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Analyses of population dynamics and establishment of harvest-based  
population estimation methods in the sika deer (*Cervus nippon*) in  
Hokkaido, Japan

(北海道に生息するニホンジカ(*Cervus nippon*)個体群の動態解明と  
捕獲数を用いた個体数推定法の確立)

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## Chapter 1

### General Introduction

#### *Why should we control deer populations?*

Overabundance has been a common problem in the world and represents one of the greatest challenges facing wildlife professionals during the 21st century (Warren 1997). Animals are diagnosed as “overabundant” when they (a) threaten human life or livelihood, (b) are too many for their “own good”, (c) depress the densities of economically or aesthetically important species, or (d) cause ecosystem dysfunction (Caughley 1981). We require management to ensure that their numbers do not affect other land-use objectives, including agriculture, forestry and habitat requirements for other species (Gill 1992, McShea et al. 1997).

Although various species are diagnosed as overabundant to date (e.g. the wild boar *Sus scrofa*, Gortázar et al. 2006; the greater snow geese *Anser caerulescens atlanticus*, Menu et al. 2002; the raccoon *Procyon lotor*, the otter *Enhydra lutris*, and the seal *Leptonychotes weddelli*, Garrot et al. 1993), the taxon of Cervidae includes a large number of species in state of “overabundance”. Many cervid species have increased dramatically throughout Europe, North America and Japan over the last century (the red deer *Cervus elaphus*, Clutton-Brock et al. 2004; the roe deer *Capreolus capreolus*, Anderson and Linnell 2000; the sika deer *Cervus nippon*; Kaji et al. 2000; the Ministry of the Environment of Japan 2004; the white-tailed deer, *Odocoileus virginianus*, Knox 1997). As for causes of the overabundance, increasing availability of forage due to changing land use is listed as well as reduced predation from large carnivores, strict hunting regulation, and recent mild winter (reviewed in Côté et al. 2004). Consequently, dense deer populations are exerting an increase in grazing and browsing pressure on agriculture (Conover 2001) and forestry (Akashi 1998, 1999); Tilghman (1989) clearly

demonstrated density-dependent browsing effect on forests using white-tailed deer in enclosures. Browsing by deer affects plant community structure and abundance of rare species (Alverson et al. 1988, Brandner et al. 1990, Kaji et al. 1991, Yokoyama and Shibata 1998) and the population and community composition of many invertebrates, birds, and small mammals (Côté et al. 2004, Hino et al. 2006). Moreover, deer-vehicle and -train collisions have been dramatically increasing (Groot and Hazebroek 1996, Uno et al. 1995, HIES 1997, Ohtaishi et al. 1998). High population densities of deer appear to increase the transmission risk of tick-borne zoonoses (Wilson and Childs 1997, Ostfeld and Keesing 2000).

To stabilize or reduce high-density populations causing severe and irreversible impact on forests, a number of techniques have been developed: defensive methods such as fencing, repellents, and offensive methods such as population control by contraception, immunosuppression and culling (Brown et al. 2000, Brinkman et al. 2004). Although fencing is effective in reducing damage in a specific area, deer move to another place looking for favorable habitat and cause other damage. The effectiveness of repellents increases with their concentration but decreases with time since application, attractiveness of the food, deer hunger and rainfall (Côté et al. 2004). Therefore, defensive methods may not be an essential solution for overabundance and thus population control is required. Nonlethal population control techniques such as contraception, immunosuppression are labor intensive (Nettles 1997), and has not been ready to broad scale management application (Smith and Coggin 1984, Garrott et al. 1993, McCullough et al. 1997, McShea et al. 1997). Therefore, culling is the most practical way of population control (Diefenback et al. 1997, Healy et al. 1997, Brown et al. 2000, Koval and Mertig 2004).

*Current population management in deer: establishment of population estimation methods and*

*evaluation of population cull.*

For population control, wildlife managers have manipulated season length and bag limit of 'hunting' that includes voluntary action by hunters and 'pest control' that is motivated to reduce agricultural damage (Diefenback et al. 1997, Healy et al. 1997). Thus, 'culling' aiming for population control actually utilizes opportunities for hunting and pest control with different incentives. In this study, deer killed by human regardless of incentives (hunting and pest control) is expressed as "harvest". Since cervids are polygenous, culling adult females is more effective in reducing population growth than culling males and thus game laws have been reformed to allow culling of more does and fawns (Smith and Coggin 1984, Diefenback et al. 1997, Matsuda et al. 2002, Côté et al. 2004). Harvesting accounts for the majority of mortality where effective predators are few or absent (Gaillard et al. 1998), and adult female mortality is the vital rate with the highest elasticity (i.e., the factor in which a given variation affects dynamics the most; Gaillard et al. 1998, 2001, Lebreton and Clobert 1991). Empirical studies have shown that changes in mortality rates by intensive hunting can dominate population fluctuation (Fryxell et al. 1991, Ferguson et al. 1996, Solberg et al. 1999, Bowyer et al. 1999).

However, there are few examples in which deer abundance has been successfully reduced to a target density level. In Japan, although 31 out of 44 prefectures where deer occur are trying to decrease deer population sizes, there are only two prefectures (Iwate prefecture and Hokkaido prefecture) that limited the population increase, and no area where population size was reduced down to a targeted density level (Uno et al. 2007). Growth in cull size is apparently lower than population growth (Milner et al. 2006a), indicating that culling pressure is not enough. There are three reasons to explain why. First, targeted cull size may be smaller than needed because of underestimation of population sizes (Matsuda et al. 2006). Estimates of absolute population size based on observation indices often underestimate population size due to the low visibility of

deer, e.g., in the mixed coniferous-deciduous forests (Matsuda et al. 2002, Kaji 2006, Uno et al. 2007). Second, current way of culling may not be very efficient: we are not sure if current way of age- or sex-specific culling is effective to control population size, because quantitative effects of culling on population growth are still poorly understood (Milner et al. 2006b). Third, hunters who contribute to population cull are lacking (Milner et al. 2006a): number of hunters is decreasing due to less familiarity of hunting to young generations. The third reason must be overcome from human dimension by sociologists. The first two challenges originate from the difficulty in estimating absolute population size with accuracy and precision. Although good population estimates may be possible by Capture-Mark-Recapture methods (CMR), sufficient number of marked individuals during many years (over 100 for adult deer; Gaillard et al. 1998) is required. This indicates too labor consuming to perform CMR methods in population management. Therefore, we have to explore cost effective way of estimating absolute population size and quantifying effect of culling on population growth for successful population management (Macnab 1985, Matsuda 2006, Milner et al. 2006a).

#### *Double-scale sampling*

To achieve these challenges, here I introduce population estimation methods targeting two hierarchal scales: a large scaled area and a modeled small area within the large area. For a large scaled area, cheap methods are applied to estimate absolute population sizes. Within that area, we set up a particular area as a modeled area to collect intensive data enough to quantify effect of culling on population growth rate. Then, we obtain a population dynamics model from the modeled area and apply the model into population estimation in the large scale. I focus on two set of data: harvest data and population index by spotlight survey. Harvest data is most available in wildlife management (Bender and Spencer 1999) and represents the minimum size of a

population. By investigating ages of harvested animals, harvest-at-age data becomes informative and can be analyzed in various ways. The other data, population index from spotlight survey has shown to reflect temporal trend in population dynamics (Uno et al. 2006). These two data sets are usually available in areas where population management is carried out. Thus, using harvest data and population index by spotlight survey, establishment of cost effective and accurate estimation methods for absolute population size and quantification of culling on population growth will be possible.

