ECOLOGICAL MANAGEMENT OF VOLES;
POPULATION DYNAMICS, REPRODUCTION AND PREDATOR EFFECTS
IN AOMORI ORCHARD

A DISSERTATION
SUBMITTED TO THE UNITED GRADUATE SCHOOL OF
AGRICULTURAL SCIENCES, IWATE UNIVERSITY

IN PARITAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Chie Murano
December 2019

Contact Address

Chie Murano
The United Graduate School of Agricultural Sciences,
Iwate University
Bunkyocho 3, Hirosaki, Aomori, 036-8224 JAPAN

chiemurano116@gmail.com

ii

Abstract

　ハタネズミ *Micr otusmontebelli* は、日本固有で日本に生息する唯一の *Micr otus*属の小型哺乳類であり、青森県をはじめとした寒冷地の農地における主要な哺乳類害獣である。毎年、特に積雪が多い地域においては、積雪期に果樹の幹を食害する。ひどい時には樹を枯死させるため、その被害はかなり深刻であるが、これまで日本の積雪地帯では、ハタネズミの生態調査はほぼ行われてこなかった。ハタネズミの被害防除には、長らく殺鼠剤が利用されてきたが、現在国内の農地で利用可能な殺鼠剤が十分な防除効果を持つとは言い難い一方で、殺鼠剤がネズミの捕食者も含めた農地の生態系に及ぼす悪影響が懸念されており、より環境影響の少ない管理手法が求められている。

世界的にみると *Micr otus* 属はその近縁種が北半球全体に広く分布しており、その生態や個体数動態は比較的よく研究されている生物である。これらの膨大な研究から、これらの小型哺乳類の個体数変動には、周辺の捕食者の種類、同種の生息密度、繁殖生態や積雪等の気象条件が大きな影響を及ぼすことが分かっている。

これらを踏まえ本研究では、より生態学的な個体数管理の手法の確立を目指し、まず青森県の津軽地域におけるハタネズミの年間の基本的な個体数動態と、月ごとの繁殖状況を調査した。個体数動態は、非積雪期の月 1 回程度の個体識別を伴う捕獲再捕獲調査のデータをもとに、Jolly-Seber モデルを基にした階層モデルによって、年間を通した総個体数と生存率、加入率を推定した。さらに、リンゴ園に生息する哺乳類捕食者を自動撮影カメラによってモニタリングし、哺乳類捕食者の出現数がハタネズミの生存率に影響を及ぼすかどうかを検証した。繁殖状況は、月ごとにサンプリングした標本を解剖し、内部観察を行った。さらに、より積極的な生物防除の手法として、ハタネズミを積極的に捕食することで知られるフクロウ *Strix ur. alensis* の誘致実験を行った。人工的に園地にフクロウの巣箱を設置し、営巣地の周辺と営

巣のない農地におけるハタネズミの個体数密度の季節変化の違いを比較し、農地におけるフクロウの繁殖がハタネズミの防除につながるかどうかを検証した。最後に、EU の有機農法における食害防除手法の一つとされる冬季の代替餌供給について、日本のリンゴ園における実行可能性と有効性を検証した。

　本研究の結果、青森県の積雪地である津軽地域において、ハタネズミは春の消雪直後に個体数のピークが表れる、独特の個体数動態を持っていることが示された。この動態は、これまで他地域で行われてきた既存研究のどの個体群のものとも異なるものであった。このユニークな個体数動態が形成される要因として、非積雪期、特に5 月から7月にかけての低い生存率と、冬季の積雪下における高い繁殖率が考えられた。夏までの生存率低下には、捕食者の出現率が有意に影響しており、本研究の農地において、生態系サービスが獣害管理に重要な役割をはたしていることが明らかになった。一方で、本地域のハタネズミは多雪な地域環境に適応した繁殖生態を持ち、安定した積雪がある冬季に最も高い妊娠率を示すことが明らかになった。またそれにより総個体数密度は、2～3 倍に急回復することが示された。これらの個体数動態と繁殖生態を踏まえると、個体数が最も低下する夏から秋にかけての生息密度を把握し、それに基づいて冬季の食害防除計画を立てることが重要であると考えられた。次に、鳥類捕食者であるフクロウの繁殖を誘致する実験によって、周辺農地のハタネズミの個体数密度は 5 月から 11 月にかけて平均 63％減少し、捕食者の誘致がハタネズミの個体数抑制につながることが示された。さらにフクロウは、ハタネズミの生息密度が高い園地を選択的に繁殖場所として利用していることが示唆され、鳥類を利用した害獣管理が、広域的にバランスの取れたハタネズミの個体数抑制につながる可能性が示された。代替餌供給の実験では、青森における一般的な果樹管理によって廃棄される剪定枝を餌資源として利用した。剪定枝の供給によって、半数の園地で食害量を有意に低下させる効果があることが示された。今後、供給場所を改善することで、被害防除効果をより高めることができると考えられる。

　本研究によって、青森県のハタネズミ個体数は多様な捕食者に大きく影響されていることが明らかになった。本研究で得られたデータは、ハタネズミの生態学的管理が十分に可能であることを示している。今後は、フクロウ以外の捕食者効果のより詳細な検証とともに、本研究で得られた生態系サービスによる害獣防除の効果について、地域の理解を深めていく必要があるだろう。また、冬季の被害防除のため、人為的な追加の個体数管理が必要かどうかを判断する判断基準を確立したり、冬季の積雪下でのハタネズミの生態をより詳しく調査し、被害発生のメカニズムを理解したりすることで、生態学的な管理をベースとする、より持続可能な害獣管理手法の確立が可能になるだろう。

Contents

Chapter 1

Introduction

The importance of biological pest control in agroecosystems is increasingly recognised (Bommarco et al., 2013; Chaplin‐Kramer et al., 2011). In 1992, the United Nations Conference on Environment and Development concluded that integrated pest management (IPM), which combines biological control, host plant resistance, and appropriate farming practices while minimising pesticide use, is the best option for sustainable agriculture (UNCED, 1992). Numerous studies on arthropod pests have estimated the effects and economic values of biological pest control services (Barbaro et al., 2017; Losey & Vaughan, 2006; McMurtry & Croft, 1997; Mols & Visser, 2002; Rusch et al., 2016; Thies et al., 2011). However, studies on the biological control of rodent pests causing considerable damage to agriculture and timber production (Paz et al., 2013; Pelz, 2003; Singleton et al., 2010) are still very limited (Labuschagne et al., 2016; Sekercioglu, 2006). Rodenticides are currently the dominant pest control measure, but misuse or overuse of chemicals may cause widespread poisoning of non‐target wildlife, as well as the secondary poisoning of predators (Berny, 2007; Jacquot et al., 2013). Accordingly, more ecologically safe measures are essential to managing rodent pest populations.

My study field is the orchard area in Hirosaki, Aomori prefecture. In orchards, one of the major animal pests which have been frustrating land

managers is a small native rodent, Japanese field vole *Microtus montebelli* (Abe, 2002). Especially at heavy snow area like Hirosaki, land managers have to find many apple trees damaged or even killed by voles following snowmelt every spring. The problem is there is no way to assess or forecast the vole abundance. What land managers can do had been the stopgap measures such as reducing the number of voles with rodenticide and covering all apple tree trunks with protectors to prevent voles debarking. Despite the many decades of vole damages, the biology or ecology of voles in orchards had not been really thought back. There is not even basic information available for land managers, such as mean population abundance or breeding seasons in orchards. This is such a contrast to the story of grey sided vole *Clethryonomys rufocanus*. Grey sided vole is a major pest in Hokkaido forestry and its population had been largely and systematically assessed for few decades resulting in population forecasting model (Nakata et al., 2009, Nakata, 2015). Furthermore, these long-time population dynamics data contributed substantially to rodent population biology (e.g. Saito et al., 1998, Stenseth et al., 2003, Saito et al., 2006).

For effective, sustainable management of pest damage, we need to understand the biology of voles, and we need to be conscious of the ecosystem affecting vole population abundance. What surprised me during my survey was the population abundance of Japanese field vole in Hirosaki seemed to be quite different from any of them known from existing studies. Furthermore, the vole abundance was strongly affected by the ecosystem service more than the artificial management, and the vole abundance was not necessarily proportional to the volume of vole damage. Those surprises made me realized, that they understand the mechanism of vole damage requires several steps; first is to understand the basic biology and population dynamics of voles, then the second is to find out the factors provoking voles to debark fruit tree.

In this thesis, I mainly studied the basic biology and population dynamics of Japanese field vole in Hirosaki, Aomori prefecture. And also, the possibility of population management of voles was explored with an experiment manipulating native predators. The verifications on factors provoking voles to debark are entrusted to the future studies, but the possible candidates of factors are discussed. I hope this study becomes a step for a better understanding of Japanese field voles in an orchard and evolving an

ecological management of voles in orchards.

Chapter 2

Current state; what we know about the vole and its agricultural damage

2.1 The biology of the Japanese field vole

Japanese field vole *Microtus montebelli* is a common and endemic microtine rodent of Japan. Aomori is the northern limit of this species, and Hokkaido does not have this vole (Kaneko 2008). It is nominated as a locally endangered species in more than ten prefectures, especially in Kyushu islands and big cities such as Tokyo, Kanagawa, Aichi, Osaka. There are many studies about basic biology as it had been major rodent pest at all over Japan (Watanabe 1962; Kaneko 1975). However, social biology such as mating system, dispersion or density dependence had barely been investigated for this species. Here, the basic biology of Japanese field vole known from existing studies is summarized.

The Japanese field vole feeds mainly on herbaceous plants and seeds, almost any kinds of plants but mugwort *Artemisia indica* (Watanabe 1962, personal observation). With well-advanced appendix which contains endosymbiotic bacterium, *Microtus* vole can digest cellulose (Stevens & Hume

1988). It is the most extreme herbivory among all rodents inhabit Japan (Iwao et al. 1960).

Japanese field vole population is considered to have only seasonal fluctuation although there are no long-term studies on population dynamics of this species. The studies to estimate the seasonal density of the voles had been facilitated in Iwate (Abe 1974), Kyoto (Kaneko 1976), Fukushima (Kimura et al., 1980) and Kyushu (Arai & Shiraishi 1982). Historically, there are several records of outbreaks in open forests (Udagawa et al. 1956; Ito 1975) and riverbank (Kitahara 1980). Some of those outbreaks had been reported following the simultaneous flowering of bamboo grass, but the correlation has not been scientifically investigated.

The vole reaches its sexual maturity at around 60 - 80 days in captivity (Kaneko 1975; Nakatsu 1977) and the gestation length is 21 days in laboratory observation (Yoshinaga et al. 1997). It takes at least 2 weeks for juveniles to weigh 10 to 15 g and come out of the nests to look for food (Yoshinaga et al. 1997). Considering common vole *Microtus arvalis*, which is most common species in European continent agriculture land, can start reproduction at two weeks after the birth (Hayssen et al. 1993), the fecundity of Japanese field vole is not as explosive.

They are territorial (Kaneko 1975) and their home ranges are approximately 30 m for male and 25 m for female (Odachi et al, 2015), although the home ranges could vary according to the population density of the vole. Physiographically, the vole prefers hollowed, wet low land to convexed dry land. The voles burrow beneath the ground at the depth of 30 to 50 cm, and the burrows have many openings. The diameter of burrows is approximately 3 - 4 cm width in horizontal and 2 – 3 cm width in vertical (Kaneko 1975). In Japan, Japanese shrew-mole *Urotrichus talpoides*, another burrow builder, may inhabit sympatrically. Although the openings of burrows created by shrew-moles usually have a heap of soil around them and can be distinguished from the flat opening created by the voles, Japanese filed vole and Japanese threw-mole can sometimes share their burrows (Kaneko, 1975). Therefore, the number of burrow openings might help to estimate the abundance of voles loosely, but some consideration may be required when the population are to be estimated by the burrow openings method (Liro, 1974).

Japanese field vole is the most dominant rodent species in agriculture

land and open forest in the Tohoku region. Although they damage grains and vegetables, most of agricultural damage by voles in Aomori occurs in orchards (Ministry of Agriculture, Forestry and Fisheries 2019). The vole debarks trees during snow season. The reason for debarking could be the lack of other food resources (Servello et al. 1984). However, the biology of voles under snow have barely been investigated, and the factor inducing the debarking is not scientifically confirmed.

2.2   Existing data and monitoring method

As previously mentioned, there is no long-term data of population dynamics of Japanese field vole in Japan. Instead, as for Aomori, there are two long-term data of agricultural damage caused by voles as far as I know; one is the estimations of yearly economical damage amounts caused by animal pest damage are published by Ministry of Agriculture, Forestry and Fisheries online (e.g. for Tohoku region; http://www.maff.go.jp/tohoku/ seisan/tyozyu/higai/index.html). The other is the rate of damaged tree calculated through sampling survey conducted by Aomori prefecture and Aomori Prefectural Agricultural Pest Control Office.

As for economical damage amount data, the total damage at each prefecture is estimated through the questionnaire to cities. The detail of cost estimation method for Aomori is described in the reports issued by the Department of Agriculture, Forestry, and Fisheries, Aomori Prefecture (2016). The extraordinal damage by rodent pest can be observed occasionally from the estimation (Fig. 2-2-1), this tendency is observed for not only in Aomori prefecture but also other prefectures as well (http://www.maff.go.jp/tohoku/ seisan/tyozyu/higai/index.html). Although this damage amount estimation shows some tendency, it is open to doubt if the reality of rodent pest damage is reflected, as the largest year has more than 100 times larger damage than the mean of the rest of years. Furthermore, the severe rodent pest damages were observed in my study site even in 2015 and 2017 (personal observation),

Agricultural damage estimation in Aomori
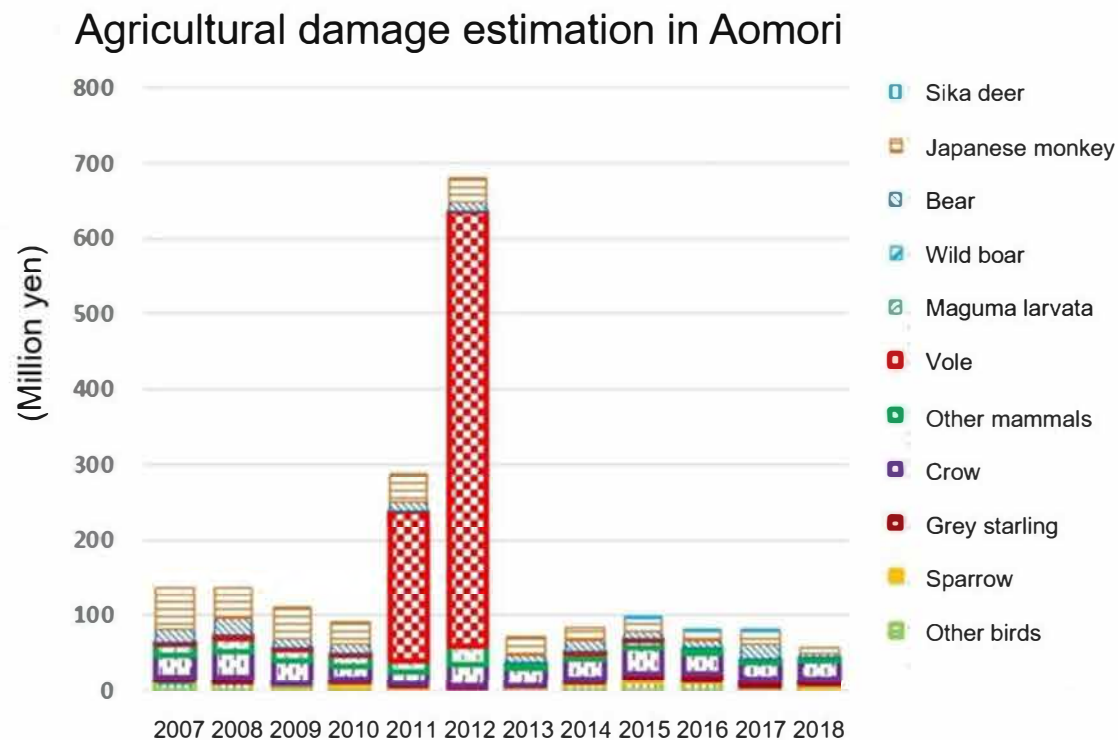
Fig. 2-2-1. Estimated yearly pest damage in Aomori Prefecture. The damage to fruit production consists of 59 % of agricultural damage in Aomori. http://www.maff.go.jp/tohoku/seisan/tyozyu/higai/index.html

but the estimation is almost zero in 2015 and 2017 in this data. The unnaturalness of the data could be partially due to the scheme of how the damage surveys were facilitated. In normal year, the rodent damages are surveyed by the city government with questionnaires to several agricultural organizations and reported to the prefecture. In heavy snow year, the damages caused by voles are surveyed by the prefectural government survey team in conjunction with the snow damage survey. Obviously, there would be differences in assessment criterion and survey efforts between usual year and heavy snow year, with the risk of underestimation of rodent pest damage during small or medium snow year.

The another assessing data is the number and the rate of trees

damaged by voles, reported by Aomori Prefectural Agricultural Pest Control Office. They have surveyed apple tree damages qualitatively by sample surveys since 1988. They split Aomori prefecture into two areas; Tsugaru (east part of Aomori) and Kennan (west part of Aomori), and select sample sites within each area arbitrarily every year (six to 29 survey sites for Tsugaru area and three to five survey sites for Kennnan area). At each survey site, from 50 to 100 apple trees were selected to quantify the damage level (small, medium, large and fatal) for each tree. The percentage of each level was calculated by dividing the number of trees at each level by the total number of trees assessed. The table 2-2-1 and 2-2-2 show the yearly tree damage rates in Tsugaru and Kennan respectively. Generally, the Tsugaru area has a higher rate of vole damage every year. Unfortunately, the damage survey was not facilitated in 2011 and 2012, the years when financial damage was extraordinal.

Fig. 2-2-2 shows the comparison of two data; the total rate of damaged trees in the Tsugaru area and the estimation of damage cost. Although there are some similarities between two data (e.g. relatively high in 2005, and almost no damage in 2007), they are far from linked. I do not have information for making a decision which is more reliable, although the data from Aomori pest control centre seems to be closer to the impression through my fieldwork from 2015 to 2019.　What we can learn from those two data is almost 10% of trees on average get some kind of vole damages every year, and once the conditions go right (Table 2-2-1), the damage could become extreme high (Fig 2-2-1).

The difficulty of analysing the damage data is the financial cost of a certain area of vole damage can be largely different depending on the vulnerability of apple trees. For example, the area voles must debark to kill an apple tree with 50 cm diameter is ten times larger than the one with 5 cm diameter tree. Even there was the same number of voles, debarking the same amount of tree barks, many more trees face the risk to be killed when there were skinnier trees in orchards. Furthermore, Shimada (2018) pointed that Japanese field vole has a clear preference for the JM7 cultivar which is most widely selected rootstock for dwarfed apple tree production. Generally, dwarf trees stay small diameter and replacement cycles are shorter. Recently, the production with dwarfed trees is increasing according to the promotion by the national government. The change of cultivation method should also be taken

into consideration when we look at the yearly change of financial damage amount. If the quantitative information, such as the quantity of area debarked by voles, was recorded on top of the damage level, it would be more informative to grasp the reality of damage.

Table 2-2-1. The rate of apple tree damaged by rodent pest in Tsugaru area, assessed by Aomori pest control centre. The orchards for assessment were selected arbitrarily and the number of assessment sites varies from six to ten. At each orchard, approximately 50 to 100 trees were assessed to calculate the damage rate. Each tree damage was classified into five categories (Fatal; tree trunk is debarked around and unrecoverable, Large; trunk and main branches are partially debarked resulting in large yield reduction, Medium; branches are partially debarked resulting in some yield reduction, Small; trunk or branches are slightly debarked not resulting in yield reduction, None; no damage).

