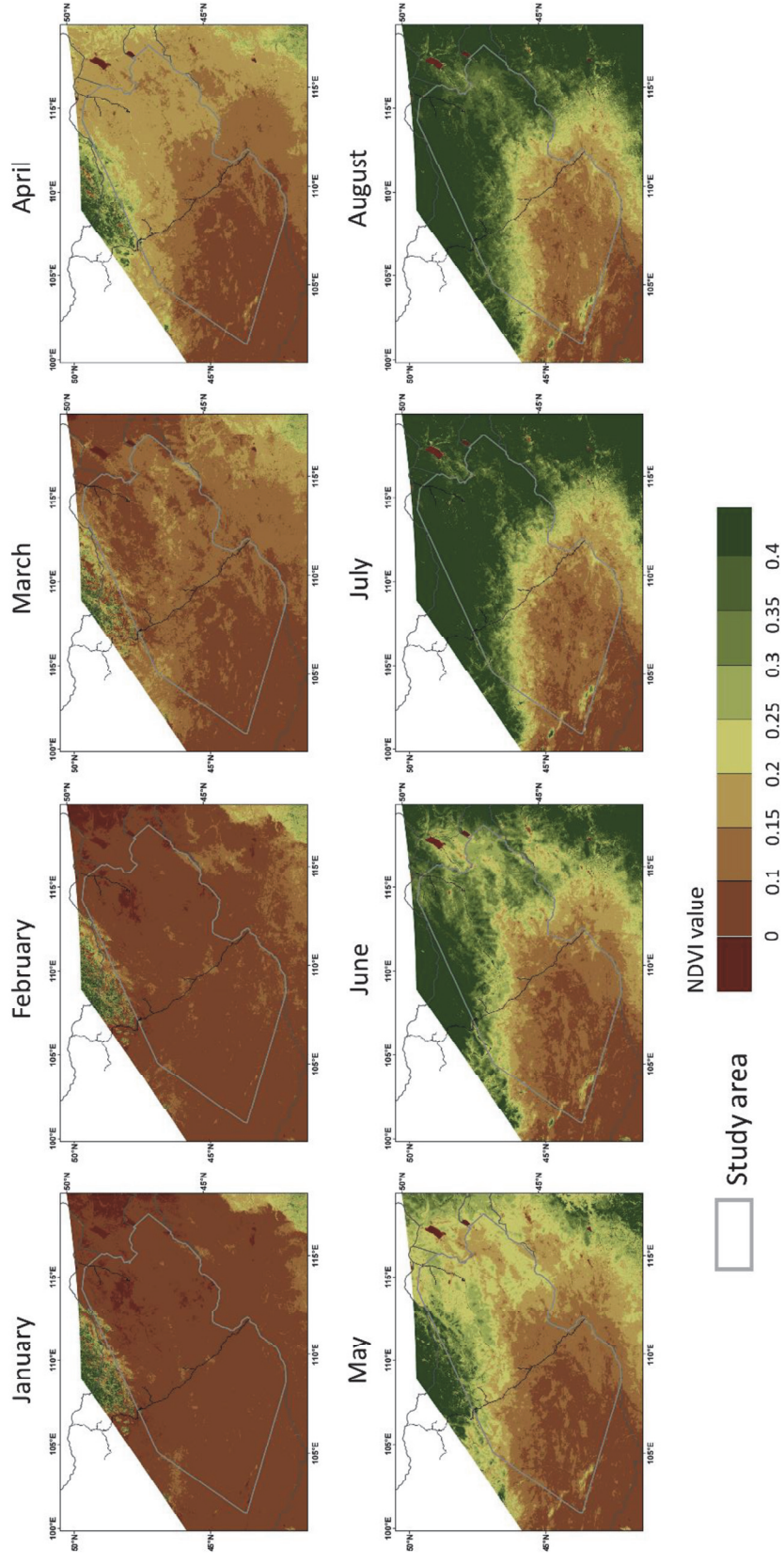


Figure S4.6. Monthly change (from January to August) in the spatial distribution of mean NDVI values from 2003 to 2012 in the study

area.

