Population maintenance mechanisms in the Great Spotted Woodpecker in a fragmented forest landscape

（分断化された森林地域におけるアカゲラの個体群維持機構）

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Acknowledgements

Chapter 1

General Introduction

Forest habitat loss and fragmentation due to human activities are major factors influencing species loss all over the world (Fahrig 2003, Thomas et al. 2004). These are typically caused by modification and management of landscapes to produce food or other agricultural commodities for human consumption (Stattersfield et al. 2004, Foley et al. 2005). Agricultural land currently occupies approximately 38% of the planet's land surface, or around half its habitable area (Clay 2004, cited in Donald & Evans 2006). In an effort to reduce species loss, investigations of the effects of habitat loss and fragmentation and ways to mitigate them are a significant research field in ecology, conservation biology, landscape ecology and natural resource management (Lindenmayer & Fisher 2006). It is especially important to elucidate the maintenance mechanisms of animal populations in fragmented forests in agricultural landscapes.

Woodpeckers are often considered as key cavity providers to other species in forest ecosystems (Martin & Eadie 1999, Martin et al. 2004), and as good indicators of forest condition in managed forests (Mikusiński & Angelstam 1998, Mikusiński et al. 2001). Thus understanding the population dynamics of woodpeckers has practical applications as well as theoretical interest (McClelland & McClelland 1999). Although there exists a considerable literature on woodpecker abundance, habitat use and foraging behavior, much less is known about how populations of these species are regulated, and what role demographic parameters play with respect to woodpecker population dynamics (Pasinelli 2006), except for two cooperatively breeding species: the Acorn Woodpecker *Melanerpes formicivorus* (e.g. Koenig & Mumme 1987) and the Red-cockaded Woodpecker *Picoides borealis* (e.g. Letcher et al. 1998, Schiegg et al. 2005). Cooperative breeding is rare not only in woodpeckers but also in other birds (Arnold & Owens 1998). The Great Spotted Woodpecker *Dendrocopos major*

(GSW hereafter) is monogamous and common species in fragmented forests in Europe and northern Japan, where other woodpecker species are rare (Short 1982, Anada & Fujimaki 1984, Ito & Fujimaki 1990, Glue & Boswell 1994, Hinsley et al. 1996, Yamauchi et al. 1997, Birdguides Ltd. 2004). In such habitats, the GSW is an important cavity provider (Virkkalla 2006). Thus, understanding population maintenance mechanisms in the GSW would contribute to forest ecosystem conservation and management. Also, it would be possible to apply the knowledge obtained for this species to the conservation and management of closely related, monogamous, threatened woodpeckers such as Okinawa Woodpeckers *Sapheopipo noguchii*. Therefore my goal was to determine GSW population maintenance mechanisms in a fragmented forest habitat surrounded by agricultural land of Hokkaido, the northernmost island of Japan.

How can we understand population maintenance mechanisms? Local population size is determined by the balance between the increase of individuals through birth (B) and immigration (I), and loss of individuals through death (D) and emigration (E). The biological significance of the population maintained is distinctly different depending on the balance of these four demographic parameters (Pulliam 1988, Pulliam & Danielson 1991, Watkinson & Sutherland 1995, Thomas & Kunin 1999). Pulliam (1988) and Pulliam and Danielson (1991) defined source and sink populations on the basis of whether local births exceed deaths, or vice versa, at equilibrium. Source populations export surplus individuals to surrounding populations (B>D, E>I). Inversely, sinks consume individuals (B<D, E<I) and go extinct without immigration from the source.

However, these demographic parameters are not invariable but fluctuate stochastically or depending on the population density. Although pseudo-sinks (Watkinson & Sutherland 1995) also consume individuals (B<D, E<I) at high density, they will not go extinct in the absence of immigration, because birth rate exceeds death and emigration rates at low density. Also, stochastic variation in B or D could result in a population acting as a source in some years and as a sink in others (Thomas & Kunin 1999, Murphy 2001b). Thus, point measurements of demographic parameters could be misleading when assessing population quality.

Time-series demographic data are required to determine the fluctuation pattern of demographic parameters correctly, which is crucial for understanding the process and mechanisms of population dynamics. For example, marginal populations of the Pied Flycatcher *Ficedula hypoleuca* in northern Finland were not self-sustaining in a seven-year study mainly because of three cold summers, and immigration from the south (acting as a source) was required to avoid local extinction (Järvinen & Väisänen 1984). However, to measure demographic parameters, it is necessary to monitor a population in which most individuals are identified. Most natural vertebrate populations do not lend themselves to this kind of study.

The fluctuation in demographic parameters at the population scale emerges from adaptive behavior of individuals. In recent years, an individual-based approach for understanding population properties has been attracting greater attention (Sutherland 1998, Grimm & Railsback 2005). Individuals are assumed to respond to spatio-temporally heterogeneous environments and select the best habitat to maximize their fitness. Thus, the fluctuation processes of the demographic parameters are suggested by the spatio-temporal patterns observed between habitat configuration and individual behavior, such as territory occupancy, reproduction, migration and dispersal (Brown 1969, Fretwell & Lucas 1970, Rodenhouse et al. 1997, Sergio & Newton 2003). Understanding of the process that gives rise to emergent patterns is important, because it facilitates extrapolation of the findings of one landscape to another that has not been studied (Lindenmayer & Fischer 2006). In this context, I assume two ideal conditions for my population dynamics study of Great Spotted Woodpeckers. First, the distribution and breeding performance of most breeding birds in the study site are detectable. Second, habitat structure can be categorized simply and accurately. Some successful studies of avian population dynamics met these two conditions (e.g. Koenig & Mumme 1987, Arcese et al. 1992, Holmes et al. 1996, Letcher et al. 1998, Murphy 2001a, b).

However, habitat selection by individuals may be determined not only by characteristics of a given local site but also constraints at larger spatial scales (Wien 1989, Pulliam & Danielson 1991, Levin 1992, Hanski 1999). Different cues may determine the behavior of individuals at

different scales. As a result, the patterns observed between individual behavior and habitat configuration often seem to be different at different scales. The most common approach to dealing with such scale issues is to compare patterns among several arbitrarily selected points of a scale spectrum (Wien 1989). Such multi-scale approaches provide a better understanding of the process that gives rise to observed patterns. For example, the Black Kite *Milvus migrans*, which prefers to forage over water bodies and positively selects urban areas near the water at the landscape scale (i.e., foraging range), but avoids the same features at the local scale (i.e., nest site and its immediate surroundings) (Sergio et al. 2003). High availability of safe nest sites may result in poor foraging and breeding performance of kites if the sites are located too far from preferred foraging habitat.

The GSW populations in fragmented forest landscape can meet the two above-mentioned ideal conditions for a study of population dynamics. That is, it is possible to collect data on birth, death, migration, and breeding attempts of many identified individuals in large tracts of land with clear habitat configuration. Thus, the spatio-temporal fluctuation patterns of demographic parameters can be detected from direct observations of individual behavior in a spatially heterogeneous habitat.

The aim of this study is to shed light on the maintenance mechanism of GSW population in a fragmented forest landscape at multiple spatial scales. The composition of this thesis and the contents of each chapter are as follows (Fig. 1). The thesis consists of six chapters. Chapter 2 following this general introduction describes the study site and materials. Chapter 3 describes foraging habitat use on a home-range scale, and then discusses the important factors for maintaining a year-round territory. Chapter 4 tests the ideal despotic distribution model on a scale over home range and the study site, and discusses site-dependent density effects on reproductive output and survival rates. Chapter 5 describes demographic parameters and their temporal fluctuation patterns and ranges on a landscape scale over the study site and its similar surroundings, and then discusses the environment-dependent fluctuations in population size and composition. Finally, chapter 6 provides a general discussion about the population maintenance mechanisms in the GSW in a fragmented forest

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landscape based of the results of the earlier chapters.
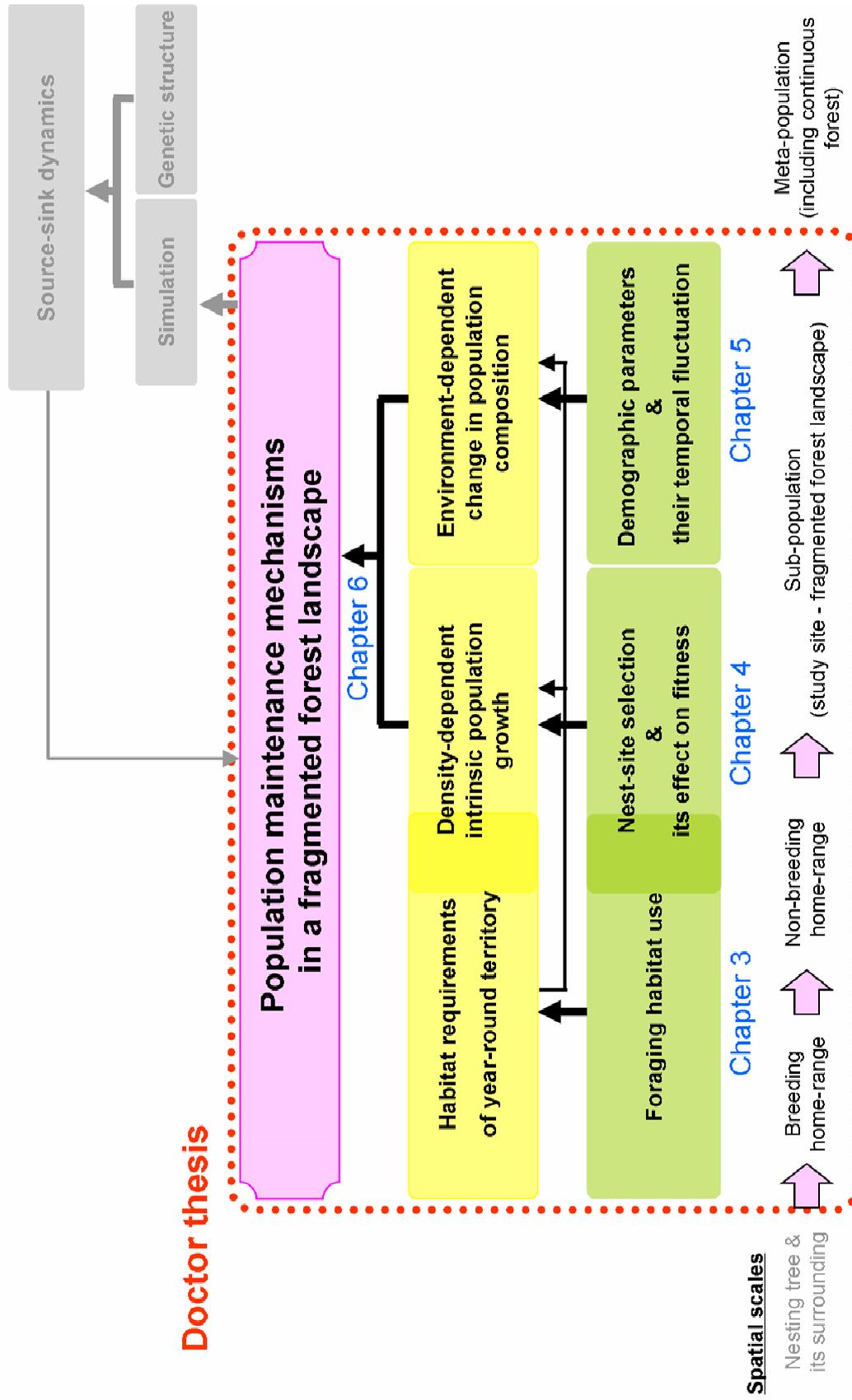
Fig. 1 The composition of this study and the contents of each chapter.

Chapter 2

Study Site and Materials

Study site

The study site was a 40 km^2 tract of agricultural land in southern Obihiro City (42°46'N, 143°05'E), Hokkaido, Japan (Fig.1). Hokkaido is the northernmost of the four main islands of Japan, and ranges in the subarctic zone. The average August temperature of Obihiro is around 20°C, and the average January temperature ranges from -14°C to -2°C (Japan Meteorological Agency 2008). The study site is located in the Tokachi Plain, which occupies about 10% of Hokkaido's entire area. The Tokachi Plain was originally covered by broad-leaved deciduous forest, but has been transformed into an agricultural landscape during the last 100 years (Himiyama et. al. 1995). Presently, the study site consists of flat agricultural fields (the main crops are wheat, sugar beets, potatoes, meadows, and beans) mixing with forest habitat which covers about 6% of the total area. The nearest continuous forest is at the foot of the Hidaka mountains and is about 5 km away from the site.