Tsugaru	Damage rate(%)					Total rate of damaged trees (%)	Data Source
	Fetal	Large	Medium	Small	None		
1988	2.0	0.3	2.2	4.3	91.2	8.8	a
1989	0	0.6	0.7	2.0	96.7	3.3	a
1990	0	0	0	1.7	98.3	1.7	a
1991	–	–	–	–	–	–	a
1992	–	–	–	–	–	–	a
1993	–	–	–	–	–	–	b
1994	–	–	–	–	–	–	b
1995	–	–	–	–	–	–	b
1996	1.9	1.1	2.0	6.3	88.8	11.2	b
1997	–	–	–	–	–	–	b
1998	–	–	–	–	–	–	b
1999	0	0.8	1.4	13.9	84.0	16.1	b
2000	1.5	1.8	3.2	6.9	86.6	13.4	b
2001	1.2	2.2	2.4	3.9	90.3	9.7	b
2002	0	0.2	1.3	4.2	94.3	6.1	b
2003	0	0.2	1.4	2.4	96.1	4.8	b
2004	0	0.1	1.2	3.4	95.4	4.6	b
2005	0	1.4	5.8	12.6	80.2	19.8	b
2006	0.3	0.4	2.1	6.6	90.7	9.3	b
2007	0	0	0	0.1	99.9	0.1	b
2008	0	0	0.8	5.3	93.9	6.1	b
2009	0.4	1.2	1.6	3.3	93.5	6.5	b
2010	0.1	0.2	1.6	4.3	93.8	6.2	b
2011	0	0.0	0	7.5	92.5	7.5	c
2012	–	–	–	–	–	–	c
2013	–	–	–	–	–	–	c
2014	0.8	3.3	1.2	12.5	82.2	17.8	c
2015	0	1.4	0	27.9	70.7	29.3	c
2016	0	0.2	0.1	5.3	94.4	5.6	c
2017	0	2.5	3.7	37.5	56.3	43.7	c
2018	0	0.4	1.0	20.9	77.7	22.3	c

Table 2-2-2. The rate of apple tree damaged by rodent pest in Kennan area, assessed by Aomori pest control centre.

| Kennan	Damage rate(%)					Total rate of damaged trees (%)	Data Source
	Fetal	Large	Medium	Small	None		
1988	0	0	0	0	100	0	a
1989	0	0	0	0	100	0	a
1990	0	0	0	0	100	0	a
1991	—	—	—	—	—	—	a
1992	—	—	—	—	—	—	a
1993	—	—	—	—	—	—	b
1994	—	—	—	—	—	—	b
1995	—	—	—	—	—	—	b
1996	0	0	0	0	100	0	b
1997	—	—	—	—	—	—	b
1998	0	0	0	1.0	99.0	1.0	b
1999	0	0	0	0.3	99.7	0.3	b
2000	0	0	0	0	100	0	b
2001	0	0	0	0	100	0	b
2002	0	0	0	0	100	0	b
2003	0	0	0	5.0	95.0	5.0	b
2004	0	0	0	0	100	0	b
2005	0	0	0	0	100	0	b
2006	0	0	0	2.8	97.2	2.8	b
2007	0	0	0	0	100	0	b
2008	0	0	0.3	0	99.7	0.3	b
2009	1.1	1.0	1.9	2.7	93.3	6.7	b
2010	0	0	0	0	100	0	b
2011	0	0	0	0	100	0	c
2012	—	—	—	—	—	—	c
2013	—	—	—	—	—	—	c
2014	0	0	0	2.8	97.2	2.8	c
2015	0	0	0	0	100	0	c
2016	0	0	0	0.8	99.2	0.8	c
2017	0	0	0	0	100	0	c
2018	0	0	0	0	100	0	c

* Alphabets in data source indicate as follow;

     a: 有害動植物発生予察事業結果書 (Aomori Prefecture)

     b: 有害動植物発生予察事業年報 (Aomori Prefecture)

     c: 有害動植物発生予察事業年報 (Aomori Prefectural Agricultural Pest Control Office)

Fig. 2-2-2. The total ratio of damaged tree in Tsugaru area (bars), in comparison with the economical estimation (grey line).
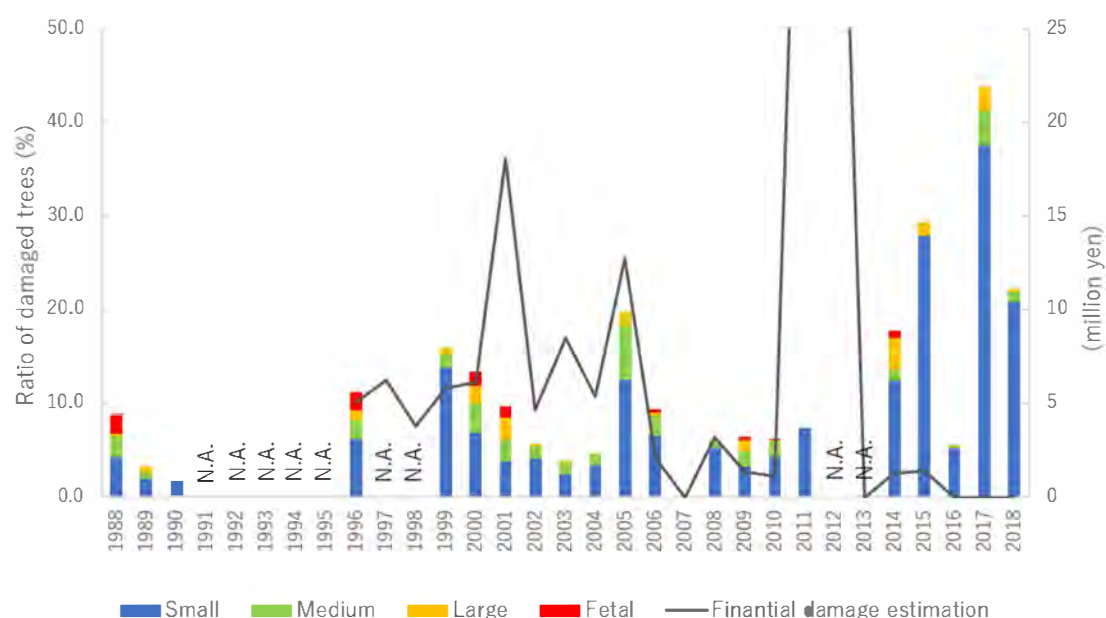
2.3　Overview of my study site

The study site is the orchard area in the south-west of Hirosaki (40° 36′ N, 140° 27′ E), Aomori prefecture. Hirosaki city is located in the flat low land in Tsugaru basin, and the gentle hill slopes surrounding the flat area. Most of those hilly areas is used as apple orchards. The mountains around the orchard area are covered with a mixed plantation of Japanese cedar Cryptomeria japonica and natural forest which consists of mainly Japanese beech *Fagus crenata*, Japanese oak *Quercus crispula*, and Japanese red pine *Pinus densiflora*. The mean temperatures in Hirosaki is 10.2°C, and the mean maximum snow depth is 83 cm. Snowfall occurs from December to March.

Fig. 2-3-1 The location of study site and the land use.
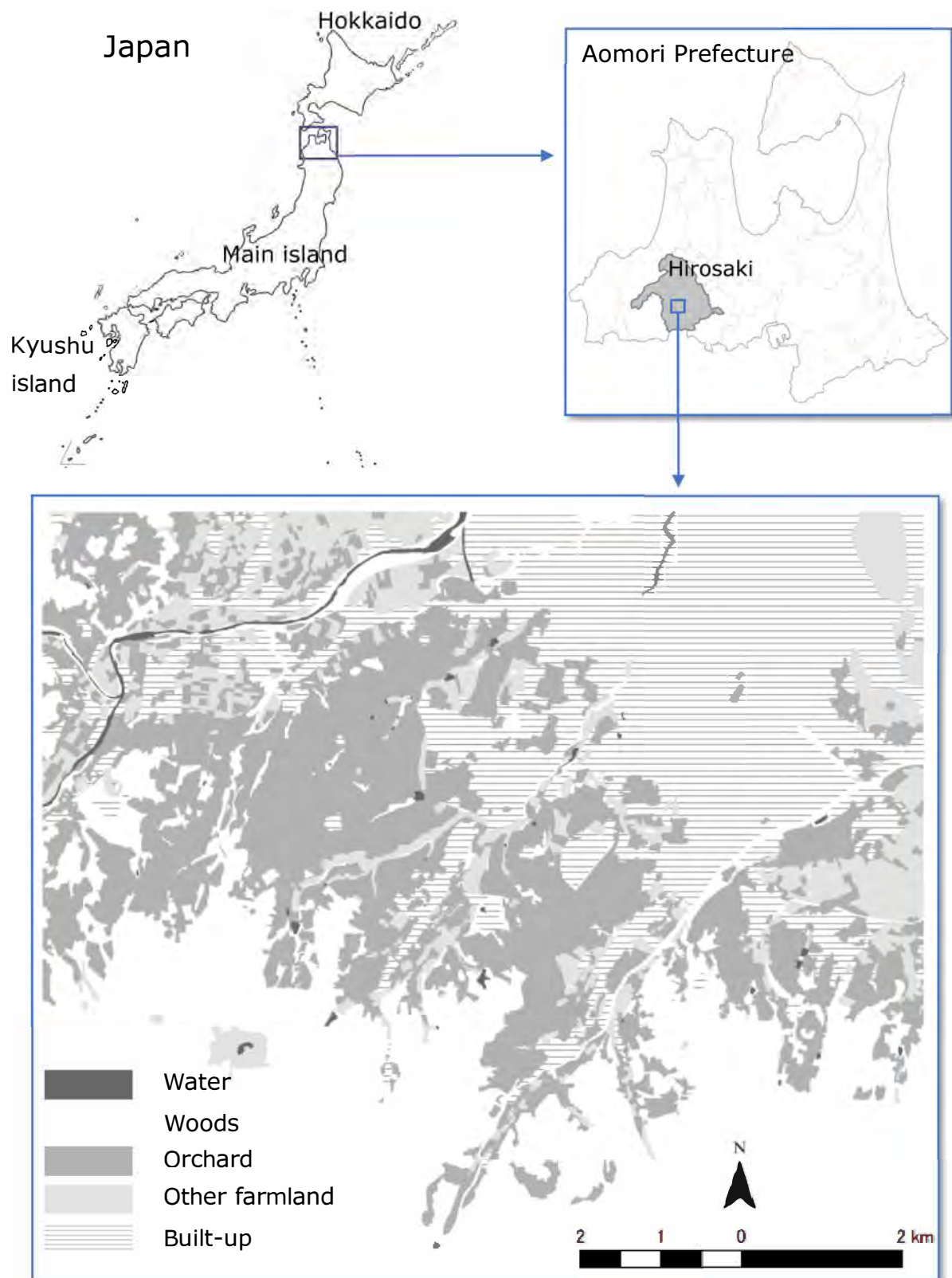
Chapter 3

Seasonal population dynamics of Japanese field vole in orchards

3.1 Introduction

It is necessary to understand rodent population dynamics to manage their populations and decrease the amount of agricultural damage rodents cause. Studies of rodent populations have been performed since the early 20th century. These studies suggest that extrinsic processes, such as food availability and predation (e.g., Hanski et al., 1991; Hanski et al., 2001), and intrinsic processes caused by predator–prey interactions, such as physiological or behavioural changes (Lima, 1998; Prevedello et al., 2013; Vibe‐Petersen et al., 2006), help determine rodent population dynamics. Studies in Fennoscandia have shown that generalist predators can reduce rodent population oscillations as well as their reproductive rates (Klemola et al., 2002; Salo et al., 2010; Sundell, 2006). Although these studies were performed in a boreal region, similar population dynamics may apply in other regions.

Capture-recapture survey and Jolly-Seber model are the golden

standard method to estimate wildlife abundance, survival probability, and detection (capture) probability in open population. In heavy snow region as Hirosaki, it is not easy to conduct capture-recapture survey by a constant interval throughout a year because of the accessibility to the trapping site during winter and the seasonal change of ground cover condition. Hierarchical model (Royle & Dorazio 2008) that are composed from ecological process model and observation model make it possible to estimate targeting parameters under such irregular and incomplete observation.

In this study, we investigate the seasonal population abundance of Japanese field vole inhabiting snowy area and estimate the recruit and survival. Comparing the result to the data from previous studies in similar air temperature but different snow condition, we aim to extract the effect of snow on population dynamics of Japanese field vole.

3.2   Materials and Methods

3.2.1   Study site and trapping design

The study site is located within the hilly terrain of apple orchards surrounding Hirosaki city (40°36′ N, 146°27′ E), Aomori prefecture, Japan (Fig. 3-2-1). Aomori is the most northern prefecture of Honshu, located to the south of Hokkaido Island. The west side of Aomori prefecture including Hirosaki has annual heavy snowfall accumulation. The mean monthly air temperatures and the recorded snow depths from 2016 to 2019 of Hirosaki, are shown Fig. 3-2-2A and Fig. 3-2-2B. The elevation of the study site varies between 93-154 m.

At the study site, six open quadrats (five quadrats of 50 m × 50 m and one quadrat of 50 m × 30 m) were measured off within six arbitrarily chosen orchards (Fig. 3-2-1). All quadrats were a minimum of 200 m apart from known Ural owl nests, to avoid owl's overwhelming negative influence on the vole population during the owl's breeding season (Murano et al. 2018).
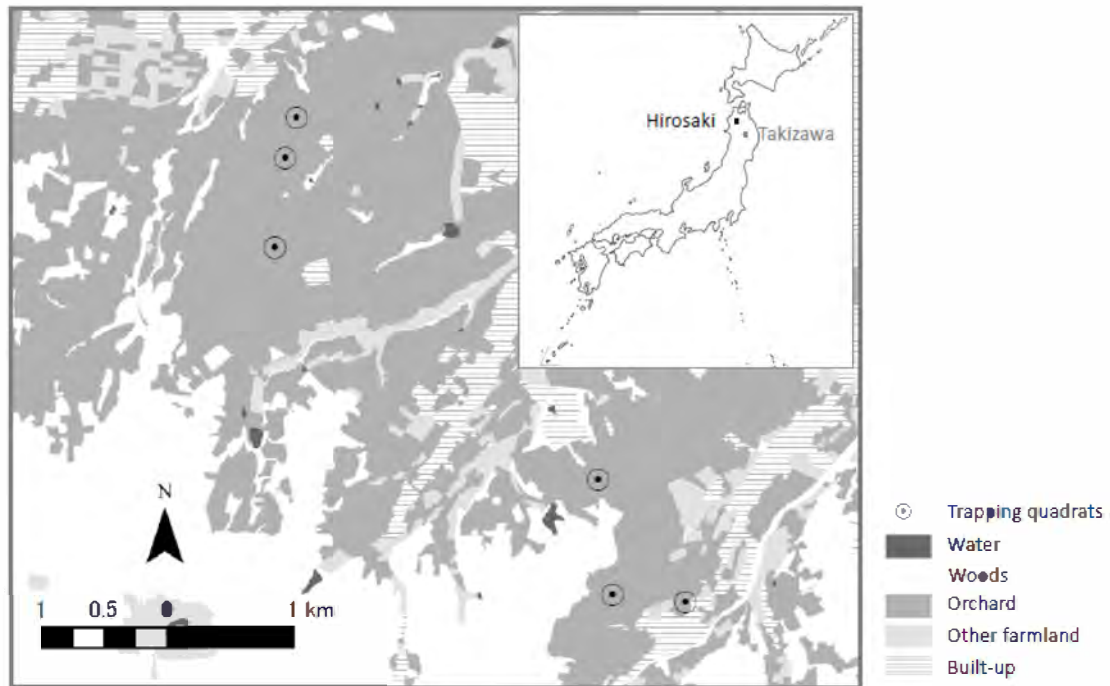
Fig. 3-2-1 The locations of study site (Hirosaki) and the trapping sites. The location of Takizawa where existing study by Abe (1974) was facilitated is also shown in country map.

Fifty live-traps (27 × 7 × 9 cm; Hokkaido Forest Management Corporation, Japan) within five quadrats and thirty live-traps within one smaller quadrat were set near vole ground burrow openings over three consecutive nights. The live-trap surveys were undertaken between April 2017 and May 2019 with regular surveys conducted monthly excluding the periods with snow cover (December to March). Sunflower seeds were used as bait and traps were stuffed with loose cotton as insulation to prevent vole death from cold. Traps were set in the evening and checked twice daily over three consecutive days in the morning after sunrise and the evening before sunset. Captured voles were numbered with ear tags, and the sex and weight of each vole were recorded.

During January and February of 2019, additional live-trappings were conducted to measure the breeding rates under snow cover. For this survey, live-trappings were conducted in three quadrats only; the other quadrats would become inaccessible during mid-winter because of snow. Thirty vole
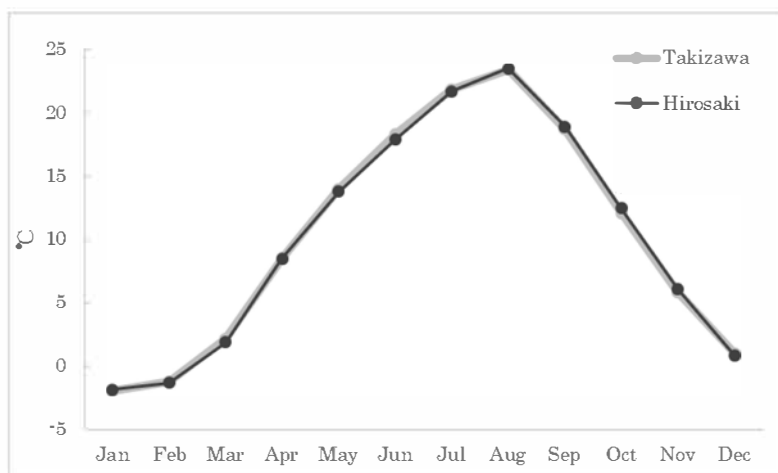
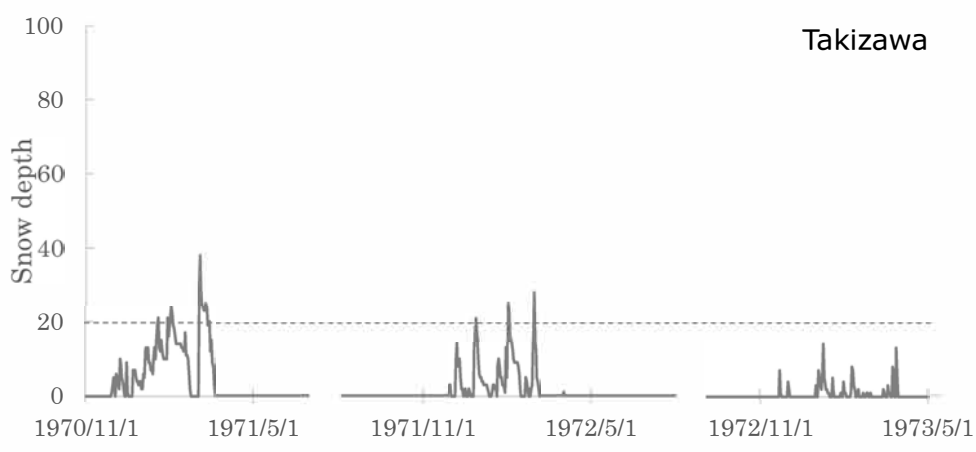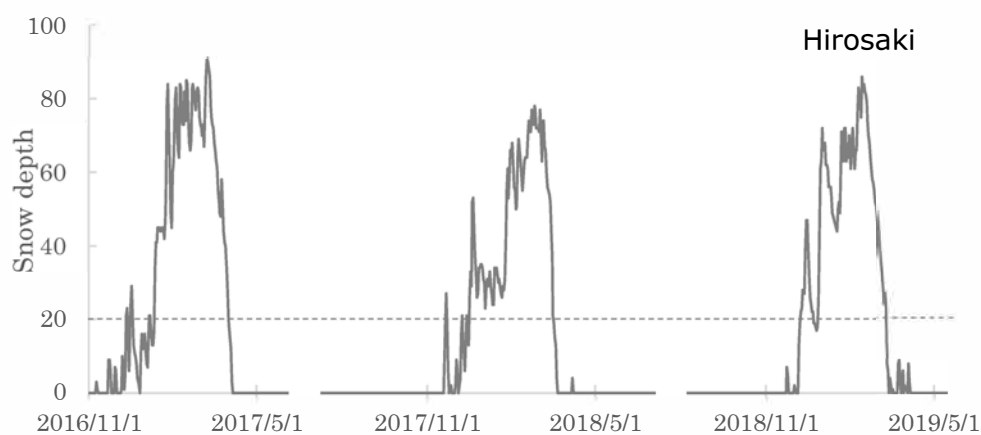Fig.3-2-2A   Monthly mean air temperature in Hirosaki, in comparison with the on in Takizawa

Fig.3-2-2B Snow depth in Hirosaki (2016 November - 2019 May) and Takizawa (1970 November – 1973 May)

burrow openings within three orchards were covered with chimneys before the start of snow season, and a live-trap was set in each chimney for one to three nights in mid-January and mid-February. The breeding status of female voles is determined visually, as advanced pregnancy is recognizable by a bellied abdominal and lactation status is by prominent mamillae.