*Current status of sika deer population in Hokkaido Japan.*

The sika deer population in Hokkaido gradually recovered in abundance and distribution from the bottleneck (-1950s) under government protection, and by the mid-1970s the population occupied most available habitats in eastern Hokkaido (Kaji et al. 2000). Increase in availability of bamboo grass (*Sasa* spp.) after logging, increase of agricultural land and increase of forested landscapes at an early successional stage since 1960s may have provided abundant, high-quality food that may have increased carrying capacity of deer habitat (Kaneko et al. 1998). As sika deer expanded their distribution range, agricultural and forest damage increased and thus Hokkaido government has relaxed hunting regulations (Kaji et al. 2000, Matsuda et al. 2002). To reduce the damage caused by deer, doe hunting was allowed in restrict areas for 10 days in 1994. Doe hunting was allowed in wider areas for 1 month. Ultimately the hunting chance increased 20-fold by 1997. From 1998, the catch limit increased to 2 does or 1 doe and 1 buck per day per hunter, and deer hunting was allowed for 3 months (Matsuda et al. 2002, Table 3.1, Table 4.1). The relative population index calculated based on spotlight survey increased from 1992 to 1998 and then became stable after some reduction (Uno et al. 2006, Yamamura et al. 2008). Nevertheless, population density is still high above a target density (Uno et al. 2007). We

need to quantify the performance of sex-specific culling and changes in culling opportunities as a population control.

Hokkaido government conducted a structured data collection, one is intensive research focused on specific areas; the other is applied to entire area of Hokkaido island using low-cost methods. Intensive research includes pregnancy rate measure, age determination of harvested animals, and absolute count of an island population, whereas large scale research includes harvest inventory based on annual reports from hunters, spotlight survey, and calculation of damage on agriculture and forestry (Uno et al. 2006). Thus, collection system of harvest data in Hokkaido suits for examining an establishment of population estimation methods targeting two hierarchal scales.

#### *Aim of this thesis*

Aim of this thesis is to establish harvest-based population estimation methods and evaluate sex-specific culling as a population control qualitatively and quantitatively. I conducted following three studies using harvest data of a moose population in Norway and a sika deer population in Eastern Hokkaido in Japan. First, we examined and modified an estimation method by population reconstruction using harvest-at-age data to apply to large terrestrial mammals (Chapter 2). Second, I reconstructed a sika deer subpopulation in Eastern Hokkaido using the method examined in Chapter 2 and analyzed the dynamics of a deer population to examine effect of sex-specific culling on the population (Chapter 3). Third, I established a large scale population estimation method by combining intensively surveyed data at subpopulation scale with data by a low-cost method at an entire population scale (Chapter 4). Finally, I discussed application of harvest-based population estimation methods examined in this thesis for sika deer management (Chapter 5).

## Chapter 2

### Application of cohort analysis for harvest data on large terrestrial mammals

#### 2.1 Introduction

Modern wildlife management often depends on good estimates of population size and growth. Although radio-telemetry surveys provide reliable estimates of population sizes via capture-mark-recapture methods (Lebreton et al. 1992), their efficacy depends on the number of individuals animals included in the surveys, making the method time- and labor-intensive in many cases where accuracy of estimation is of importance. On the other hand, large harvest data sets for game species, often collected by age and sex as part of wildlife agency management programs (Skalski and Millspaugh 2002; Conn et al. 2008), are more readily available; under many circumstances, these data can be useful for population estimation.

Cohort analysis (also known as virtual population analysis, VPA) is a method for population reconstruction applied to age-specific harvest data (harvest-at-age). Originally developed in fisheries science (Gulland 1965; Pope 1972), the technique has been applied to commercially harvested fish stocks (bigeye tuna *Thunnus obesus*, Nishida and Takeuchi 1999; chub mackerel *Scomber japonicus*, Yatsu et al. 2002; Pacific cod *Gadus macrocephalus*, Ueda et al. 2006), aquatic mammals (sperm whale *Physeter macrocephalus*, Shirakihara 1991; minke whale *Balaenoptera acutorostrata*, Fujise et al. 2005; minke whale, Mori et al. 2007) and terrestrial mammals (red deer *Cervus elaphus*, Lowe 1969; white-tailed deer *Odocoileus virginianus*, McCullough 1979; marten *Martes americana*, Fryxell et al. 1999; roe deer *Capreolus capreolus*, Lowe and Thompson-Schwab 2003). Cohort analysis is based on the principle that individuals born in a particular year (a cohort) will die either from natural causes or from harvesting (i.e., human exploitation) and that mortality may occur at any point in time

up to the cohort's oldest age-class. Cohort analysis enables calculation of the number of individuals in a particular age-class (number-at-age) by aggregating the numbers of animals harvested from that age class ( $a$ ) to the point when they reach oldest age-class ( $A$ ); the natural mortality rate is also incorporated into the calculations. By combining calculations for various cohorts, population size in each year can be reconstructed. Thus, cohort analysis can be a useful method for population reconstruction when harvest-at-age data are available for each year, and the assumptions of a closed population (no immigration or emigration) and a particular natural mortality rate are fulfilled.

There are, however, two major cost- and time-related problems. One is that a long time series of data is required. To calculate total population size for any previous year, data must span a period extending beyond the lifespan of individuals born in that year. This requirement becomes especially problematic in large terrestrial mammals, such as cervids, which can live up to 20 years (Lowe 1969; Solberg et al. 2000). The second problem, arising from the first, is that it is not possible to calculate recent population sizes. We adapted this original cohort analysis to make it more cost effective and to provide real-time estimates for large terrestrial mammals using harvest data.

This estimation can be achieved by combining three models with the original cohort analysis: (1) a model for age-specific harvesting mortality rate in the most recent year, ( $Y$ ; Model A), (2) a model for the rate of harvesting mortality in a composite age class of ( $p$ ) and the older, (plus-group,  $p+$ ; Model B), and (3) a model for the age distribution in the plus-group (Model C), which has been used routinely in fisheries science (Ueda et al. 2006; Yamaguchi and Matsuishi 2007). Applying Models A, B, and C, number-at-age in year  $Y$  and number at age  $p+$  in each year can be estimated. Subsequently, the numbers-at-age for any year can be computed in the same way as the original cohort analysis. Cohort analysis combining the three

models, therefore, is expected to be cost effective and provide real-time estimates for large terrestrial mammals.

However, there has been no cohort analysis for large terrestrial mammals combining these three models. Because each model has particular assumptions regarding rates of harvesting mortality or age distribution in the plus-group, the reliability of estimated numbers-at-age will, in turn, depend on meeting the assumptions. The issue needs to be investigated before cohort analysis combining three models can be applied routinely to large terrestrial mammal harvest data.

With a sufficiently long data set, we can reconstruct a population using the original cohort analysis by assuming that harvest-at-age for the oldest age-class is equal to number-at-age for that age-class. Then, we can compare calculated number-at-age from the original cohort analysis with number-at-age estimated by modeling to test assumptions and to explore potentially more realistic assumptions. This approach is similar to retrospective analysis (e.g., Shimoda et al. 2006). Pope (1972) demonstrated theoretically that estimates will be more robust when aggregated harvests-at-age make up the greatest proportion of the estimates (represented by the rate of age-specific cumulative harvesting mortality). We can therefore examine robustness of the estimates by quantifying the age-specific cumulative harvesting mortality rate. We used harvest-at-age data for moose in Norway collected over a sufficiently long period to enable calculation (by the original cohort analysis method) of number-at-age over a period of several years.

To develop a method for large terrestrial mammal population reconstruction, our objectives were to explore ways to meet realistic assumptions for each of the models A, B, and C, and to determine the extent to which the assumptions affect the robustness of estimated number-at-age. For the first objective, we calculated number-at-age by using the original cohort analysis

method, and then tested previously-used assumptions for Models A, B, and C, exploring comparable alternative assumptions for more reliable estimates. As part of this process, we demonstrated a cohort analysis combining three models using limited periods of harvest data, and tested the performance of comparable alternative assumptions. For the second objective, we quantified the age-specific rate of cumulative harvesting mortality to examine the robustness of number-at-age estimations.