Table S4.1. Information of movement and benefit of tracked Mongolian gazelles.

ID	Year	Movement type	Sex	Age (years)	Winter range				Summer range				Cumulative distance ratio	Duration (days)	Benefit			
					Date of start	Date of end	Latitude (°N)	Longitude (°E)	Date of start	Latitude (°N)	Longitude (°E)	Whole period			Movement period	Summer period		
37572	2003	Linear	F	adult	* Feb 14	Apr 11	45.38	108.39	May 9	45.20	108.94	82.5	117.5	1.42	28	-0.086	-0.027	-0.059
37573	2003	Linear	F	3-5 (adult)	* Feb 14	Feb 28	43.72	101.80	Apr 4	43.96	103.06	104.8	129.8	1.24	35	0.349	0.013	0.336
25381	2004	Linear	M	1-2	* Mar 20	Mar 20	48.03	115.49	Jul 3	49.07	115.09	101.2	168.6	1.67	105	-0.720	-0.196	-0.524
37572	2004	Linear	F	adult	* Apr 29	Apr 29	47.19	107.34	May 27	45.42	108.67	221.7	237.3	1.07	28	0.459	-0.012	0.471
41243	2004	Linear	F	2-3	* Jan 29	Apr 18	45.33	108.46	May/23	44.81	108.58	89.9	126.0	1.40	35	-0.034	0.015	-0.049
42645	2004	Linear	F	adult	* Jan 10	May 15	47.99	115.25	May/22	47.87	113.73	114.5	114.5	1.00	7	-0.038	—	-0.038
41243	2005	Linear	F	3-4	* May 11	May 11	46.99	105.77	Jun 22	45.79	108.35	238.8	341.7	1.43	42	-0.253	-0.168	-0.085
42645	2005	Linear	F	adult	* Jan 8	Mar 19	47.62	112.26	Apr/16	48.00	113.37	93.0	110.7	1.19	28	0.182	-0.038	0.220
67929	2008	Linear	M	1-2	* Feb 16	Apr 12	46.27	108.27	Jun 15	46.51	107.75	48.3	78.6	1.63	64	0.148	0.059	0.089
67932	2008	Linear	F	adult	* Mar 3	May 30	46.64	110.88	Jun 15	47.52	111.60	111.5	116.6	1.05	16	-0.172	-0.042	-0.130
78511	2008	Linear	F	2-3	* Feb 16	Apr 12	43.65	110.10	Apr 20	43.39	109.17	80.7	80.7	1.00	8	0.119	0.000	0.119
67921	2009	Linear	F	3	* Feb 18	Feb 18	45.36	110.70	Jun 2	46.39	110.94	116.1	228.4	1.97	104	-0.174	0.031	-0.205
67928	2009	Linear	F	adult	* May 1	May 1	46.67	106.81	May 25	46.19	107.74	89.4	96.4	1.11	24	0.457	0.044	0.413
78510	2009	Linear	F	2-3	* Feb 18	Apr 23	43.27	110.22	May 25	43.30	109.11	90.4	94.6	1.05	32	0.073	0.009	0.063
78511	2009	Linear	F	3-4	* Jan 25	Mar 6	42.79	108.74	Apr 15	43.29	109.03	60.8	91.4	1.50	40	0.172	-0.028	0.199
78511	2010	Linear	F	4-5	* Feb 5	May 20	42.84	109.71	Jun 5	43.33	108.69	98.8	118.0	1.19	16	0.139	0.021	0.118
37571	2003	Nomadic	F	1-2	* Feb 7	Mar 21	45.46	109.20	Jul 21	45.33	109.30	16.4	477.9	29.08	122	0.025	0.025	0.000
25363	2004	Nomadic	F	2-3	* Jan 8	Apr 24	46.63	114.42	—**	—**	—**	76.0	370.2	4.87	126	0.049	0.049	—
25448	2004	Nomadic	M	3	* Jan 8	Mar 26	45.91	116.12	—**	—**	—**	132.8	717.6	5.40	154	0.436	0.436	—
37571	2004	Nomadic	F	2-3	* Feb 16	Feb 16	45.58	109.55	Jun 24	45.42	108.98	47.9	456.3	9.53	129	-0.117	-0.098	-0.019
25363	2005	Nomadic	F	3-4	* Mar 26	Mar 26	46.75	114.65	—**	—**	—**	75.6	379.1	5.02	154	-0.304	-0.304	—
37571	2005	Nomadic	F	3-4	* Mar 6	Mar 6	46.86	106.01	May 29	46.09	107.66	182.5	467.0	3.06	84	-0.026	0.033	-0.059
67921	2008	Nomadic	F	2	* Feb 24	Feb 24	45.96	108.97	Jul 25	46.07	109.96	78.3	264.3	3.37	152	0.463	0.423	0.039
67925	2008	Nomadic	F	1	* Feb 16	Feb 16	46.01	107.96	Jul 11	45.08	109.24	64.3	576.6	8.97	136	-0.016	0.019	-0.035
67927	2008	Nomadic	M	2	* Feb 8	Feb 8	46.70	105.38	Jun 7	47.08	106.07	66.9	235.4	3.52	120	0.081	-0.091	0.172
67928	2008	Nomadic	F	adult	* Jan 15	Jun 7	45.73	106.92	—**	—**	—**	57.9	167.9	2.90	80	-0.002	-0.002	—
67931	2008	Nomadic	F	1	* Feb 16	Feb 16	45.71	110.71	Jul 11	45.59	110.85	17.3	424.4	24.46	136	0.271	0.265	0.006
67933	2008	Nomadic	F	adult	* Mar 3	May 6	45.33	109.07	Jul 25	45.00	109.12	37.1	144.0	3.88	80	0.038	0.017	0.021
67923	2008	Sedentary	M	1	—	—	45.48	110.90	—	—	—	56.0***	275.5	—	—	—	—	—
75810	2010	Sedentary	F	3-4	—	—	42.97	110.20	—	—	—	12.2***	55.5	—	—	—	—	—
78510	2011	Sedentary	F	4-5	—	—	42.97	110.18	—	—	—	8.1***	105.9	—	—	—	—	—
78511	2011	Sedentary	F	5-6	—	—	43.29	109.05	—	—	—	9.1***	66.3	—	—	—	—	—