3.2.2   Study animal

The Japanese field vole is common, endemic, and the only *Microtus* rodent in Japan. Aomori prefecture is the most northern prefecture in Honshu island, and the northern limit of the species (Kaneko 2008). The Japanese field vole is territorial (Kaneko 1975) with a home range of approximately 20 m × 20 m within an agriculture field (Abe 2002). This vole feeds primarily on herbaceous plants, but during winter snow cover season it may feed on the bark of orchard trees. In Aomori prefecture, this vole is a prevalent pest within apple orchards (Abe 2002). Although several population outbreaks are on record (e.g. Ito, 1975; Kitahara, 1980), multiannual fluctuations in populations have yet to be recorded. The Japanese field vole reaches sexual maturity within 60 - 80 days in captivity (Kaneko 1975; Nakatsu 1977) and has a gestation period is 21 days (Yoshinaga et al. 1997). Within 14 days after birth, when juveniles reach a weight of 10 - 15 g juvenile voles will begin foraging for food (Yoshinaga et al. 1997). A mature female vole weighs at least 22 g, and a mature male vole weighs at least 25 g, observed in Aomori prefecture (Murano, unpublished).

3.2.3   Predator survey

The mammalian predators whose territories include the study site are all generalists predators; The Japanese Red Fox Vulpes vulpes japonica, domestic cat Felis silvestris catus and the Japanese marten Martes melampus. Although the study area is within the territory of Least weasel Mustela nivalis, it is designated as a near threatened species in the region (Ministry of

Environment, 2019), and none were detected during our survey either by live-traps nor sensor cameras. The avian predators whose territories include the study site include the Ural owl *Strix uralensis* and the Eastern buzzard *Buteo japonicus* also generalist predators. In order to count the number of predators visiting the quadrats, sensor cameras (Ltl-6210MC; Ltl Acorn, China) were employed in each quadrat from May to November, two cameras per quadrat. The sensors cameras were relocated every four weeks to random locations within the quadrats in order to maximize coverage. Cameras were set with 30 seconds delay interval between triggers to avoid multiple triggers by a single animal pass. For each vole survey, the numbers of animals captured by cameras and tallied by species.

3.2.4   Statistical Analysis

We estimated the abundance, survival probability, and entry of voles by Jolly-Seber model (Jolly 1965, Seber 1965) based on the capture-recapture survey method. Amongst the methods in which the Jolly-Seber model may be implemented, we adopted the super population approach (Williams et al. 2002) implemented as a hierarchical model (Kéry and Schaub 2012).

The hierarchical model is composed of a process model and an observation model; firstly, we explain the process model. The survival probability model of each field and survey timing is as below.

$$mean\_phi \sim N(0, 10^3)$$
$$logit\_phi_{f,1} \sim N(mean\_phi, \sigma^2_{field})$$
$$logit\_phi_{f,t} \sim N(logit\_phi_{f,t-1}, \sigma^2_{transition})$$
$$phi\_day_{f,t} = \frac{1}{1 + \exp\left(-logit\_phi_{f,t}\right)}$$

$$\varphi_{f,t} = phi\_day_{f,t}^{Interval_{f,t}}$$

mean_phi is the mean daily survival probability in a logit scale, $logit\_phi_{f,t}$ is the daily survival probability of *f*th field and *t*th survey interval in a logit scale, σ_{field} and $\sigma_{transition}$ are the standard deviation of Normal distribution, $Interval_{f,t}$ is the survey interval between *t*th survey and *t*-1th survey, $\varphi_{f,t}$ is the survival probability

of fth field and tth survey. Because the survey interval differed in each field and survey timing, we firstly modeled the daily survival probability and powered the daily survival probability by the survey interval. It should be noted that we cannot distinguish the mortality of vole and eternal emigration of vole. Then, the survival probability of our model is the mixture of them. Prior distributions of σ_{field} and $\sigma_{transition}$ are a vague uniform distribution U(0, 100) (Gelman 2006).

The model about the entry (recruitment or immigration from outside of target population) probability of vole is as below.

$$b_t \sim \text{Dirichlet}(\boldsymbol{\alpha})$$

$$\eta_1 = b_1, \eta_2 = \frac{b_2}{1 - b_1}, \cdots, \eta_t = \frac{b_t}{1 - \sum_{i=1}^{t-1} b_i}$$

b_t is the entry probability of tth survey, $\boldsymbol{a}$ = [a_1, a_2, …, a_t] is the parameter of Dirichlet distribution, and η_t is the conditional entry probability of tth survey. In this case, each component of $\boldsymbol{a}$ was set as 1 (a non-informative prior distribution).

By using the survival probability and the conditional entry probability, we can model the survival and entry of each vole in each survey timing as below.

$$z_{i,1} \sim \text{Bernoulli}(\eta_1)$$

$$z_{i,t}|z_{i,t-1}, \cdots, z_{i,1} \sim \text{Bernoulli}\left(z_{i,t-1}\varphi_{f,t-1} + \eta_t \prod_{k=1}^{t-1}(1 - z_{i,k})\right)$$

$z_{i,t}$ is the latent variable about the existence or absence of ith individual in tth survey in the target population. The second equation indicate that the existence or absence of ith individual in tth survey is determined by the survival of ith individual ($\varphi_{f,t-1}$) that existed in the target population in the previous survey timing ($z_{i,t-1}$) and the products of absence probability until t-1th survey ($\prod_{k=1}^{t-1}(1 - z_{i,k})$) and the entry probability in tth survey (η_t).

Next, we will explain the observation model. The model about detection probability is as below.

$$\text{mean\_p} \sim N(0, 10^3)$$

$$\text{logit\_p}_t \sim N(\text{mean\_p}, \sigma_p^2)$$

$$p_t = \frac{1}{1 + \exp(-\text{logit\_p}_t)}$$

mean_p is the mean detection probability in a logit scale, logit_p$_t$ is the detection probability of tth survey in a logit scale, σ_p is the standard deviation of Normal distribution, and p_t is the detection probability of tth survey. Because we expect that the detection probability will differ depending on the presence/absence of vegetation, we divided the survey timing by season (i.e., December to April or

May to November). Prior distributions of σ_{p} is a vague uniform distribution U(0, 100) (Gelman 2006).

As the precise detection of voles is not possible, we account for the potential quantity of voles which were undetected to estimate population abundance through the use of "parameter-expanded data augmentation (PX-DA)" technique (Royle et al. 2007). PX-DA consists of two components: (1) adding an arbitrary number of zeros to the data set and (2) analysing a reparameterized version of the original model. Let's assume that n is the number of marked voles, N is the latent population abundance, and M is the augmented data size. The relationship among them is $n < N < M$ and $N = \psi M$, while ψ is the inclusion probability. Then, the data with zeros added to the original data should be larger enough than N. The zeros can be divided into two components: i.e., a "existed" but unmarked vole or a vole that never exist in practice. The sum of n and the number of "existed" but unmarked vole is the estimator of N. With the augmented data, the estimation of latent state of M voles can be modelled as below.

$$\omega_i \sim \text{Bernoulli}(\psi)$$

ω_i is the latent variable about the existence (1) or absence (0) of ith individual in the target population during the whole survey and ψ is the inclusion probability as stated above.

By using the above parameters, we can model the observed data including the added zeros as below.

$$y_{i,t}|z_{i,t} \sim \text{Bernoulli}(\omega_i z_{i,t} p_t)$$

$y_{i,t}$ is the detection (1) or non-detection (0) of ith vole in tth survey.

Estimation of the posterior distribution of the model was conducted by the Markov chain Monte Carlo (MCMC) method that was implemented by R (R Core Team 2018), JAGS (Plummer 2003), and the package "rjags" (Plummer 2018) of R (R Core Team 2018). We ran three parallel MCMC chains and retained 100000 iterations after an initial burn-in of 30000 iterations. We thinned the sampled values to 1% (i.e., obtained 1000 samples as posterior distributions for each chain). MCMC sampling was considered to be converged when the "R hat" value became < 1.1 (Gelman et al. 2004).

Furthermore, we examined the effect of mammal predator abundance on the daily survival probability (phi_day$_{f,t}$) by a generalized linear model (GLMM) with beta error structure. Although it is better to examine the effect directly in the above hierarchical model, we evaluated the number of photographed mammal predators by sensor camera and we could not set the camera traps

during winter because of heavy snow in our study site. Then, the camera data is lack for some survey timing. The response variable is phi_day$_{f,t}$ and the explanatory variable is the sum of photographed mammal predator (i.e., the total number of photographs of red foxes, domestic cats, and Japanese marten as stated above) per day. Each field and survey timing were included as random effects. We estimated the parameters of GLMM by the "glmmTMB" package (Brooks et al., 2017) of software R (R Core Team, 2018). We evaluated the significance of the estimated coefficient by the Wald X^2 test.

3.3　Result

During the survey period, we captured and tagged 596 voles (14280 trap-nights). The estimated total vole abundance (N) with a 95% credible interval was 1124 (1061-1314) (Fig. 3-3-1). The augmented data size (M=1788) was much larger than the total abundance, indicating that the number of added zeros for data expansion was sufficient. Additionally, the estimated detection probability with green vegetation (May to November) was slightly lower than that without green vegetation (December to April) (Fig. 3-3-2). The estimated abundance was 1.9 times the number of real captures.

The estimated population size (Fig. 3-3-3) showed the yearly peaking in April following snowmelt and decreasing from May to July. During winter snow cover, the population recovered to double or triple of the population level in November. The result indicated higher entries of new individuals in May, June, August and during winter snow season. The weights of trapped voles at each survey are shown in Table 3-3-1. The juveniles weighing less than 15 g were observed primarily during June and October, while very few juveniles were captured in April and May (Table 3-3-1), though the appearance of juvenile does vary seasonally.

The estimated daily survival probabilities during with snow cover were relatively high compared to the probabilities during without snow cover (April to November), particularly notable is the difference in 2017 (Fig. 3-3-4). The lowest survival rates were observed in May or June. The mammalian predators had a significant adverse effect on the survival rate of voles (Table

3-3-2, Fig. 3-3-5). The number of avian predators captured on camera was limited; hence any influence by avian predators on the vole population or survival rate could not be identified.

The breeding status of live-trapped voles under snow cover during January and February is shown in Table 3. Over 60 per cent of the females were found to be in an advanced stage of pregnancy during January and February.
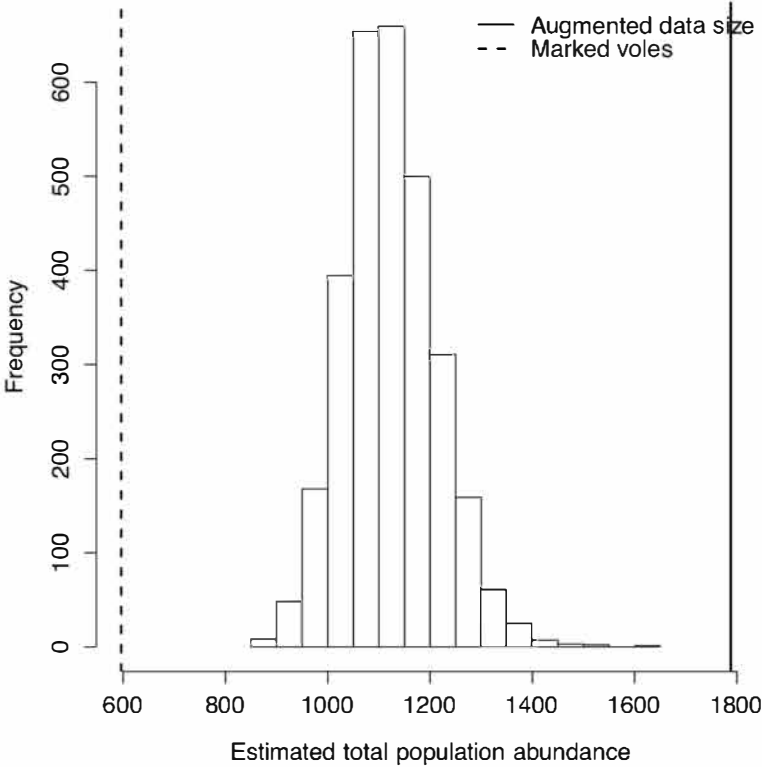

Fig. 3-3-1 Posterior of estimated total abundance in relation to the number of marked voles and the augmented data size
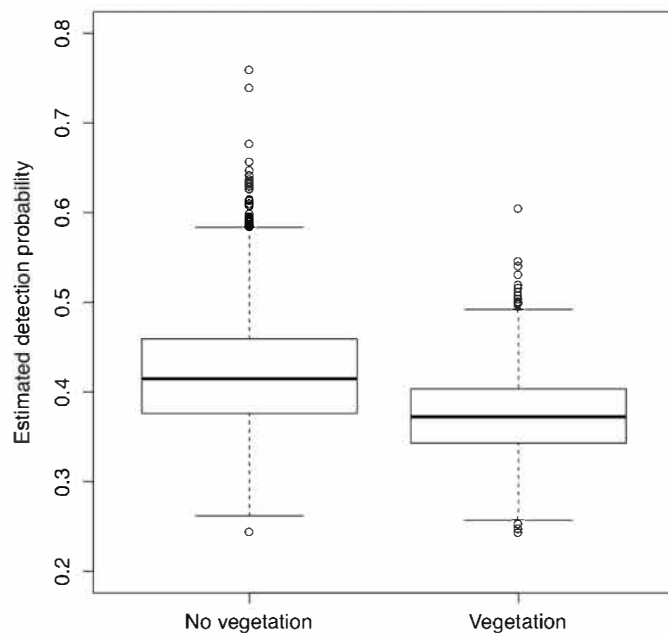
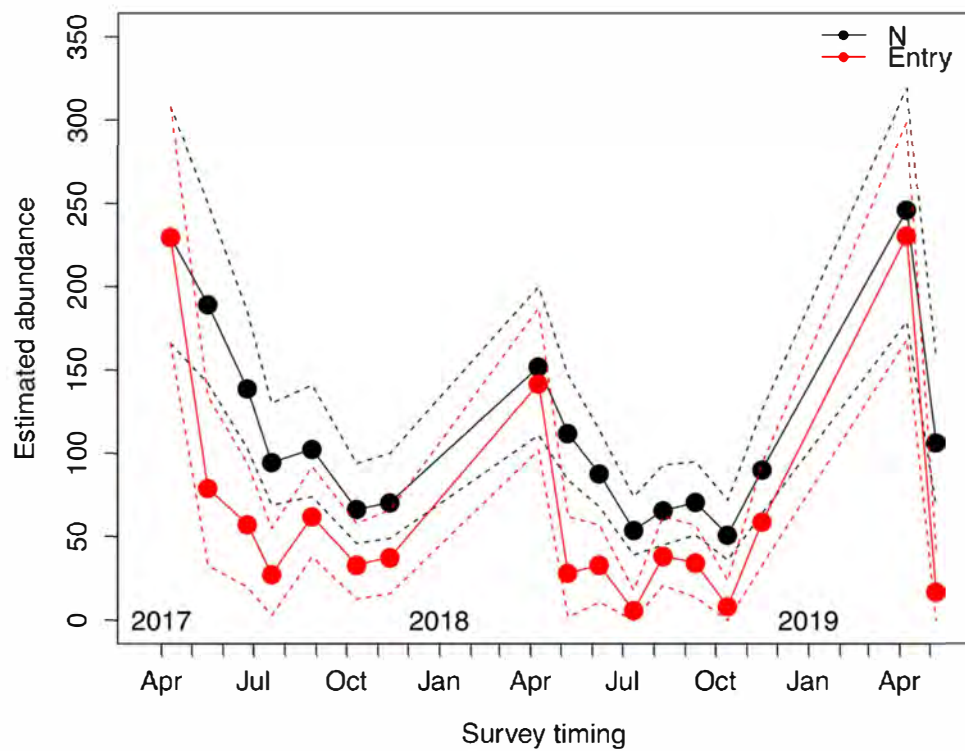Fig. 3-3-2 Boxplot of posterior samples about detection probability

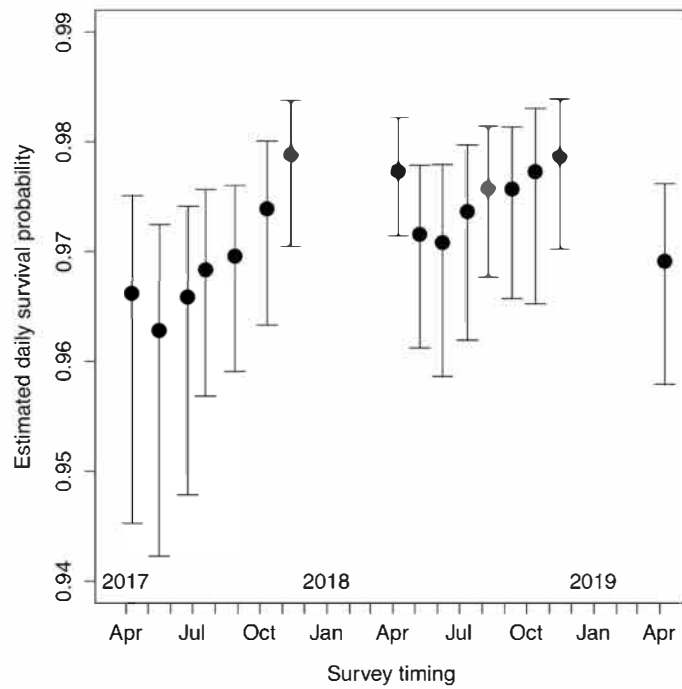Fig.3-3-3 Estimated seasonal abundance of vole in Hirosaki.

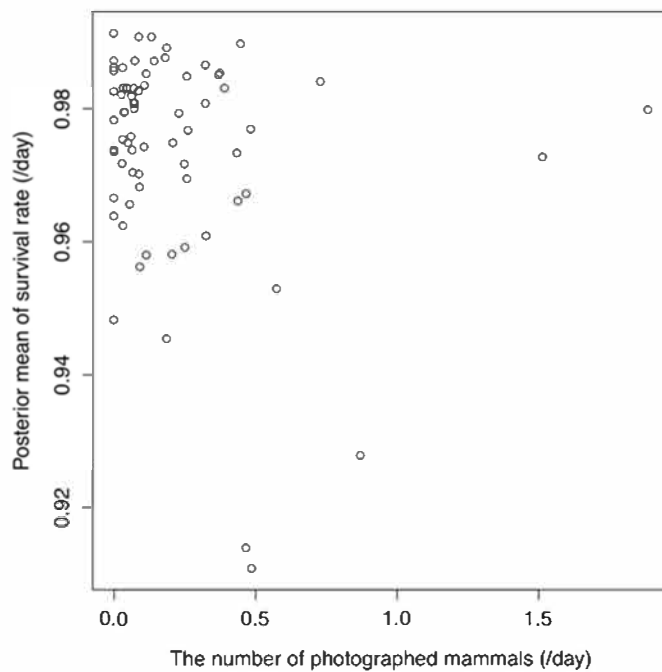Fig. 3-3-4 Seasonal dynamics of estimated daily survival probability

Fig. 3-3-5 The relationship between the estimated daily survival probability and the number of photographed mammal predators

Weight (g)	2017							2018								2019	
	April	May	June	July	August	October	November	April	May	June	July	August	September	October	November	April	May
35 <	20	15	9	5	8	1	4	15	16	12	8	3	3	2	9	21	7
25 - 35	49	49	22	17	21	8	10	35	24	12	5	9	19	7	18	57	20
15 - 25	25	8	14	8	8	6	10	15	1	10	4	8	2	3	8	23	10
< 15	1	0	8	5	1	8	3	2	1	5	0	2	1	3	2	3	0
Total	95	72	53	35	38	23	27	67	42	39	17	22	25	15	37	104	37

Table 3-3-1 Monthly body weight distribution of voles trapped.

Table 3-3-2 Summary of GLMM about the effect of mammal predator on the estimated daily survival probability

| | Estimated coefficient | | | |
	Mean	SE*	z value	*p* value
Intercept	3.737	0.119	31.419	0.000
Photographed mammal predators (/day)	-0.388	0.166	-2.329	0.020

* SE is standard error of estimated coefficients.

Table 3-3-3 Result of live-trapping and the breeding rate of voles in January and February.

| | 2019 | |
	January	February
Number of captured Males	14	7
Number of captured females	10	12
Matured female (>22g)	9	11
Females in later pregnancy	6	8
Pregnancy rate	0.67	0.73

3.4   Discussion

The study results highlight two prominent observations: Firstly, the substantial increase in population during winter snow cover, and secondly the decrease in population following snowmelt (Table 3-3-1).