## 2.2 Material and methods

### Data

We used harvest-at-age data for female moose in Gausdal municipality, Oppland county, southern Norway (61°26'N, 9°83'E). In the period 1981-2004, 2314 moose were killed in the area and age was determined for 2235 (96.5%) (Solberg et al. 2006). The annual proportions of animals within age groups (0 year-old moose was classified as 'young', 1 year-old as 'yearlings', and  $\geq 2$  year-old as 'adults') ranged between 87% and 100%. To correct for missing individuals, the annual number of moose harvested within each age group was multiplied by a factor correcting for the number of missing individuals in the data set. For example, when only  $x$  of  $y$  adults were harvested and aged in a particular year, the harvest number within each adult age-group for the year was multiplied by  $y/x$  to correct for the deviation. The study area and harvest-at-age data are more fully described by Solberg et al. (2002, 2006).

The following notation was used for analyses:  $C_{a,y}$ , the corrected number of harvest-at-age  $a$  in year  $y$ ;  $N_{a,y}$ , the calculated number of individuals alive at age  $a$  in year  $y$  based on the original cohort analysis;  $F_{a,y}$ , the harvesting mortality rate at age  $a$  in year  $y$  based on the calculated number-at-age;  $M$ , the assumed natural mortality rate. Mortality "rate" in this study

was actually represented by a mortality coefficient rather than a rate. Nevertheless, we refer to mortality rate, as this term is in more general use.

### **Natural mortality rate ( $M$ )**

$M$  was assumed to be 0.05 for young and 0.03 for yearlings and adult individuals (Solberg et al. 1999, 2000, 2006). The choice of  $M$  was based on the very low natural mortality estimated from radio-collared moose in a number of Scandinavian populations (Solberg et al. 2005). No annual variation in  $M$  and no age-specific variation in  $M$  among adult females were assumed. Because survival rate for yearlings and adults is generally high and stable, the effect of these assumptions may be of minor importance in large mammals (Fowler 1987; Sæther 1997; Gaillard et al. 1998; Gaillard et al. 2000). However, because senescence has been detected after 7-9 years of age in ungulate populations (Gaillard et al. 1993, Loison et al. 1999, Festa-Bianchet et al. 2003), higher natural mortalities for older individuals may make the reconstructed population more realistic. Nevertheless, we did not have quantitative data on age-specific natural mortality rate to differentiate older individuals.

### **Testing separate assumptions for Model A, B, and C**

#### **Original cohort analysis**

Let June (birth season) be the start of a year. Assuming that hunting is a pulse-like event that occurs in the middle of the year and that animals are subject to  $M$  throughout the year, the number-at-age ( $N_{a,y}$ ) is given by the following equation (Pope 1972; Yatsu et al. 2002):

$$N_{a,y} = N_{a+1,y+1} \exp(M) + C_{a,y} \exp(M/2) \dots\dots\dots (1).$$

The initial value for calculation by original cohort analysis was the number of individuals at oldest age  $A$  ( $N_{A,y+A-a}$ ). We assumed that  $N_{A,y+A-a}$  was equal to the number harvested at the oldest age ( $C_{A,y+A-a}$ ). Then,  $N_{a,y}$  can be obtained by backward calculation of the number

of individuals from the initial values using Equation (1).

In the original cohort analysis, number-at-age is calculable only for cohorts for which harvest-at-age data were available from  $a$  to  $A$  (Fig. 2.1-a: number-at-age shaded in gray). We used harvest-at-age data from 0 to 14 years of age ( $A = 14$ ) because the number of individuals beyond 14 age is negligibly small (Solberg et al. 1999, 2000, 2006). Thus, using data for the period 1981-2004, we were able to calculate number-at-age for all ages in cohorts alive during the period 1981-1990. Using the calculated number-at-age,  $N_{a,y}$ , we also calculated the age-specific harvesting mortality rate  $F_{a,y}$  as follows (Pope 1972; Yatsu et al. 2002):

$$F_{a,y} = -\ln\left(1 - \frac{C_{a,y} \exp(M/2)}{N_{a,y}}\right) \dots\dots\dots (2).$$

We tested separate assumptions for Models A, B, and C using calculated number-at-age and calculated age-specific harvesting mortality rates for all ages in cohorts alive during the period 1981-1990. The plus-group was set to 9 years of age ( $p = 9$ ) because pooling  $C_{a,y}$  beyond that age made the harvest numbers at ages  $p+$  and  $p-1$  exceed zero in every year.

**Assumptions for Model A**

A model for rate of age-specific harvesting mortality in the most recent year (Model A for  $\hat{F}_{a,y}$ ) assumes that  $\hat{F}_{a,y}$  is equal to the age-specific harvesting mortality rate in the preceding year (Model A-I: Hiramatsu 2001), the arithmetic mean of age-specific harvesting mortality rates during the 3 preceding years (Model A-II; Ueda et al. 2006) or during the preceding 5 years (Model A-III; Yatsu et al. 2002), taking into consideration the circumstances of harvest. These assumptions are differentiated by the period of years they represent. We also examined another model that assumes that  $\hat{F}_{a,y}$  is equal to the arithmetic mean of age-specific

harvesting mortality rates during the preceding 7 years (Model A-IV).

To test which assumption is most realistic, we compared the difference between an estimated value based on a model and a calculated (observed) rate of age-specific harvesting mortality in year  $Y$  ( $Y = 1988, 1989, 1990$ ) between four models:

$$SSR = (F_{a,Y} - \hat{F}_{a,Y})^2 \dots\dots\dots(3).$$

**Assumptions for Model B**

Previous studies have assumed that if there are no differences in behavior or distribution of individuals between consecutive older age classes (ages  $p-1$  and  $p+$ ); the rate of harvesting mortality at age  $p+$  may be assumed to be proportional to the rate of harvesting mortality at age  $p-1$  in all years, with a slope of  $\alpha$  without an intercept. For simplicity,  $\alpha$  was set at 1 (Restrepo and Powers 1991; Shepherd 1999; Hiramatsu 2001; Yatsu et al. 2002; Ueda et al. 2006):

$$F_{9+,y} = \alpha F_{8,y} + \beta \dots\dots\dots(4),$$

where  $\alpha = 1, \beta = 0$  (Model B-i).

We tested Model B-i using rates of calculated harvesting mortality in the last two age classes in the period 1981-1998.

We also modeled harvesting mortality rate at age  $p+$  using the relationship between calculated rates of harvesting mortality for the last two age classes that are calculable for early years using the original cohort analysis. Here, we introduced a simple linear-regression equation for the rate of harvesting mortality at age 9+ against that same mortality rate at age 8:

$$F_{9+,y} = \alpha F_{8,y} + \beta \dots\dots\dots(5),$$

where  $\alpha$  and  $\beta$  were estimated from calculated rates of harvesting mortality in the last two age classes, which are calculable from the original cohort analysis (Model B-ii).

We compared the estimated rate of harvesting mortality at age 9+ ( $\hat{F}_{9+,y}$ ) against the calculated

value ( $F_{9+,y}$ ) for the period 1981-1998 between Model B-i and Model B-ii in order to test which is the more realistic.

### **Assumptions for Model C**

According to Hiramatsu (2001), the sum of number-at-age within the plus group for one year (i.e.,  $N_{9,y} + N_{10,y} + N_{11,y} + N_{12,y} + N_{13,y} + N_{14,y}$ ) is assumed to be equal to the sum of number-at-age within the plus group for a particular cohort (i.e.,

$$N_{9,y} + N_{10,y+1} + N_{11,y+2} + N_{12,y+3} + N_{13,y+4} + N_{14,y+5}).$$

To test the reliability of this assumption, we calculated and compared the sum of number-at-age within the plus group for one year in the period 1981-1999 against the sum of number-at-age within the plus group for corresponding cohorts.

### **Demonstration of cohort analysis combining three models**

#### **Cohort analysis combining three models (Fig. 2.1-b)**

We estimated number-at-age in the period 1981-1990 (i.e.,  $Y = 1990$ ) using  $C_{a,y}$  for this period from cohort analysis combining three models. We examined the performance of eight scenarios (Model A-I, -II, -III, -IV combined with Model B-i, -ii and Model C).

For Model B-ii, we introduced a regression equation of the calculated rate of harvesting mortality at age 9+ against that at age 8 in the period 1981-1984 using  $C_{a,y}$  over this time span (see gray area in Fig. 2.1-a).