F: female. M: male. *: Gazelles were already in the winter range on the first date of analysis. **: Gazelles that did not have an estimated summer range. ***: Linear distance in sedentary gazelles was calculated as the maximum linear distance between two points in the winter range. —: No data available

Chapter 5

General discussion

In the present thesis, I analyzed multiple elements in the movement of Mongolian gazelles over a wide and continuous distribution, and revealed the different regional trends among the elements. Mongolian gazelles were generally nomadic throughout their distribution range (Chapter 2). However, latitudinal trends were observed in annual home-range sizes (Chapter 3) and spatial distribution in spring movement strategies (Chapter 4). The latitudinal trends were different between movement elements. The annual range size (annual movement distance) linearly increased from south to north, although a spring movement strategy, “searcher” was most prominent at mid-latitudes (Fig. 5.1). Such differences in regional trends between movement elements could be explained by the spatiotemporal heterogeneity of vegetation conditions in the habitat of the Mongolian gazelle.

Although the temporal predictability of vegetation conditions in Mongolia is relatively low compared to other regions of the globe (von Wehrden et al. 2012), vegetation conditions were spatially different within the Mongolian gazelle’s habitat. Vegetation quantity in summer increase with increase in precipitation from south to north (Chapter 3, Yu et al. 2003, Vandandorj et al. 2015). However, vegetation quality for Mongolian gazelles in summer was highest in the mid-latitude (Chapter 4, Fig. 5.1), which is explained by the forage maturation hypothesis (Fryxell et al. 1998). Selection of areas with intermediate vegetation amounts by Mongolian gazelles has also been reported in previous studies (Mueller et al. 2008, Olson et al. 2010). In the northern area, which had higher vegetation quantities than the mid-latitude, the optimal vegetation

conditions were observed in early spring. Vegetation quantity and quality in winter were almost similar in all regions or marginally higher in the central and south regions, since larger areas in the north were covered in snow, while shrubs were more likely to be available in the central and south regions, which had less snow cover. Therefore, seasonal changes in vegetation quantity and quality would be greater in the north (Chapter 3, Fig. 5.1). However, as mentioned above, the seasonal and regional differences in the peak periods with maximum vegetation quantity and quality values would be critical in understanding seasonal movements of Mongolian gazelles.