3.4.1   Population increase and breeding

Some species of *Microtus* are known to breed under snow cover occasionally subject to food supplies (e.g. Tast & Kaukusalo, 1976; Norrdahl & Korpimaki

2002) and heavy snowfalls (Beer & MacLeod 1961). Though these observations were sporadic, hence considered a minor influence as the proportion of breeding females observed was low (Norrdahl & Korpimaki 2002).

In our study, the population increase over winter was primarily due to a large number of new entry (Table 3-3-1), which most likely correlate with breeding during January and February (Table 3-3-3). Our findings indicate that under certain abiotic conditions, *Microtus* breeding under snow cover can influence population dynamics. Observations revealed that it was only during winter snow cover that a substantial increase in population occurred.

The two existing studies reported that the breeding of Japanese fields vole ceased during winter. One of the studies was conducted within pastureland in Takizawa (39°45' N, 140°56' E) (Abe 1974) (Fig. 3-2-1), located on the east side of Honshu. The air temperatures are similar to Hirosaki (Fig. 3-2-2A) but the annual snow accumulations are much less and lacking persistent winter snow cover. The snow depths recorded at around Abe's study period (1972) are shown in Fig 3-2-2B. The climate data is from the City of Morioka observatory, closest to Takizawa. In Takizawa, vole population abundance peaks in June, and breeding ceases from January to March (Abe 1974). The other study was conducted within a grassy field in Yatsugatake (36°06' N, 138°14' E) (Miyao, 1966) (Fig. 3-2-1). Yatsugatake, located at a high elevation (1400 - 1500 m), with a mean temperature lower than Hirosaki (Fig. 3-2-2A). While the study lacks data on snow depth, the mean precipitation from December to February between 2007 and 2017 was approximately 10 % less than Takizawa's; we extrapolate that the depths of snow cover in Yatsugatake may be similar or less than Takizawa. In Yatsugatake, the vole population was lowest in April and increases during spring breeding season with a peak in August and no breeding activity between December to April. In contrast, within our study site, the Japanese field vole did breed during winter, under snow cover.

The effect of snow accumulation on the subnivean conditions have been discussed in the field of soil physics. Higashi (1954) estimated the depth in which soil freezes with the relationship to the depth of accumulated snow cover physically. Inferring with an approximation formula that the freezing depth of soil was proportional to the square root of the accumulated freezing index, he calculated that the soil freezing would cease progressing with 15

cm snow cover in the climate of Hokkaido. This result was confirmed by Ishikawa and Suzuki (1964) by field measurements. Decker et al. (2003) also reported that with a snow depth of 20 cm or more, that snow cover provided an insulating effect as observed in Northern Vermont, United States. In cool-temperate climate regions, snow depth of 15 - 20 cm is sufficient depth to provide an insulating effect to prevent the ground from freezing, and the temperature in subnivean environment should be kept slightly above 0 ℃ degreed. Snow covers insulating effect would also help to prevent freezing of ground vegetation, which subsequently prolongs the food supply for voles. We believe these factors contribute to promoting the intensive breeding of voles under snow cover.

It is also notable that the breeding ceases following spring snowmelt (Table 3-3-1). The first four or five weeks immediately following snowmelt, the absence of widespread vegetation cover can be critical as vole survival rates decrease because of limited food supply and the exposure to predators. The very high pregnancy rate under snow cover (Table 3-3-3) may be an instinctive survival investment to offset population decrease after snowmelt.

A higher number of juvenile voles weighing less than 15 g were captured in June and October (Table 3-3-1), these were most likely born on the study site. Few juveniles were captured during April and May (Table 3-3-1). The new entries captured in May were likely due to migration of sub-adult voles.

3.4.2   Population decline and predators

Another notable aspect of our study findings is the decrease in population between April to July. In previous studies in Takizawa (Abe 1974) and Yatsugatake (Miyao 1966), populations increased between April to June. At our study site, the survival rates were relatively low from May to July and highest during winter snow cover (December to March) (Fig. 3-3-4), with the decrease of the population during the optimum breeding season in June. The low survival rate without snow cover can be explained by the number of medium-sized mammalian predators, which were photographed by sensor cameras (Table 3-3-2, Fig. 3-3-5). The practice of routine vegetation

management (grass cutting) employed within orchards contribute to the predator effect by limiting the height of ground vegetation; making small rodents are more easily detected and preyed upon by predators. Our findings indicate that predation by medium-sized mammals does influence the vole population dynamics in agriculture fields. Regrettably, the presence of avian predators within the study site was beyond the camera's detection capacity, such that we could not attribute any noticeable effect to avian predators. Our findings indicate that the difference in vole's survival rates during periods with snow cover and without can be considered as an ecosystem service by terrestrial predators in the study site.

The highest survival rates observed during snow cover (Fig. 3-3-4) would confirm the common understanding that the snow cover does provide protective cover for small mammals inhabiting the subnivean space from the terrestrial and avian predators (Hansson and Henttonen 1985; Duchesne et al. 2011). During our study in Hirosaki, snow depths between 20 – 90 cm were recorded in January and February; this is likely sufficient depth to reduce predation. Within the study site, the risk of predation by least weasels, which is the only major predator of small mammals within the subnivean, was considered insignificant due to the low population density of Least weasel in the region (Ministry of the Environment 2019). Huitu et al. (2003) revealed in experiments with *Microtus agrestis* that the vole population did increase up to its maximum carrying capacity under snow cover in the absence of predators and sufficient food supplies were available. Within our study site, similar conditions to the experiments conducted by Huitu et al. (2003) could be realized in open quadrats. Without snow cover, the vole population remained low until November due to predation, which reduces the competition for food among the voles, and with winter snow cover, there is also relief from predators, allowing the population increase.

This study provides an essential basic information to manage the vole population.   also indicates the importance of biological pest control provided by ecosystem service managing the vole population abundance low, especially during no-snow season.   there were no predators in orchards, the population abundance could go much higher. Considering the survival probability stays high during snow season, it is important to reduce the vole abundance as much as possible before winter. Predators seems to give high predation pressures on voles in spring, but the effect seems to

slow down after July. It could be most effective to support predators until summer and concentrate artificial vole management efforts on after August if needed. With further studies, the thresholds where artificial vole management was required could be identified.

Chapter 4

Breeding seasons of Japanese field vole in heavy snow region

4.1   Introduction

The breeding seasons of small rodents had been most classical, basic information for understanding of population dynamics and effective management of vole population. In population biology, three rodent families have been well investigated for its population dynamics; *Microtus*, *Myodes* (*Clethrionomys*) and *Lemmus*, as some species of those families exhibit outstanding multiannual population fluctuation. Generally speaking, *Microtus* family seems to have relatively flexible breeding biology and the breeding under snow were recorded occasionally (Beer & MacLeod 1961; Tast & Kaikusalo 1976; Ylonen & Viitala 1985; Norrdahl & Korpimaki 2002) as well as *Lemmus* family (MacLean et al. 1974), while *Myodes* family seems to breed only from spring to fall (Ylonen & Viitala 1985; Saito et al. 1998; Norrdahl & Korpimaki 2002). Considering this flexibility, for *Microtus*, it is more important to understand the breeding seasons at each region for effective management.

Japanese field vole is the only one *Microtus* rodent in Japan (Odachi,

32

2015). Their breeding timing is known to vary even inside of Japan according to the surrounding environment (Miyao et al., 1966; Abe 1974; Kaneko, 1976; Saito et al. 1980; Kimura et al. 1980). Kaneko (1975) pointed, the voles seems to stop breeding during hot summer with air temperature over than 26℃, while in the cooler climate region (Iwate and Nagano), their breeding was considered to cease during winter. The unique population dynamics observed in Hirosaki (Chapter 3) suggests different breeding pattern of voles, especially the breeding under snow. To validate this assumption and explore the detail of breeding biology of voles, I investigate the monthly breeding status of Japanese field vole anatomically.

4.2　Materials and methods

The 131 vole samples with 72 females and 59 males collected through the trappings from 2015 to 2019 at orchards within the study site (Fig 1-3-1). All samples were weighed, dissect and sorted by the month they were captured. The breeding status of each sample was examined referencing to Nagorsen & Peterson (1980); for male voles, the major axis of testes was measured and the visibility of tubules in the cauda epididymis were checked if the tubules were visible, the sample could be considered to be reproductively active. For female voles, the visibility of teats and the status of mammary tissue were observed, and then the condition of the uterus are examined. The sample was determined as "pregnant" if there were any embryos exist in its uterus. If a sample has heavily developed mammary tissue, it was regarded as "lactating".

4.3　Result

4.3.1　Male

Total 59 males were examined (Table 4-3-1); the heaviest individual was 44.7 g and the lightest one was 16.3 g. Of 59 males, 48 samples have clear visible tubules in their cauda epididymis, while 11 samples did not. Almost all samples with clear tubules in their cauda epididymis have testes with the axis longer than 9.0 mm, except two samples (8.9 mm and 8.4 mm). Thus, the males with testes more than 9.0 mm long could be regarded as reproductively positive. Fig. 4-3-1 shows the plots of length of major axis of testes against its body weights. Most of males reproductively positive are over 25 g, except one sample (22.6 g in April). This implies that the voles need to be at least 25 g to become reproductively active in Hirosaki, which means 51 out of 59 males should be considered as adult. On a monthly basis, more than 75 % of males are reproductively positive throughout the year, although there is no data for December and January (Table 4-3-1).

Fig. 4-3-1 The plot of the length of major axis of testes against the body weight of male Japanese field vole in Hirosaki (n=59).
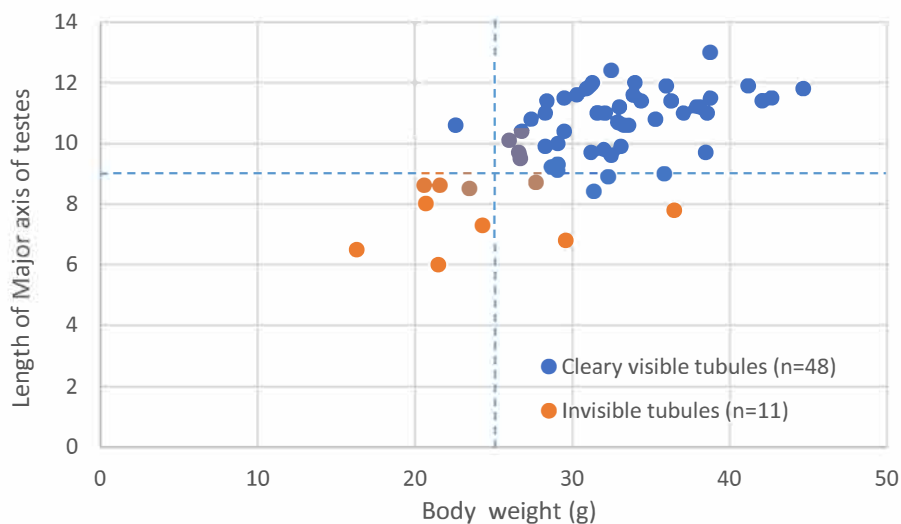
Table. 4-3-1 The number of male samples examined (n=59).

		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
N	Number of samples examined (Male)	-	1	4	15	9	4	4	3	5	4	10	-
A	Number of samples above 25g	-	1	4	9	9	3	4	3	5	4	9	-
B	Number of samples with visible epididymal tubules	-	1	3	9	9	3	4	3	4	4	8	-
	Breeding rate (B/A)	-	1.00	0.75	1.00	1.00	1.00	1.00	1.00	0.80	1.00	0.89	-

4.3.2 Female

Total 72 females were examined (Table 4-3-2); the heaviest, not pregnant female was 37.4 g, while the lightest one was 15.1 g. Of 72 samples, 22 females were pregnant, 36 females had heavily developed mammary tissue, and 45 females have visible teats. The mean number of embryos per one female was 4.45. The placental scars were invisible once the uterus was restored, thus the presence or absence of birth experience was not confirmed. Most of pregnant female were over 22 g except one sample (18.0 g in May). Therefore, the female voles over 22 g could be considered as adults which

Table 4-3-2 The sample size and breeding status of female Japanese field vole examined.

|		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
N	Number of samples examined	5	4	6	11	14	5	2	0	3	9	13	0
A	samples weighing above 22g	3	3	4	9	11	5	2	0	3	9	8	0
B	Number of samples pregnant	2	1	0	1	7	2	1	0	1	5	2	0
C	Samples with advanced mammary tissue and enhanced uterus	0	0	0	0	2	1	1	0	1	1	2	0
D	Sanokes with advanced mammary tissue and normal uterus	1	2	0	1	0	2	0	0	0	2	3	0
	Breeding rate ((B+C+D)/A)	1.00	1.00	0.00	0.22	0.82	1.00	1.00	-	0.67	0.89	0.88	-
	Pregnancy rate (B/A × 100)	0.67	0.33	0.00	0.11	0.64	0.40	0.50	-	0.33	0.56	0.25	-
	Mean number of pupps	3.0	4.0	0.0	5.0	4.7	3.5	6.0	-	5.0	4.8	4.0	-
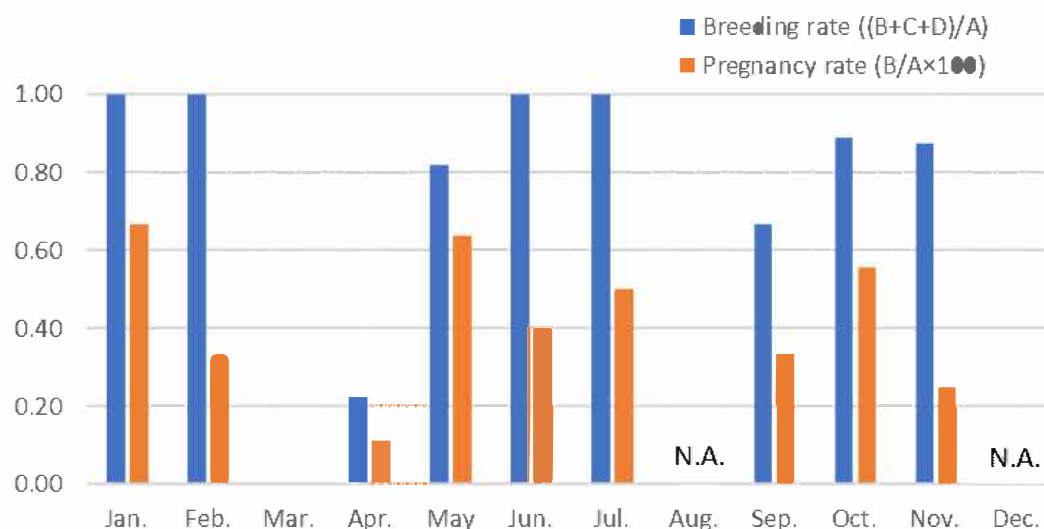
Fig. 4-3-2 The rate of females in pregnancy and breeding. Total rate of females with advanced mammary tissue and pregnant were shown as "breeding".

could be sexually matured and reproductively active. This implies 57 out of 72 samples were grown up enough to be considered as adult.

Table 4-3-2 and Fig 4-3-2 shows the monthly rate of females which were considered reproductively active. Although there is no data for August and December, the highest pregnancy rate was observed in January with 67 % of matured females, followed by May (64 %) and October (56 %). Additionally, in January, February, June and July, all of adult females were involved in reproductive activity, either pregnant or lactating, and in May, October and November, more than 80 % of females were reproductively active. In March, on the other hand, no breeding activity was observed. Even in April, the rate of females which were reproductively active was very low.

4.4   Discussion

This study revealed the breeding pattern of the Japanese field vole inhabiting Hirosaki for the first time. The voles continuously breed through the year except March and April, and they most intensively breed in January under

snow. This would be the first report of the Microtus breeds regularly under snow, and the assumption made in Chapter 3 was verified. And this study indicate that the volume of snow could be the factor to make effect on breeding season of Japanese field vole.

The rate of females being involved in reproductive activity was 100% in January, February and June. Note that July also has 100 % rate, but it was held aside as I have only small sample size (n=2). This is very high compared to the data presented in previous study (Abe 1974). There are some studies indicating that the matured females suppress younger female's sexual maturation when the population density of voles goes beyond the threshold, called "density dependency" (e.g. Rodd & Boonstra 1988, Saito 2002). Probably, the density of voles in the orchard was quite low compared to the environmental carrying capacity. Thus, voles would not have to face the competition for food resources. Therefore, the almost all females could start the reproduction activity when the environment became suitable for them.

The results of this study indicate that voles have a good energy supply enough to breed in January and February. This indication, however, could conflict with the general understanding of winter debarking; pest voles debark trees because of lack of more preferable food resources (Servello, et al, 1984). The mechanism inducing voles debarking under snow needs further exploration.

Regardless of new questions, the regular breeding of Japanese field vole under deep snow had been confirmed with the experiment in this chapter. This would be an example of adaptation to heavy snow environment by *Microtus* vole, and this should be taken into consideration to develop ecological pest management.

Chapter 5

Effectiveness of vole control by owls in apple orchards

5.1   Introduction

Raptors are predators that influence rodent population dynamics (Ims & Andreassen, 2000; Korpimäki & Norrdahl, 1991). As most raptors are purely carnivorous (König et al., 1999), they are less likely to damage crops and fruit compared with omnivorous mammalian predators. Moreover, some cavity‑nesting species, such as owls, can be effectively attracted by erecting nest boxes (Meyrom et al., 2009). Currently, studies on rodent pest control by raptors are restricted to particular species such as the barn owl Tyto alba (Labuschagne et al., 2016). Despite the widespread erection of nest boxes for barn owls, very few field studies have quantified how effective this is as a means of pest control (Kross et al., 2016; Meyrom et al., 2009; Munoz‑Pedreros et al., 2010; Paz et al., 2013; Wood & Fee, 2003).

The Ural owl *Strix uralensis* inhabits a wide region in mid‑latitude Eurasia, extending to Japan (König et al., 1999). This species is a large cavity‑nesting owl and considered a generalist predator (Klemola et al.,

38

2002; Korpimäki & Sulkava, 1987; Lundberg, 1981) that primarily preys on small rodents (Cramp et al., 1985). Investigating the diet of this owl and quantifying its effect on pest density can help reveal the role of Ural owls in orchards and determine whether the species may be beneficial as a pest control agent.

In Japan, Ural owls inhabit a variety of environments, from forest to agricultural land (Kobayashi, 1978; Takano et al., 1985) and frequently nest in the hollows of apple trees in orchards located in the Aomori Prefecture of northern Japan (Azuma, 2007). The Japanese field vole Microtus montebelli is the dominant rodent species in orchards (Abe, 2002) and can cause severe damage to the trunks and roots of apple trees during the winter when they covered in snow (Abe, 2002; Azuma, 2007). Apple orchard land managers have historically appreciated the ability of owls to reduce rodent abundance; however, the impact of owls on vole population has not been scientifically studied. Several decades of promotion of intensive fruit production (Ministry of Agriculture, Forestry and Fisheries, 2016) have resulted in widespread replacement of old apple trees with young dwarf trees. By the beginning of the 21st century, the number of apple trees with cavities suitable for owl breeding had declined accordingly. The loss of potential nest sites in turn caused owl populations to decline (König et al., 1999). If owls do provide considerable pest control in apple orchards, the loss of native nest sites could be compensated for by providing supplemental nest sites inside apple orchards. This practice would be mutually beneficial to land managers, who receive biological pest control, and owls, who gain breeding sites.

In this study, I evaluated the effectiveness of Ural owls as biological control agents as a means of developing IPM schemes for orchards. To quantify the predator effect of Ural owls on rodents, I conducted two surveys. First, I determined the diet of Ural owls breeding in apple tree hollows during the rearing period. Second, I encouraged the owls to breed in apple orchards by setting nest boxes. I then monitored the seasonal changes in vole population sizes in orchards with and without breeding owls. I also examined whether the distance from the forest edge to nest boxes, as well as vole density around nest boxes, influenced Ural owl nest site selection.