The present forest habitat consists of second-growth broad-leaved deciduous remnant woodlands, narrow shelterbelts (<15m width), wide shelterbelts (*ca.* 30-100m width), riparian shrubs, and small groves beside scattered private dwellings. The second-growth broad-leaved deciduous remnants were composed mainly of Kashiwa Oak *Quercus dentata*, Japanese Elm *Ulmus davidiana*, Japanese Ash *Fraxinus mandshurica*, and Japanese Alder *Alnus japonica*. The Kashiwa Oak and the other species were mainly found in dry and wet habitat, respectively. Many narrow shelterbelts of Japanese Larch *Larix kaempferi* were found growing in the study site. In the wide shelterbelts, both coniferous and deciduous broad-leaved species were growing. The dominant coniferous species were Larch, Eastern White Pine *P. strobus*, but other evergreen pine species were also inter-mixed. Both the narrow and wide coniferous shelterbelts were under forestry management, so damaged,

snagged, and rotten trees were rare. As for the deciduous broad-leaved species, oak, elm, ash, alder and Japanese White Birch *Betula platyphylla* grew in the wide shelterbelts. The riparian shrubs were composed mainly of Willows *Salix* spp. Broad-leaved deciduous remnants were not under forestry management, so damaged, snagged, and rotten trees were comparatively common. The groves planted around private dwellings were very small, composed of Korean Pine *P. koraiensis* and various garden trees. Broad-leaved deciduous trees in the remnant forest and wide shelterbelts were often semi-natural, and provided many snags and damaged trees which were suitable for the nesting tree of the GSW. By contrast, coniferous shelterbelts
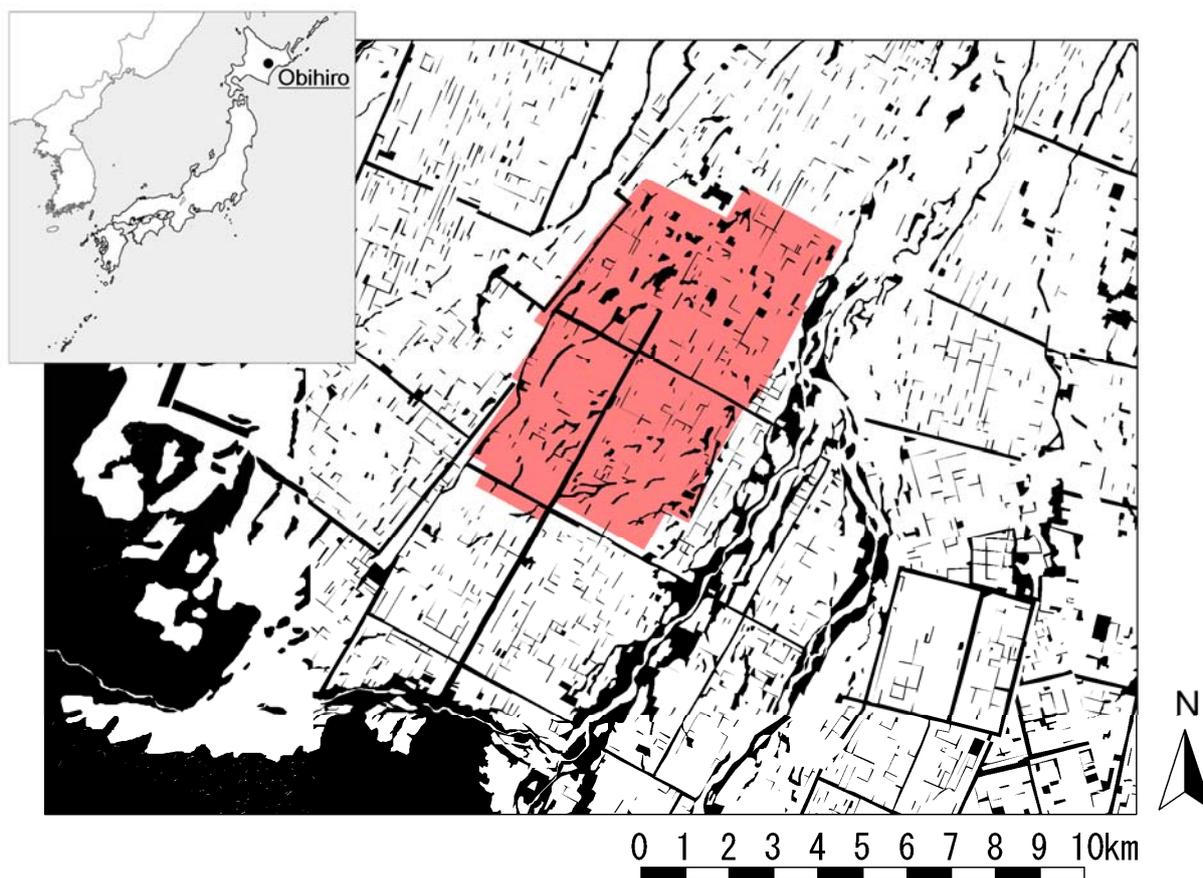
Fig. 1 The Map of the study site in Obihiro city, Hokkaido (the northernmost of the four main islands of Japan). Black polygons and a pale red polygon indicate forested areas and the study site, respectively. White areas were mainly agricultural fields. The continuous forest shown in the southwestern portion of the map is the foot of the Hidaka mountains. The data were provided by the Natural Environmental Information GIS (Environmental agency of Japan 1997).

were under forestry management, and groves around private dwellings were also managed by residents. Consequently, snags and damaged trees were few in these vegetation types.

The Great Spotted Woodpecker

   The GSW is a medium-sized resident woodpecker species (average body length 24 cm; Fig. 2). It has typically monogamous mating system. Breeding birds excavate a nest hole on tree trunk or limb and have one brood a year. GSWs utilize a range of tree species with sufficient growth and hardness for nesting (Mazgajski 1998, Matsuoka 2008). GSWs forage omnivorously on various arthropods, tree seeds, and fruits (Matsuoka 1977, Birdguides Ltd. 2004). The distribution range is wide, from Arctic taiga, through boreal to temperate zones (Short 1982, Winkler et al. 1995, Birdguides Ltd. 2004). It is a common species in fragmented forests both in urban and agricultural areas in Europe and Hokkaido (Japan), where the other woodpecker species are rare (Short 1982, Anada & Fujimaki 1984, Ito & Fujimaki 1990, Glue & Boswell 1994, Hinsley et al. 1996, Yamauchi et al. 1997, Birdguides Ltd. 2004). The GSW therefore provides the majority of cavities for secondary cavity users in such environments

Fig. 2 The Great Spotted Woodpecker. Left: male, Right: marked female

(Virkkala 2006, Kotaka & Matsuoka 2002, Muraki & Yanagawa 2006). In this context, the GSW is the most intensively studied species of European woodpeckers (Pasinelli 2006). Considerable number of studies on the GSW has been conducted in Europe, however, little is known on population regulation, and what role demographic parameters play with respect to its population dynamics (Pasinelli 2006).

Chapter 3

Foraging habitat use in a year-round territory

Abstract

Foraging habitat use in a year-round territory of the Great Spotted Woodpecker *Dendrocopos major* was studied in a fragmented forest landscape, in Obihiro City, Japan. I observed four males and three females of the four pairs at three sites in the breeding seasons of 1999-2001 and winter of 2001. Three of the four pairs kept their pair bond during the study period and showed nest-site fidelity. Foraging habitat use in the breeding season varied among individuals, years and sites. Their home-ranges in the breeding season were typically restricted to the vicinity of their nest trees, but in the winter, their home-ranges enlarged. In winter, all individuals visited small pure or mixed Korean Pine groves which were distant from their prior nesting trees (up to 970 m). Individuals exclusively foraged Korean Pine seeds in Korean Pine groves. In one breeding season, one of the four pairs foraged Korean Pine seeds and had a home-range as large as the winter home-ranges of the other individuals. Korean pine seeds are thought to be an energetic, efficient and stably supplied food resource during the winter season. Foraging habitat use in the breeding season was flexible, so it might not have restricted territory selection strongly. The availability of stably supplied efficient food, such as conifer seeds, during winter may be a key factor to the maintenance of year-round territory of the Great Spotted Woodpecker in marginal habitat, such as the northern limit of the species' distribution range and fragmented forest landscape like that in my study site. In this study site, the seeds of Korean Pine were suggested to be an important food resource.

Introduction

The Great Spotted Woodpecker *Dendrocopos major* (GSW hereafter) is omnivorous, feeding on arthropods, tree seeds and fleshy fruits (Matsuoka 1977, Birdguides Ltd. 2004). Their foraging habits vary in different habitats. During summer months, the GSW is mainly insectivorous. However, conifer seeds (mainly pine *Pinus* and spruce *Picea*) become an important food resource during the winter, and more so in northern populations (Birdguides Ltd. 2004). The range of distribution of the GSW is wide, from Arctic taiga through boreal to temperate zones (Short 1982, Birdguides Ltd. 2004). The GSW is a common species in fragmented forests both in urban and agricultural areas of Europe and Hokkaido, Japan (Short 1982, Anada & Fujimaki 1984, Ito & Fujimaki, 1990, Glue & Boswell 1994, Hinsley et al. 1996, Yamauchi et al. 1997, Birdguides Ltd. 2004).

The breeding habitat requirements of the GSW in fragmented forest landscapes have previously been discussed on the basis of breeding biology, nesting tree characteristics and minimum forested area inside their breeding home-range (Kawata 1980, Yamauchi et al. 1997, Kotaka & Kameyama, 2001). These methods did not assess whether or not individuals could keep year-round territory at the nesting site, although it had been reported in a continuous forest that GSWs exhibited strong site fidelity to a home-range, once settled, and used the same breeding area for six to eight years (Birdguides Ltd., 2004). It is necessary to know the habitat requirements for securing the survival of individuals at sites once settled throughout the year in order to understand the population maintenance mechanisms of the GSW.

Rolstad et al. (1995) confirmed plasticity in the feeding habitat selection of the GSW during the breeding season in a relatively continuous Scandinavian middle boreal forest. They predicted that territory selection of the GSW might depend on the availability of conifer seeds, which were crucial for winter survival in their research area. Their study was conducted on a population that was close to the species' northern limit, in other words, a marginal region. Conifer seeds may be an efficient energetic food resource, where invertebrate food resources such as surface-living arthropods and wood-boring insects are either unobtainable or more costly to forage in cold winters. Fragmented forest landscapes are also assumed to be

somewhat marginal region for the GSW, because the GSW inhabits forested habitat. Thus, the GSW in a fragmented forest landscape may also rely on a compensatory food resource in winter.

The aims of this study are to 1) describe foraging habitat use of the GSW in a fragmented forest landscape in both breeding season and winter, then 2) discuss important factors in keeping year-round territory in marginal habitat.

Methods

The study site was a 40 km^2 agricultural area in southern Obihiro City (42º46'N, 143º05'E), Hokkaido, Japan. Flat agricultural fields (mainly wheat, sugar beets, potatoes, meadows and beans) covered about 94% of the study site, in which there were scattered shelterbelts and small forest stands.

The foraging habitat use of GSWs was investigated in the late nestling period, when the birds required the most food, and in the winter, when they faced food shortages. The GSWs had one brood per year. They started excavating nest cavities in mid-May and all nestlings had fledged by early July. Foraging habitat use in the late nestling period was investigated for four breeding pairs (pairs A, B1, B2 and C) in 1999-2001. Finally, six data sets on foraging habitat use were obtained from these four pairs in the breeding season. The duration and period of field observation for each data set were as follows: Pair A (1999): 11 hrs on 22-25 June; Pair B1 (1999): nine hrs on 19-21 June; Pair B2 (2000); seven hrs on 23-27 June; Pair B2 (2001): 17 hrs on 21-26 June; Pair C (2000): 11 hrs on 2-6 July; and Pair C (2001): 15.5 hrs on 22-30 June. Of these, three pairs were also observed in the winter of 2001 (Pair A: 25 hrs on 22 January-17 March; Pair B2: 15 hrs on 13 January-13 February; and Pair C: 36 hrs on 18 January-17 March). Pair A was not investigated in 2000 and 2001, but they kept their pair bond and settled in the same nest site through the end of this study. The male (mB1) of Pair B1 disappeared after 1999, and then the female (fB) formed Pair B2 with another male (mB2) from 2000. Pair C settled in their nest site in 2000 and kept their bond through the end of this study.

All of the birds were captured at their nests or roosting holes by means of a mist net or a bag net. The captured birds were individually marked with three coloured rings and one metal ring. The birds were observed directly with 8×20 binoculars, and their location was marked on vegetation maps (1: 5,000 and 1: 10,000) every minute. Radio transmitters were also attached to four birds (mA, mB2, fB, fC) in winter to assist direct observation. The transmitters were attached to the base of a central tail feather shaft with epoxy resin glue and fine copper wire. The antennas were tied to the feather shaft with fine copper wire and extended to the distal end of the feather. The transmitters could be easily removed by cutting the wire or would fall off with the moulted tail feather. The behavior of the birds seemed unaffected by the transmitters which were 1.2-2.4 g (< 3 % of GSW body weight).

For analysis, only spatially and temporally independent fixes were employed to avoid the effect of spatial autocorrelation of successive fixes. In the breeding season, spatial independence of a fix was assumed when the fix was separated from the previous one by more than five minutes, or when a bird had moved more than 50 m from the previous fix within five minutes. In winter, temporal and spatial minima of 15 min and 50 m were adopted. These criteria were based on the nest-visiting interval of parent birds and winter movement characteristics. In the fragmented habitat of the study site, vegetation separated by 50 m was typically very different.

Vegetation was classified into three types. Type 1 was deciduous broad-leaved forest in which Japanese Ash *Fraxinus mandshurica*, Japanese Elm *Ulmus davidiana*, Japanese Alder *Alnus japonica*, Kashiwa Oak *Quercus dentata*, Japanese White Birch *Betula platyphylla*, and Willows *Salix* spp. constituted the main tree species. This type was found mainly in forest remnants and along riversides. Type 2 was coniferous forest (excluding Korean Pine *Pinus koraiensis*). Japanese Larch *Larix kaempferi* constituted the main tree species of this vegetation type and many narrow shelterbelts (< 15m width) of this species were growing in the study site. Eastern White Pine *P. strobus* and other pine species were also inter-mixed in some of these plantings. Type 3 was pure, or mixed, Korean Pine groves. The groves of this species were typically very small and had been planted only around private dwellings.

The home-range of each individual was estimated as a 100% maximum convex polygon. The distances from a pair's nest to the farthest located fix were compared between the breeding season and winter by Mann-Whitney's U test. The farthest fix in winter was defined based on the following breeding season's nest. The proportion of Type 3 vegetation use was compared between the breeding season and winter by Mann-Whitney's U test.

Results

The distances between the nest and the farthest fix were significantly greater in winter than in the breeding season ($U=12$, $P=0.025$; Fig. 1). The home-range sizes of each bird are
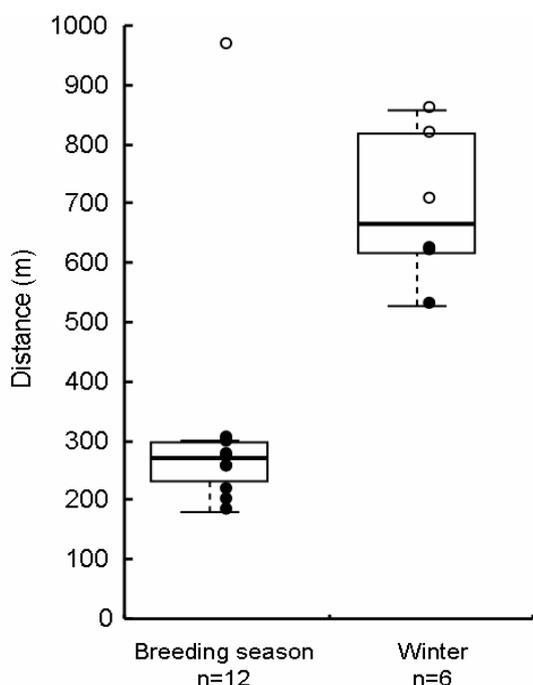
Fig. 1. The distance from the nest to the farthest fix in each season.

The boxes, bold lines, and horizontal lines indicate the quartile deviation, median, and extremum, respectively.

○: Type 3 groves, ●: Other vegetation types

Table 1. Utilization of each vegetation type indicated by observation of the number of fix-points.