Larger interannual variations in vegetation condition in summer in the mid-latitude than in the north and south in Mongolia have been reported based on NDVI analyses (Eckert et al. 2015, Vandandorj et al. 2015). Although the interannual variation in vegetation conditions in summer could be synchronous over wide areas in similar latitudes, spatial heterogeneity of vegetation conditions would also be high in the mid-latitude zones of the study area, based on the levels of precipitation in the area. The high frequency of gazelles considered to adopt “searcher” strategies in the mid-latitude (Chapter 4) would indicate coarse spatial heterogeneity of the vegetation conditions in the area (Fig. 5.1). Therefore, vegetation conditions can be divided into two categories; linearly changing or maximizing/minimizing at the mid-latitude along the latitudinal gradient.

Such varying spatial patterns in vegetation factors along latitudinal gradients could explain the regional and individual differences in movement patterns and strategies of Mongolian gazelles, despite the generally low interannual predictability of vegetation conditions (von Wehrden et al. 2012), in addition to why Mongolian gazelles are generally nomadic (Chapter 2, Mueller et al. 2011). The linear changes in vegetation

factors along a latitudinal gradient would explain the regional differences in annual range sizes (annual movement distance). Mongolian gazelles do not move considerably throughout the year in the south, where seasonal changes in vegetation conditions are minimal. Conversely, in the north to mid-latitudes, where the seasonal changes in vegetation conditions are greater, gazelles move over long distances seasonally. Consequently, range sizes and the spatial heterogeneity of the vegetation conditions within annual ranges would be greater (Chapter 3).

The coarse spatial heterogeneity in vegetation quantity and quality in summer and their low interannual predictability in the mid-latitudes are potentially responsible for the high frequency of gazelles considered “searchers” in the area, and the movements of gazelles considered “jumpers” towards the mid-latitudes from the north and south (Chapter 4). Low interannual predictability of vegetation conditions would lead to both groups obtaining and losing benefits through spring movements in gazelles. Therefore, both strategies could have coexisted. Movements of some gazelles considered “searchers” towards north in early spring and back to the mid-latitudes before summer (Chapter 4) suggest that vegetation quality was higher in the north in early spring and then areas with high quality vegetation shifted to the mid-latitudes. In addition, the gazelles “jumping” over long distances for short periods suggests high interannual predictability of suitable vegetation conditions over a lower spatial scale.

The present thesis revealed spatiotemporal heterogeneity in vegetation conditions even in the habitat of Mongolian gazelles, in addition to their relationships with regional differences in annual movement distances (annual range size) and spring movement strategies of the gazelles. Among the vegetation factors influencing movement elements of Mongolian gazelles, there are factors that change linearly along the latitudinal

gradient and those maximizing/minimizing at the mid-latitude. In addition, the spatial differences in vegetation conditions include temporal factors such as the magnitude and predictability of seasonal and interannual changes. Large-scale vegetation factors along the latitudinal gradient influence annual movement distances, annual home-range sizes, and medium spatial-scale vegetation factors. For example, the spatial heterogeneity at similar latitudinal (vegetation) zones influences the number of gazelles adopting different spring movement strategies. Smaller-scale spatial heterogeneity such as spatial variation within similar plant communities would also influence movement and habitat selection of gazelles, although such factors were not examined in the present thesis.

In addition to the spatial scale, there are different temporal scales in predictability of vegetation conditions that influence animal movement. In this thesis, I revealed the influence of large (interannual) and medium (seasonal) scale changes in vegetation conditions on Mongolian gazelle movements. Finer-scale temporal heterogeneity in environmental conditions such as within seasons or diurnal changes would also influence animal movement. Studies on the effects of changes at different spatiotemporal scales on animal movement and habitat selection have been increasing recently (Kie et al. 2002, van Moorter et al. 2013), and the results of this thesis would be an important case study.