We first estimated age-specific harvesting mortality rate in the most recent year,  $\hat{F}_{a,y}$ , and the rate of harvesting mortality at age  $p+$  in all years,  $\hat{F}_{p+,y}$ , based on Models A and B, respectively. Details of the computation of  $\hat{F}_{a,y}$  and  $\hat{F}_{p+,y}$  are shown in Appendix I.

Using these estimates, we computed the age-specific number of moose in the most recent year  $Y$  (Hiramatsu 2001):

$$\hat{N}_{a,y} = \frac{C_{a,y}}{1 - \exp(-\hat{F}_{a,y})} \exp\left(\frac{M}{2}\right) \dots\dots\dots (6).$$

Similarly, we computed the number of moose of age  $p+$  in all years as follows (Hiramatsu 2001):

$$\hat{N}_{p+,y} = \frac{C_{p+,y}}{1 - \exp(-\hat{F}_{p+,y})} \exp\left(\frac{M}{2}\right) \dots\dots\dots (7).$$

We estimated the number of moose of age  $p$  from the number of moose of age  $p+$  using following equation, which is obtained analytically from Model C (Hiramatsu 2001):

$$N_{p,y} = N_{p+,y} (1 - \exp(-(F_{p+,y} + M))) \dots\dots\dots (8).$$

The remaining number-at-age throughout the period was computed by Equation (1).

To examine the performance of these scenarios, we obtained the estimation error for number-at-age:

$$\nu(\hat{N}_{a,y}) = \left( \frac{N_{a,y} - \hat{N}_{a,y}}{N_{a,y}} \right)^2 \dots\dots\dots (9).$$

Estimation error in total population size was expressed as follows:

$$\tau(\hat{N}_{total,y}) = \left( \frac{N_{total,y} - \hat{N}_{total,y}}{N_{total,y}} \right)^2 \dots\dots\dots (10).$$

### **Robustness of the number-at-age estimate**

According to Pope (1972) and Siddeek (1982), proportional error in number-at-age

$\rho(\hat{N}_{a,y})$  of a cohort is expressed theoretically as:

$$\rho(\hat{N}_{a,y}) \cong \left( \frac{F_{s,t} - \hat{F}_{s,t}}{\hat{F}_{s,t}} \right) (\exp(-Q_{a,y})) \dots\dots\dots (11),$$

where  $\hat{F}_{s,t}$  is the rate of terminal harvesting mortality at age  $s$  in year  $t$  of that cohort, i.e., the rate of age-specific harvesting mortality in the most recent year ( $\hat{F}_{a,y}$ ) from Model A, or the rate of harvesting mortality at age  $p$  ( $\hat{F}_{p,y}$ ) from Models B and C.  $Q_{a,y}$  is the rate of age-specific cumulative harvesting mortality defined as the sum of calculated age-specific harvesting mortality rates from age  $a$  to  $s-1$  within the cohort (i.e.,

$$F_{a,y} + F_{a+1,y+1} + F_{a+2} \dots + F_{s-1,t-1}; \text{ Pope 1972).}$$

Equation (11) indicates that, although the estimation error depends on the authenticity of Models A, B, and C, the extent of dependency is lower as  $Q_{a,y}$  becomes larger. We calculated  $Q_{a,y}$ , and then examined the relationship between the estimation error in number-at-age and  $Q_{a,y}$ .

## 2.3 Results

### Testing separate assumptions for Models A, B, and C

#### Assumption for Model A

For Models A-I through -IV, differences were not great between model-estimated values of age-specific harvesting mortality rates in the most recent year ( $Y= 1988, 1989, 1990$ ) and a calculated (observed) value (Fig. 2.2).

#### Assumption for Model B

The relationship between calculated rates of harvesting mortality at age 9+ ( $F_{9+,y}$ ) and age 8

( $F_{8,y}$ ) did not support Model B-i ( $F_{9+,y} = F_{8,y}$ ; Fig. 2.3). When  $F_{8,y}$  was  $< 0.2$ ,  $F_{9+,y}$  was

highly variable. Conversely, when  $F_{8,y}$  was  $> 0.2$ ,  $F_{9+,y}$  appeared negatively linearly correlated with  $F_{8,y}$ . Coefficients of the regression relationship were statistically different from 1 for the slope ( $t = -5.88, p < 0.01$ ) and different from 0 for the intercept ( $t = 6.54, p < 0.01$ ). Although the simple linear least-squares regression for  $F_{9+,y}$  against  $F_{8,y}$  was not significant (Model B-ii:  $Y = -0.21X + 0.44, r^2 = 0.06, p = 0.32, n = 18$ ), estimated harvesting mortality rates at age 9+ from Model B-ii were closer to the line than values estimated with Model B-i (Fig. 2.4).

### **Assumption for Model C**

The estimated sum of number-at-age  $\geq 9$  years old for a year was close to, but not equal to the sum of number-at-age  $\geq 9$  years old calculated by cohort analysis (Fig. 2.5). Thus, the assumption that the sum of number-at-age within the plus group for one year is equal to the sum of number-at-age for a particular cohort was not always met.

### **Demonstration of cohort analysis combining three models**

#### **Estimation errors in numbers-at-age in 1990**

Model A-IV estimation errors in number-at-age in 1990, were lowest among versions of Model A (Models A-I through A-IV) for six of nine age-classes (Table 2.1). For two of the age-classes, Models A-III and Model A-II reduced the error most. Model A -I reduced the error to the greatest extent for only one age-class. Moreover, the errors using Model A-I were larger for overall age-classes than those obtained using the other three models. Thus, errors in estimating number-at-age in 1990 generally decreased when longer runs of data were included in the model (i.e. in the sequence Model A-I to Model A-IV; Table 2.1).

#### **Estimation error in the number of moose at age 9+ in all years**

Model B-ii estimation errors in numbers of moose at age 9+ were much smaller than those of

Model B-i for 5 of 10 years (mostly for earlier age classes) but were similar or larger for the last 4 years (Table 2.2).

### **Estimation error in the number of moose at age 9 in all years**

Overall estimation errors in number of moose at age 9,  $\nu(\hat{N}_{9,y})$ , ranged up to 113% (Table 2.2). The error in number of moose at age 9 was not different between Model B-ii and Model B-i (Table 2.2).

### **Estimation errors in number-at-age and total population size throughout the period**

We calculated estimation errors in number-at-age using a combination of Models A-IV, Model B-ii, and Model C (Table 2.3). Estimation errors were smaller for younger ages in earlier years. The estimation errors in number-at-age  $\leq 3$  years old up to 1987 were less than 20%, whereas the estimation errors in number-at-age  $\geq 4$  years old and the estimation errors in number-at-age in 1988 and after were more than 20% (Table 2.3). Estimation errors in total population size were smaller than those of number-at-age (Table 2.3).

The estimation errors in total population size were larger for later years for every combination of models (Table 2.4). The estimation error for late years was differentiated by four variants of Model A; the error tended to decrease as longer periods of data were included in the model (i.e., in the sequence Model A-IV to A-I).

### **Robustness of the number-at-age estimate**

The relationship between proportional error in number-at-age,  $\rho(\hat{N}_{a,y})$  and age-specific cumulative harvesting mortality rate ( $Q_{a,y}$ ) was consistent with theoretical values (Fig. 2.6).

As  $Q_{a,y}$  increased, the estimation error converged to smaller values regardless of model misspecification; the error ranged from -64% to 81% below a  $Q_{a,y}$  of 0.5, whereas error was

between -16% and 34% above a  $Q_{a,y}$  of 1.0.

The magnitude of  $Q_{a,y}$  ranged from 0.1 to 1.9 (Fig. 2.6). Most of the values were below 1.5.