Season	bird	Vegetation type 1	2	3	Total
Breeding season					
Pair A					
1999	mA	19	18	0	37
	fA	18	13	0	31
Pair B1					
1999	mB1	10	3	3	16
	fB	1	10	1	12
Pair B2					
2000	mB2	7	16	0	23
	fB	6	13	0	19
2001	mB2	23	25	0	48
	fB	17	26	0	43
Pair C					
2000	mC	30	0	0	30
	fC	19	0	0	19
2001	mC	59	0	0	59
	fC	46	0	0	46
2001 Winter					
Pair A	mA	29	11	20	60
	fA	10	7	7	24
Pair B2	mB2	14	7	15	36
	fB	14	15	9	38
Pair C	mC	27	0	3	30
	fC	48	5	11	64
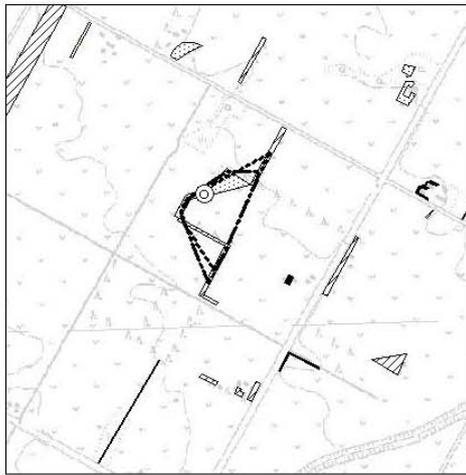
Pair A (1999)
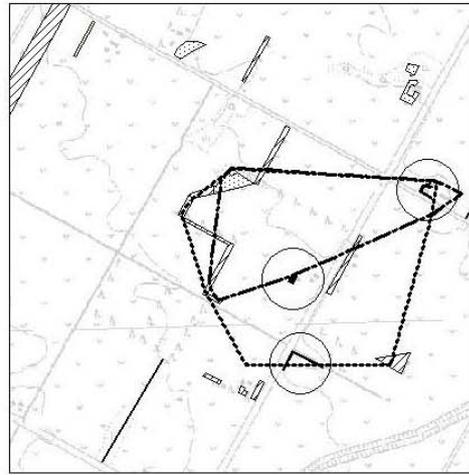
Pair A (Winter)
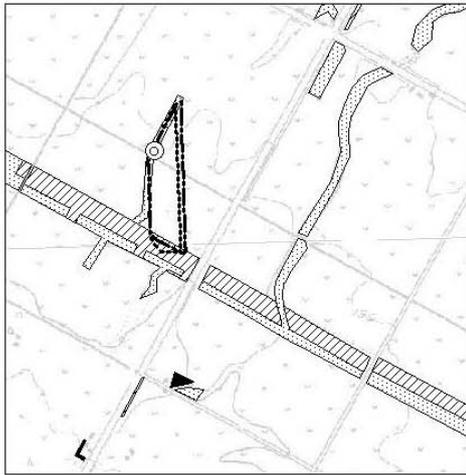
Pair B2 (2000)
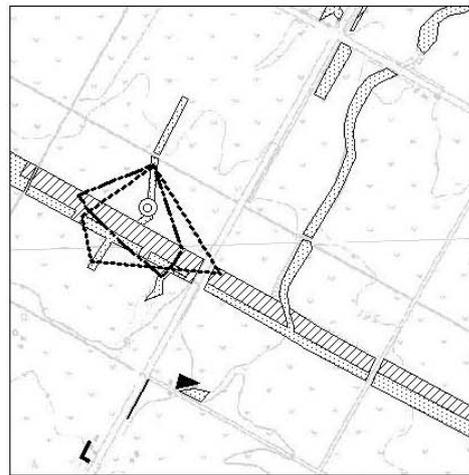
Pair B2 (2001)
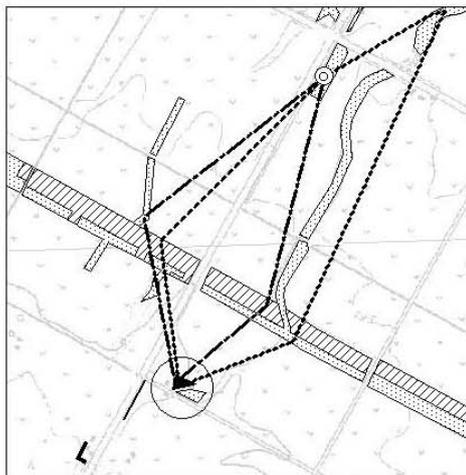
Pair B1 (1999)
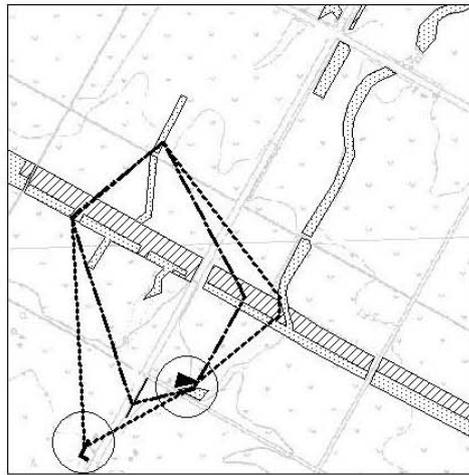
Pair B2 (Winter)

Fig. 2, Continued on the next page

Continued from the previous page

Pair C (2000)

Pair C (2001)

Pair C (Winter)

◎ Nest
Male home-range
Female home-range

Type 1
Type 2
Type 3

0   200   400   600   800   1000 m

N
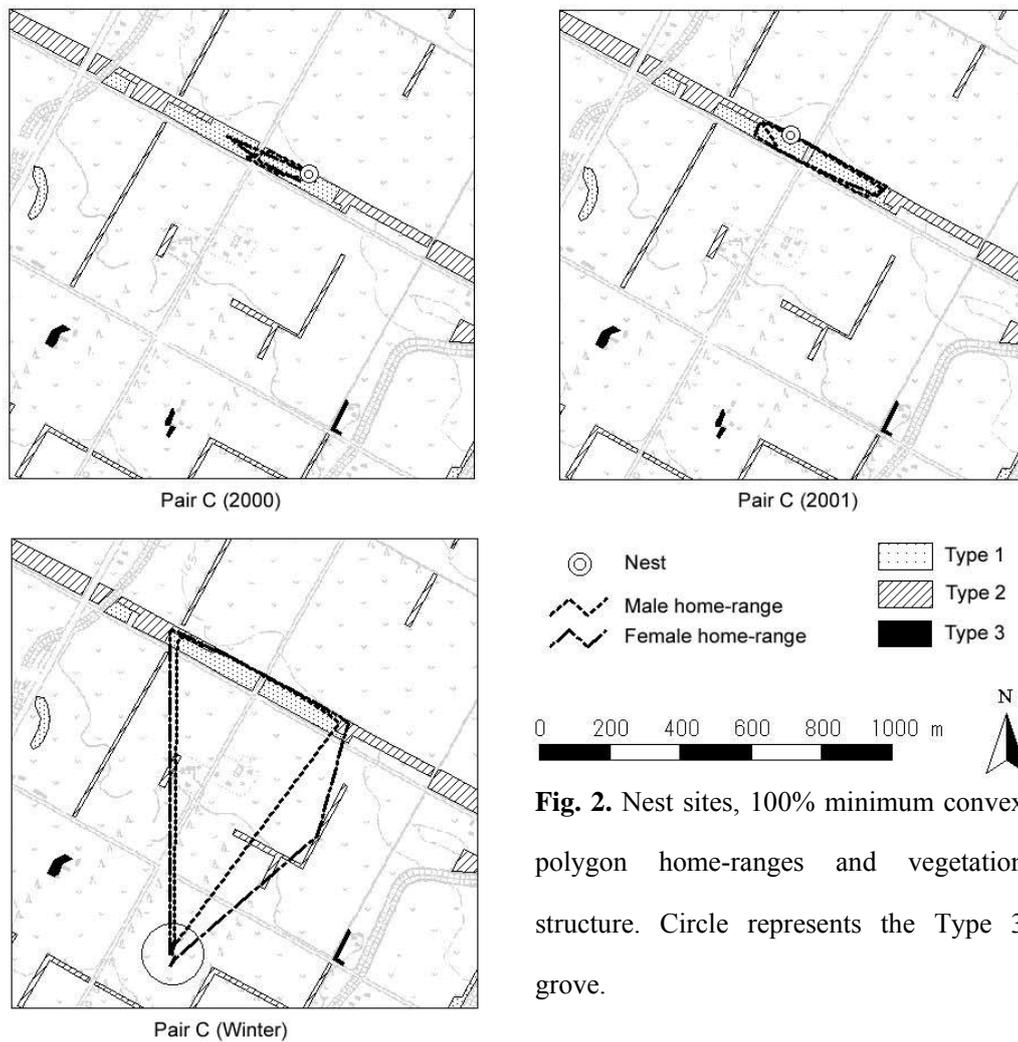
Fig. 2. Nest sites, 100% minimum convex polygon home-ranges and vegetation structure. Circle represents the Type 3 grove.

shown in Appendix 1. In winter, all birds visited vegetation Type 3, where they fed exclusively on pine seeds. Only Pair B1 did so in breeding season (Table 1). In the other vegetation types, all birds foraged invertebrates from inside the tree or under the bark in winter. The proportion of Type 3 use was significantly greater in winter than that in breeding season (U=70, P<0.001; Table 1). Type 3 groves were always located on the edge of a home-range (Fig. 2; the sizes of home-range were shown in Appendix 1), and defended and exclusively used by one pair. The maximum distance from a nesting tree to the farthest used Type 3 grove in winter was 810 m (Pair C).

Pair B1, which nested in a small forest, had an exceptionally large breeding season

home-range, which was as large as winter home-ranges of the other pairs. Pair B1 visited a Type 3 grove (970 m from the nest; Fig. 1) and fed on pine seeds during the breeding season. Other breeding pairs fed almost exclusively on insects (*e.g.*, caterpillars, aphids and ants), taking them from the surface of trees, and did not feed on pine seeds during the breeding season.

Discussion

The foraging habitat use of GSWs in breeding season was restricted to Type 1 and 2 in five out of the six cases. Pair B1 (1999) was an exceptional case in that they used Type 3 vegetation also in breeding season. They relied on Korean Pine seeds during summer, which probably compensated for the shortage of animal food in their home-range. The GSW is known to be mainly insectivorous in the breeding season (Matsuoka 1977, Birdguides Ltd. 2004). The range of foraging habitat in the breeding season was known to be mainly 100-600 m and up to 1,100 m away from the nest (Birdguides Ltd. 2004). The maximum distance from the nest to a Type 3 grove was 970 m in the present study (Pair B1, 1999). That is, it was close to the known limit of their foraging range.

The foraging habitat use of GSWs varied among pairs and years in the breeding season. Heterogeneous fragmented forests in the present study site provided different vegetation in the vicinity of each nest site. The result in the present study matched up to the general notion that GSWs select foraging habitat flexibly in the breeding season according to food availability (Rolstad et al. 1995, Birdguides Ltd. 2004).

Rolstad et al. (1995) predicted that the GSW would select its territory based on the availability of conifer seeds (pine and spruce), a food resource crucial for winter survival in a relatively continuous middle boreal forest in Scandinavia. In the present study, GSWs used Korean Pine groves that were up to about 1 km from the nest. Conifer seeds are an efficient energetic food for the GSW (Pogorelov 1992). The Korean Pine, in particular, produces one of the most energetic seeds containing much protein, fat, and carbohydrate (López-Mata 2001). The seeds mature in autumn and rest inside the cones on the branch for a long time, so

Korean Pine seeds are assumed to be a stably supplied efficient food during winter. The GSWs spend 10-42% of their time in Type 3 vegetation in winter, but energy obtained from the seeds is expected to occupy a higher proportion of their total energy income. Thus, the Korean Pine presumably provides an important food resource affecting GSWs' settlement in the fragmented habitat of this study site. Scandinavian GSWs may represent "a special position" in terms of foraging habits, due to the marked seasonal shift in their diet, from invertebrate summer foods to conifer seeds in winter (Rolstad et al. 1995). Plant foods, in particular conifer seeds, are important for most GSWs, but more so in more northerly populations (Birdguides Ltd. 2004). The fragmented forest of the present study site may represent nearly marginal habitat for the GSW, in much the same way that high latitude forests represent a marginal range. Food availability throughout the year is an important factor in keeping year-round territory by GSWs inhabiting marginal habitat.

Appendix 1. The home-range size for each individual calculated as a 100% maximum convex polygon.

Season		Bird	Home-range (ha)
Breeding season			
Pair A			
	1999	mA	3.3
		fA	3.5
Pair B1			
	1999	mB1	34.8
		fB	20.5
Pair B2			
	2000	mB2	2.8
		fB	3.3
	2001	mB2	6.8
		fB	4.9
Pair C			
	2000	mC	0.7
		fC	0.5
	2001	mC	1.7
		fC	1.9
2001 Winter			
Pair A		mA	32.0
		fA	15.5
Pair B2		mB2	30.6
		fB	21.4
Pair C		mC	20.8
		fC	29.4

Chapter 4

Effects of ideal despotic distribution on reproductive output and survival rates: a sign of site-dependent density effect

Abstract

A population is regulated by density-dependent processes such as competition for food or other resources, and predation. In this study, I estimated the process of density-dependent population regulation in a breeding population of the Great Spotted Woodpecker *Dendrocopos major*, by comparing observed settlement patterns with theoretical prediction of ideal despotic distribution and site-dependent population regulation. The data were collected from a marked breeding population of this species in a fragmented forest landscape (40 km^2) in 1999-2001 and 2005-2008. The observed patterns were that: 1) there exists preferred breeding areas and avoided ones, 2) at the population scale, a greater percentage of less-preferred breeding areas were occupied in years of higher breeding densities compared to years of low breeding density, 3a) forest coverage was higher in the preferred breeding areas, 3b) birds resided longer in preferred areas, 3c) the reproductive output (clutch size, fledging success, and fledgling number) did not differ among breeding areas, and 3d) the pressure of inter-species interference, the major cause of nesting failure, was higher in preferred areas. The observed patterns 1, 2, 3a, and 3b were consistent with the theoretical scenarios, but 3c and 3d were not. These antinomies may result from cost-benefit trade-off. Birds settled in the less-preferred breeding areas with low forest coverage should pay high travel cost for foraging, but these birds might obtain the benefit of low inter-species interference. Thus, the site-dependent density effect may act through the survival rate of breeding birds, but not through the reproductive output in the studied population.