Nevertheless, the present study has some limitations. Quantification of temporal predictability and spatial heterogeneity of environmental conditions, analysis of differences based on sex and age, and movement strategies in seasons other than spring were not conducted. Benefit losses through movement were identified, suggesting the high spatial heterogeneity and low interannual predictability in the study area (Chapter 4). However, the benefits were calculated solely based on changes in vegetation indices.

Therefore, more quantitative evaluations would be required to examine the relationships between vegetation index and vegetation quality for Mongolian gazelles and the benefit gains and losses associated with movement. Age and sex influence movement patterns of ungulates (Millner-Gulland et al. 2011, Singh et al. 2012). Therefore, research, on the effects of such factors on movement patterns of Mongolian gazelles could be insightful. Spring movements have studied relatively well due to the relative ease of analyzing relationships between animal movements and vegetation conditions (Sawyer et al. 2011, Bischof et al. 2012, Aikens et al. 2017, Middleton et al. 2018). However, strategies for surviving the harsh seasons could be important for enhancing animals' fitness through mortality and fecundity. Mongolia is one of the regions that experiences severe cold and food shortage in winter. Therefore, movement in autumn would have greater influence on fitness and could be more important for understanding the evolutionary roles of their movement strategies. Studies on autumn movements are fewer than studies on spring movements (Bischof et al. 2012). Mongolian gazelles inhabiting various spatiotemporally heterogeneous environments in their habitat would be suitable study species for examining movements in autumn.

Development activities are on the rise in Mongolia, and the impact of habitat fragmentation and human activities on migratory ungulates are a source of concern in Mongolia (Batsaikhan et al. 2014) and many other countries. The results of the present study have several implications for conservation. In addition to the importance of maintaining the ability to migrate over wide ranges, which has already been pointed out, conservation strategies that consider the regional differences in environmental conditions, as explored in the present thesis, are required. The determination of the existence and locations of areas with high interannual predictability area with suitable

vegetation conditions based on movements of gazelles considered “jumpers” would be also important. Studies on Mongolian gazelles could facilitate the better understanding of animal movement ecology, by accumulating and analyzing tracking data of gazelles under various environmental conditions within their distribution ranges.