5.2   Materials and methods

5.2.1   Study sites

This study was conducted in apple orchards in Aomori Prefecture, Japan. From 2000 to 2007, Ural owl diets were monitored at site A in Namioka (40° 42′ N, 140° 34′ E; Figure 5-1-1a). From 2014 to 2017, the quantification of pest control by breeding Ural owls was conducted at site B in Hirosaki (40° 36′ N, 140° 27′ E; Figure 5-1-1b). This was done by attracting owls to orchards with nest boxes. Sites A and B are approximately 20 km apart. The flatlands in both study sites are surrounded by gently sloping hills adjacent to a mountain. Most of the hilly areas are used for apple production, and the steeper hill ranges are covered with a mixed plantation of Japanese cedar *Cryptomeria japonica* and natural forest. Both sites are in the beech forest zone, which consists of Japanese beech *Fagus crenata*, Japanese oak *Quercus crispula*, and Japanese red pine *Pinus densiflora*. The mean temperatures in Namioka and Hirosaki are 10.4 and 10.2°C, respectively, and the mean maximum snow depths are 107 and 83 cm respectively. Snowfall occurs from December to March.
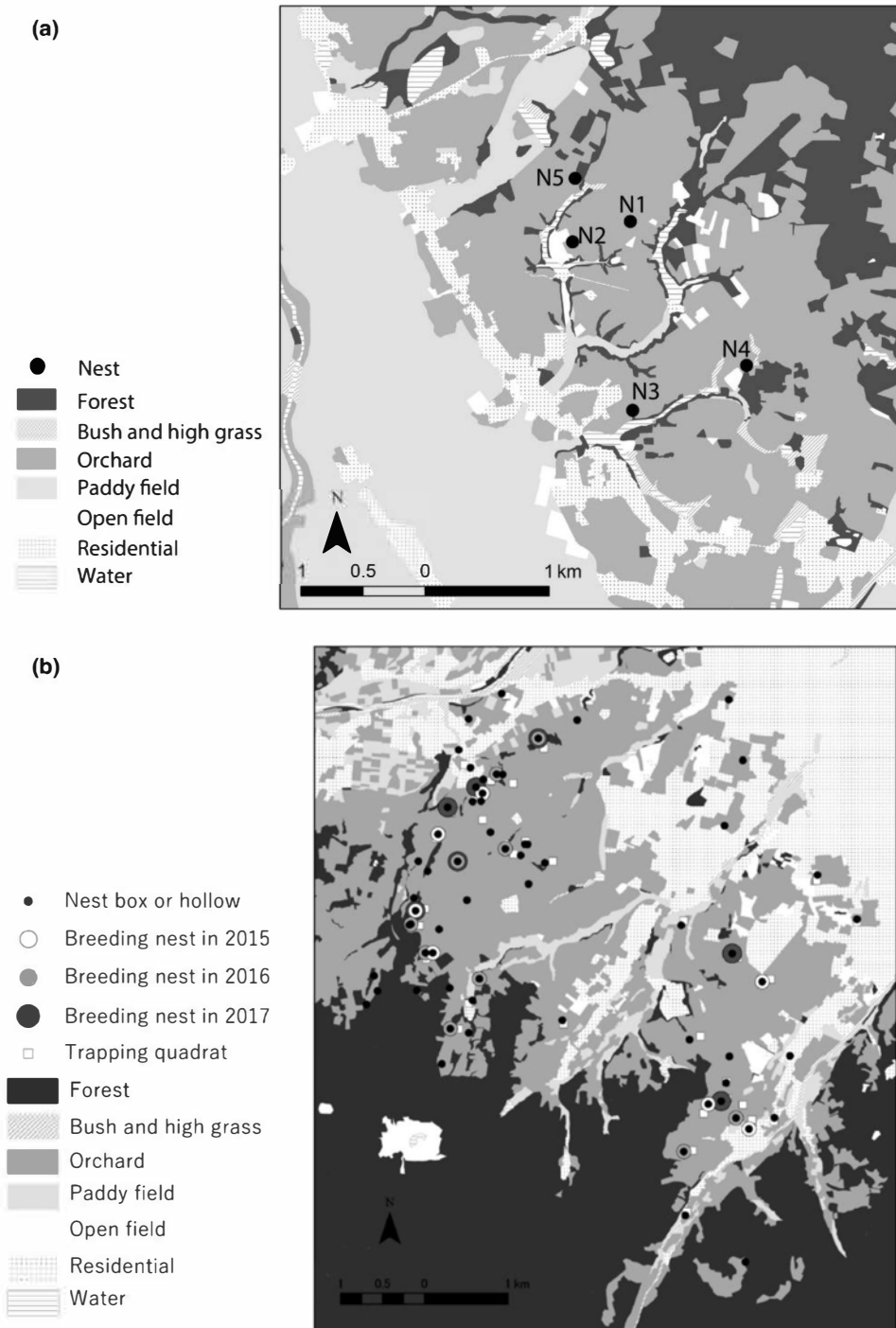
Fig. 5-2-1 (a) Study site A in Namioka, with the location of Ural owl nests in apple hollows. The letters indicate Nest ID. The area specified as "Open field" includes fallow field, a vegetable garden, and bare land. (b) Study site B in Hirosaki used for the nest box experiment. The nests surrounded by circles indicate occupied nests, and the nests surrounded by two circles were occupied twice during the study

41

5.2.2   Ecology of the Ural owl and the Japanese field vole

Ural owls typically begin laying eggs in March (Watanabe, 1989). Incubation lasts 28–35 days, and owlets leave the nest approximately 35 days after hatching (König et al., 1999). Because of the need for parental care after fledging, young owls stay with their parents for another 3 months before dispersing in late August or early September (Cramp et al., 1985). Ural owls have rarely been observed to lay replacement clutches (Lundberg, 1981). Adult Ural owls are territorial and generally stay within the same territories throughout the year (König et al., 1999). However, there is no data regarding the home ranges of Ural owls that inhabit agricultural areas.

The Japanese field vole is a territorial, herbivorous vole. Populations of the species show seasonal fluctuations (Abe, 1974), although they also may produce outbreaks once per several decades after the blossom of the sasa (*Sasa kurilensis*; Ito, 1975). A previous study conducted in northern Japan has found the vole population density to be 20–100 voles per hectare in grassland (Abe, 1974). Vole breeding peaks in spring and fall (Kaneko, 2008; Kimura et al., 1980), with a mean of 4.3 offspring per female (Abe, 1974). Around 14 days after birth, young voles become ambulatory and begin to forage (Yoshinaga et al., 1997). Within 30–40 days after birth, the voles obtain a young adult weight (Yoshinaga et al., 1997) and may disperse from their nests. Within 100–120 days, voles reach sexual maturity (Kaneko, 1975).

5.2.3   Monitoring of Ural owl prey animals

From 2001 to 2007, we conducted a diet study of Ural owls nesting in apple orchards at study site A (Figure 5-3-1a). Video cameras (DCR‐PC9, DCR‐SR100, and DCR‐TRV300 [Sony, Japan]; and HHCIR‐S38BCIR [Hoga, Japan]) were attached to the inside of the apple tree nests and used to monitor the prey brought to nests by adult owls. Recordings were conducted 24 hr a day for 12–37 days at six nests. Prey animals were identified to genus

by body size, auricle shape, and tail length. The proportion of each species in the diet was calculated by dividing the number of each prey species by the total number of identified preys.

5.2.4 Nest box installation

Sixty nest boxes were installed in 55 orchards at site B (Figure 5-3-1b) in November 2014. The distribution of nest boxes was not uniform as nest boxes could only be installed in orchards where permission had been obtained from land managers. The mean distance ± SD between nest boxes was 349 ± 271 m. Each nest box was 36 × 36 × 70 cm with an 18 cm diameter front entrance. The material to produce a nest box cost approximately US $25. Nest boxes were visited once in late March and once in May each year to detect all nesting owls. Additionally, the owls breeding in apple tree hollows were identified by interviewing land managers.

Assessing the environmental requirements for owls breeding in agricultural areas is important for increasing occupancy rates and harnessing owls as biological control agents. To determine whether breeding owls require a nearby forest patch for breeding, we measured the distance from each occupied and unoccupied nest box to the nearest forest patch. Furthermore, prey vole population densities in April (the measurement method is described in the next section) were compared between orchards that had occupied and unoccupied nest boxes. The mean distance ± SE from occupied nests to quadrats for measuring vole density in orchards with breeding owls was 39 ± 6 m, while the mean distance to quadrats in orchards without breeding owls was 1026 ± 168 m.

5.2.5 Vole population density estimation by live‐trapping

We measured vole population changes in 39 orchards (29 in 2016 and 10 in

2017) in which at least one nest box had been installed. Of the 39 orchards, 10 had breeding owls, and the other 29 orchards were selected arbitrarily. The mean area ± SE of the 39 orchards was 1.06 ± 0.18 ha. The ages of the apple trees within the 39 orchards varied from 2 to over 80 years old. Within each orchard, we live‐trapped voles in a single 25 × 30 m quadrat to estimate their population size and seasonal variations in abundance. The mean distance ± SE between quadrats was 471 ± 48 m. Two quadrats were only 164 m apart but deemed to be independent because a paved road and public facility separated them, providing 35 m of separation between two orchard edges. As the home range radius for a Japanese field vole is approximately 20 m (Abe, 2002), and given that there are paved roads, forested areas, and non‐arable lands between all orchards that obstruct the free migration of voles, we considered all quadrats to be independent.

The population counts of small mammals by live‐trapping were repeated three times each year. The first count was conducted in April, before the owl rearing period; the second was in May, following owlet fledging; and the third was in November, just before snow cover. Reducing the population density of rodents before snow cover is critical for orchard damage control. Thirty live‐traps (27 × 7 × 9 cm; Hokkaido Forest Management Corporation, Japan) were placed in each quadrat. The live‐traps were set in front of burrow openings with bait and checked on three consecutive mornings. Each captured vole was weighed and marked by painting inside of one auricle with pigment paint to distinguish recaptures. The total number of voles captured, excluding recaptures, was deemed to be the vole population for that quadrat and used to calculate the vole density around each nest box (Bjørnstad et al., 1999; Nakata, 2015). In 2016, it took approximately 3 weeks to complete each series of live‐trapping in 29 quadrats. As the count in May coincided with the vole's peak breeding season, many pregnant voles were captured at the beginning of the count series, and later many juveniles were captured in the quadrats. In some instances, voles gave birth overnight in live‐traps. To eliminate the data skew which was caused by the time‐lag of survey, juveniles were excluded from population counts in May. We identified juveniles by weight, as voles weighing <22 g were born within the previous 30 days (Yoshinaga et al., 1997). Among the 39 quadrats in May, 16 quadrats contained vole breeding nests with juveniles. The mean number of vole juveniles was 1.57 per quadrat within the owl breeding territory, and

1.84 for quadrats outside the owl breeding territory.

5.2.6 Defining "breeding territory" of the Ural owl

To quantify the pest control effects of breeding owls, we estimated the range in which owls foraged during nesting periods. Normally foraging areas should be confined to territorial areas (Cramp et al., 1985). Thus, the mean distances between two simultaneously occupied nests over the 3 years of our study (753, 612 and 964 m) were used to estimate foraging area. Depending on the abundance of prey, not all Ural owl pairs breed every year (Lundberg & Westman, 1984; Pietiainen, 1989); therefore, the distance calculated during better breeding years should reflect their minimum territorial radius. Thus, we used 306 m as the Ural owl "breeding territory" radius in the orchards we studied, which was half the shortest mean distance over the 3 years. To validate the breeding territory radius that we had defined, we plotted vole population decreases in each quadrat during the rearing period (between April and May) against the distance from the nearest owl nest. To specify the threshold where the owl effects became negligible, a piecewise regression was applied using the software package Segmented (version 0.5 - 3.0; Muggeo, 2008) in r (version 3.2.3; R Core Team, 2017). The occupancy rate of nest boxes was calculated by excluding any neighbouring nest boxes that were within the breeding territory. We used ArcGIS (version 10; ESRI software) for GIS analysis.

5.2.7 Analysis of Ural owl effects on voles

Among the 39 quadrats for live - trapping of small mammals, 14 were within the estimated breeding territory of Ural owls, and 25 were not. One of the 14 quadrats within a breeding territory was 371 m away from the nearest known nest, but ululation and pellets were frequently observed during breeding

season within this quadrat. Thus, this quadrat was an exception and categorised as being within a breeding territory. The mean distance ± SE from owl nests to quadrats within breeding territories was 73 ± 19 m, whereas the mean distance to quadrats outside of breeding territories was 1,148 ± 183 m.

To analyse the effect of breeding owls on the vole population, we used a GLMM with Poisson distribution and a log‑link function. The response variable was "Count," which represented the vole population of quadrats in May and November. The five experimental variables were "Month," "Owl," "Young tree," "Forest," and "Residential" (Table 5.2.1). "Residential" was chosen as an experimental variable because the surrounding land‑use should affect vole density (Delattre et al., 2009; Michel et al., 2006). The value of the variable "Owl" was set at one for quadrats within a breeding territory, and zero for quadrats outside of a breeding territory. The interaction of "Owl" and "Month" was also analysed to separate the effect into two seasons: during and after rearing season. To calculate vole population changes from April, the variable "April" was used as an offset term. Quadrat ID and year were set as random effects with Gaussian distribution to take into account the effects of repeated samplings in the same quadrat as well as

Table 5.2.1 Definitions and range of variables for generalised linear mixed model analysis to examine the effect of breeding owls on vole density. The quadrat ID and year were set as random effects

Variables	Definition	Range
Response		
Count	The number of voles captured in May and November	n=78, 0-25
Explanatory		
Month	Vole trapping season (May or November)	May or Nov
Owl	If the quadrat is within breeding territory (Yes: 1/No: 0)	0 or 1
Age of tree	The age of apple trees in orchard (1: < 5years old / 0: >5 years old)	0 or 1
Forest	If orchard lot is bordering forest or not (Yes: 1 / No: 0)	0 or 1
Residential	If orchard lot is bordering residential area or not (Yes: 1 / No: 0)	0 or 1
Offset		
Capacity	The number of voles captured in April	n=39, 1-31

yearly differences. Although there was a moderate positive correlation between "Owl" and "Forest" (Pearson's r = 0.45), multicollinearity was not observed. Other correlations among variables were low (Pearson's r < 0.35). Therefore, we used all the variables in our GLMM analysis. The best models were selected based on the Akaike information criterion. We used the software package lme4 (version 1.1‑13) for GLMM analysis in r (version 3.2.3; R Core Team, 2017).

5.3   Results

Prey fed to young at six breeding Ural owl nests in apple orchards are shown in Table 5-3-1. Voles were the primary prey around all nests and consistently accounted for more than 80% of the identified prey. Other notable prey identified were mice and small birds (Table 5-3-1).

Table 5-3-1 Prey items brought to nests by Ural owls in orchards and their contribution (2001–2007). Nest locations are shown in Figure 5-2-1 (a) with Nest IDs. "Vole" includes *M. montebelli* and Anderson's red‑backed vole *Eothenomys andersoni*; "Mouse" includes large and small Japanese field mice; "Rat" includes the Norway rat *Rattus norvegicus* and black rat *Rattus tanezumi*; and "Shrew‑mole" includes Japanese shrew‑mole and Dsinezumi shrew

Study year		2001	2002	2006			2007
Nest ID		N1	N1	N2	N3	N4	N5
Recording days		28	37	23	12	23	20
Number of feedings		197	335	126	152	195	148
Number of prey identified		114	280	121	121	153	122
	Vole	0.82	0.92	0.90	0.88	0.90	0.80
	Mouse	0.12	0.02	0.09	0.05	0.08	0.07
Contribution of	Rat	0	0	0.01	0.01	0.01	0.02
each prey type	Shrew-mole	0.02	0	0	0.02	0.01	0
	Bird	0.04	0.06	0	0.02	0	0.11
	Anura	0	0	0	0.01	0.01	0

Four owl nests were discovered in apple tree hollows during our study, and thus there were a total of 64 available nest sites at site B (Table 5-3-2). The total number of occupied nest sites was 24, with 21 nest sites occupied once, and three nest sites repeatedly occupied. The occupancy rate of nest boxes was less than 20% over the duration of the study (Table 5-3-2). Sixteen of 24 occupied nest sites were observed in the western half of site B, mainly in orchards alongside swathes of forest (Fig. 5-2-1b). In orchards surrounded by residential areas, nest boxes were not occupied (Fig. 5-2-1b). Vole density in April was significantly higher in orchards with owl nests in 2016 (Mann–Whitney U test, $p < 0.05$) but not in 2017 ($p = 0.61$) (Fig. 5-3-1). The mean distance ± SE (minimum to maximum) to the nearest forest patch from the owl nests and unoccupied nest boxes was 103 ± 28 m (0–423) and 145 ± 23 m (0–642), respectively, and no significant difference was observed. Nineteen of 21 occupied nest sites contained woodland within a 306 m radius circle (presumed breeding territory), and 39 of 43 unoccupied nest sites had woodlands within a 306 m radius. The smallest woodland patch within a breeding territory was 0.6 ha.

Table 5-3-2 Ural owl breeding status in study site B

Year	2015	2016	2017	Total
Number of Breeding	7	10	7	24 *
Nest box	5	8	7	20
Apple tree	2	2	0	4
Mean distance between nests; m (SD)	753 (144)	612 (41)	964 (219)	
Occupancy rate (%)	13.5	20.0	13.2	
Number of vole quadrats on orchard with owl nests	-	6	4	10
Number of vole quadrats within owl breeding territory	-	9	5	14
Number of vole quadrats out of owl breeding territory	-	20	5	25

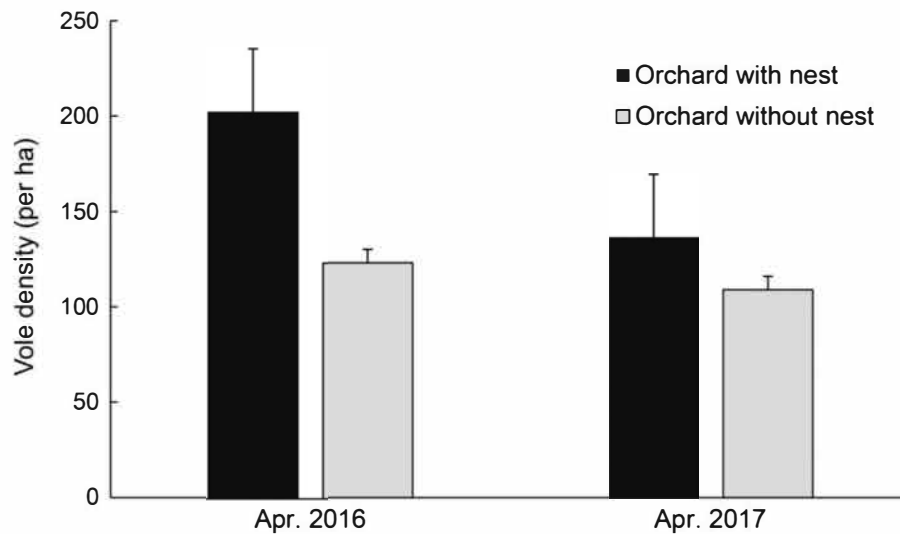＊:Three nest boxes were occupied twice during the study)

Figure 5-3-1 Comparison of mean vole density per hectare in April (with SE) between orchards where Ural owls selected nest sites, and orchards where Ural owls did not select nest sites

During our two live‐trapping years, with 10,530 trap nights, five small mammal species were captured: Japanese field vole *M. montebelli*, large Japanese field mouse *Apodemus speciosus*, small Japanese field mouse *A. argenteus*, Dzinezumi shrew *Crocidura dsinezumi*, and Japanese shrew‐mole *Urotrichus talpoides*. We captured a total of 1,391 small mammals, of which 959 were unique individuals and 432 were recaptures. The Japanese field vole accounted for 940 (98.0%) of the unique individuals. Therefore, we only analysed owl effects on the Japanese vole.

The piecewise regression model suggests the potential for a breakpoint ($\pm$SE) at which the owl effect on the vole population becomes negligible, at around 183 m (50–662 m; exp [5.21 $\pm$ 1.28]) from the owl nests (Fig. 5-3-2). Although the difference between the two slopes was not significant ($p = 0.50$), the breakpoint distance was within the presumed owl breeding territory radius.