Introduction

    A population is regulated by density-dependent processes such as competition for food or other resources, predation, and parasitism (or infectious diseases) (Newton 1998). In territorial animals, ideal despotic distribution (Fretwell & Lucas 1970) is expected to be the basis of density-dependent processes of population regulation. Pulliam and Danielson (1991) advocated ideal preemptive distribution in the source-sink scenario, which is the same idea as ideal despotic distribution. Ideal despotic distribution model assumes that the highest quality or the first arriving individuals occupy the best quality habitats preemptively, and defend such habitat from other individuals territorially. Therefore, lower-quality or later-arriving individuals can not access high-quality habitats, and are driven away to lower-quality habitats. Thus, individuals settled in high-quality territories gain better fitness than those settled in low quality territories. The key point of this model is that the benefit of fitness depends on the quality of the territory settled. Fitness is closely related to life-time reproductive success (Käär & Jokela 1998), which is the product of survival rate and reproductive success (Krebs 2001). Ideal despotic distribution in a heterogeneous habitat produces the "buffer effect" (Brown 1969) at the population scale. That is, the proportion of lower quality territories occupied increases with population density. Consequently, progressive use of low quality territories causes a decline in mean per capita reproductive output and/or survival rate. As a result, this acts as a negative feedback on population growth at high population densities. These processes were been named "site-dependent population regulation" by Rodenhouse et al. (1997).

    Ideal despotic distribution and site-dependent population regulation have been considered mainly in avian species (e.g. Newton 1991, Krüger & Lindström 2001, Sergio & Newton 2003). The occupancy of breeding territory has been frequently used as a measure of territory quality, and a relationship between the occupancy and reproductive output have been described to investigate the hypotheses of these theories (reviewed in Sergio & Newton 2003). Both reproductive output and survival rate are deterministic factors of fitness, but few studies have examined them simultaneously.

The aims of this study are to: 1) test whether the actual breeding bird distribution follows the ideal despotic distribution model, and exhibits site-dependent population regulation based on observed reproductive output and survival rate; and 2) speculate the processes of the density-dependent effects on the population regulation in the GSW.

Materials and Method

MATERIAL

The GSW is widely distributed from the Arctic taiga through to boreal and temperate zones, using a range of tree species with sufficient growth and hardness as a nest tree (Mazgajski 1998, Birdguides Ltd. 2004, Matsuoka 2008). It is a common species in fragmented forests both in urban and agricultural areas in Europe and the northernmost (Hokkaido) of the four main islands of Japan (Short 1982, Anada & Fujimaki 1984, Ito & Fujimaki 1990, Glue & Boswell 1994, Hinsley et al. 1996, Yamauchi et al. 1997, Birdguides Ltd. 2004). The breeding birds exhibit strong site fidelity to a home range once settled and this lasts throughout the year (Birdguides Ltd. 2004, Mori 2005, see also chapter 3). These birds lay one brood per year, but occasionally re-nest after failure, but only if it failed in its early stages. In the studied population, breeding birds typically excavate new nest holes for each nesting attempt, and they hardly re-use old nest holes. They roost in old nest cavities, natural cavities, or in roughly excavated new cavities. They food habit is omnivorous, but mainly fed on surface-living arthropods (e.g. defoliators) found in a wide range of trees depending on the availability during the summer (cf. Rolstad et al. 1995, Mori 2005, Jiao et al. 2008, see also chapter 3).

STUDY SITE

The study site was a 40-km^2 tract of agricultural land, south of Obihiro City (42°46'N, 143°05'E), Hokkaido. Flat agricultural fields (mainly wheat, sugar beets, potatoes, meadows and beans) are widespread in this region. Forest habitat occupied 6% of the site. The nearest continuous forest was about 5 km from the site at the foot of the Hidaka mountains.

The forest habitat consisted of second-growth broad-leaved deciduous remnant woodlands, narrow shelterbelts (<15m width), wide shelterbelts (*ca.*30-100m width), riparian shrubs, and small groves around private dwellings. Broad-leaved deciduous trees inside the remnant and wide shelterbelts were semi-natural, and provided many snags and damaged
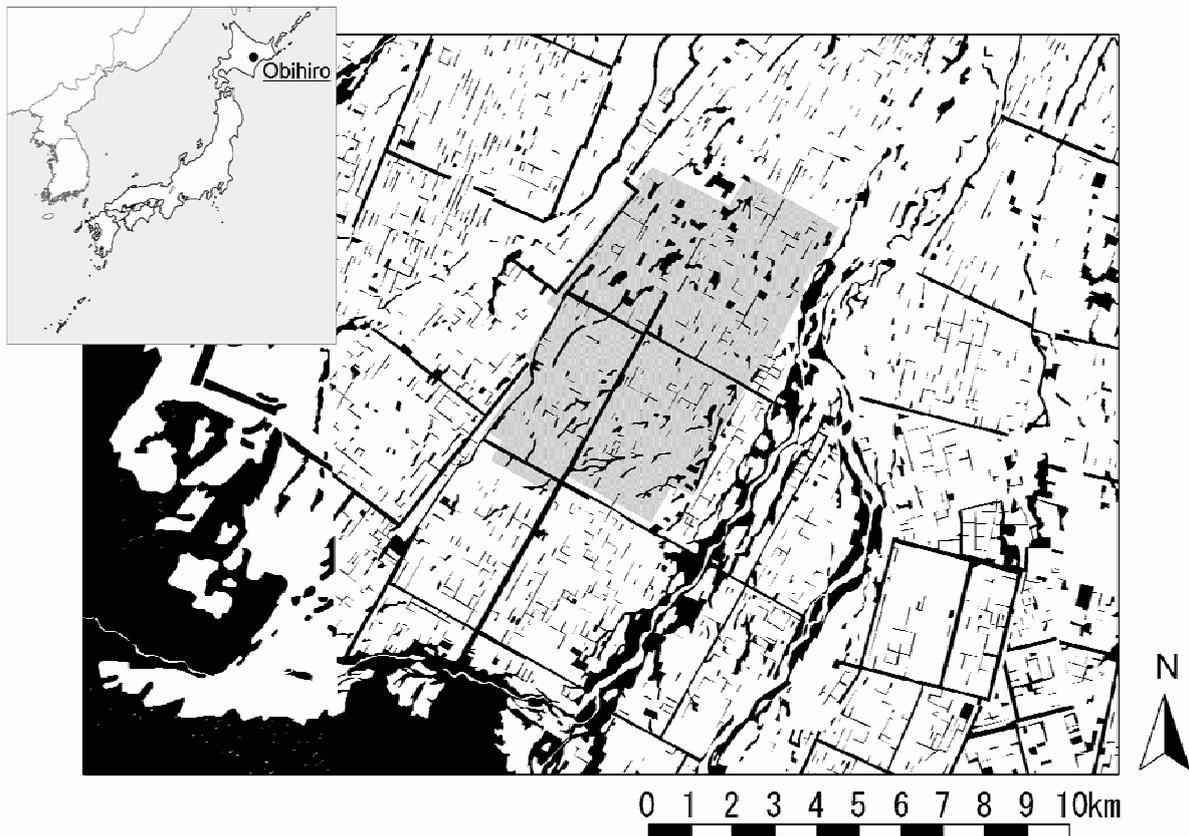
Fig. 1 The study site, a 40 km^2 agricultural landscape in Obihiro, and its surroundings based on the Natural Environmental Information GIS (Environmental agency of Japan 1997). Black polygons and the pale gray polygon indicate forested areas and the study site, respectively. White areas were mainly agricultural fields. The continuous forest shown in the southwestern portion of the study site is the foot of the Hidaka mountains.

trees which were suitable for nesting by the GSW. In contrast, narrow and wide coniferous shelterbelts were under forestry managements, and the groves around private dwellings were managed by residents. Thus, snags and damaged trees were few in these vegetation types. Detailed information about the vegetation is described in Mori (2005) (see also chapters 2 and

3).

The data on vegetation cover in the study site were collected using aerial photographs and field observation. The woodlands were digitally mapped and the associated data entered into the Geographic Information System (GIS) using Arcview 3.2 (ESRI, CA, USA).

BREEDING POPULATION MONITORING

The location of nests and individually identified breeding woodpeckers in the site were monitored from early May to early July in 1999-2001 and 2005-2007 (six years in total). Additionally, data on the survival of breeding birds marked in prior years were collected in 2008. Most birds started nest excavation in mid-May and all nestlings fledged by early July. Nests were detected by repeated intensive search. Breeding pairs showed conspicuous nest defense behavior, and nestlings made loud begging calls, which served as effective cues for searching.

Breeding birds were captured at their nests or at roosts with a mist or a bag net. A caged female and/or the playbacks of drumming and calls were used to attract individuals to the nets since 2005. Captured birds were individually marked with 1-3 plastic color rings and one metal numbered ring. Some breeding birds had been captured and marked at their natal nests as nestlings/fledglings from earlier years. Nestlings were captured using a pick-up tool and/or by hand without destructing nests. Fledglings were captured by mist nets or bag nets when they fledged from the nest.

Any cavity containing at least one egg was classified as a nest. When birds re-nested after a failure, only the re-nesting data was used to calculate fledging success and the total number of successful nests by the pair.

Once found, excavated nest cavities were checked repeatedly by interior or exterior observation throughout the entire breeding season until the nestlings fledged. Nests were checked at least once per three days in the egg-laying period, hatching period, and the late nestling period to confirm clutch size, hatching date, fledging success, and the number of fledglings. A small light and mirror, or an infrared CCD camera was used to observe the

inside of nest holes to determine clutch size, nestling growth, and the number of fledglings. Fledging success was recorded in the following cases: 1) fledglings were observed directly at the nest, 2) fledged young were observed in the periphery of the nest, 3) fledglings were found being fed by an adult, or with adults around the nest, 4) nestlings over 20 days of age, or nestlings of unknown age with well-developed plumage were observed within three days prior to their disappearance from the nest. In Obihiro, nestlings left the nest at about 20 days (ranged 17-25 days) after hatch (Kawata 1980). The number of fledglings was determined as the number of nestlings that was observed at least 20 days from hatching, or those observed within three days prior to their disappearance from the nest.

PREDICTED SCENARIOS AND STATISTICAL ANALYSIS

Prior to the analysis, the term "breeding area" was determined as any area containing more than one nest. If multiple nests existed within a 300m radius of each other, these nests were considered to be in one breeding area (Fig. 2). The radius of 300m was applied based on the approximate breeding home range size of GSWs in the fragmented forests of Hokkaido (Kotaka & Kameyama 2002) and the distance of nest location shift within the study site (see chapter 6). Nests were occasionally distributed very close each other (minimum 85m). Such breeding areas containing multiple nests in a given year were assumed to have reached the maximum carrying capacity of observed pairs that year (Fig 2).

To verify that the studied population followed the ideal despotic distribution model and
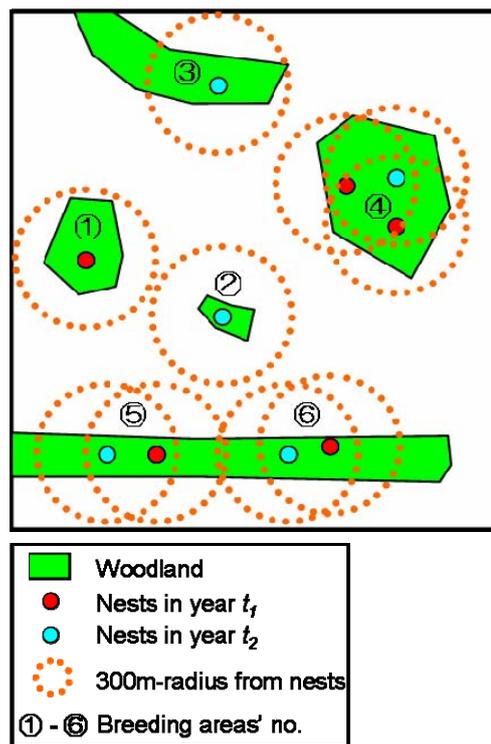
Fig. 2 The schema of definition of breeding area. In this example, the breeding area only no.4 has carrying capacity of two pairs.

site-dependent population regulation, the scenarios predicted by theory were compared with the observed occupation rate and quality indices of the breeding area. If breeding area selection in the GSWs follows the ideal despotic distribution model, some breeding areas should be occupied more frequently than others, indicating the existence of preferred areas and avoided areas. This is a precondition in testing ideal despotic distribution. Thus, the scenario first examined was that 1) preference and avoidance of breeding areas existed within the study site. Then, the following scenarios were predicted by the ideal despotic distribution model and site-dependent population regulation: 2) at the population scale, a greater percentage of less-preferred breeding areas were occupied in years of higher breeding densities compared to low; 3) the occupation rate of breeding areas reflected their quality. The third condition implied that: 3a) preferred breeding areas provided the higher availability of resources, 3b) preferred breeding areas had better survivability of birds, 3c) preferred breeding areas had lower inter-species interference pressure, and 3d) preferred breeding areas had the better reproductive output.

Scenario 1 was tested by examining whether the observed occupation rate of breeding area significantly differed from a random pattern. I modified the method of previous studies (Korpimaki 1988, Newton 1991, Sergio & Newton 2003) for this comparison. In previous studies on raptors, the observed pattern of breeding area occupancy was compared to the Poisson pattern, which was expected if territories were occupied at random, independently of previous history. In the present study, the carrying capacity of breeding areas was considered, and the random pattern was generated according to the observed fluctuation in the number of nest by simulation. The mean value of random occupation rate derived from 10,000 replicated simulations was compared with the observed pattern by chi-square test.

Scenario 2 was tested by examining whether the mean occupancy rate of breeding areas decreased with increasing population density by linear regression.

To test scenario 3a, the mean forested area contained within a 300m radius from each nest was used as the index of availability of resources in a given breeding range (cf. Kotaka & Kameyama 2002). Since forests provide crucial resources for the GSW, such as sites for

nesting, roosting, and foraging, this was deemed appropriate. The correlation between the mean forested area and the occupancy rate of the breeding areas were examined using Spearman's rank correlation test.

To test scenario 3b, the number of years that marked birds resided in the same breeding area was counted, and its correlation with the occupancy rate was examined using Spearman's rank correlation test. Additionally, the tendency of breeding area shift of marked breeding birds was found to complement the testing of this scenario. The unit of observation used for this purpose was one 'bird year', thus birds observed in more than two successive years counted more than once. Birds marked in 1999, 2005, and 2006 were included in these analyses, because it was possible to track their fate for at least three years.

To test scenario 3c, nesting failures caused by inter-specific interference per nesting attempt was calculated for each class of the occupation rate of breeding area. It was then examined whether the inter-specific interference rate decreased with increasing occupation rate of breeding areas by linear regression. Nesting attempts were only counted if the nest hole was completely excavated. In this study site, a major cause of nesting failure of GSWs was nest cavity usurpation by secondary cavity users such as the Russian Flying Squirrel *Pteromys volans orii* and the Chestnut-cheeked Starling *Sturnus philippensis* (cf. Mori 2006).