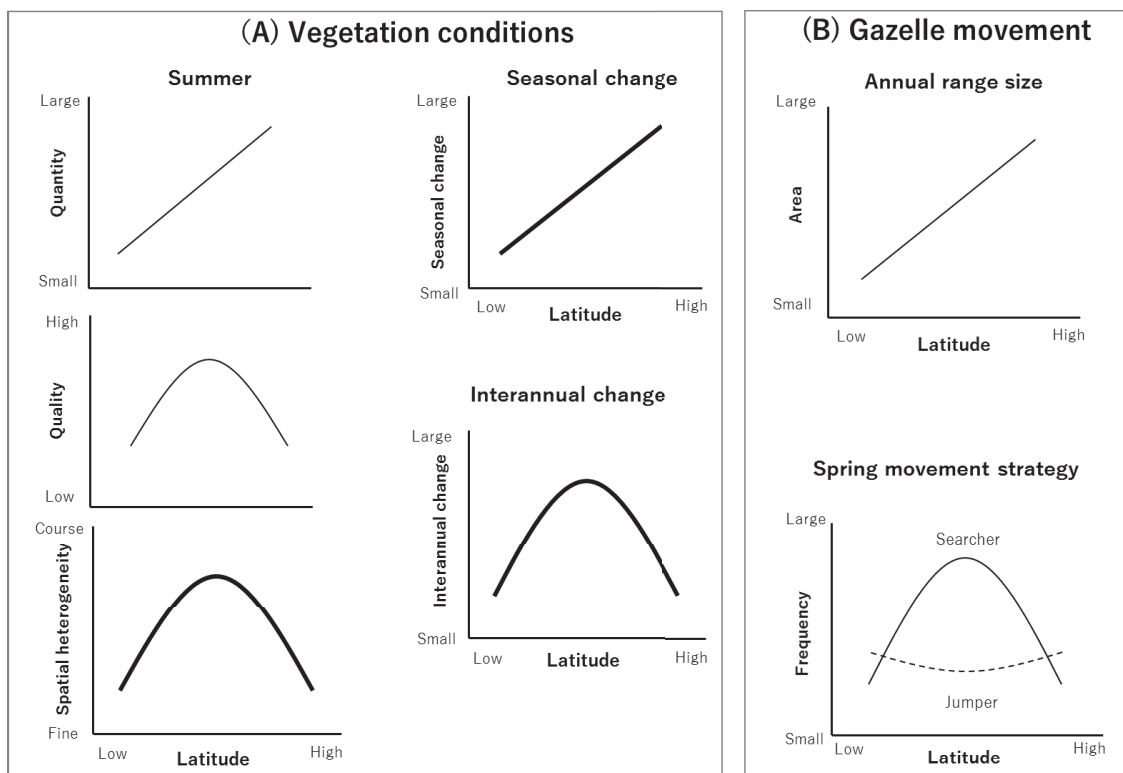


Figure 5.1 General regional trends in vegetation conditions (A) and movement patterns of Mongolian gazelles (B) in the major and wide continuous distribution ranges of Mongolian gazelles. Bold lines in (A) indicate similar regional trends in both vegetation quality and quantity.

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Summary

Spatiotemporal heterogeneity of environmental conditions influences animal movement patterns. In the case of large terrestrial herbivores, spatial heterogeneity and seasonal and annual change of vegetation conditions are important. Typical seasonal migration between specific seasonal ranges is predicted in areas with high seasonal changes and high temporal predictability in vegetation conditions, and has been reported in numerous species. In contrast, nomadism, which is characterized by irregular movement based on both locations and seasons, is predicted in areas with low temporal predictability in vegetation conditions. However, studies that have examined the relationship between animal movement and environmental conditions have remained limited due to the challenges of tracking animals and evaluating environmental conditions over wide geographical ranges. To understand the relationships between movements of terrestrial herbivores and environmental conditions better, studies in various environments including areas with low temporal predictability of environmental conditions are required. Therefore, the aim of the present study was to reveal relationships between movements of a migratory ungulate, Mongolian gazelle (*Procapra gutturosa*), inhabiting Mongolia's grasslands, where the temporal predictability of environmental conditions and spatiotemporal heterogeneity of vegetation conditions are relatively low compared to in other regions on the globe.

The Mongolian gazelle is a suitable study species for examining relationships between movement patterns and vegetation conditions because the species is distributed continuously over a wide geographic and ecological range, including in various vegetation zones ranging from steppe to desert in Mongolia. Movement data from the gazelle's wide distribution range would facilitate the analysis of the relationships

between movement and vegetation conditions. I analyzed the relationships between movement data from 20 gazelles from 2002–2012 and vegetation conditions using NDVI data derived from satellite remote sensing tools. I analyzed the general movement patterns of Mongolian gazelles and their regional differences using movement models (Chapter 2). I also analyzed the relationships between annual range sizes of Mongolian gazelles and vegetation conditions (Chapter 3). In addition, I attempted to elucidate the movement strategies of Mongolian gazelles in spring (vegetation growth season) (Chapter 4). Based on the results, I summarized the vegetation conditions in the distribution range of the Mongolian gazelles and discussed their relationships with the movement patterns of Mongolian gazelles (Chapter 5).

Based on the NSD modeling approach, the mixed migration type was the most observed type among the five statistically determined movement types. Some movement types were also identified as migratory or sedentary. However, most of the NSD modelled seasonal changes in the annual movements of gazelles were irregular, suggesting nomadic movements of individuals. Most gazelles tracked over more than a year shifted their movement types annually, and the movement periods differed among individuals. The results also indicate nomadic movement in the species, although some challenges in modeling nomadism using the NSD approach were encountered.

The maximum individual annual range size was more than 40 times the minimum (range: 900–37,000 km²). Annual range size increased with increasing vegetation amount, spatial heterogeneity, and seasonal change in vegetation amount. Many tracked gazelles changed their ranges between summer and winter, and the ranges represented relatively minor proportions of their annual ranges. The lower annual range sizes in the areas with lower vegetation amounts could be explained by the lower seasonal changes

and spatial heterogeneity in vegetation amounts.