In both 2016 and 2017, vole population densities were highest in April, and decreased more in the quadrats within owl breeding territories than in quadrats outside breeding territories in both May and November (Fig. 5-3-3). The best models derived from GLMM analysis included three variables: "Owl",

"Young tree," and "Residential" (Table 5-3-3). GLMM results indicated that vole population densities (±SE) within owl breeding territories were 37% (30%–47%; exp [−0.98 ± 0.22]) in comparison to the predicted population density if there was no "Owl" effect (Table 5-3-3). The vole population decreased significantly after April in orchards with trees less than 5 years old, and in orchards adjacent to residential areas (Table 5-3-3).
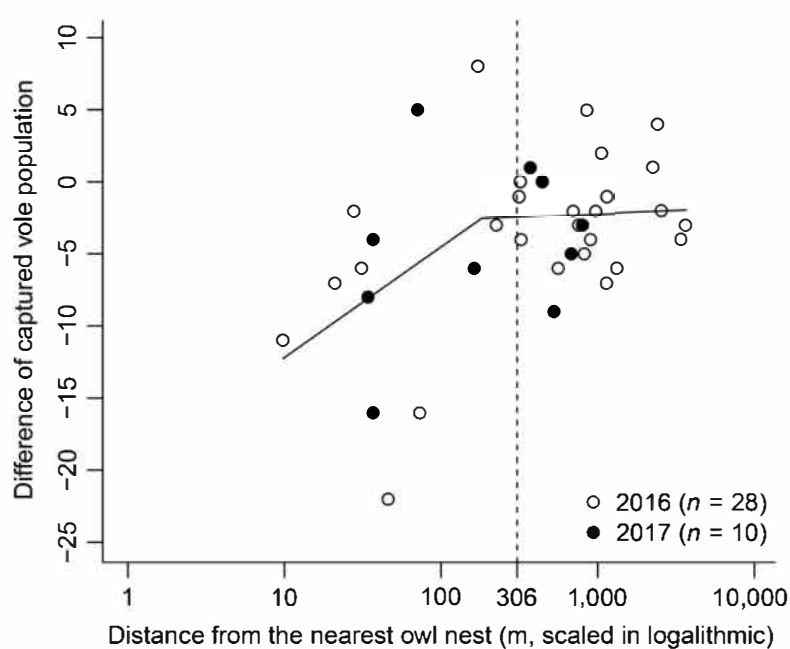

Fig. 5-3-2   Scatter plot of differences in captured vole populations from April to May against the distance from the nearest Ural owl nest to a quadrat (on the logarithmic scale). The dashed line indicates the border of the breeding territory area (306 m). Solid lines show regression values estimated from the piecewise regression model (r^2 = 0.23)
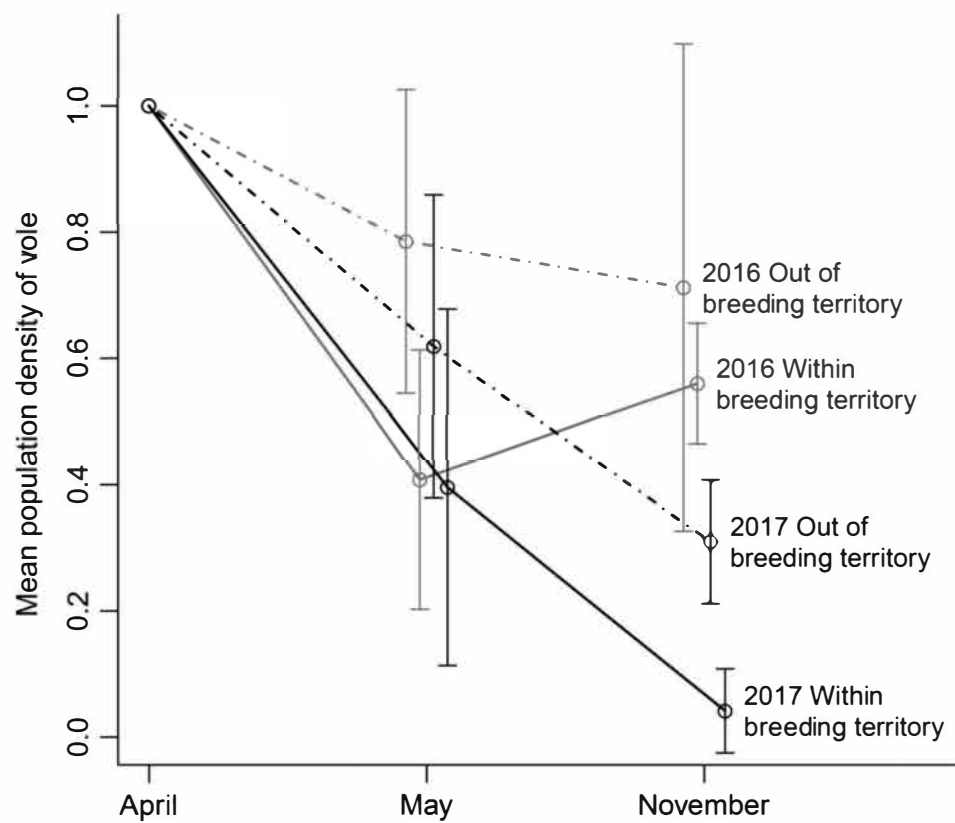
Fig. 5-3-3 Comparison of seasonal changes in mean vole population densities between orchards within Ural owl breeding territories and outside breeding territories. The population densities in May and November are expressed as ratios compared with the count in April. Error bars indicate SE

Table 5-3-3   Generalised linear mixed model results for the effect of Ural owls on vole density. Variables included in best - fit models selected by Akaike information criterion are indicated with plus and minus signs for positive and negative effects, respectively. Parameter estimates, standard error (*SE*), Wald statistics value (*z*), 95% confident interval, and probability (*p*:Pr < |*z*|) of the best model are also shown

	Model rank						Best model result					
Variables	1	2	3	4	5	6	Estimate	SE	z	2.5% CI	97.5% CI	P
Owl	-	-	-	-	-	-	-0.98	0.22	-4.41	-1.41	-0.54	<0.001
Young Tree	-	-	-	-	-	-	-1.06	0.37	-2.90	-1.78	-0.35	<0.01
Residential	-	-	-	-	-		-0.71	0.34	-2.09	-1.38	-0.04	0.03
Month Nov		-		-	-							
Forest			+	+		+						
Month Nov × Owl					+							
df	6	7	7	8	8	6						
AIC	458.5	459.2	459.3	460	460.3	460.5						
delta	0	0.66	0.79	1.46	1.73	1.99						

5.4　Discussion

Ural owl breeding pairs had a measurable effect on vole population densities in apple orchards, supporting our hypothesis that they can act as a biological pest control agent. To our knowledge, this is the first study undertaken to test the possibility of pest control by Ural owls. In this study, Japanese field voles were the most numerous small mammal species in apple orchards and the primary prey of breeding Ural owls in the area (Table 5-3-1). Although vole densities varied between years, the densities in orchards with breeding owls were significantly higher (Fig. 5-231); this indicates that owls can detect orchards with more prey. Previous studies on the diet of Ural owls in Japan showed elasticity in their primary prey (mice, voles, or sparrows) based on habitat and prey availability (Matsuoka, 1977; Morii & Shioiri, 1996; Shiraishi & Kitahara, 2007). Moreover, Suzuki et al., (2013) reported that the proportion of voles in the Ural owl diet decreased with increasing distance from owl nests to vole‐inhabited pasture areas. This finding suggests that the proportion of prey in Ural owl diets is correlated with land‐use around their nests. We expect that the majority of voles fed to owl nestlings came from apple orchards, the voles᾽ primary habitat type in our study area. These results indicate the importance of sustaining Ural owl nest sites inside orchards to enhance pest control by these owls.

　　　We also found that nesting owls in orchards reduced Japanese field vole populations by 53%−70% in breeding territories during the rearing period (Table 5-3-3). Moreover, vole suppression was significant in both May and November (Table 5-3-3). Although it was not statistically significant, our piecewise regression model suggested that vole densities decreased largely around the center of owl breeding territories (Fig. 5-3-2), which indicates that the core foraging area should exist inside the presumed breeding territory. One factor contributing to the strong suppression of vole numbers in May and November may be the direct predation by Ural owls in April. Extrapolating from the results shown in Table 5-3-1, a pair of breeding owls prey on approximately 150−300 voles during the rearing period, which is before the vole spring breeding season. The considerable decrease in the number of voles of breeding age in April could potentially impact the population later in the year. Another potential factor in reducing vole population sizes could be

53

the indirect effect of owls as predators, such as driving rodent dispersal (Prevedello et al., 2013; Vibe‐Petersen et al., 2006), reducing rodent activities, and lowering survival or reproductive rates (Abramsky et al., 1996; Haapakoski et al., 2012; Jochym & Halle, 2013; Korpimäki et al., 1994). Preisser et al., (2005) showed that indirect effects of predators on prey density could be as significant as direct effects. Thus, the interaction of direct and indirect effects of predators on voles could cause long‐term reduction of vole densities within Ural owl breeding territories. The impact of the variable "Residential" was consistent with previous studies (e.g., Delattre et al., 1996). The negative effect of the variable "Young trees" is inconclusive but may have occurred because there was less preferred habitat for voles during summer, with less shade and more exposure to predators, compared with neighboring orchards with older trees.

Future research should investigate whether Ural owls can suppress vole density at a regional scale, as our study only verified owl effects within breeding territories. Paz et al. (2013) detected vole suppression effects by kestrels around their nest boxes but failed to detect effects at a regional scale (within 2,000 ha plots). The impact of Ural owls outside of breeding territories is not discussed in this study, as we have no data on their diet or home range after the rearing period. To assess the Ural owl impact as a pest control agent at the regional scale, the number and locations of owl breeding and vole population densities need to be monitored over a longer period of time.

Another challenge is how to increase nest box occupancy rates. The occupancy rate at site B was relatively low (Table 5-3-2) compared with the mean occupancy rate (58%) from previous studies (Labuschagne et al., 2016). The reason for the low occupancy rate could be biological differences between Ural owls and other raptors. Higher occupancy rates were mainly obtained in studies on barn owls. Barn owls, because of their biology, tend to have high occupancy rates; they have weak territoriality, breed more than once a year depending on prey abundance (König et al., 1999) and population sizes vary based on prey availability (Dupuy et al., 2009). Such biological traits, however, might lead to the destabilization of rodent populations (Hanski et al., 2001). Conversely, Ural owl density is stable despite prey abundance changes (Dupuy et al., 2009), which is important for stabilizing rodent populations. The Ural owl occupancy rate could be increased by efficient nest box installation taking their territory size into account. In site B,

54

multiple breeding pairs occupied nest sites with a mean separation of 600 m, indicating that 600 m is the suitable distance between nest boxes (Table 5-3-2). We could not ascertain owl preference regarding the distance between nest sites and forest edge, as woodland is scattered throughout our study site and all nests were within 650 m of woodland or forest. Owls were frequently observed roosting in forest patches during our survey, and 19 of the 21 breeding territories monitored did include woodlands. The woodland patches near nests do not need to be large or continuous, but they are important as they provide suitable places to roost and hunt, and refuge from predators, which is essential for fledging owlets with low mobility. More importantly, forest patches provide additional hunting grounds for alternative prey, such as wood mice and songbirds, when vole populations in orchards are low. As owls appear to benefit when their territories contain woodlands, nest boxes should be installed near forest patches. An observed exception was two pairs of owls without any forest patches within their presumed breeding territories. These owls nested in the hollows of old apple trees, which the land managers stated had been occupied consecutively for 20 years. Thus, orchards with older trees may resemble a forest patch. Providing long‐term nest sites may improve the affinity of owls for more homogeneous orchard environments. To obtain a more detailed understanding of the landscape requirements of Ural owls breeding in agricultural areas, further investigation of their year‐round home ranges is required.

Additionally, programs that support predator breeding in and around agricultural areas should be implemented carefully with consideration of both local and regional ecosystems. Ural owls are predators that prey on many kinds of small mammals, birds, frogs, and insects (König et al., 1999), including endangered species. Furthermore, artificial nest boxes will typically wear and decay within 5 years unless regularly maintained (Lindenmayer et al., 2009).

I conclude that Ural owls have potential as biological pest control agents because they have a diverse range of habitats and can be attracted to orchards using nest boxes. This approach could be applied to a variety of orchards and other crop types with neighboring forest patches, such as vineyards, rice paddy fields, and annual crop fields. In the future, because of the considerable effects of predators on rodent population dynamics, other native generalist raptors could also be explored as potential biological rodent

control agents. Supporting native raptor inhabitation in agricultural areas could be an option for IPM and could contribute to sustaining regional biodiversity.

Chapter 6

Non-rodenticide practices to manage vole populations and damages

Until now, this thesis showed the impact of the biological pest control service provided by ecosystem on Japanese field vole. Chapter 3 showed that the pest vole abundance was decreased by half in orchards without artificial treatment from April to July, and the abundance would increase double or triple under snow cover. Chapter 5 showed the Ural owls, the native avian predator, would suppress the density of voles by 63 % around their nests. These biological pest control service could be more efficient than the effect of rodenticide (. If we could make use of this service into agriculture practices in an effective way, the use of rodenticide could be reduced. The importance of ecosystem service, however, has not gained enough awareness, and rodenticide is being used widely without any verification of the effect on vole abundance.

But there is a sign of change in the world. In Europe and North America, more ecological management practices other than rodenticide are being discussed actively according to the increasing market demands for organic fruits. The conferences to exchange information and seek for better management scheme are organized year to year.

In this chapter, I review the rodenticides used in Japan at first and review the ecological pest management schemes being developed or discussed. Finally, I present the practical consequence of one of the suggested ecological management schemes, "winter feeding" at my study site, to verify if it could prevent vole damage under snow cover.

6.1   The history of rodenticides in Japan

The history of rodenticide in agriculture starts in the middle of Meiji era (Editorial committee of Shokubutsu boueki kouza, 1982). Until the end of World War II, the Salmonella typhimurium was the most frequently used rodenticide in the field (Misaka, 1954). The bacteria were cultured and bottled into beer bottles to spread to fields, and it was appreciated by farmers (Misaka 1954) although there were criticisms that the infectability of Salmonella typhimurium was too low (Ueda et al., 1966). When WWII ended, the use of the Salmonella typhimurium was forbidden as it could be harmful to human beings, and instead, chemical rodenticides were introduced into Japan one after another (Misaka 1954). The major rodenticides being introduced since 1945 were α-naphthyl thiourea (called "Antu"), Sodium mono-fluoroacetate (called "Fratol" in Japan, "1080" in the U.S.A), Zinc phosphide and varieties of Coumarinne compounds (Misaka 1954).

The α-naphthyl thiourea was known as one of three major scientific inventions with penicillin and DDT (Misaka 1954).   is highly poisonous to Norway rat *Rattus norvegicus*, however, the effectivity on herbivorous voles was low. Because of a poor result from the field experiments, it was not applied to practical use (Ueda et al., 1966), and the registration as agricultural rodenticide had been expired in 1974 in Japan (Food and Agricultural Materials Inspection Center (2019).

Sodium mono-fluoroacetate was the rodenticide registered in 1957, with the strongest toxicity and high persistency. Almost 100% of removal rate of voles were reported from field experiments (Udagawa, 1953, Ueda et al, 1966).   was widely diffused, but because of its strong toxicity and persistency inside of dead bodies, it caused unexpected poisoning of pet

58

animals (Misaka 1954), wild animals including predators (Ota 1960), and even human beings. For its severe toxicity, the use of Sodium mono-fluoroacetate was technically restricted to groups of people under the licenced professionals' supervision by governmental order. For land managers of orchards in Aomori, it had been the trump card rodenticide (Murano, personal communication) until it was finally forbidden in 2010 (Food and Agricultural Materials Inspection Center (2019).

Zinc phosphide was invented in Germany during WWII (Nose, 1969). It is an inorganic rodenticide and has an immediate effect. Zinc phosphide gets decomposed by moisture, and voles were reported to avoid feeding after the repetitive use of it (Nose, 1969). Several products are available until now such as "Z.P." or "Ratemin" in Japan. Probably this is currently the most widely used rodenticide in orchards in Aomori. The toxic substance is considered to be the hydrogen phosphide gas produced as the result of hydrolysis of zinc phosphide (Nose 1969; Editorial committee of Shokubutsu boueki kouza, 1982). The zinc phosphide would not have risk to cause secondary poisoning, as it is considered to lose toxicity after releasing hydrogen phosphide gas in rodent (Editorial committee of Shokubutsu boueki kouza, 1982). However, it presents strong toxicity as well when other non-target mammals and avian take directly.

All of the coumarin compounds are anticoagulant chemicals. When animals feed on coumarin compounds for more than three days in a row, it causes visceral bleeding resulting in death. Coumarin compounds can produce its effect only when the animals feed on it continuously (Editorial committee of Shokubutsu boueki kouza, 1982). The effect in the field is not as effective as other rodenticides, but pregnant female voles could be more vulnerable to this rodenticide (Editorial committee of Shokubutsu boueki kouza, 1982). Several products have been registered and available for agriculture use. There are few reports of mice which develop resistance for coumarin rodenticide (Editorial committee of Shokubutsu boueki kouza, 1982). After 1960th, new rodenticides similar to coumarin rodenticide were developed and introduced to Japan, such as diphacinone or chlorophacinone (Editorial committee of Shokubutsu boueki kouza, 1982). But the side effect for non-target wildlife of those anticoagulant has not been scientifically verified in Japan.

All anticoagulant chemicals currently permitted in Japan are grouped

as "first-generation Anticoagulants", though there are rodenticides grouped as "second-generation Anticoagulants", which are widely used in Europe and Canada (Albert et al., 2010; Jacquot et al., 2013; Ruiz-Suarez et al., 2014). Those second-generation anticoagulants are reported to be accumulated within both avian and mammal predators (Albert et al., 2010; Ruiz-Suarez et al., 2014) and concerned to affect the predator populations (Jacquot et al., 2013).

At this time, the rodenticides permitted for fruit production in Japan are zinc phosphide and coumarin compounds. They do not present an absolute control effect as the sodium mono-fluoroacetate, thus there is a demand for more effective rodenticide. However, the intensive use of rodenticide could have a high risk of damaging predators, which will result in tearing apart the regulating service provided in orchards by the ecosystem. The alternative vole management scheme should be developed and tested, around the biological pest control services observed in this study.

Additionally, it would be important for land managers to hold some remedies like rodenticide just in case of an emergency. To enhance the development of better remedy, we need to enrich our understanding of the biology of voles, ecosystem service and mechanism of vole damage.

6.2   Ecological pest management being developed

There are quite few studies to verify more ecological pest management schemes in the world, although the rodenticide is still the major management method worldwide. Here I introduce the ecological management schemes including developing ones, referring Pelz et al. (2003), Witmer et al. (2009), Sullivan et al. (2018) and Schlötelburg et al. (2019).

Migration barriers (fencing) and trapping

The dispersal and migration are considered to be one of the major factors

affecting the population dynamics of rodents in fields (Gauffre, 2009). When voles were removed from a certain area, the vacancies will be quickly re-colonized from neighbouring populations (Pelz et al., 2003). Furthermore, voles in agriculture area survive by changing their habitat responding to habitat change caused by agricultural operations (Bonnet et al., 2013). Therefore, to prevent invasion and reduce the survivability of voles, the migration barriers could be useful. Saucy (2004) recommends a semi-permeable fence with one-way exit, which allows voles to leave the plots, but prevent them from coming back in. It had been observed that vole population abundance was relatively smaller in the small area isolated from a continuous agricultural area (Delattre, et al., 1992; Murano, unpublished).

There are some studies to combine traps with migration fences. Variety of fences are suggested. For example, Fuelling et al. (2010) creates multi capture live traps with two entrance doors, combined with mesh wire fence. The lid of box-like trap could be opened by a predator, so that predators can prey on voles captured. Traps with similar concept are proposed by other researchers such as Walther & Fuelling (2010) and Schlötelburg et al. (2019).

It is very common to have uncultivated grassland surrounding orchards in Aomori, and thatgrass land tends to work as a refugee for voles. Fencing orchards where vulnerable young trees and separating orchards and the source of voles could be one of the options to consider for reducing vole damage.

Supporting vole predators

The vole suppression effect by mammals and owls had already been verified in Chapter 3 and Chapter 5. Owls could be attracted to orchards with nest boxes, and actually, the number of nest box installed in apple orchards are drastically increasing after our study was published. The volume of vole damage after nest box installation should be monitored to verify the effect of predator attraction.

Mammal predators, on the other hand, have not been well investigated in Aomori yet. Japanese Red fox *Vulpes vulpes japonica* was observed to occur in relatively high density through our camera trap experiments (Murano,

unpublished). By investigating their requirement for habitat could help to support fox inhabitation within orchards. Domesticated cat and dogs are also known to suppress the small mammal's activity (Mahlaba et al., 2017).

Additionally, there are more candidate predators which could be providing regulating service by foraging in an orchard, such as eastern common buzzard *Buteo buteo* and least weasel *Mustela nivalis*. Eastern common buzzard occurs in high density in Aomori as well as the Ural owl. They require high trees for breeding and perches for hunting (Meunier et al., 2000). To provide an environment to make buzzard easier to hunt or breed near agricultural area could enhance the predator effect on voles. Least weasel is the one of the major predators investigated as a specialist predator within studies of population dynamics of northern voles. In Aomori, however, very little is known about its biology, abundance or habitat requirement, and further studies are required.