To test scenario 3d, clutch size, fledging success, and the number of fledglings per successful nest were used as indices of the reproductive output, and their correlations with the occupancy rate of breeding areas were examined using Spearman's rank correlation test. A cavity containing at least one egg was classified as a nest.

Results

SCENARIO 1: PREFERENCE AND AVOIDANCE OF BREEDING AREAS EXISTED WITHIN THE STUDY SITE.

In 1999-2001 and 2005-2007 (six years in total), the numbers of nests found were 30, 12, 26, 24, 34, and 29, a total of 155 nests. The numbers of occupied breeding areas were 27, 11, 25, 22, 26, and 24, a total of 49 breeding areas. Out of these breeding areas, six breeding

areas had carrying capacity of multiple pairs. Three breeding areas had carrying capacity of three pairs, and the rest had carrying capacity of two breeding pairs. Random occupation patterns were simulated 10,000 times based on the observed total number of breeding areas, carrying capacity of each breeding area, and the fluctuation in the number of nests. In comparing the observed and expected frequencies, the upper two classes (i.e. 5 and 6) were combined into one class in order to avoid cells with expected frequencies less than five. The observed occupation frequency of breeding areas differed from that expected by simulation (Fig. 3; $\chi_4^2 = 10.7$, *P*=0.03). Some breeding areas were found to be occupied more or less than expected, either for many or few years, implying that there was some level of preference for breeding areas. Therefore, scenario 1 was supported.
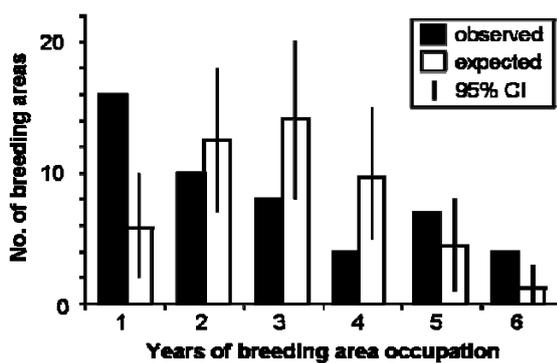
Fig. 3 Observed and expected occupancy of GSW breeding areas over 6-year period (1999-2001 and 2005-2007). The observed occupancy of breeding areas significantly differed from that expected ($\chi_4^2 = 10.7$, *P*=0.03).
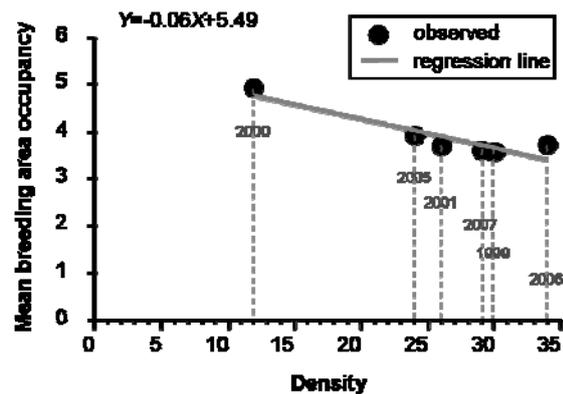
Fig. 4 The relationship between mean occupancy of GSW breeding areas and breeding density (1999-2001 and 2005-2007). Each point represent one year of study. Mean breeding area occupancy in a year was calculated as the average occupancy of all the breeding areas occupied that year. Less-preferable breeding areas were significantly occupied more at higher breeding densities ($\hat{R}^2 = 0.80$, n=6, *P*<0.01).

SCENARIO 2: AT THE POPULATION LEVEL, A GREATER PERCENTAGE OF LESS-PREFERRED BREEDING AREAS WAS OCCUPIED IN YEARS OF HIGHER BREEDING DENSITIES THAN COMPARED TO YEARS OF LOW BREEDING DENSITIES.

The mean occupation rate of breeding areas (Y) decreased as the number of nests increased (X)(Fig. 4; $Y=-0.06X+5.49$, $\hat{R}^2=0.80$, n=6, $P<0.01$). Thus, scenario 2 was supported.

SCENARIO 3: THE OCCUPATION RATE OF BREEDING AREAS REFLECT THEIR QUALITY.

The occupation rate of breeding areas was positively correlated with mean forested area within 300m radius from nests (Fig. 5; $r_s=0.51$, n=49, $P<0.001$). Scenario 3a was supported.

The number of birds marked in 1999, 2005, and 2006 were 43 males and 49 females.
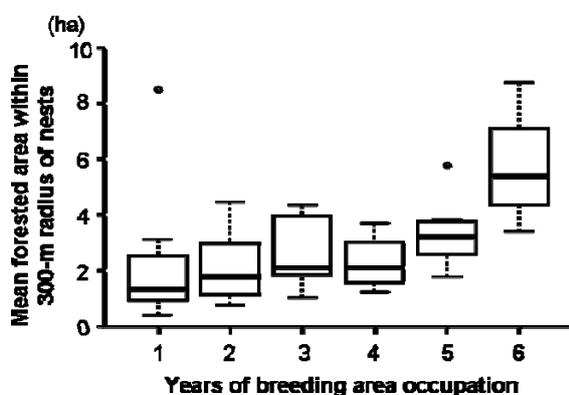
Fig. 5 The mean of forested area within 300-m radius from nests in each breeding area. It increased with occupancy: $r_s=0.51$, n=49, $P<0.001$.

The boxes, bold lines, and horizontal lines indicate the quartile deviation, median, and extremum, respectively.
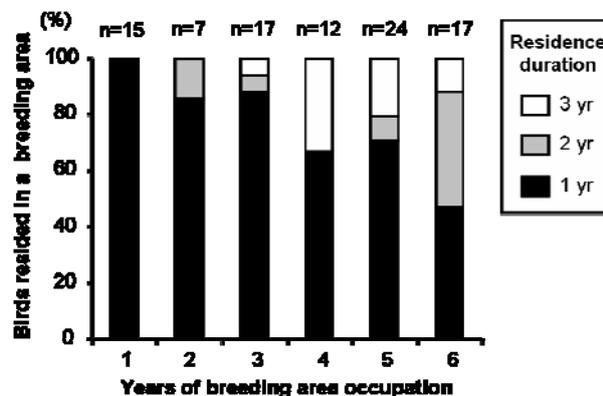
Fig. 6 The residence duration of breeding GSWs in breeding areas of differing occupancy. The years of residence increased with occupancy: $r_s=0.36$, n=92, $P<0.001$.

The residence duration of marked birds was positively correlated with occupancy rate of the breeding area (Fig. 6; r_s=0.36, n=92, P<0.001). Scenario 3b was supported. Of 92 birds, 52 birds were observed for only one year, and 18 and 22 birds were observed for two years and three years, respectively. No birds were observed for four years (i.e. the birds marked in 2005

Table 1. The tendency of breeding area shift of breeding GSWs marked in 1999, 2005, and 2006.

Years of breeding area occupation	Disappeared		Stayed on same area		Moved to a different area of same or higher occupancy		Moved to a different area of lower occupancy		Total
	n	%	n	%	n	%	n	%	n
1	12	70.6	-	-	5	29.4	-	-	17
2	7	50.0	3	21.4	4	28.6	0	0.0	14
3	15	75.0	2	10.0	2	10.0	1	5.0	20
4	8	50.0	8	50.0	0	0.0	0	0.0	16
5	17	53.1	13	40.6	1	3.1	1	3.1	32
6	15	51.7	11	37.9	2	6.9	1	3.4	29
Total	74	57.8	34	28.9	37	10.9	3	2.3	128

The birds observed in more than two years figure more than once, as the unit of observation was one 'bird year'.

were not observed in 2008). The tendency of breeding area shift is shown in Table 1. Of the total 128 bird years counted, 28.9% (n=34) settled in their previous breeding area. Of the birds that changed the breeding areas, a majority moved to a breeding area of the same or higher occupation rate than their previous breeding area (Table 1).

The total observed number of nesting attempts was 134 in six years (1999-2001 and 2005-2007). Out of the 38 nesting failures, causes were unknown for 16 cases.
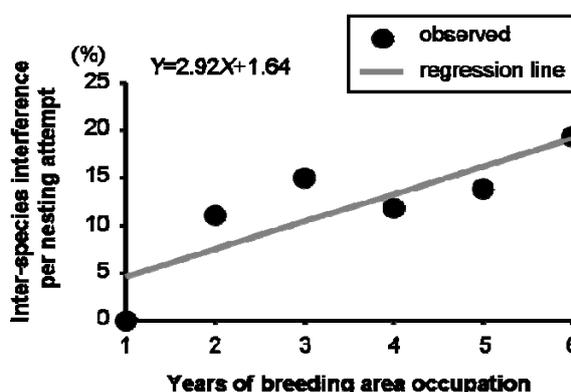
Fig. 7 Inter-species interference per nesting attempt in breeding areas of differing occupancy. The interference significantly increased with occupancy ($\hat{R}^2$=0.63, n=6, P=0.04).

Incidents of inter-specific interference was found in 67 % (n=18) of the known causes (n=27). Other causes of failure were due to un-hatched eggs and starvation (n=6), and nest destruction (n=3). The inter-specific interference per nesting attempt (*Y*) increased with the increase in occupation rate of breeding areas (*X*)(Fig. 7; *Y*=2.92*X*+1.64, $\hat{R}^2$=0.63, n=6, *P*=0.04). Thus, the result indicated the opposite pattern to the one expected. Scenario 3c was not supported.

The indices of the reproductive output, clutch size, fledging success, and the number of fledglings per successful nest, were not correlated with the occupancy rate of breeding areas (Table 2; clutch size: r_s=-0.07, n=76, *P*=0.52, fledging success: r_s=0.05, n=129, *P*=0.55, fledgling number: r_s=-0.02, n=60, *P*=0.90). Scenario 3d was not supported.

Table 2. The reproductive outputs of GSWs in breeding areas of differing occupancies.

Years of breeding area occupation	Clutch size		Fledging success		No. of fledglings	
	mean ± SE	n	%	n	mean ± SE	n
1	5.7 ± 0.8	6	92.3	13	4.0 ± 1.3	7
2	6.3 ± 0.9	10	77.8	18	3.6 ± 1.7	9
3	5.5 ± 1.0	15	75.0	20	4.0 ± 1.1	8
4	6.2 ± 0.8	10	81.3	16	3.4 ± 1.4	9
5	5.3 ± 1.0	17	67.6	34	3.8 ± 0.8	12
6	5.8 ± 0.9	18	82.1	28	3.7 ± 1.1	15
Total	5.8 ± 0.9	76	77.5	129	3.8 ± 1.2	60

The reproductive output was not correlated with the occupancy of breeding areas (clutch size: r_s=-0.07, n=76, *P*=0.52, fledging success: r_s=0.05, n=129, *P*=0.55, fledgling number: r_s=-0.02, n=60, *P*=0.90)

Discussion

The results showed that the observed settlement pattern of GSWs were consistent in principle with the scenarios predicted by the ideal despotic model and site-dependent population regulation (Fretwell & Lucas 1970, Rodenhouse et al. 1997). Scenarios 1 and 2 were completely supported, and scenario 3 was partly supported.

The observed patterns consistent with the scenarios were that: 1) preferences exist for

breeding areas (Fig. 3), 2) at the population scale, a greater percentage of less-preferred breeding areas was occupied in years of higher breeding densities compared to years of low breeding density (Fig. 4), 3a) the forest coverage, an index of resource availability, was higher in the preferred areas (Fig. 5), and 3b) birds resided longer in more preferred areas (Fig. 6).

The observed patterns 1 and 2 indicated that the occupation rate of the breeding area could be used as a reliable measure of the breeding area preference. Thus, the patterns 3a and 3b suggested that the forest coverage and the residence duration of birds reflected the quality of breeding area. The forest coverage may be a cue for GSWs' breeding area selection, because it was the one visible environmental feature for GSWs throughout the year. GSWs forage mainly on surface-living arthropods (e.g. defoliators) on a wide range of trees during summer. It is probably difficult for GSWs to predict the future availability of such resources directly when settling in breeding areas before spring, because food source per se generally emerge in patchy and ephemeral manners (cf. Matsuoka 1977). On the other hand, availability of suitable trees for nesting or roosting is readily predictable for the GSW. GSWs use a range of tree species with sufficient growth and hardness for nesting (Matsuoka 2008) and typically excavate new nests every year in the study site. Available breeding area may be determined by the availability of suitable trees for nesting. However, since the purpose of this study was to test the settlement pattern in available breeding areas, I did not describe the condition for determination of available breeding areas. The result suggested that GSWs may be using forest coverage as a measure of food resource availability, when selecting breeding areas from ones available.

In contrast to forest coverage, residence duration of birds showed effects of breeding area selection. The observed pattern 3b along with complementary data (Table 1) suggested that the residence duration of birds in a breeding area was probably correlated with the true survival years. Of 92 birds in total, 52 birds were observed in the study site for only one year. Most of these disappeared birds probably died, because the known nest location shift distance was typically less than 1,200 m (Chapter 5). Most of the survived birds, once settled in a breeding area, resided there in the following year (68.5%; Table 1). Additionally, when birds

successfully changed their breeding area, most of them (82.4%) moved to another breeding area of equal or higher occupation rate than their previous breeding area. These birds continued to survive for two or three more years, even though they initially settled in a breeding area of low occupation rate. Thus, birds probably achieved better survival probability in preferred breeding areas.

The other scenarios 3c and 3d were not supported. The observed patterns against these scenarios were: 3c) the reproductive output (clutch size, fledging success, and fledgling number) did not differ among breeding areas, and 3d) the pressure of inter-species interference, the major cause of nesting failure, was higher in preferred areas. The observed pattern 3c was, in particular, contradictory to theoretical scenario.

As mentioned above, birds probably preferred breeding areas with high forest coverage, which reliably predicted its high quality. Although reproductive output shows effects of breeding area selection by birds, pattern 3c indicated that the breeding area selection did not improve the reproductive output. This may have resulted from the increased pressure of the inter-species interference in preferred breeding areas. The inter-species interference pressure should be predictable for the GSW, because starlings and flying squirrels were common cavity usurpers in any population of the GSW (e.g. Mazgajski 2000, 2002, Kotaka & Matsuoka 2002, Mori 2006, Smith 2006). However, GSWs in the study site seemed to mis-predict these pressures. This antinomy may result from the cost-benefit trade-off due to forest fragmentation. Since forest coverage surrounding the nest was smaller in less-preferred breeding areas, the birds settled there tend to use remotely located woodlands for foraging. This forces birds to pay a higher travel cost. However, such breeding areas may not be accessible for flying squirrels, because their gliding ability is restricted to less than 30-50m (Asari et al. 2007, Tsuji et al. 2004). As for starling and several other secondary cavity-using birds, they may prefer areas of high cavity availability. They not only usurp active nests but also use old cavities. Less-preferred breeding areas should have less numbers of old cavities, in contrast with preferred breeding areas, which are occupied repeatedly. Thus, this condition may drive a decrease in usurpation of active nests by the secondary cavity using birds.