The gazelles continuously preferred areas with intermediate NDVI values from May to July, and spatial and temporal shifts of the distribution of preferred areas would explain the long-distance movements of many gazelles in spring. Three movement types were identified: sedentary type (12.5%), linear movement type (50.0%), and nomadic movement type (37.5%). The period with high individual variations in benefit was different between the linear movement type and the nomadic movement type. During the movement period, the variance in benefit was larger in the nomadic movement type, whereas during the summer period, it was larger in the linear movement type, suggesting the existence of different movement strategies in the Mongolian gazelle. Linear long-distance movements over short periods in the linear movement type suggested the “jumper” strategy, whereas other movement patterns could be “searcher” strategy. The cases of benefit gains and losses through movements of individuals in both strategies would indicate low interannual predictability of vegetation conditions in the study area, and it would explain the co-existence of multiple movement types or strategies in spring in the Mongolian gazelle.

The present study revealed the spatiotemporal heterogeneity of vegetation conditions in the habitat of Mongolian gazelles and its relationship with the regional differences in annual movement distances (annual range size) and spring movement strategies of Mongolian gazelles, although the Mongolian gazelle exhibits a nomadic annual movement pattern. The relatively low interannual predictability of vegetation conditions would explain the nomadic movement being the general pattern of the species. However, different spatial patterns based on different vegetation factors could explain the regional and individual variations in movement patterns and strategies in

Mongolian gazelle in addition to the spatial differences in vegetation conditions including temporal factors such as the magnitude and predictability of seasonal and interannual changes. Linear changes on vegetation factor along the latitudinal gradient would be explained by regional differences in annual movement distances and annual range sizes. Vegetation factors maximizing/minimizing at the mid-latitude of the gazelle distribution range—higher vegetation quality, coarse spatial heterogeneity, and lower annual predictability in the mid-latitude in summer—would explain the high frequency of “searchers” in the mid-latitude and the movement of “jumpers” from north and south to the mid latitude in spring. Different spatial scales—latitudinal gradient (large scale) and heterogeneity in a vegetation zone (middle scale)—and different temporal scales—interannual changes (large scale) and seasonal changes (middle scale)—in vegetation conditions also influence the movement of Mongolian gazelles. This thesis revealed the effects of spatiotemporal heterogeneity of vegetation conditions including at different spatiotemporal scales on animal movements could facilitate the comprehensive understanding of animal movement ecology, particularly in Mongolian gazelle.

学位論文概要

環境条件の時空間的不均一性は動物の移動パターンに影響を及ぼす。陸上大型草食獣の場合には、食物である植物の空間的不均一性とその季節変化、年変動が重要な環境条件だと考えられている。植生条件の季節変化や年変動の予測可能性が高い地域では、特定の季節行動圏の間を季節的に移動する典型的な季節移動が予測され、多くの季節移動の研究事例がある。一方、植生条件の時間的予測可能性が低い地域では、移動時期や滞在地在が不規則な遊動が予測されるが、動物追跡や環境評価の難しさなどから実証的な研究事例は少ない。陸上大型草食獣の移動と環境条件の関係の総合的な理解には、植生条件の時間的予測可能性が低い地域を含む、さまざまな環境での動物の移動の研究が必要である。そこで、世界的には環境条件の時間的予測可能性が低いモンゴルの草原地帯に生息する移動性有蹄類モウコガゼル(*Procapra gutturosa*)を対象として、移動と植生条件の時空間的不均一性の関係を明らかにすることを目的とした。