Note that manipulating predator animals would always require careful consideration for the local biodiversity, as they could cause conflict with non-targeted wild animal conservation.

Provision of alternative food

This is a method to provide preferred food artificially to satisfy the food requirements of a target pest species. This scheme aims to divert vole's foraging pressure from vulnerable fruit tree with some kind of attractive food. If the cause of voles debarking in winter was the limited food source, supplying alternative food could be an effective scheme. There is a history of studies mainly facilitated in Canada. Servello et al. (1984) study indicated that the apple tree bark would not be the most preferable food for voles, but the sugar content of root bark was significantly higher in winter, and that could invoke voles debarking during food shortage time in winter. Food supplement experiment were conducted in Canadian apple orchards (Sullivan, 1988), and the results indicated that the alternative food supply could be a method deserving further exploration (Pelz, 2003).

All schemes for ecological management of rodent is still developing, but there is a growing demand for them. EU organizes conferences of "organic fruit growing" inviting European scientists to exchange information about ecological production and pest management within EU countries every two years, and the proceedings are available online through their website.

Furthermore, the understanding of rodent ecology is advancing, and that scientific knowledge could provide useful inspiration for ecological management of voles. For example, formerly, the predator effect was considered as "predation" itself. But recent studies are revealing the predator is also creating an effect called "fear", such as suppression of activities or enhancing emigration, and its effect on population dynamics is as strong as direct predation. I believe the understanding of conspecific and interspecific interaction could be a help to develop the schemes for vole damage management.

6.3   Experiment to supply alternative food in apple orchards

To verify the effect of alternative food supplement, an experiment was facilitated at orchards in the study site. In apple production, pruning of branches is the usual, essential process during snow season. I frequently observed the branches cut and left on the snow were debarked intensively or brought into the burrows created by voles. The young branches trimmed could be an option for vole's alternative food during winter. Here I facilitated an experiment to verify if providing apple branches at suitable timing could reduce the apple tree damages.

6.3.1   Materials and method

The study was facilitated in orchards in Hirosaki from 2018 and 2019 (Fig. 6-3-1). The study was carried out in one orchard (A) in 2018, and two more orchards (total three orchards; A, B and C) in 2019. Within an orchard, the
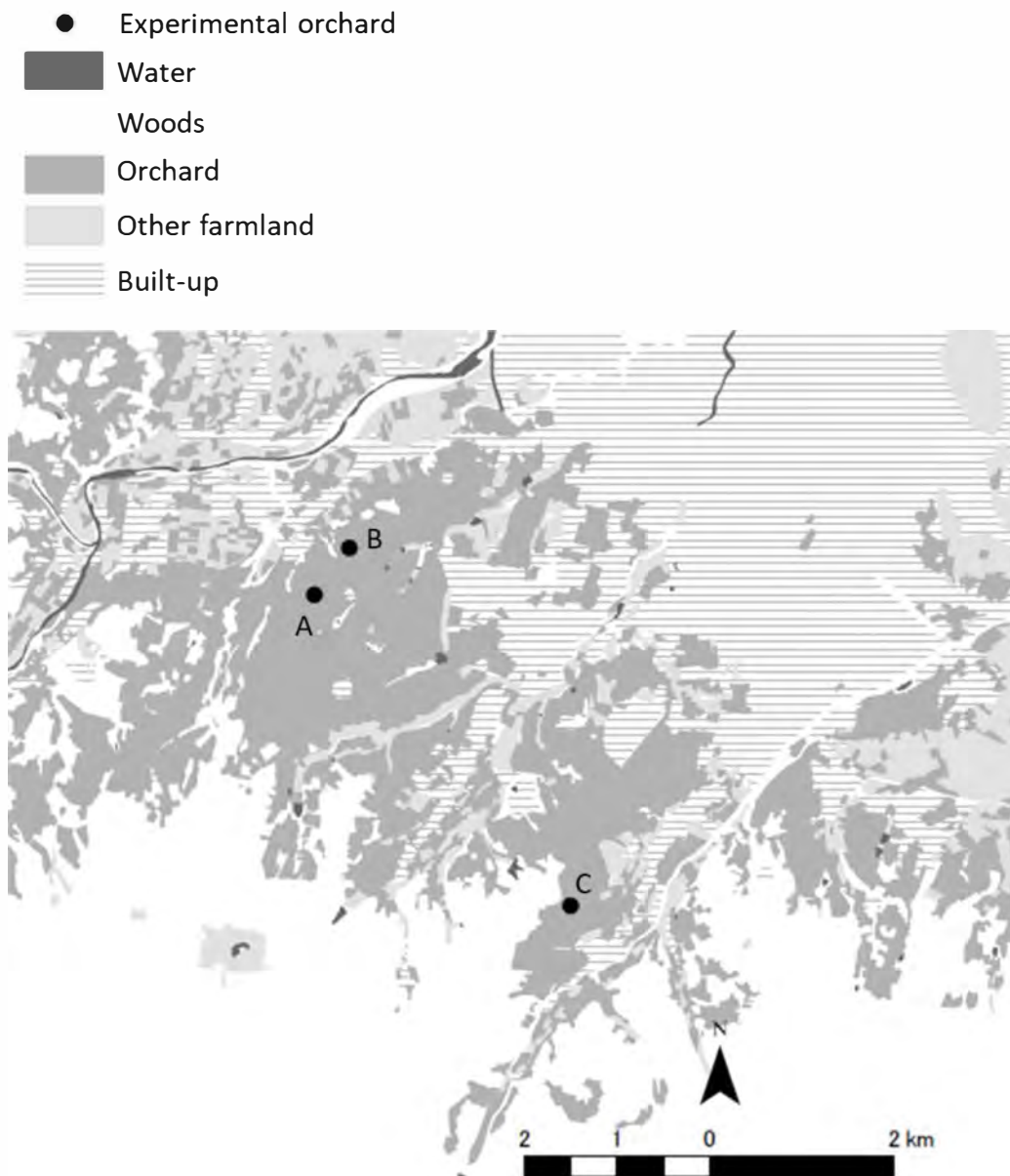
Fig. 6-3-1 The location of orchards for experiments.

two quadrats with approximately the same number of apple trees (21 to 56 apple trees) were set in January. Two quadrats were located at least 20 m apart considering the home range of Japanese field vole. In a treatment quadrat, the apple trees were pruned in January, and all pruned branches were left on the snow so voles could reach. In a control quadrat, the apple pruning was held until the middle of March, just before the snowmelt, and no

branches were supplied during January and February. In April after snowmelt, the area debarked by voles were measured with scales and calculated into an area (cm^2) per each tree. The damage area difference between treatment and control was tested with Welch's t-test.

6.3.2 Result

Among four treatment quadrats, one in 2018 and one in 2019 had significantly smaller damage by voles compared to their control sites (Fig. 6-3-2). In 2019, however, the treatment quadrat in orchard A had significantly larger damage (Fig. 6-3-2). In orchard B, the treatment did not make significant difference to damaged area in 2019. In orchard C, there was no damage occurred in the treatment site, which was significantly different from the damage at the control site.
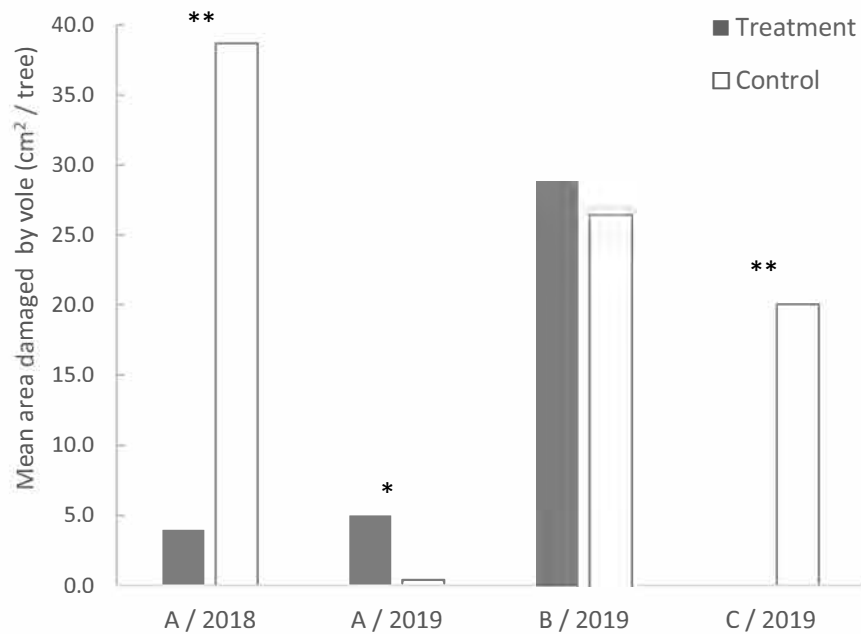
Fig. 6-3-2 Mean area damaged by vole in four orchards.

6.3.3　Discussion

The significant reductions of vole damaged area were observed in two orchards out of four, although the significant difference could not be detected when all samples were combined. As the damage level could vary year to year, additional experiments are required to conclude the effect of the alternative food supply.

　　　　Generally, the debarked area was 5 cm^2 or less in treatment quadrats except for orchard B. This would be the acceptable damage level in most of the orchards. In orchard B, where the treatment did not present any reduction of debarked area, there were no vole burrows on the surface of accumulated snow around branches. The result in orchard B might be because voles could

not detect the branches on the snow. In a further experiment, the way to spread branches should be improved so that voles can easily detect the branch supply.

  Pruning branches are a part of the regular maintenance process of apple production. If the branches could be the supplemental food resource for vole, it could be an easily employable scheme without any further expenses for land managers.

Chapter 7

Conclusions

My five years study revealed several interesting facts about the management of Japanese field vole in orchards in Aomori. At the same time, it also brought up many challenges and unsolved questions.

As reviewed in this paper, Japanese field vole has flexible breeding biology, and its population dynamics are varied according to the climate of each region. This means the management scheme of voles should also be different in each region. To develop an effective vole management scheme, it is very important to understand the population dynamics of each region and find the critical timing for artificial management.

For Aomori, the population of voles decrease naturally from spring to early summer in most of the orchards. These population dynamics were considered to be driven by mammalian and avian predators (Chapter 3 and Chapter 5). This is an encouraging result, which indicates that the main agent managing vole population, in fact, is the regulating service provided by ecosystem including predators, and it is not impossible to develop an ecologically sound management scheme of pest voles in orchards in Aomori. After the result of our nest box study (Chapter 5) was published, many more nest boxes had been installed in orchards for owls in Aomori. Now we need to focus on the long-term change of vole damage in the area with nest boxes,

to verify the predator effect on a larger scale. At the same time, the other predator's population and ecology also should be explored, and their contribution to ecological service should be accurately evaluated. A non-poisoning management scheme should be also widely disseminated and tested in the field.

The mechanism which drives voles debarking is still an open question. Obviously, there seems to be a general tendency that higher vole abundance during winter tends to result in larger vole damage. But the damage does not always occur when the vole abundance was high. Those factors to influence vole's behaviour and induce debarking, including both biological condition and abiotic environment need to be further explored in the future. Once we could understand the important factors, we can forecast the expected damage level from the vole abundance in fall and decide if we should add additional treatments or not. To disentangle the mechanism of vole damages and find the threshold for additional treatment, a long-term, basic assessment is essential. Luckily, Aomori Prefectural Agricultural Pest Control Office had been assessing the vole damage in apple orchards quantitatively for the last three decades. Hopefully in the future, the abundance of Japanese field vole in spring and fall will also be monitored for an in-depth understanding and providing accurate information for land managers.

Bibliography

Abe, T. (1974). An Analysis of Age Structure and Reproductive Activity of *Micortus montebelli* Population Based on Yearly Trapping Data. *Japanese Journal of Applied Entomology and Zoology*, 18, 21– 27. https://doi.org/10.1303/jjaez.18.21. (In Japanese)

Abe, T. (2002). *Waika deno Mondaiten II, Choujuugai: Nezumi* [Issues of dwarfing pomology II, Bird and animal damage: Vole]. In: Rural Culture Association Japan (ed.) *Nougyou Gijutsu Taikei: Kaju [Agriculture technique system: Fruits]* (pp. waza 417- waza 420-2). Tokyo, Japan: Rural Culture Association Japan. (In Japanese)

Abramsky, Z., Strauss, E., Subach, A., Kotler, B. P., & Riechman, A. (1996). The effect of barn owls (Tyto alba) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia*, 105, 313– 319. https://doi.org/10.1007/BF00328733

Albert, C.A., Wilson, L.K., Mineau, P., Trudeau, S. & Elliott, J.E. (2010). Anticoagulant rodenticides in three owl species from western Canada, 1988–2003. *Archives of Environmental Contamination and Toxicology*, 58, 451-459. https://doi.org/10.1007/s00244-009-9402-z

Arai, S. & Shiraishi, S. (1982). Population Ecology of the Japanese field vole (*Microtus montebelli*) in Kyushu: I. Changes in population size and home range. *Science bulletin of the Faculty of Agriculture, Kyushu University*, 36, 89-99. (In Japanese with English abstruct)

Azuma, N. (2007). *Ringoen to Fukurou* [Apple orchard and owls]. *Wild Birds*, 706, 15. (in Japanese)

Barbaro, L., Rusch, A., Muiruri, E. W., Gravellier, B., Thiery, D., & Castagneyrol, B. (2017). Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. *Journal of Applied Ecology*, 54, 500– 508. https://doi.org/10.1111/1365-2664.12740

Beer, J. R. & MacLeod, C.F. (1961). Seasonal reproduction in the meadow vole. *Journal of mammalogy*, 42, 483-489.

Berny, P. (2007). Pesticides and the intoxication of wild animals. *Journal of Veterinary Pharmacology & Therapeutics*, 30, 93– 100. https://doi.org/10.1111/j.1365-2885.2007.00836.x

Bjørnstad, O. N., Stenseth, N. C., & Saitoh, T. (1999). Synchrony and scaling in dynamics of voles and mice in northern Japan. *Ecology*, 80, 622– 637. https://doi.org/10.2307/176640

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for fool security. *Trends in Ecology & Evolution*, 28, 230– 238. https://doi.org/10.1016/j.tree.2012.10.012

Bonnet, T., Crespin, L., Pinot, A., Bruneteau, L., Bretagnolle, V., & Gauffre, B. (2013). How the common vole copes with modern farming: Insights from a capture-mark-recapture experiment. *Agriculture, Ecosystems and Environment*, 177, 21-27.

Brooks, M.E., Kristensen, K., Van Benthem. K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Ma¨chler, M. & Bolker, B.M. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378– 400 DOI 10.32614/RJ-2017-066.

Chaplin‐Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta‐analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, 14, 922– 932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Cramp, S., Brooks, D. J., Dunn, E., Gillmor, R., Hollom, P. A. D., Hudson, R., … Wilson, M. G. (1985). *Handbook of the birds of Europe, the middle East and North Africa. The birds of the Western Palearctic (Vol. 4)*. Oxford, UK: Oxford University Press.

Decker, K. L. M. Wang, D. Waite, C. & Scherbatskoy, T. (2003) Snow removal and ambient air temperature effects on forest soil temperatures in northern Vermont. *Soil Science Society of America journal*, 67, 1234–

1243.

Delattre, P., Giraudoux, P., Baudry, J., Musard, P., Toussaint, M., Truchetet, D., Stahl, P.A., Poule, M.L., Artois, M., Damange, J.P., & Quere, J. (1992). Land use patterns and types of common vole (Microtus arvalis) population kinetics. *Agriculture, Ecosystems & Environment*, 39, 153-168.

Delattre, P., Giraudoux, P., Baudry, J., Quéré, J. P., & Fichet, E. (1996). Effect of landscape structure on Common Vole (Microtus arvalis) distribution and abundance at several space scales. *Landscape Ecology*, 11, 279–288. https://doi.org/10.1007/BF02059855

Delattre, P., Morellet, N., Codreanu, P., Moit, S., Quere, J. P., Sennedot, P., & Baudry, J. (2009). Influence of edge effects on common vole population abundance in an agricultural landscape of eastern France. *Acta Theriologica*, 54, 51– 60. https://doi.org/10.1007/BF03193137

Department of Agriculture, Forestry and Fisheries, Aomori Prefecture (2016) '*Heisei 25 nen Ringo tou kaju no kisho saigai to taisaku - Kirokuteki na oyuki ya oame ni tachimukatta kiroku –* [The weather hazards on fruit production and our countermeasures in 2013 – Report of our effort for extreme snow and heavy rain-]'. Ringo kajuka Shiryo 410 [Report 410, Department of Apple and Fruit, Aomori prefecture] 78pp. Aomori, Japan. (In Japanese)

Duchesne, D., Gauthier G. & Berteaux,D. (2011) Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia*, 167, 967–980. DOI 10.1007/s00442-011-2045-6

Dupuy, G., Giraudoux, P., & Delattre, P. (2009). Numerical and dietary response of a predator community in a temperate zone of Europe. *Ecography*, 32, 277– 290.
https://doi.org/10.1111/j.1600-0587.2008.04930.x

Editorial committee of Shokubutsu boueki kouza (1982). '*Shokubutsu boueki kouza*' [Plant epidemic control cource]. Japan Plant Protection Association, Tokyo, 259pp.

Food and Agricultural Materials Inspection Center (2019). 'Shikkou nouyaku ichiran' [Database of lapsed agrichemicals], available at:
https://www.acis.famic.go.jp/toroku/index.htm (Accessed on 2019, December 02).

Fuelling, O., Walther, B., Nentwig W. & Airoldi J. (2010). Barriers, Traps and

Predators – An integrated approach to avoid vole damage. *Proceedings of the Vertebrate Pest Conference, 24*. R. M. Timm & K. A. Fagerstone, Eds., University of California, Davis, 222-227. https://doi.org/10.5070/V424110631

Gauffre, B., Petit, E., Brodier, S., Bretagnolle, V. & Cosson, J.F. (2009). Sex-biased dispersal patterns depend on the spatial scale in a social rodent. *Proceedings of the Royal Society B*, 276, 3487-3494.

Gelman, A., Carlin, J., Stern, H. S. and Rubin, D. B. (2004). '*Bayesian Data Analysis, Second edition*'. Chapman&Hall/CRC, Boca Raton, 668 pp.

Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis* 1(3):515-534

Haapakoski, M., Sundell, J., & Ylönen, H. (2012). Predation risk and food: Opposite effects on overwintering survival and onset of breeding in a boreal rodent. *Journal of Animal Ecology*, 81, 1183– 1192. https://doi.org/10.1111/j.1365-2656.2012.02005.x

Hanski, I., Hansson, L., & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, 60, 353– 367. https://doi.org/10.2307/5465

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L., & Turchin, P. (2001). Small‐rodent dynamics and predation. *Ecology*, 82, 1505– 1520.

Hansson, L. & Henttonen, H. (1985). Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia*, 67: 394-402. https://doi.org/10.1007/BF00384946

Hayssen, V., A. van Tienhoven, and A. van Tienhoven. (1993). '*Asdell's patterns of mammalian reproduction: A compendium of species-specific data*'. Cornell University Press, New York.

Higashi, A. (1954); Hokkaido no dojo touketsu; Sekisetsu tono Kankei [Soil freeze in Hokkaido; In relationship with snow depth]. *Nougoubutsuri Kenkyujo Houkoku*, 34, 145-157. (In Japanese)

Huitu, O., Koivula, M., Korpimäki, E., Klemola, T. & Norrdahl, K. (2003). Winter food limits growth of northern vole populations in the absence of predation. *Ecology*, 84. 2108-2118. 10.1890/02-0040.

Ims, R. A., & Andreassen, H. P. (2000). Spatial synchronization of vole population dynamics by predatory birds. *Nature*, 408, 194– 196. https://doi.org/10.1038/35041562

Ishikawa, M. & Suzuki, T. (1965). Distribution of maximum freezing depths in

the ground in the winter of 1964-1965 in Hokkaido. *Annual Report of the Hokkaido Branch Forest Experiment Station 1964*, 238-241. (In Japanese)

Ito, T. (1975). Outbreaks of the field vole, *Microtus montebelli*, in Kansai and Chugoku districts. *Bulletin of the Forestry and Forest Products Research Institute*, 271, 39– 92. (in Japanese)

Iwao, T., Kitazawa, T. & Morozumi, M. (1960). On the relations of length of large intestine and caecum against the length of small intestine in Rats. *Zoological magazine*, 69, 171-176.