## 2.4 Discussion

### Exploring ways to reach realistic assumptions for Models A, B, and C

#### Assumption for Model A

Age-specific harvesting mortality estimation errors in the most recent year, ( $Y= 1988, 1989, 1990$ ) were not very different among Models A-I through -IV (Fig. 2.2). Nevertheless, number-at-age estimation errors in 1990 ( $\hat{N}_{a,1990}$ ) decreased with models that included age-specific harvesting mortality rates spanning longer time periods (i.e., in the sequence Model A-I to Model A-IV; Table 1). It is difficult to conclude that Model A-IV is superior to other variants from this result alone. However, numbers-at-age between ages in the most recent year are indirectly connected to one another; estimation error in number-at-age at a particular age in the most recent year is subject to the magnitude of the estimation error in number-at-age at for animals one year older in the most recent year. Nevertheless, the extent of the influence becomes smaller with a Model A version using age-specific harvesting mortality rates over a longer period; estimated number of moose at age  $a$  in the most recent year becomes increasingly independent of the estimation error in number-at-age for  $a+1$  years old with Model A variants using data over a longer period. Therefore, the best model for avoiding chain-reacting estimation errors uses the longest period of age-specific harvesting mortality rates, provided there is no trend in rates of age-specific harvesting mortality over years.

#### Assumption for Model B

The relationship between calculated rates of harvesting mortality in the last two age-classes (8

and 9+ years old) did not support Model B-i (Fig. 2.3). Model B-i might not have been realistic because of hunting regulations that include a quota system. The calculated harvesting mortality rate at age 9+ was highly variable when the rate at age 8 was  $< 0.2$ , whereas the relationship tended to be negative when the rate at age 8 was  $> 0.2$  (Fig. 2.3). Because the total number in the harvest is limited by quota, the number of moose harvested in a specific age group will always depend on the number harvested in other age groups. As moose at age 8 are harvested and become a smaller proportion of the total harvest, the remaining age classes should form a larger proportion of the total harvest, but this is not always the case for moose harvested at age 9+. Indeed, when moose at age 8 make up an increased proportion of the total harvest, the proportion of harvested moose in the other age classes (including age 9+) should be smaller. This pattern will be also seen in harvesting mortality rate, unless size and age structures in the population change greatly. Thus, harvest data from a quota system might limit the usefulness of Model B-i.

Estimated harvesting mortality rate at age 9+ ( $\hat{F}_{9+,y}$ ) from Model B-ii was closer to the observed value than the estimate from Model B-i (Fig. 2.4). This is a reasonable outcome because Model B-ii was estimated by least-squares analysis based on the calculated relationship between those variables.

The estimation error for early years in the number-at-age 9+ from Model B-ii was smaller than that from Model B-i (Table 2.2). Although estimation errors in number of moose at age 9+ from Model B-ii were considerably larger than those from Model B-i for later years (Table 2.2), we could find no logical reason why Model B-i would be better than Model B-ii for those years. We therefore suggest it might be better (for a more reliable estimate of harvesting mortality at age  $p+$ ) to construct a study-specific Model B from observational data (Model B-ii) instead of applying a previously used model (Model B-i). Although we introduced Model B-ii

as a simple linear regression, the structure and shape of a model will depend on the data used for construction. Because Model B-ii was obtained from the original cohort analysis, it is applicable to species for which age determination is accurate through the older age-classes.

### **Assumption for Model C**

The Model C assumption was not met in this study (Fig. 2.5). Nevertheless, we showed that this assumption is not very influential in population estimation compared with Model A, which we discuss below.

The estimation error in number of moose at age 9 was not reduced even with application of Model B-ii (Table 2.2). The estimation error in number of moose at age of 9, however, was still high.

We could not examine an alternative Model C assumption because of the difficulty in meeting the assumption of some relationship between number-at-age in a year and number-at-age within a cohort. Although Hiramatsu (2001) introduced an alternative to Model C, this alternative was analytically obtained using Model B-i, for which the assumption was not met in this study.

### **Robustness of the number-at-age estimate**

As the age-specific cumulative harvesting mortality rate,  $Q_{a,y}$ , increased, the proportional error in number-at-age converged to a smaller value, indicating that the estimation was less subject to misspecification of Models A, B, and C (Fig. 2.6). Because  $Q_{a,y}$  is larger for younger ages in earlier years, the number-at-age estimation error was smaller for younger ages in earlier years, but larger for older ages in earlier years and for all ages in later years (Table 2.3). The magnitude and pattern of total population size estimation errors were consistent with those for number-at-age estimation errors for young ages (Table 2.3); >50% of the population was

composed of ages 0-2 (Appendix II).

The total population size estimation errors for late years were differentiated by comparable alternative assumptions of Model A (Table 2.4). This outcome occurred because number-at-age estimation errors for young ages in late years were largely subject to the reality of Model A. Thus, meeting the assumption of Model A is more important for the reliability of the population estimate than assumptions of Models B and C, consistent with findings of Hiramatsu (2001).

According to Pope (1972), number-at-age estimation is robust regardless of Model A, B, and C misspecifications when the age-specific cumulative harvesting mortality rate exceeds 2.0. Although it is difficult to quantify age-specific cumulative rate of fishing mortality, the estimated rate of age-specific fishing mortality is sufficiently high to approach the critical value of 2.0 (e.g., Arcto-Norwegian cod *Gadus morhua*, Pope 1972; sardine *Sardinops sagax*, Cergole 1995; sandfish *Holothuria scabra*, Watanabe et al. 2005; Pacific cod *Gadus macrocephalus*, Ueda et al. 2006). Conversely, age-specific cumulative harvesting mortality rates in our study ranged from 0.1-1.9, and most of the values were  $< 1.5$  (Fig. 2.6), indicating that number-at-age estimation error for large terrestrial mammals will be more sensitive to model misspecification than the error for fish populations. Thus, the assumption of a reliable population size estimate must be met in the case of large terrestrial mammals, even for Model B.

Cohort analysis has been applied to aquatic species including whales and tuna, which are long-lived. While performance of models, influence of aging error in the data, and stochastic variation in population parameter estimates have been intensively studied (Shimoda et al. 2006; Mori et al. 2007), performance of Model B has not been examined. Abundance of large terrestrial mammals in the plus group is small, around  $10^{-10^2}$  (Fig. 2.1; Ueno et al. unpublished), while it is  $10^3$  for tuna (Nishida and Takeuchi 1999). This suggests that estimates of plus group

individuals in large terrestrial mammals will tend to be subject to demographic stochasticity in harvesting mortality rate. Because the performance of Model B-ii was not markedly superior to that of Model B-i (Table 2.2), more simulation studies are required to examine the performance of Model B.

In our study, harvest-at-age was assumed to be measured without error. Possible measurement errors will come from the difficulties in accurate age determination or erroneous correction of harvest-at-age using a portion of harvest supplied for age determination (Restrepo and Powers 1991; Hiramatsu 1992; Yamaguchi and Matsuishi 2007). Nonetheless, accuracy of age determination for ungulates (85.1-100%) has been verified from several studies of known-age animals (Erickson and Seliger 1969; Keiss 1969; Lockard 1972; Hamlin et al. 2000; Rolandsen et al. 2008). Jawbones of almost all harvested individuals are supplied for age determination when hunters report date, locality, sex and carcass mass (Solberg et al. 1999). Therefore, harvest-at-age measurement error in ungulates is assumed to be small; these estimates will likely be robust to measurement errors.

In contrast, Gove et al. (2002) and Conn et al. (2008) introduced a method for statistical population estimation of large terrestrial mammals when harvest-at-age is measured with error. Their method will be useful when the reported rate is low or unknown because of an insufficient reporting system or poaching. Nonetheless, some conditions must be met to apply their method. First, it is necessary to estimate a large number of harvesting mortality parameters to determine number-at-age during the period of interest, which often leads to estimation failure (Radomski et al. 2005). Alternatively, practical application requires a reduction in the number of parameters by assuming a simple pattern in harvesting mortality rate across age-classes, e.g., harvesting mortality rate is constant over years and across ages (Gove et al. 2002), which may diverge from the actual pattern. Secondly, this method requires data on survival rate collected

by radio-telemetry surveys. There are few areas where harvest-at-age data are collected concurrently with radio-telemetry surveys. We advise against applying survival estimates from natural causes and hunting in one area to another area because of great spatial variation in harvesting mortality rate. The method is applicable where radio-telemetry surveys are conducted and when annual pattern in the rate of harvesting mortality is similar across ages. Cohort analysis combining the three models introduced here can be applied to areas without such conditions, and will be reliable unless harvest-at-age is assumed to be greatly subject to measurement error.