Consequently, birds settled in less-preferred breeding areas with low forest coverage might pay high travel costs for foraging, but obtain benefits of low inter-species interference. This hypothesis may be supported by high reproductive output of this study site, which was comparable to the known reproductive output in the continuous forests of Europe (Table 3; Bavoux 1985, Michalek et al. 2001 cited in Pasinelli 2006, Mazgajski 2002, Mazgajski & Rejt 2006).

In conclusion, the settlement pattern and site-dependent density-dependent population regulation in this GSW population were estimated as follows. GSWs preferred highly forested breeding areas, using the level of forestation as indicators for good breeding areas. Breeding pairs may inhabit progressively low-forested breeding areas as population density increases, and this may lead to reduced per capita survival rate. In short, the site-dependent density effect in this studied population may act through survival rate of breeding birds, but not through the reproductive output in this population.

Table 3. The reproductive outputs of GSWs in continuous forests of Europe.

Clutch size		Fledging success		No. of fledglings		Remark	Location of study sites	Source
mean ± SD	n	%	n	mean ± SD	n			
				2.7 ± 0.8	98		France	Bavoux (1985)
5.4 ± 0.89	5					in 1996	Central Poland	Mazgajski (2002)
5.67 ± 0.87	9			2.91 ± 0.83	21	in 1997		
5.5 ± 1.29	4			4.1 ± 0.72	16	in 1998		
		81.3	32			in 1996-1998		
				3.9	7	nestlings counted between days 17 to 23 after hatching	E Austria	Michalek et al. (2001) cited in Pasinelli (2006)
5.69 ± 0.85	13	83.3	12	3.92 ± 0.77	24	in 2-55ha forest	Central Poland	Mazgajski & Rejt (2006)
6.5 ± 0.89	16	84.6	13	4.48 ± 1.03	21	in >120ha forest		

Chapter 5

Breeding population dynamics influenced by food abundance and weather severity in winter

Abstract

The dynamics of a marked breeding population of the Great Spotted Woodpecker *Dendrocopos major* was monitored in a fragmented forest landscape (40 km^2) in 1999-2001 and 2005-2008. The population parameters of survival, emigration and immigration were estimated from the monitoring data. The population composition (i.e. survivor, immigrant breeder, and natal dispersing immigrant) were detected from these parameters. Winter food supply (seeds of Korean pine) and winter severity (temperature) were considered as possible environmental factors affecting population dynamics. The breeding population size fluctuated three-fold, between 12 and 34 pairs. The breeders typically stayed in their previous breeding area, and their survival rate showed strong positive correlation with the seed crops of Korean pine. The population was found to be maintained by immigrants, compensating for declines of previous breeders during the winter. In four of the five years, immigrants composed more than half the breeding population. Most such immigrants were assumed to be natal dispersers from outside of the study site. The population dynamics of the Great Spotted Woodpecker may be complicated by the different responses to winter food and winter severity by individuals of different status.

Introduction

Elucidating patterns and processes that generate fluctuations in population size over time is essential to understand the mechanisms of population regulation, which is one of the fundamental objectives of ecology (Begon et al. 2005). Fluctuation in population size is often correlated with environmental factors, such as food-supply and weather, because those strongly affect the survival of individuals, which then affects the composition of subsequent breeding populations (Lack 1966, Sæther et al. 2004, Newton 1998). Many avian species, especially at high latitude, rely on non-renewing food resources during winter. The importance of food-supply during winter for over-winter survival has been investigated descriptively, correlatively and experimentally in many species. Survival rates have been found to be higher in winters with abundant food (e.g. beech mast for seed eaters or hares for predators) than those with scarce food (Källander 1981, Houston & Francis 1995). Most experimental studies reveal that well-fed birds have a better chance of surviving than controls (Krebs 1971, Jansson et al. 1981, Brittingham & Temple 1988). Weather conditions during the non-breeding season also affect the size of population fluctuations in numerous avian species (Sæther et al. 2004). In particular, winter temperatures have often been correlated with annual changes in survival rate and spring population size (Graber & Graber 1979, Nilsson 1987, Arcese et al. 1992, Peach et al. 1995, Lahti et al. 1998).

Most of these studies, however, have discussed the effects of the environmental factors on survival and/or breeding population size without separating the effects of survival, recruitment, and immigration in a breeding population. Survivors, recruitments, and immigrants (including natal disperser) are expected to respond differently to the environmental factors, because environmental factors have been found to affect animals of different status (e.g. age, sex and immigration status) in different ways (Colbert 1988, Lahti et al. 1998, Coulson et al. 2002, Robinson et al. 2007). These status-dependent responses have been explained as result of status-dependent social dominancy, dispersal tendency, reproductive cost, and so on (Fretwell 1969, De Leat 1985, Ekman 1990, Langen & Rabenold 1994). The sum of all the patterns of fluctuations in the independent components of the

population is thought to suggest the overall process of fluctuation in population size. To estimate the population composition, it is necessary to obtain basic demographic parameters of survival, emigration, and immigration from time-series data by tracking many identified individuals over multiple years.

In this study, a marked breeding population of the Great Spotted Woodpecker (GSW hereafter) was monitored in a fragmented forest landscape in Hokkaido, Japan in 1999-2001 and 2005-2008. This species is common in fragmented forests, and breeding individuals there are detected and captured more easily than those in a continuous forest habitat. These features made it possible to derive demographic parameters from the monitoring data. The woodpeckers in this study site rely on the seeds of Korean pine *Pinus koraiensis* throughout winter. This serve as an efficient energetic food resource (López-Mata 2001, Mori 2005; Chapter 3), where invertebrate food resources such as surface-living arthropods (e.g. defoliators) and wood-boring insects are either unobtainable or more costly to forage in cold winters (cf. Jiao et al. 2008; maximum temperature in January is ca. -2.0 ˚C in my study site). The aimes of this study are to 1) estimate the parameters of survival, emigration, and immigration, 2) describe the fluctuations of independent components of the population, and 3) infer the effect of the environmental factors (the seed crops of Korean pine, winter temperature) on the process of population dynamics in a breeding population of GSWs inhabiting a fragmented forest landscape in Hokkaido, Japan.

Material and Methods

MATERIAL

The GSW is widely distributed from the Arctic taiga through to boreal and temperate zones, using a range of tree species with sufficient growth and hardness as a nest tree (Mazgajski 1998, Birdguides Ltd. 2004, Matsuoka 2008). It is a common species in fragmented forests both in urban and agricultural areas in Europe and the northernmost (Hokkaido) of the four main islands of Japan (Short 1982, Anada & Fujimaki 1984, Ito & Fujimaki 1990, Glue & Boswell 1994, Hinsley et al. 1996, Yamauchi et al. 1997, Birdguides

Ltd. 2004). The breeding birds exhibit strong site fidelity to a home-range once settled and individuals have been found to use the same breeding area for 6-8 years (Birdguides Ltd. 2004). Their food habit is omnivorous, but mainly insectivorous during the summer months. Conifer seeds (mainly pine *Pinus* and spruce *Picea*) become important food resource during the winter, and more so in northern populations. The seeds of Korean pine are known to be the preferred winter food resource in the studied population (Mori 2005; Chapter 3).

STUDY SITE

The study site was a 40-km² tract of agricultural land, south of Obihiro City (42°46'N,

Fig. 1. The study site, a 40 km² agricultural landscape in Obihiro, and its surroundings based on the Natural Environmental Information GIS (Environmental agency of Japan 1997). Black polygons and the pale gray polygon indicate forested areas and the study site, respectively. White areas were mainly agricultural fields. The continuous forest shown in the southwestern portion of the study site is the foot of the Hidaka mountains.

143°05'E), Hokkaido (Fig. 1). Flat agricultural fields (mainly wheat, sugar beets, potatoes, meadow and beans) are widespread in this region. Forest habitat occupied 6% of the site. The nearest continuous forest, the foot of the Hidaka mountains, was about 5 km from the site.

The forest habitat consisted of second-growth broad-leaved deciduous remnant woodlands, narrow shelterbelts (<15m width), wide shelterbelts (*ca.*30-100m width), riparian shrubs, and small groves around private dwellings. The Korean pine *P. koraiensis* was a dominant tree at small groves around scattered private dwellings. Detailed information about the vegetation is described in Mori (2005) (see also chapters 2 and 3).

MONITORING DATA

The location of nests and individually identified breeding woodpeckers in the site were monitored from early May to early July in 1999-2001 and 2005-2008. Most birds started nest excavation in mid-May and all nestlings had fledged by early July. The nests were detected by repeated intensive search. The breeding pairs' conspicuous nest defense behavior and nestlings' loud begging calls were often effective cues for the search. Thus, the number of breeding individuals was considered as the breeding population size in the study site. The study site was visited for nine days in June 2002, and only data on the nest location shift of the marked breeding birds were included in analyses for this particular year.

The breeding birds were captured at their nests or roosting cavities with a mist or a bag net. A female in a cage and/or the playback of drumming and call were used to attract individuals to the nets starting in 2005. Nestlings and fledglings were also captured at their natal nests and marked in 1999 and 2005-2008 to obtain supplemental data on natal dispersal. The nestlings were captured by a pick-up tool and/or by hand without destructing nests. The fledglings were captured by means of a mist net or a bag net when they left the nest. Captured birds were individually marked with 1-3 plastic color rings and one metal numbered ring. A cavity containing at least one egg was classified as a nest. When re-nesting was observed after a failure, only the re-nesting data was used for the pair.

ESTIMATION OF DEMOGRAPHIC PARAMETERS

The survival, nesting attempts and dispersal of marked birds were directly observed. The estimated demographic parameters were survival rate, emigration rate and immigrant number in breeding woodpeckers. The breeding population composition (i.e. survivor, immigrant breeder, and natal dispersing immigrant) was estimated from these demographic parameters. Local recruitment within the study site was assumed to be almost negligible, because the known mean natal dispersal distance was 16.5km (Paradis et al. 1998).

Survival rate

The apparent survival rate (S_t) was calculated as the proportion of marked breeding birds that survived and bred in both year, t, and the following year, $t+1$, in the study site. The true survival rate was calculated by adding the emigration rate (see next section) to the apparent survival rate.

Emigration rate

The shifts of nest locations were assumed to illustrate most of the emigration. Such distances were measured on a GIS map, from locations where marked individual bred successively. Since the distances were not significantly different between sexes, shift directions, or years, all the data were pooled and the distances were classified into 50-m classes (Fig. 2: sexes: U=1054, P =0.15, n=85, shift directions (four cardinal points): H=2.74, P=0.43, n=85, years: H=9.17, P=0.10, n=85). The frequency distribution of the distance of nest location shift was approximated by exponential regression. The expected proportion of nest location shift was estimated by integrating the exponential regression curve. To simplify the measurement and calculation, the expected proportion of nest location shift were divided into 300-m intervals (i.e. n classes). Then, 300-m concentric circular were generated around every nest in year t using GIS. The probability for each individual to shift its nest location outside of the study site from year t to $t+1$ was considered as the expected emigration rate. Thus, the emigration rate for the breeding population in the study site in year t (E_t) was

estimated by the following equation:

$$E_t = \sum_{i=1}^{n}(Do_i \times P_i)$$

where Do_i is the proportion of the sum of buffer areas outside the study site to the sum of buffer areas in class i, and P_i is the expected proportion of the nest shift occurrence in class i.

Immigrant number

The total immigrant number from year t-1 to t was calculated as

$$I_t = N_t - (N_{t-1} \times S_{t-1})$$

where N is the number of breeding individuals, and S is the apparent survival rate. The immigrants were considered to be only either the immigrant breeders that had nests in the previous year in neighboring areas of the study site, or new breeders that might have dispersed a longer distance from their natal nest (e.g. Mori 2006; Chapter 5). The number of immigrants and the number of emigrants constituted by breeders in the previous year were assumed to be balanced inside and outside of the study site, since the environments were comparably. Thus, the natal dispersing new breeders (hereafter natal dispersing immigrants) were assumed to compose the rest of the population other than survived breeders, and immigrant breeders from the neighboring area of the study site:

$$Y_t = I_t - (N_{t-1} \times E_{t-1})$$

where Y is the number of natal dispersing immigrants, and E is emigration rate. The numbers of individuals were estimated as the integral number truncating the decimal fraction.

ENVIRONMENTAL FACTORS

Winter food abundance and severity were considered to be environmental factors that affected the demographic parameters of the GSW.

Korean pine seed crops

The seed crops of Korean pine, a mast-seeding species and the preferred food by GSWs,

were monitored in the winter
seasons in Hokkaido, Japan (Mori
2005; Chapter 3). The Korean
pine is an exotic species, and
typically planted in small groves
around private dwellings. The
cones grow to about 12-16 cm
long, green before maturity, and
ripen about 18 months after

Table 1. Cone production ranks (0 to 5) of Korean pine in each grove.

		Cone number per fruited tree			
		<5	5-15	≥15	≥50
Pines with cones	0%	0			
	<10%	1	1	2	4
	10-80%	1	2	3	4
	≥80%	2	3	3	5

pollination (October). The large green cones were observed from the ground in early-July of
2006 and 2007, and crop levels were classified as poor, moderate or rich. Inside the study site,
there were 68 groves containing Korean pine, and when those in the neighboring area were
included (<1 km from the boundary), 76 and 80 groves were found in 2006 and 2007,
respectively. The proportion of the Korean pine trees with cones to the total number of
Korean pine trees were recorded (0%, <10 %, 10-80%, or ≥80 %), and the approximate
average cone number per fruited tree (< 5, 5-15, ≥15, or ≥50) in each grove. The cone
production of each grove was classified into five ranks as shown in Table 1. The seed
production of coniferous species is known to be synchronous over large areas (Koenig &
Knops 1998). So, the seed crop in 1998-2001 and 2004-2005 were determined by comparison
with the production of that in 2006 and 2007, which were based on within-site personal
observations by the author and observations of the site periphery by the group, Ezorisu-no-kai
(2008)(a line census was conducted in the Obihiro Forest, about 9 km north of the study site).
A poor crop year is obvious because most Korean pine groves bear no or very few cones. In
rich crop years, most groves bear plenty of cones and some mature cones with seeds still
remaining on branches until the next summer.

Winter severity

As measures of winter severity, air temperatures during November-April in 1998-2001

and 2004-2008 at the Obihiro meteorological observatory, about 15 km north-east of the study site, were used. The data were taken from the web-accessible database of Japan Meteorological Agency. The mean daily temperature was summed for each winter.