モウコガゼルはモンゴルの草原地帯から砂漠に近い環境までを含む、連続的で広大な地域に分布しており、異なる地域を利用する個体や個体群により、利用地域の植生条件が異なると考えられるため、広い地域で移動データを集められれば、移動と植生条件の関係を研究する上で好適な対象である。2002年から2011年までに、分布域の広域で衛星追跡された20個体のモウコガゼルの移動データと、衛星リモートセンシングによる植生指数データから、モウコガゼルの移動と植生条件の関係を解析した。まず、移動データと移動モデルを用いてモウコガゼルの全体的な移動パターンとその地域差を明らかにした(第2章)。つぎに植生指数(NDVI)データも組み合わせ、モウコガゼルの年間行動圏と植生条件の関係を解析した(第3章)。さらに植物の生育期である春に注目し、植生条件の予測可能性が低いと考えられる地域における春の移動戦略の解明を試みた(第4章)。これらの結果から、モウコガゼル分布域内の植生条件を整理し、モウコガゼルの移動との関係を議論した(第5章)。

モウコガゼル追跡個体の1年間の移動を5つのNet squared displace (NSD) モデルを用いて移動型を分類したところ、混合季節移動型に分類されたものが最も多かったが、季

節移動型や移動型などすべての移動型に分類され、特定の移動型に集中はしなかった。また、ほとんどの個体の NSD の季節変化パターンは不規則であり、複数年追跡できた個体の移動型は年によって異なった。NSD アプローチによる遊動のモデル化の困難さも示されたが、これらの結果はモウコガゼルが全体的には遊動的であることを支持した。

年間行動圏面積には 40 倍以上 (900-37,000 km²) の個体差があり、行動圏内の植物現存量とその空間的不均一性、季節変化が大きいほど行動圏が大きかった。多くの追跡個体は夏と冬で行動圏を変え、各季節行動圏が年間行動圏内に占める面積は小さかった。植物現存量が小さい地域で年間行動圏が小さかったことは植物現存量の季節変化と不均一性が小さいためと説明された。

春の移動に注目すると、モウコガゼルは 5 月から 7 月まで継続的に NDVI が中程度の地域を選択し、好適 NDVI 値の地域の季節的・空間的な変化が多くのモウコガゼル個体の春の長距離移動を説明した。春の移動は定住型 (12.5%)、直線移動型 (50.0%)、遊動型 (37.5%) に分けられ、移動による利益の個体差が大きい時期が直線移動型と遊動型で異なった。移動期には遊動型で、夏 (移動先到着後) には直線移動型で個体差が大きかったことはモウコガゼルに異なる移動戦略が存在することを示唆し、短期間の直線移動はジャンパー戦略、ほかの移動パターンはサーチャー戦略である可能性がある。両戦略ともに、移動により利益を損失した個体が出たことは本地域の予測可能性の低さを示唆し、これが複数の移動戦略 (移動型) の共存を可能にするのかもしれない。

以上から、モウコガゼルは全体的には遊動的であるが、モウコガゼルの分布域内の植生条件の時空間的不均一性が存在し、それがモウコガゼルの移動要素の地域差と関係することが示された。植生条件の年次的な予測可能性が他地域に比べ全体的に低いことが、モウコガゼルの移動が全体として遊動的である要因だと考えられたが、植生条件の緯度方向の環境傾度に異なる変化パターンが混在することが、モウコガゼルの移動パターンや戦略の地域差や個体差を説明するだろう。緯度方向に直線的に変化する植生条件が年間の移動距離や行動圏面積の地域差の要因であり、中緯度で夏の植生の質と空間的不均一性が高く、年次的な予測可能性が低いことが、中緯度で春のサーチャー戦略が多く、北部や南部からジャンパー戦略の個体の中緯度に向かう要因だろう。分布域全体の環境

傾度という大きな空間スケールと同一植生帯内のような中程度の空間スケールや、年変動という大きなスケールと季節変化という中程度の時間スケールが、移動要素に対しそれぞれ異なる影響及ぼすことも明らかにした。異なる時空間スケールを含む、植生条件の不均一性の移動への影響を明らかにした本研究は、動物の移動生態の総合的な理解に貢献するだろう。

List of Publications

Shunsuke Imai, Takehiko Y. Ito, Toshihiko Kinugasa, Masato Shinoda, Atsushi Tsunekawa and Badamjav Lhagvasuren. 2019. Nomadic movement of Mongolian gazelles identified through the net squared displacement approach. *Mammal Study* 44 (2), April 2019 (Accepted, this article covers **Chapter2**).

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