To conclude, we have shown that meeting model assumptions is more important for population estimation of large terrestrial mammals than of fish. We recommend using the longest period of age-specific harvesting mortality rates for modeling rates of age-specific harvesting mortality in the most recent year, so long as there is no trend in age-specific harvesting mortality rates over years; and we recommend using a study-specific model based on data for rates of harvesting mortality at age  $p+$  in all years.

age	year									
	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
0	12	10	12	23	18	24	26	22	27	27
1	7	11	16	11	8	10	8	12	18	19
2	0	4	10	5	6	6	2	4	2	9
3	12	7	6	4	7	7	5	8	9	8
4	2	6	1	0	7	5	4	7	7	8
5	2	2	4	1	0	7	1	5	4	4
6	6	1	1	2	1	3	6	8	5	2
7	2	1	5	0	5	1	0	4	9	3
8	6	1	1	2	1	6	2	1	1	2
9	0	1	1	0	1	2	2	1	1	0
10	2	1	1	2	2	0	2	0	0	5
11	0	2	0	1	0	1	1	0	0	3
12	0	0	0	1	1	1	2	1	1	0
13	0	0	2	0	0	1	3	0	0	0
14	0	2	0	0	1	0	0	0	2	0

Fig. 2.1a

Harvest-at-age for female moose during 1981-1990. From this data, only the number-at-age highlighted in gray is calculable by the original cohort analysis.

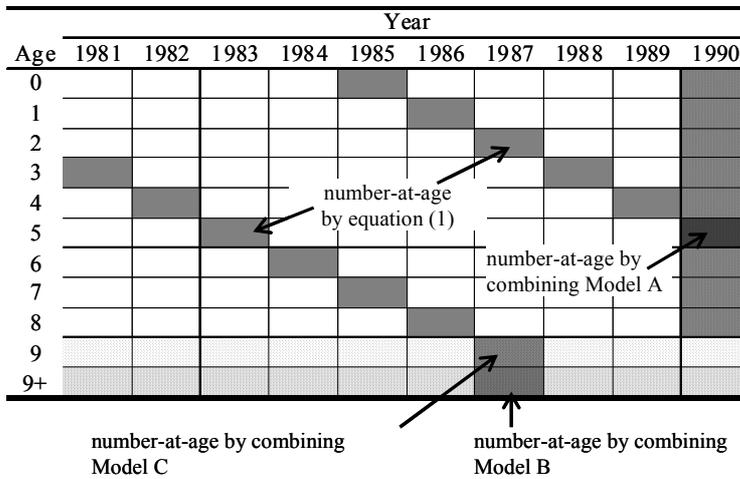


Fig. 2.1b.

A diagram of cohort analysis combining three models. Number-at-age throughout the period is estimated from harvest-at-age of Fig. 1-a combining three models with the original cohort analysis. First, numbers-at-age in the most recent year,  $Y$ , and the number at age  $p+$  in each year are computed using estimates from Model A, B following Equation (4) and Model C following Equation (5). Subsequently, the remainder of number-at-age throughout the period is computed using Equation (1).

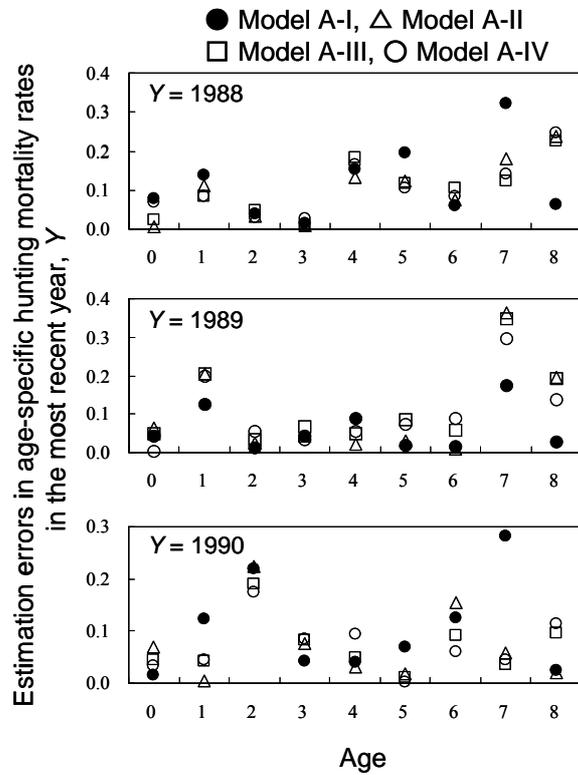


Fig. 2.2.

Differences between estimated model values of age-specific harvesting mortality rates and calculated values for the most recent year  $Y$  ( $Y = 1988, 1989, 1990$ ) using four variants of Model A. Models assume (1) that age-specific harvesting mortality rate is equal to the age-specific harvesting mortality rate in the preceding year (Model A-I, ●), (2) the arithmetic mean of the age-specific harvesting mortality rates in the preceding 3 years (Model A-II, □), (3) 5 years (Model A-III, □), and (4) 7 years (Model A-IV, ○).

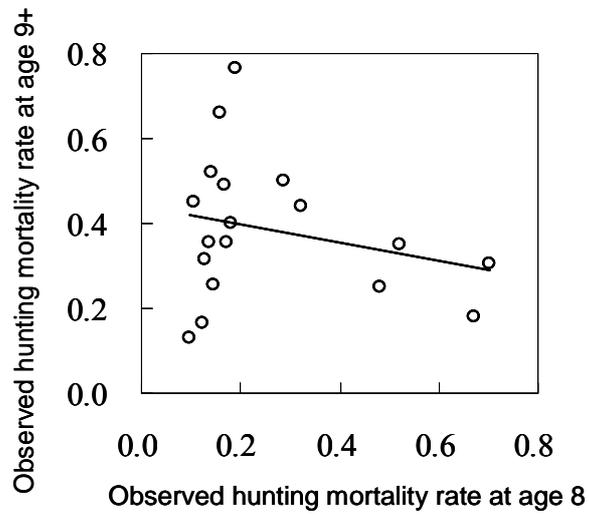


Fig. 2.3.

Calculated harvesting mortality rate at age 9+ against calculated harvesting mortality rate at age 8 for the period 1981-1998. The linear regression line fitted by least squares analysis (Model B-ii) is not statistically significant ( $Y = -0.21X + 0.44$ ,  $r^2 = 0.06$ ,  $p = 0.32$ ).



Fig. 2.4.

Model B-i (●) and Model B-ii (△) estimated harvesting mortality rates at age 9+ against calculated harvesting mortality rate at age 9+ for the period 1981-1998. Model B-i assumes that the harvesting mortality rate at age 9+ is equal to that at age 8 ( $F_{9+,y} = F_{8,y}$ ). Model B-ii is a linear regression equation for calculated harvesting mortality rate at age 9+ against that at age 8 ( $F_{9+,y} = -0.21F_{8,y} + 0.44$ ).

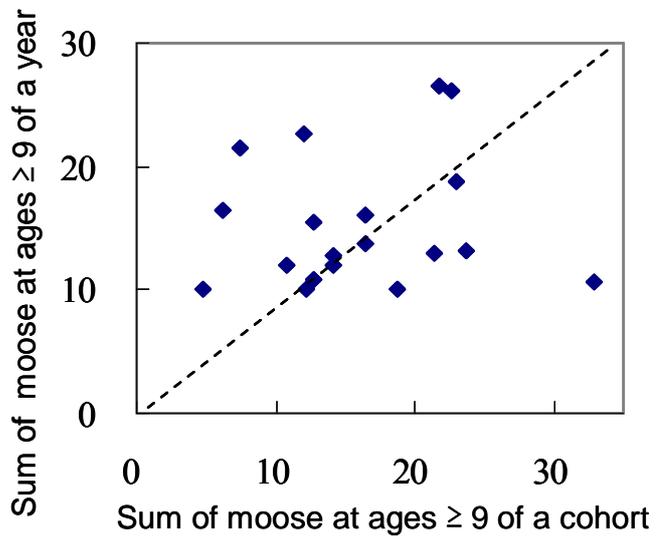


Fig. 2.5.