STATISTICAL ANALYSIS

The studied breeding population was assumed to be composed of survivors, immigrant breeders, and natal dispersing immigrants (see above). Although the pre-analysis suggested that the number of neighboring breeders immigrated into the study site depended on the constant nest location shift tendency, survivors and natal dispersing immigrants may be affected by previous winter environmental factors differently. The correlation between S_t or Y_t and the environmental factors in previous winter (i.e. Korean pine seed crops or temperature) were examined using Spearman's rank correlation test.

Results

POPULATION DATA

The yearly numbers of nests found in the study site were 30, 12, 24, 26, 34, 29, and 31 (Table 2). The breeding population size was the smallest in 2000, which was half or less than that of the other years. A total of 90 breeding males and 87 breeding females, and 159 nestlings and fledglings were marked. Although not all nestlings were marked at several nests, 145-150 marked nestlings/fledglings were considered to have fledged successfully from the nest monitoring data (Table 2).

DEMOGRAPHIC PARAMETERS AND DISPERSAL

Distances of nest location shifts observed in the study site (n=85) were biased toward the shorter end of the distribution, and the maximum distance was 2360m (Fig. 2). The exponential regression curve was expressed by the following equation: *Frequency* = 32.7859 × exp (-0.41317 × *Distance*) (R^2=0.62, *P*<0.001). The expected probability of a nest site shift for each 300-m distance class was estimated as 87.3 %, 11.6 %, 1.0 %, and 0.1 % until 1200m,

Table 2. Numbers of nests and individually identified birds.

Year	Nest	Breeding adult		Nestling	
		N	Marked	Marked	Fledged
1999	30	60	32	11	11
2000	12	24	23	0	0
2001	26	52	19	0	0
2005	24	48	22	31	22-23 [b]
2006	34	68	55	48	44-46 [b]
2007	29	57 [a]	52	68	51-53 [b]
2008	31	62	58	20	17

The marked birds observed for years were counted more than once in the table. A total of 90 breeding males and 87 breeding females, and 159 nestlings and fledglings were marked.

a) A female re-nested with another male after the former mate and eggs were predated at the former nest. b) The numbers of fledglings were estimated within the estimated range by repetitive monitoring, where nestlings were partially marked at the nest.
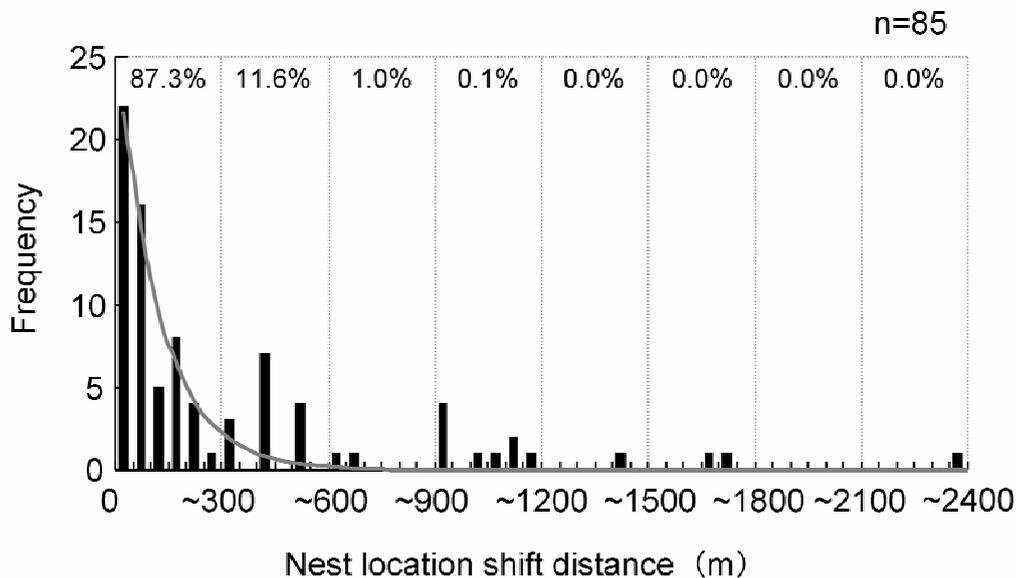
Fig. 2. The frequency distribution of the distance of nest location shift (histogram) and the exponential regression curve (*Frequency* = 32.7859 × exp (-0.41317 × *Distance*), $R^2 = 0.62$, $P < 0.001$). The probability of nest location shift within each 300-m class (P_i), shown in the graph area, were calculated by integrating the regression curve.

in order from the smallest class (Fig. 2). The estimated value in the class over 1200m approached asymptotically to zero. The emigration rates of the breeding population were estimated to be relatively stable, and the mean ± SD was 5.2 ± 1.0%. The estimated number of emigrating breeders was 0-3 birds (Table 3).

The apparent survival rates were about 30% in 1999-2000 and 2006-2007, 54.9% in 2007-2008, and more than 60% in 2000-2001 and 2005-2006 (Table 3). Thus, the true survival rates ($S_t + E_t$) were estimated as 22.8-62.8%.

The total immigrant number was estimated as 8, 38, 36, 36, and 31 in each of the five years (Table 3). The immigrants composed 33%, 73%, 53%, 63%, and 50% of the breeding birds in each year. Most of immigrants were assumed to be natal dispersing immigrants, because the immigration of neighboring breeders should be equal the number of emigrated breeders (i.e. 0-3 individuals) (Fig. 3a). The number of natal dispersing immigrants was estimated to be 5, 38, 34, 33, and 28 in each year, subtracting the immigrated neighboring breeders from the total amount of immigrants.

Table 3. Demographic parameters of emigration, survival, and immigration of Great Spotted Woodpeckers in a fragmented forest landscape.

Year	Emigration		Apparent Survival		Immigration
	E_t(%)	N	S_t(%)	N	I_t
1999	5.4	3	28.1	16	-
2000	3.6	0	60.9	14	8
2001	6.2	3	-	-	38
2005	5.4	2	68.2	32	-
2006	4.8	3	30.9	21	36
2007	6.7	3	54.9	31	36
2008	4.4	2	-	-	31

Observed examples also indicated that distances of natal dispersal were much longer than the breeders' nest location shift (Appendix 1). The shortest distance between the natal

nest and first breeding nest was at least 2205m. Additionally, one female, which fledged in 1999, was found outside the study site at a location about 8000m from the natal nest in February, 2000.

ENVIRONMENTAL FACTORS

The seed crop of Korean pine was poor in 2006: 45, 21, and 10 of 76 observed groves were ranked as 0, 1, and 2, respectively. Note that more than half the groves bore no cones at all. In 2007, the seed crop was moderate: 16, 16, 15, 22, and 11 of 80 observed groves were ranked as 0, 1, 2, 3, and 5, respectively. Seed crops were classified as rich in 1998, 2000, and 2005, moderate in 2004, and poor in 1999 (S Mori, Personal observation, Fig. 3b). The trends observed in the study site roughly corresponded with those in the Obihiro Forest (Ezorisu-no-kai 2008). In the study site, most groves had no cones in July of 1999, similar to the situation in 2006. Plenty of mature cones and premature cones were observed in most Korean pine groves in the winter of 2000-2001 (cf. Mori 2005; Chapter 3), and in July of 2005, respectively, and the abundance of cones per fruited tree in those years were much more than that in 2007. In the Obihiro Forest, the number of cones in 2005 was 12-fold of that in 2007 (Ezorisu-no-kai 2008). The seed crops in 1998 in the study site were also presumably rich, because many mature cones still remained on the branch in the breeding season of 1999 (cf. Mori 2005; Chapter 3), and many dropped cones were observed under the trees.

The winter of 2006-2007 was the warmest (Fig. 3b). The coldest winter was that of 2000-2001, and the second coldest was that of 1999-2000.

STATISTICAL ANALYSIS

The survival rate had significant positive correlation with the Korean pine seed crops (r_s=0.95, P=0.01, n=5). No other significant correlation was found (S_t & temperature: r_s=-0.20, P=0.01, n=5, Y_t & seed crops: r_s=0.79, P=0.11, n=5, Y_t & temperature: r_s=-0.3, P=0.62, n=5).

Discussion

The Korean pine seed crop may have had a direct impact on the survival of breeding adults. The survival rate had significant strong positive correlation with the Korean pine crops (Table 3, Fig. 3). GSWs are thought to remain faithful to their initial breeding site (Birdguide Ltd. 2004). In my study site during the winter, pairs maintained enlarged home-ranges around their previous nest site to feed on the seeds in Korean pine groves, and they defended the groves from the other individuals (Mori 2005; Chapter 3). If food resources other than Korean pine were hardly available, the seed crops are expected to have a straightforward impact on the survival of adult GSWs in the winter of this study site.

However, the breeding population size was not determined by the adult survival rate, and the amount of seed crop. The breeding population size was maintained by immigration, which was not correlated with the seed crop in four of the five years; where the year 2000 was the only exception (Table 3, Fig. 3a). I assumed that the rest of the birds, other than survived breeders and immigrant breeders from the neighboring area of the study site, were natal dispersing immigrants. This assumption seemed to be reasonable because observed natal dispersal was much longer than the breeders' nest location shift (Fig. 2, Appendix 1). As a result, most of the immigrants were expected to be natal dispersing immigrants. It is difficult to distinguish yearlings from the older individuals in the breeding season, because fledglings molt into their adult plumage by October (Short 1982). However, duller black and worn feathers indicated that newly marked breeders included many yearlings.

Because the natal dispersing immigrants were not enough to compensate for the great loss of breeders caused by the previous winter's poor pine seed crop, the breeding population size in 2000 was about half of that in the other years. The winter of 2006-2007 had poor pine seed crop, yet, the number of natal dispersing immigrants and the breeding population size in 2007 was similar to those in 2001, 2006 and 2008.

Winter severity may explain the discrepancy in the number of natal dispersing immigrants between year t and t+1 when the preceding winter had poor pine crops. The number of natal dispersing immigrants seemed to be negatively affected by winter severity
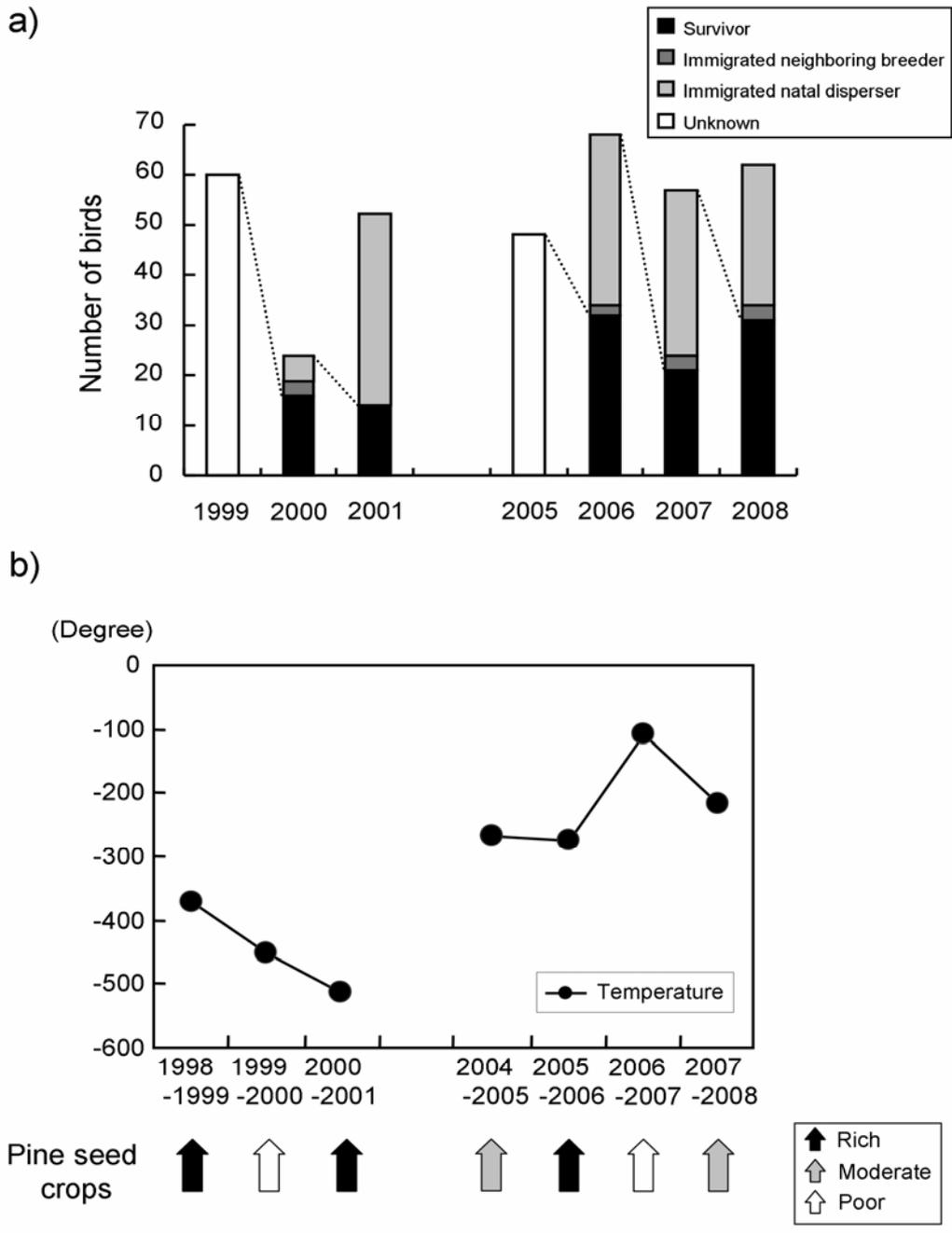
Fig. 3. a) The breeding population composition of the Great-spotted Woodpecker in the study site. These compositions were derived from the demographic parameters described in Tables 1 and 2. b) The fluctuation of environmental factors (winter severity and Korean pine seed crops). Winter severity (November-April) is presented as the sum of mean daily temperatures (●).

only when the seed crop was poor. The winter of 1999-2000 was the second coldest winter during the studied period, 1998-2007 (Fig. 3). In contrast, the winter of 2006-2007 was the warmest winter. Winter severity may increase mortality through energy shortage; it may be difficult to obtain sufficient net energy when the days are very cold and short, and when food resources are depleted (Grubb & Pravosudov 1994, Lahti et al. 1998). Severe winter weather is known as a factor contributing to breeding population fluctuation in many avian species (Sæther et al. 2004). However, the present study implies that the weather per se might not have critical impact on the breeding population size, but might reinforce the negative impact of a poor food supply on the breeding population size by decreasing natal dispersing immigrants. The winter of 2000-2001, the coldest winter, but with a rich pine crop, resulted in high survival rate of breeders, normal amount of natal dispersing immigrants, and normal size of population in 2001 (Table 3, Fig. 3).