Jacuot, M., Coeurdassier, M., Couval, G., Renaude, R., Pleydell, D., Truchetet, D., Raoul, F. & Giraudoux, P. (2013) *Journal of Applied Ecology*, 50, 1406-1414. doi: 10.1111/1365-2664.12151.

Jochym, M., & Halle, S. (2013). Influence of predation risk on recruitment and litter intervals in common voles (*Microtus arvalis*). *Canadian Journal of Zoology*, 91, 281– 286. https://doi.org/10.1139/cjz-2012-0249

Jolly G.M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52(1-2):225-248

Kaneko, Y. (1975). Mammals of Japan (12): Order Rodentia, Genus *Microtus*. *Mammalian Science*, 30, 3-26. (in Japanese)
DOI: https://doi.org/10.11238/mammalianscience.15.1_3.

Kaneko, Y. (1976). Reproduction of Japanese field vole, *Microtus montebelli (Milne-Edwards)*, at Iwakura, Kyoto, Japan. *Japanese Journal of Ecology*, 26, 107-114.

Kaneko, Y. (2008). Japanese grass vole; *Microtus montebelli (Milne‐Edwards, 1872)*. In H. Abe (Ed.), A guide to the mammals of Japan (2nd revised ed.,). Tokai University Press, 206 pp, Hadano, Japan.

Kéry, M. & Schaub, M. (2012) *'Bayesian population analysis using WinBUGS: a hierarchical perspective'.* Academic Press, p.555.

Kimura, Y., Saito, K., & Hachiya, T. (1980). On the breeding activity of the Japanese field voles, *Microtus montebelli*, at Mizuhara in Fukushima City. *Science reports of the Faculty of Education Fukushima University*, 30, 33– 40. (in Japanese with English abstract)

Kitahara, E. (1980). Notes on Ecological Respects of High Dense *Microtus* Population. *The Journal of the Mammalogical Society of Japan,* 8(4),

144-147. https://doi.org/10.11238/jmammsocjapan1952.8.144

Klemola, T., Tanhuanpää, M., Korpimäki, E., & Ruohomäki, K. (2002). Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos*, 99, 83– 94. https://doi.org/10.1034/j.1600-0706.2002.990109.x

Kobayashi, K. (1978). *'Birds of Japan in natural colours'. New edition*. Osaka, Japan: Hoikusha Publishing. (in Japanese)

König, C., Weick, F., & Becking, J.‐H. (1999). '*Owls: A guide to the Owls of the world'*. Sussex, UK: Pica Press.

Korpimäki, E., & Norrdahl, K. (1991). Do breeding nomadic avian predators dampen population fluctuations of small mammals? *Oikos*, 62, 195– 208. https://doi.org/10.2307/3545265

Korpimäki, E., Norrdahl, K., & Valkama, J. (1994). Reproductive investment under fluctuating predation risk: Microtine rodents and small mustelids. *Evolutionary Ecology*, 8, 257– 268.

Korpimäki, E., & Sulkava, S. (1987). Diet and breeding performance of Ural Owls Strix uralensis under fluctuating food conditions. *Ornis Fennica*, 64, 57– 66.

Kross, S. M., Bourbour, R. P., & Martinico, B. L. (2016). Agricultural land use, barn owl diet, and vertebrate pest control implications. *Agriculture, Ecosystems and Environment*, 223, 167– 174. https://doi.org/10.1016/j.agee.2016.03.002

Labuschagne, L., Swanepoel, L. H., Taylor, P. J., Belmain, S. R., & Keith, M. (2016). Are avian predators effective biological control agents for rodent pest management in agricultural systems? *Biological Control*, 101, 94– 102. https://doi.org/10.1016/j.biocontrol.2016.07.003

Lima, S. L. (1998). Nonlethal effects in the ecology of predator–prey interactions. *BioScience*, 48, 25– 34. https://doi.org/10.2307/1313225

Lindenmayer, D. B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., … Gibbons, P. (2009). Are nest boxes a viable alternative source of cavities for hollow‐dependent animals? Long‐term monitoring of nest box occupancy, pest use and attrition. *Biological Conservation*, 142, 33– 42. https://doi.org/10.1016/j.biocon.2008.09.026

Liro, A. (1974) Renewal of burrows by the common vole as the indicator of

its numbers. *Acta Theriologica*, 19, 259-272.

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, 56, 311– 323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Lundberg, A. (1981). Population ecology of the Ural owl *Strix uralensis* in Central Sweden. *Ornis Scandinavica*, 12, 111– 119. https://doi.org/10.2307/3676035

Lundberg, A., & Westman, B. (1984). Reproductive success, mortality and nest site requirements of the Ural owl *Strix uralensis* in central Sweden. *Annales Zoologici Fennici*, 21, 265– 269.

MacLean, S. F., Fitzgerald, Jr., B. M. & Pitelka, F. A. (1974). Population Cycles in Arctic Lemmings: Winter Reproduction and Predation by Weasels. *Arctic and Alpine Research*, Vol. 6, 1-12. DOI: 10.2307/1550365.

Mahlaba TAM, Monadjem A, McCleery R, Belmain SR (2017) Domestic cats and dogs create a landscape of fear for pest rodents around rural homesteads. *PLoS ONE* 12(2): e0171593. https://doi.org/10.1371/journal.pone.0171593

Matsuoka, S. (1977). Winter food habits of the Ural owl *Strix uralensis Pallas* in the Tomakomai experiment forest of Hokkaido University. *Research Bulletin of the College Experiment Forest, Hokkaido University*, 34, 161– 173. (in Japanese with English abstract)

McMurtry, J. A., & Croft, B. A. (1997). Life‐style of phytoseiid mites and their roles in biological control. *Annual Review of Entomology*, 42, 291– 321. https://doi.org/10.1146/annurev.ento.42.1.291

Meunier, F.D., Verheyden, C. & Jouventin, P. (2000) Use of roadsides by diurnal raptors in agricultural landscapes. *Biological Conservation*, 92, 291-298.

Meyrom, K., Motro, Y., Leshem, Y., Aviel, S., Izhaki, I., Argyle, F., & Charter, M. (2009). Nest‐box use by the Barn Owl *Tyto alba* in a biological pest control program in the Beit She'an valley, Israel. *Ardea*, 97, 463– 467. https://doi.org/10.5253/078.097.0410

Michel, N., Burel, F., & Butet, A. (2006). How does landscape use influence small mammal diversity, abundance and biomass in hedgerow networks of farming landscapes? *Acta Oecologica*, 30, 11– 20. https://doi.org/10.1016/j.actao.2005.12.006

Ministry of Agriculture, Forestry and Fisheries. (2016). '*Kaju Kihonhoushin*

[Basic principle of fruit production]'. Retrieved from: http://www.maff.go.jp/j/seisan/ryutu/fruits/index.html

Ministry of Agriculture, Forestry and Fisheries (2019). '*Yasei choujugai niyoru nousakumotsu higai joukyou*' [Agricultural damage by pest mammals and avians. Retrieved from: http://www.maff.go.jp/tohoku/seisan/tyozyu/higai/index.html [Accessed on November 30, 2019].

Ministry of the Environment (2019) '*Honyurui; Kankyosho Red List 2019*' [Mammals: Ministry of the Environment Red List 2019], available at: https://www.env.go.jp/nature/kisho/hozen/redlist/index.html (In Japanese)

Misaka, K. (1954). '*Saikin no sassozai nitsuite* [About recent rodenticides]'. *Ringyo Gijutsu*, 147, 7-10.

Miyao, T., Morozumi, M. & Morozumi, T. (1966). Small mammals of Mt. Yatsugatake in Honshu, VI. Seasonal variation in sex ratio, body weight and reproduction in the vole, *Microtus montebelli*. *Zoological magazine* 75, 98-102.

Mols, C. M. M., & Visser, M. E. (2002). Great tits can reduce caterpillar damage in apple orchards. *Journal of Applied Ecology*, 39, 888– 899. https://doi.org/10.1046/j.1365-2664.2002.00761.x

Morii, R., & Shioiri, T. (1996). On the pellet contents of the Ural owl, *Strix uralensis hondoensis*. *Kagawa Seibutsu*, 23, 15– 20. (in Japanese with English abstract)

Muggeo, V. M. R. (2008). segmented: An R package to fit regression models with broken‐line relationships. *R News*, 8, 20– 25. Retrieved from https://cran.r-project.org/doc/Rnews/

Munoz‐Pedreros, A., Gil, C., Yanez, J., & Rau, J. R. (2010). Raptor habitat management and its implication on the biological control of the Hantavirus. *European Journal of Wildlife Research*, 56, 703– 715. https://doi.org/10.1007/s10344-010-0364-2

Murano, C., Kasahara, S., Kudo, S., Inada, A., Sato, S., Watanabe, K., & Azuma, N. (2018). Effectiveness of vole control by owls in apple orchards. *Journal of Applied Ecology*, 56, 677-687. https://doi.org/10.5061/dryad.cf88n7g

Nagorsen D.W. & Peterson R.L. (1980). '*Mammal Collectors' Manual: A guide for collecting, documenting, and preparing mammal specimens for*

scientific research'. Life sciences miscellaneous publications, Royal Ontario Museum, 79pp.

Nakata, K., Akashi, N. & Unno, A. (2009). Nonezumi hassei yosatsu no hensen to kongo [The history and future of rodent abundant estimation]. *Shinrin hogo*, 315, 17-21.

Nakata, K. (2015). *'Handbook for vole census methods and control (3rd ed.)'*. Sapporo, Japan: Hokkaido Forest Management Corporation. (in Japanese)

Nakatsu, A. (1977). Some observations on the Japanese field vole, *Micortus montebelli (Milne-Edwards)* in captivity II reproduction and growth of voles according to size of litter. *Bulletin of the Government Forest Experimental Station*, 297, 35-42.

Norrdahl, K. & Korpimäki, E. (2002). Changes in individual quality during a 3-year population cycle of voles. *Oecologia*, 130, 239-249. https://doi.org/10.1007/s004420100795

Nose, K. (1969). Nougyou Kouza: Nouyaku no atarashii kaisetsu 27 [Agriculture course: The latest exposit of agrichemicals 27]. Agriculture and horticulture, 44, 571-573.

Ohdachi, S.D., Ishibashi, Y., Iwasa, M.A. & Fukui, D. & Saitoh, T. (2015). *The Wild Mammals of Japan,* 2nd Edition. Shoukadoh Book Sellers and the Mammalogical Society of Japan, Sapporo, Japan.

Ota, K. (1960). Monofuluoru sakusan natoriumu (furatolu) no nijiteki dokugai no mondai. [The problem of secondary poisoning of sodium fluoroacetate (Fratol:1080)]. *Forest pests News*, 9(1), 14-15.

Paz, A., Jareno, D., Arroyo, L., Vinuela, J., Arroyo, B., Mougeot, F., … Fargallo, J. A. (2013). Avian predators as a biological control system of common vole (*Microtus arvalis*) populations in north‐western Spain: Experimental set‐up and preliminary results. *Pest Management Science*, 69, 444– 450. https://doi.org/10.1002/ps.3289

Pelz, H. J. (2003). Current approaches towards environmentally benign prevention of vole damage in Europe. In G. R. Singleton, L. A. Hinds, C. J. Krebs, & D. M. Spratt (Eds.), *Rats, mice and people: Rodent biology and management*, (pp. 233– 237). Canberra, Australia: Australian Center for International Agricultural Research. Retrieved from: http://aciar.gov.au/publication/mn096

Pietiainen, H. (1989). Seasonal and individual variation in the production of

offspring in the Ural owl *Strix uralensis*. *Journal of Animal Ecology*, 58, 905– 920. https://doi.org/10.2307/5132

Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In (Hornik, K., Leisch, F. and Zeileis, A., eds.) *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, Vienna (Austria). Available at https://www.r-project.org/conferences/DSC-2003/Proceedings/ Plummer.pdf.

Plummer, M. (2018) rjags: Bayesian Graphical Models using MCMC. R package version 4-8. Available at https://CRAN.R-project.org/ package=rjags.

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, 86, 501– 509. https://doi.org/10.1890/04-0719

Prevedello, J. A., Dickman, C. R., Vieira, M. V., & Vieira, E. M. (2013). Population responses of small mammals to food supply and predators: A global meta‐analysis. *Journal of Animal Ecology*, 82, 927– 936. https://doi.org/10.1111/1365-2656.12072

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

R Core Team. (2018). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/.

Rood F.H. & Boonstra R. (1988). Effects of adult Meadow voles *Microtus pennsylvanicus*, on young conspecifics in field populations. *Journal of Animal ecology*, 57, 755-770.

Royle, J.A., Dorazio, R.M. & Link, W.A. (2007). Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphic Statistics,* 16(1):67-85

Ruiz-Suarez, N., Henriquez-Hernandez, L.A., Valeron, P.F., Boada, L.D., Zumbado, B.M, Camacho, M & Luzardo, P.P. (2014) Assessment of anticoagulant rodenticide exposure in six raptor species from the Canary Islands (Spain). *Science of the Total Environment*, 485-486, 371-376.

Rusch, A., Chaplin‐Kramer, R., Gardiner, M. M., Hawro, V., Holland, J., Landis, D., & Bommarco, R. (2016). Agricultural landscape simplification

reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystem and Environment*, 221, 198– 204. https://doi.org/10.1016/j.agee.2016.01.039

Salo, P., Banks, P. B., Dickman, C. R., & Korpimäki, E. (2010). Predator manipulation experiments: Impacts on populations of terrestrial vertebrate prey. *Ecological Monographs*, 80, 531– 546. https://doi.org/10.1890/09-1260.1

Saito, T (2002) Mori no nezumi no seitaigaku – Kotaisu hendou no nazo wo saguru - [Biology of mice in the forest -Investigating the mysteries of population dynamics]. Kyoto University Press, Kyoto.

Saito, T., Machida, K., Inoue, S. & Takahashi, M. (1980). Reproductive activity of Microtus montebelli at Okegawa city in Saitama prefecture. *The Journal of the Mammalogical Society of Japan*, 8(4), 122-128.

Saito, T., Stenseth, N.C. & Bjornstad, O.N. (1998). The population dynamics of the Vole *Clethrionomys rufocanus* in Hokkaido, Japan. *Researches on Population Ecology*, 40, 61-76.

Saito, T., Cazelles, B., Vik, J.O., Vilijugrein, H. & Stenseth, N.C. (2006). Effect of regime shifts on the population dynamics of the grey-sided vole in Hokkaido, Japan. *Climate Research*, 32, 109-118.

Saucy, F. (2004). Manipulating dispersal as a tool in the biological control of small mammals. C. J. Feare and D. P. Cowan (Eds.), *'Advances in Vertebrate Pest Management III'*, 9-28. Filander Verlag, Fürth.

Schlötelburg, A., Plekat, A., Bellingrath-Kimura, S. & Jacob, J. (2019). Self-service traps inspected by avian and terrestrial predators as a management option for rodents. *Pest management science*. https://doi.org/10.1002/ps.5550

Seber G.A.F. (1965). A note on the multiple-recapture census. *Biometrika* 52(1-2):249-260

Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology and Evolution*, 21, 464– 471. https://doi.org/10.1016/j.tree.2006.05.007

Servello, F., Kirkpatrick, R., Webb, K., & Tipton, A. (1984). Pine Vole Diet Quality in Relation to Apple Tree Root Damage. *The Journal of Wildlife Management*, 48(2), 450-455. doi:10.2307/3801177

Shimada, T. & Moriya, S. (2018). Preference of Japanese field voles (*Microtus montebelli*) for apple rootstock genotypes: correlations with bark

characteristics. *Crop Protection*, 112, 239-245.

Shiraishi, H., & Kitahara, M. (2007). A study on the breeding ecology of the Ural Owl, *Strix uralensis*, which utilized an artificial nest, and its prey types and species at the northern foot of Mt. Fuji, Central Japan. *Mount Fuji Research*, 1, 17– 23. (in Japanese)

Singleton, G., Belmain, S., Brown, P. & Hardy, B. (Eds.) (2010). *'Rodent outbreaks: Ecology and impacts'*. Los Banos, CA: International Rice Research Institute.

Stevens, C.S., & Hume, I.D. (1988). '*Comparative Physiology of the Vertebrate Digestive System'*. New York: Cambridge Univ. Press, 320pp.

Sullivan, T.P., Sullivan, D.S. & Granatstein, D.M. (2018). Influence of living mulches on vole populations and feeding damage to apple trees. *Crop protection*, 108, 78-86.

Sundell, J. (2006). Experimental tests of the role of predation in the population dynamics of voles and lemmings. *Mammal Review*, 36, 107– 141. https://doi.org/10.1111/j.1365-2907.2006.00083.x

Suzuki, T., Takatsuki, S., Higuchi, A., & Saito, I. (2013). Food habits of the Ural owl (Strix uralensis) during the breeding season in central Japan. *Journal of Raptor Research*, 47, 304– 310. https://doi.org/10.3356/JRR-12-33.1

Takano, T., Hamaguchi, T., Morioka, T., Kanouchi, T., & Kabaya, T. (1985). '*Wild birds of Japan'*. Tokyo, Japan: Yama‐kei Publishers. (in Japanese)

Tast. J. & Kaukusalo, A. (1976) Winter breeding of the rood vole, Microtus oeconomus, in 1972/1973 at Kilpisjärvi, Finnish Lapland. *Annales Zoologici Fennici*, 13, 174-178.

Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Mobbarco, R., Clement, L. W., & Tscharntke, T. (2011). The relationship between agricultural intensification and biological control: Experimental tests across Europe. *Ecological Applications*, 21, 2187– 2196. https://doi.org/10.1890/10-0929.1

Udagawa, T. (1953). Studies on the extermination of the Field Mice, II. Thequantity of the poison and the shape of the bait used for this purpose. *Bulletin of the Government Forest Experimental Station*, 60, 81-88.

Udagawa, T., Mizuno, T. & Seki, M. (1956). A study of behaviour of the Japanese field vole (*Microtus m. montebelli*) extraordinary increased in late Autumn, 1956. *Bulletin of the Government Forest Experimental Station*, 111, 83-90. (In Japanese with English abstract)

Ueda, M., Higuchi, S., Igarashi, B., Maeda, M., Kuwahata, T., Ota, K., Abe, H., Fujimaki, Y., Fujikura, J. & Takayasu, T. (1966). Historical review of studies on the Bedford's Red-backed vole, *Clethrionomys rufocanus bedfordiae (Thomas)*. *Bulletin of the Government Forestry Experiment Station*, 191, 1-100. (In Japanese with English abstract)

UNCED. (1992). Promoting sustainable agriculture and rural development. *Agenda 21, Chapter 14*, United Nations Conference on Environment and Development.

Vibe‑Petersen, S., Leirs, H., & De Bruyn, L. (2006). Effects of predation and dispersal on Mastomys natalensis population dynamics in Tanzanian maize fields. *Journal of Animal Ecology*, 75, 213– 220. https://doi.org/10.1111/j.1365-2656.2006.01037.x

Walther, B. & Fuelling, O. (2010). Vole trapping fences - a new approach to migration barriers. Foerdergemeinschaft Oekologischer Obstbau e.V. eds. '*14th International Conference on Organic Fruit-Growing: Proceedings to the Conference*', Weinsberg, 341-345.

Watanabe, H. (1989). Breeding ecology of the Ural owl *Strix uralensis*. *Bulletin of the Nagaoka Municipal Science Museum*, 24, 55– 67. (in Japanese)

Watanabe, K. (1962). On the taxonomical and ecological studies of voles, rats and mice, from the point of view of the plant protection of agriculture. *Technical bulletin of Miyagi prefectural agricultural experiment station*, 31, 106pp.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002). '*Analysis and Management of Animal Populations*'. Academic Press, p.817.

Witmer, G.W., Snow, N.P., Humberg, L. & Salmon,T. (2009) Vole problems, management options, and research needs in the United States. *Wildlife Damage Management Conferences – Proceedings*, 140. Retrieved from:
https://digitalcommons.unl.edu/icwdm_wdmconfproc/140/

Wood, B. J., & Fee, C. G. (2003). A critical review of the development of rat control in Malaysian agriculture since the 1960s. *Crop Protection*, 22,

445– 461. https://doi.org/10.1016/S0261-2194(02)00207-7

Yoshinaga, Y., Okayama, T., Ohno, W., & Shiraishi, S. (1997). Growth, development, and reproductive patterns in the Japanese field vole, *Microtus montebelli*. *Journal of Mammalogy*, 78, 830– 838. https://doi.org/10.2307/1382941

Acknowledgment