Sum of moose at ages  $\geq 9$  within a year against sum of moose at ages  $\geq 9$  within a cohort during 1981-1999.

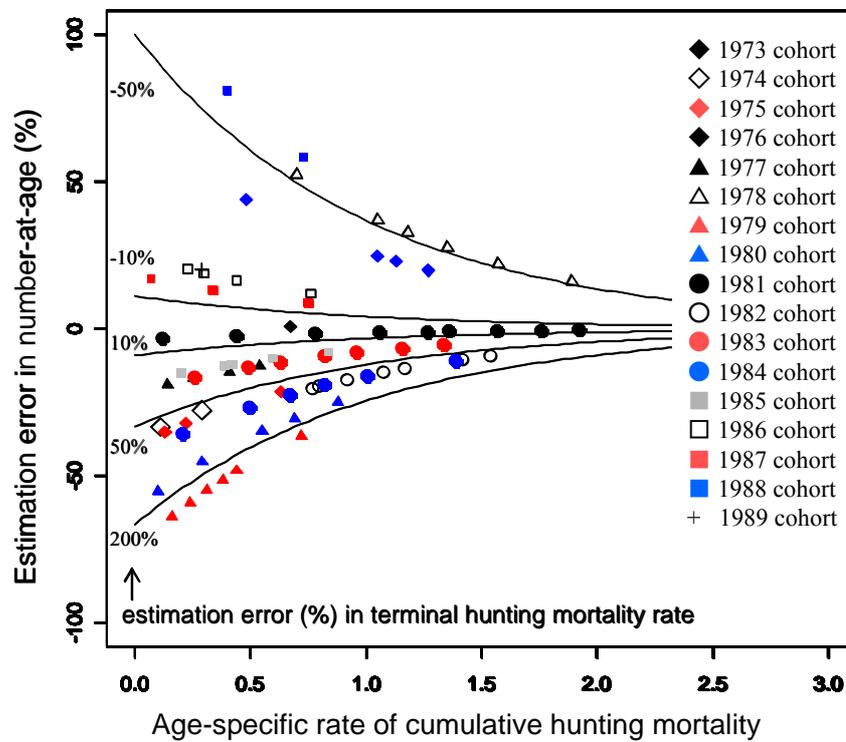


Fig. 2.6.

Relationship between estimation error (%) in number-at-age and age-specific rate of cumulative harvesting mortality. Symbols indicate cohorts born in the period 1973-1989 (i.e., cohorts alive in the period 1981-1990). Theoretical values of Pope (1972) are shown as curves. The estimation error in terminal harvesting mortality rate indicates the magnitude of misspecification by Models A, B and C.

Table 2.1. Estimation errors (%) in number-at-age in 1990 using Models A-I through A-IV as a demonstration of cohort analysis combining three models. Models assume that age-specific harvesting mortality rate is equal to the age-specific harvesting mortality rate of the preceding year (Model A-I), the arithmetic mean of age-specific harvesting mortality rates in the preceding 3 years (Model A-II), 5 years (Model A-III), and 7 years (Model A-IV).

Model A	age								
	0	1	2	3	4	5	6	7	8
I	17	41	344	8	22	45	41	22	2
II	0	15	618	0	6	20	34	15	21
III	0	10	184	3	0	9	28	8	21
IV	0	7	147	3	7	4	19	5	20

Table 2.2. Model B-i and Model B-ii estimation errors (%) in number of moose at age 9+ and Model C estimation errors (%) in number of moose at age 9 when combined with each version of Model B during the period 1981-1990. Model B-i assumes that the harvesting mortality rate at age 9+ is equal to that at age 8 ( $F_{9+,y} = F_{8,y}$ ). Model B-ii is a linear regression equation of calculated harvesting mortality.

age	Models	year									
		1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
9+	B-i	42	226	20	1	71	6	5	11	8	0
	B-ii	0	3	1	3	0	1	169	33	27	3
9	C & B-i	1	1	11	16	72	6	89	54	30	0
	C & B-ii	0	0	14	16	51	5	113	56	37	0

Table 2.3. Estimation errors (%) in number-at-age during 1981-1990 when combining Model A-IV, Model B-ii and Model C.

age	year									
	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
0	0	1	0	1	1	1	1	34	4	0
1	6	0	1	0	3	1	3	2	66	7
2	13	9	0	2	1	4	1	4	3	147
3	3	13	12	0	2	1	5	2	4	3
4	2	5	23	20	0	3	1	7	2	7
5	4	2	8	26	20	0	4	2	13	4
6	4	5	3	11	30	20	0	4	3	19
7	8	10	6	4	14	35	30	0	7	5
8	0	11	12	19	4	28	41	30	0	20
9	0	0	14	16	51	5	113	56	37	0
9+	0	3	1	3	0	1	169	33	27	3
total	0	0	1	1	1	0	0	0	1	2

Table 2.4. Estimation errors (%) in total population size in the period 1981-1990 using eight different model combinations (four for Model A combined with two for Model B and Model C).

Model A	Model B	year									
		1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
I	i	1	0	0	1	1	4	4	0	4	14
II		1	0	0	1	1	3	3	1	5	4
III		1	0	0	1	1	2	1	0	2	1
IV		1	0	0	1	0	1	0	1	3	2
I	ii	0	0	0	1	2	3	2	0	1	6
II		0	0	1	1	2	2	1	1	3	4
III		1	0	1	1	1	1	0	0	1	1
IV		0	0	1	1	1	0	0	0	1	2

Appendix 2.I. How to compute the harvesting mortality rate at age  $p+$  ( $\hat{F}_{p+,y}$ ) and the age-specific harvesting mortality rate in the most recent year  $Y$  ( $\hat{F}_{a,Y}$ ).

1. Give an arbitrary value to the harvesting mortality rate at age  $p-1$  in the most recent year  $Y$  ( $\hat{F}_{p-1,Y}$ )

2. The harvesting mortality rate at age  $p+$  ( $\hat{F}_{p+,y}$ ) is computed using Model B.

3. Number of moose at ages  $p+$  ( $\hat{N}_{p+,Y}$ ) is computed using Equation (4).

4. Number of moose at ages  $p$  ( $\hat{N}_{p,Y}$ ) is computed using Equation (5).

5. Number of moose at age  $p-1$  in one precedent year of  $Y$  ( $\hat{N}_{p-1,Y-1}$ ) is computed using Equation (1).

6. The harvesting mortality rates at age  $p-1$  in year  $Y-1$  ( $\hat{F}_{p-1,Y-1}$ ) is computed using Equation (2).

7. Back to step 2 to compute the harvesting mortality rates at age  $p+$  in year  $Y-1$  ( $\hat{F}_{p+,Y-1}$ )

8. Perform this sequentially up to the first year of data.

9. Solve for  $\hat{F}_{p-1,Y}$  to satisfy Model A. The value minimized the following objective function  $I$  is searched by the quasi-Newton method of optimization procedure using R 2.4.1.

$$I = \left\{ \hat{F}_{p-1,Y} - f(\hat{F}_{p-1,Y-1}, \hat{F}_{p-1,Y-2}, \dots) \right\}^2$$

10. Using  $\hat{F}_{p-1,Y}$  and Model A, the age-specific harvesting mortality rate in the most recent year ( $\hat{F}_{a,Y}$ ) is computed throughout the period in the same way as  $\hat{F}_{p+,y}$ .