Nilsson et al. (1992) analyzed long-term Swedish GSW census data (1975-91) and found that the population density in the breeding season was not correlated with both prior winter temperature and spruce seed supply. However, Hansson (1992), and Saari and Mikusiński (1996) have suggested that the population density in the breeding season was correlated with winter severity in Sweden and Finland. Hansson (1992) did not assess winter food, but Saari and Mikusiński (1996) analyzed long-term data (1979-95) and concluded that the density of this species was not correlated with seed crops of pine and spruce. These studies did not consider the population composition at all. The joint effect of winter severity and food abundance on the number of natal dispersing immigrants might further explain the contradictory results in these studies.

Although statistical analysis to detect that joint effect was not available because of small sample size, the known plasticity of territoriality and natal dispersal of young individuals support this hypothesis. Previous studies in birds suggested that winter weather might affect population sizes and fluctuations together with competition for territories or food resources (e.g. Nilsson 1987, Desrochers et al. 1988). In northern Europe, where GSWs mainly feed on conifer seeds in the winter (Dobrowlski et al. 1994), this species is known as a

population eruptive species (Pulliainen 1963, Eriksson 1971, Hildén 1974, Birdguides Ltd. 2004). Population eruptions in this species occur due to exceptionally large numbers of juvenile migrants (Hildén 1974) looking for food when the seed crops of pine or spruce are poor at the natal area (see Pulliainen 1963, Eriksson 1971). Young individuals occupied areas with rich pine crops preemptively, and settled down in the final winter territory in September-October when the population erupted (Pulliainen 1963). By contrast, in this study site, young individuals foraged in several Korean pine groves without territorial conflicts during the rich crop winter of 2000-2001 (S Mori, unpublished data). These young individuals usually foraged in groves that were not defended by dominant pairs, and often shared the area with other young. These results suggest stronger territoriality in poor crop years. This strategy may have been selected in this species because that gained territories providing sufficient food could survive the winter even if the weather was severe. Some of the young that shared the Korean pine groves were compelled to roost in distant sites from the foraging groves, compared to the dominant pair (S Mori, unpublished data). Most of such subordinate young might have been eliminated from the area before the winter when the seed crop was poor. This is supported by the knowledge that denser wintering populations form in areas with rich conifer crops (Eriksson 1971, Nilsson et al. 1992). Thus, the poor seed crop may reduce wintering young in the autumn, and the subsequent low survival rate caused by severe winter may further reduce the number of surviving young (i.e. natal dispersing immigrant). Further study about the settling timing and territoriality of young is needed to confirm this prediction.

This study provided basic demographic parameters and its range in the GSW, which was not known before. Additionally, this study highlights the importance of population composition through these parameters. By contrast, abundance estimates can make only weak inferences about the factors that cause changes in populations. Population composition can fluctuate independent of the changes in total population size (e.g. Coulson et al. 2002), because animals of different status have different demographic features and respond to environmental factors in different ways. It is one of the reasons that complicate the understanding of the mechanisms of population dynamics. Although sophisticated statistical

tests are still not available for the short-term data set in the present study, the results suggest differing responses to the condition of winter food and severity between breeders and natal dispersing immigrants in the GSW. A long-term study will reveal the significant pattern of fluctuations in population composition. The immigration of natal dispersers was an important factor determining the size of the breeding population. Because the study site was a part of a fragmented forest landscape and only weakly isolated from a nearby continuous forest (at least 5 km), it is possible that a significant exchange of natal dispersers occurs between these two habitats. The population dynamics process of a continuous forest should be different from the one discussed here, since Korean pine was found to be rare in a continuous habitat. To understand the mechanisms of population dynamics, it would be necessary to consider larger scale processes such as source-sink dynamics.

Appendix 1. The natal dispersal of Great-spotted Woodpeckers in the study site.

Fredging year	First breeding year	sex	Natal dispersal (m)	Remark
2006	2007	♂	3,525	
2006	2007	♂	4,655	
2007	2008	♀	3,335	
2007	2008	♀	2,205	
2007	2008	♀	3,450	
2005	2008	♀	3,470	The bird was not observed in the study site until 2008.
2006	2008	♀	2,370	The bird showed pre-breeding behavior without egg laying in 2007.

Chapter 6

General Discussion

Population maintenance mechanisms in the GSW in a fragmented forest landscape

The aim of this study is to reveal the maintenance mechanism of the GSW population in a fragmented forest landscape at multiple spatial scales. First, I described foraging habitat use on a home-range scale, and then discussed the important factors for maintaining a year-round territory (Chapter 3). Secondly, the ideal despotic distribution model was tested on a scale over the home range and the study site, and the site-dependent density effects on the reproductive output and survival rates were described (Chapter 4). Thirdly, I described demographic parameters and their temporal fluctuation patterns and ranges on a landscape scale over the study site and its similar surroundings, and then discussed environment-dependent fluctuation in population structure (Chapter 5).

The results of chapter 3 showed that the breeding pair maintained a pair bond and defended a territory around the nest site throughout the year. The pair foraged not only in the vicinity of the nest site, but also in groves of Korean Pine which were distant from the nest site. The Korean Pine seeds, which are an efficient and stable winter food, were probably important for maintaining a year-round territory in the study site. In chapter 4, the ideal despotic distribution was verified in the studied population. The results suggested that the GSW selected a "breeding area" according to the amount of forest coverage. The reproductive output was good and did not differ among breeding areas, but the survival probability was lower in less preferable breeding areas. Thus, the site-dependent density effect acts on the survival rates, but not on reproductive output. Chapter 5 showed that the annual survival rate of breeding birds was positively correlated with the size of Korean Pine seed crops in the prior winter at the population scale. The natal dispersing birds compensated for the loss of

breeding birds during the prior winter in the subsequent breeding season. However the number of natal dispersing birds would not be enough to compensate when the crop of Korean Pine was poor and the weather was severe in the previous winter.

Integrating these results shown in the earlier chapters, I can discuss the maintenance mechanism of GSW population in a fragmented forest landscape. The factors and processes that gave rise to observed patterns were suggested as follows (Fig. 1). 1) Available breeding areas that have greater forest coverage are preferentially settled by GSWs at the beginning of the breeding season. 2) The birds can achieve same reproductive output at any breeding areas. 3) The birds which settled in the preferable breeding areas can survive better than the birds which settled in the less preferable breeding areas until the next breeding season. 4) The survival rate of the breeding birds is determined not only by the forest coverage of the breeding area but also by the seed-crop size of Korean Pine. 5) The loss of the breeding birds during a winter is compensated by the natal dispersing birds in the next breeding season. 6) However, the natal dispersing birds are not enough to compensate the winter loss when the previous winter had simultaneously poor seed crops of Korean Pine and severe weather. In this case, the population density in the subsequent breeding season decreases considerably. 7) The decreased population density can recover by the next breeding season, greatly depending on the number of natal dispersing birds.

In this context, the key point for understanding the population maintenance mechanism in a fragmented forest is whether the natal dispersing birds originated from the fragmented forest landscape or from the neighboring continuous forest of the Hidaka Mountains. If the population can persist by local recruitment of natal dispersers, then the population is self-maintained. By contrast, if the population requires the immigration of natal dispersers from the outside system for persistence, it indicates the population is a sink. As I described, the study site was weakly isolated (5 km at minimum) from the continuous forest of the Hidaka mountains, where the Korean Pine does not exist and the population dynamics therefore must be different from the studied system. The natal dispersing birds in the study site were probably immigrants from the outside (see chapter 5). The range of natal dispersal

7) The decreased population density can recover by the next breeding season.

5) Natal dispersers compensate the loss of breeding birds in the next breeding season.

Mild Winter **Severe Winter**

6) The number of natal dispersers is not sufficient after a severe winter with poor seed crops.

3) The birds survive **winter** better in the preferable breeding areas than the less preferable ones.

1) Available "breeding areas" with greater forest coverage are preemptively settled in **breeding season**.

Orange circle; preferable area.
Blue circle; less preferable area.

4) A better seed crop of Korean pine results in a better survival rate.

2) The birds achieve good reproductive output at any breeding areas.

Fig.1. The maintenance mechanism of GSW population in a fragmented forest landscape.

and the rate of juvenile survival indicate that at least some of the dispersing young birds did not originate in the fragmented forest landscape where the study site was located in.

I observed some examples of the natal dispersal, and the distances ranged from >2,000 m up to about 8,000 m (see chapter 5). These observations are probably biased toward the minimal extremity of the frequency distribution of natal dispersal distance, because I did not making observations outside the study site (*ca.* 5×8 km). The bird-banding scheme in Europe provided small samples (n=15) of the natal dispersal distance for GSW, and the arithmetic mean was 16.5 km and the geometric mean was 5.9 km (Paradis et al. 1998). This indicates that birds from nearby continuous forest could immigrate to the study site through natal dispersal.

The rate of juvenile survival in the GSW is completely unknown to date. If a closed population is assumed in the fragmented forest landscape including the study site, the juvenile survival can be estimated roughly by the following formula: $\lambda = S_a + S_j F$; where λ is the annual rate of change in population size, S_a is the annual rate of adult female true survival, S_j is the annual rate of juvenile female survival from fledging to the next breeding season, and F is the number of female offspring per female per year. F is calculated as a value multiplying the number of female offspring per female by annual nesting success. In this study, λ ranged over 0.4-2.2 and the average was 1.2, S_a was 33.5-73.6% (Chapter 4, Appendix 1), the number of female offspring per female was 1.9 (assumed sex ratio is 0.5), and the nesting success was 72.4-90.0% (Chapter 5). F ranged over 1.4-1.7 (Appendix 1). As a result, the values of S_j are estimated as 3.8%, 112.7%, 46.4%, 30.6% and 35.1% for consecutively studied years. The values for 2000-2001 are especially important in understanding the population dynamics for this population, since it seemed to be a critical phase to maintain this population. It is impossible for the value of S_j excesses 100%. Thus, the estimated S_j in 2000-2001 indicates that the population in the fragmented forest landscape received immigration from the outside the studied system. In the other years, the value of S_j is estimated within a realistic range, agreeing with the general notion that S_j is lower than S_a in birds including woodpeckers (Newton 1989, Walters 1990 cited in Robles et al. 2007, Robles

et al. 2007, Rossmanith et al. 2007). When $\lambda = l$ is substituted in 2000-2001, the value of S_j is estimated as 25.7%, which is within a realistic range (Appendix 1).

Consequently, the estimated range of natal dispersal and rates of juvenile survival suggest that the population in this fragmented forest landscape at least partly received immigrants from the continuous forest. Therefore, it is still unclear that the population in the fragmented forest landscape can persist without immigrants from the continuous forest. According to the definition of source and sink populations (Pulliam 1988, Pulliam & Danielson 1991), sink populations consume individuals and go extinct without immigration from the source. Pseudo-sinks (Watkinson & Sutherland 1995) also consume individuals at high density, but they will not go extinct in the absence of immigration. In the pseudo-sinks, the immigration increases local population size above local carrying capacity and thus creates a demographic deficit at the realized high density, but birth rate exceeds death and emigration rates at low density. Stochastic variation in birth or death rates is another factor that can result in a population acting as a source in some years and as a sink in others (Thomas & Kunin 1999, Murphy 2001b). The population in a fragmented forest studied here may be a pseudo-sink or it may switch between source and sink depending on stochastic environment factors (i.e. food supply and severe weather during the winter), but may not be an absolute sink. I used rough estimation, however, and more precise evaluation of this attribute of the population is required in the future.

 The present study used multi-scale bottom-up approach to understand population maintenance mechanisms in the GSW in a fragmented forest landscape. The top-down approach in the context of source-sink system at the larger scale including continuous forest may offer further insight into population maintenance mechanisms in the GSW in a fragmented forest landscape. Pattern-oriented modeling based on the results of the present study (cf. Wiegand et al. 2003), together with the genetic structure analysis between fragmented forests and continuous forest, could be used to accomplish this (see Fig. 1 in chapter 1).

Future perspectives for conservation

Understanding the population maintenance mechanisms attracts not only theoretical interest but also practical interest today because many species are now threatened all over the world due to habitat fragmentation and loss. Knowledge of population maintenance mechanisms is required for conservation and management of target species. The results of the present study can contribute to planning for conservation and management of the GSW populations.

The GSW is common in fragmented forests in agricultural landscape of Hokkaido. However, remnant forests and shelterbelts are gradually declining today in Hokkaido. In such habitat, the GSW is known as an important cavity provider for secondary cavity users (Kotaka & Matsuoka 2002, Muraki & Yanagawa 2006). Kotaka and Matsuoka (2002) showed that the suitability of the GSW cavities for secondary cavity users decreases with time. Conservation and management of the forest habitat for GSW population persistence will enable continued production of new cavities. It should also be good for maintenance of the diversity of cavity-nesting wildlife in agriculture regions.

Additionally, it is the common practice in ecological modeling to apply the data that are available from other species as well as from other conspecific populations or subspecies if the information of such parameters is missing for a target population (Wiegand et al. 1998, Horino & Miura 2000, Wichmann et al. 2003). Although roughly 200 woodpecker species exist in the world (Sibley & Monroe 1990, Winkler & Christie 2002), our knowledge about the population dynamics of most species is lacking (e.g. Pasinelli 2006). Many woodpecker species or populations are threatened or endangered worldwide due to human-induced habitat fragmentation, loss, and degradation (e.g. IUCN 2008, Ministry of the Environment of Japan 2005). Some of these, including Japanese endemic species or subspecies, are closely related to the GSW. The information presented here on factors and processes affecting population dynamics in the GSW can be extrapolated to analyses of the populations of those species.

Appendix 1. The annual rate of population change (λ), annual breeders' survival rate (S_a), the number of female offspring per female per year (F), and the annual rate of juvenile female survival rate from fledging to the next breeding season (S_j). S_j is estimated based on the observed value of λ, or on the assumed value of $\lambda = 1$.

Year	λ	$S_a(\%)$	F	$S_j(\%)$	
				Observed λ	$\lambda = 1$
1999-2000	0.4	33.5	1.7	3.8	38.9
2000-2001	2.2	64.5	1.4	112.7	25.7
2005-2006	1.4	73.6	1.4	46.4	18.5
2006-2007	0.8	35.7	1.5	30.6	44.3
2007-2008	1.1	61.6	1.4	35.1	27.8
mean ± SD	1.2 ± 0.7	53.8 ± 18.1	1.48 ± 0.13	45.7 ± 40.6	31.0 ± 10.4

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