Appendix 2.II. Number-at-age during 1981-1990 calculated by the original cohort analysis.

age	year									
	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
0	81	88	75	75	86	91	80	81	111	117
1	40	66	74	59	49	64	63	51	55	80
2	29	32	53	56	47	39	52	53	37	36
3	44	28	27	42	50	40	33	49	48	34
4	16	30	21	20	37	41	32	27	39	37
5	15	14	24	19	20	29	35	27	19	31
6	18	13	11	19	17	19	21	33	21	15
7	12	11	11	10	17	15	15	15	25	15
8	12	10	10	6	9	11	14	15	10	15
9	2	6	8	9	4	8	5	11	13	9
9+	12	16	18	22	20	22	21	22	32	35
total	280	308	325	328	351	371	366	372	398	415

## Chapter 3

Cohort analyses of a sika deer population in eastern Hokkaido, Japan: examination of culling on population growth rate.

### 3.1 Introduction

According to Caughley (1981), “overabundance” of a given wildlife species is a value judgment based on situations when (a) the animals threaten human life or livelihood, (b) the animals are too many for their own good, (c) the animals depress the densities of favored species, or (d) the animals cause ecosystem dysfunction. Deer is the very symbolic species of overabundance. Many deer species have dramatically increased their abundance and expanded their distribution in Europe, North America, and Japan over the last century (red deer *Cervus elaphus*, Clutton-Brock and Albon 1992; white-tailed deer; McShea et al. 1997; roe deer, *Capreolus capreolus*, Anderson and Linnel 2000, sika deer *Cervus nippon*; Kaji et al. 2000). As causes for this increase, enrichment of availability of forage due to changing land use, reduced predation from large carnivores, strict control of harvesting, and recent mild winter are listed up (Côté et al. 2004). As a result, dense populations inflict major economic losses in forestry, agriculture, and transportation (Côté et al. 2004). The increase of grazing and browsing pressure has also a great impact on natural ecosystem; less preferred species are increasing in abundance and density (Côté et al. 2004, Kaji et al. 2006). Preventing deer overabundance is, therefore, an important challenge for modern wildlife management.

One of solutions is culling (Buckland et al. 1996, Brown et al. 2000, Côté et al. 2004, Gordon et al. 2004). Adult natural mortality rate is low under few predators (Gaillard et al. 1998). If we increase mortality rate of a population artificially, the population growth rate could

be reduced. Previous studies have reported that harvesting has manipulated a population size under few natural predators through changing their mortality rate (Fryxell et al. 1991, Ferguson et al. 1996, Solberg et al. 1999, Bowyer et al. 1999).

However, adult mortality is not the only component constituting population growth rate. Juvenile survival and proportion of reproductive females are also important components and are negatively influenced by density-dependent food limitation during winter (e.g. Skogland 1985, Clutton-Brock et al. 1987, 1996). Recruitment is defined as the number of yearlings entering the population. Density-dependence in recruitment rate, therefore, may work as a self-regulatory mechanism.

Although many studies have detected density-dependence in recruitment rate for large mammals (reviewed in Fowler 1987), there are few empirical studies quantifying density effect on population growth rate compared with other factors. Variation in harvesting effort had a major influence on population trends of white-tailed deer, while recruitment rate was inversely correlated to population density and mitigated the effects of harvesting (Fryxell et al. 1991). Although the number of recruitment (yearlings) into the population of moose exhibited density dependence, the population was suppressed by heavy harvest (Bowyer et al. 1999). Solberg (1999) demonstrated that an inverse relationship between recruitment rate and population density of moose, mediated by a density-dependent decrease in female body condition, could potentially have constituted a regulatory mechanism in the dynamics of the population, but this effect was masked by a human-induced demographic change. Are effects of density on population growth rate negligibly small? Otherwise, should density dependency be included in modeling dynamics of ungulate populations? Relative importance of culling and density dependence should be quantified.

Sika deer population in Hokkaido gradually recovered in abundance and distribution from

the bottleneck (-1950s) under government protection, and by the mid-1970s the population occupied most available habitats in eastern Hokkaido (Kaji et al. 2000). More recently, deer population has irrupted in eastern Hokkaido and has caused severe damage to agricultural and forested areas (Kaji et al. 2000, Matsuda et al. 2002). Aiming for population control by culling, hunting regulations were relaxed (Kaji et al. 2000, Matsuda et al. 2002, Table 3.1) and hunting effort (number of days for hunting multiplied by number of hunters) increased during 1990s (Hokkaido unpublished data). The population index calculated based on spotlight survey increased from 1992 to 1998 and then became stable after some reduction (Uno et al. 2006, Yamamura et al. 2008). The deer population in eastern Hokkaido during 1990s has been subjected to a drastic change in culling pressure from low to high. Therefore, the sika deer population in eastern Hokkaido is suitable for us to observe annual change in population growth as a mirror of possible density-dependent changes in recruitment rate, and quantify effects of density on the population growth rate.

In this study, we analyzed a dynamics of a sika deer population with changing culling pressure from low to high. First, we examined the impact of culling and recruitment rates on population growth rate. Second, we examined factors accounting for variation in recruitment rate. Finally, we discussed the importance of culling to prevent deer overabundance.

## 3.2 Materials and Methods

### **Study area**

The town of Ashoro (1408 km<sup>2</sup>) is located in eastern Hokkaido, Japan (43°20'N 143°50'E). Mean annual temperature is 5.7°C, and maximum mean monthly temperature is 19.8°C in August and the minimum is -9.5°C in January. Snow accumulation persists from late December to late March or early April (Japan Meteorological Agency). The Ashoro town comprises

mostly hilly terrain. Approximately 84% of the area is forested and the rest consists of agricultural land and residential areas (Hokkaido statistics 2000). Fifty-five percent of the forested area comprises native, deciduous broad-leaved and mixed forests. The broad-leaved forests are dominated by *Ulmus davidiana* var. *japonica*, *Quercus mongolica* var. *grosseserrata*, *Betula ermanii*, while the mixed forests include *Abies sachalinensis* and *Picea jezoensis*. The rest of the forested area is coniferous plantation including *Abies sachalinensis*, *Larix leptolepis* and *Picea jezoensis* (Hokkaido statistics 2000)

#### **Age-specific data from harvested individuals (Harvest-at-age data)**

During the study period 1990-2001, 13,761 female and 22,108 male sika deer were harvested for pest control and hunting. As a part of sika deer monitoring project of Hokkaido government, age was determined for 12,186 females (88.6%) and 5,363 males (24.3%) either from tooth replacement or by counting the number of layers of cementum of annuli of the first incisor following Ohtaishi (1980). To correct for missing individuals, the annual number of harvest within an age group was multiplied by a factor correcting for the number of missing individuals in the data set. For instances, when  $y$  adults were harvested and  $x$  were aged in a particular year, the number of harvest for each adult age-group for the year was obtained by multiplying the number of aged deer by  $y/x$ . Corrected harvest-at-age data was shown in Appendix I.

#### **Cohort analysis**

We reconstructed age-specific numbers of deer during 1990-2001 using cohort analysis combining three models. Let June (birth season) be the start of a year. We assumed that the hunting is a pulse-like event that occurs in the middle of the year and that animals are subjected to natural mortality throughout the year (Pope 1972). Age-specific numbers was computed for

all age-classes except for a composite age group beyond a particular age  $p$  and all age-classes in the most recent year by Eq (1) (Pope 1972; Yatsu et al. 2002):

$$N_{a,y} = N_{a+1,y+1} \exp(M) + C_{a,y} \exp(M / 2) \dots\dots\dots (1)$$

where  $N_{a,y}$  is number of deer at age  $a$  in year  $y$ ,  $C_{a,y}$  is number of deer harvested at age  $a$  in year  $y$ , and  $M$  is natural mortality rate. Mortality “rate” in this study was actually represented by a mortality coefficient rather than a rate. Nevertheless, we refer to mortality rate, as this term is in more general use. We assumed that natural mortality rate for individuals  $\geq 1$  years old of both sexes are fixed as 0.03 referring to the female ( $\geq 1$  years old) natural mortality rate estimated by a radio telemetry survey in neighboring areas (Igota 2004, Uno and Kaji 2006). We assumed neither annual variation nor age-related difference for natural mortality rate, which will be met for prime-aged individuals, since Gaillard et al. (2000) summarized that survival rate for prime-ages is high and stable against density-independent and -dependent factors. On the other hand, Loison et al. (1999) have shown that survival rates for old-ages were lower than that for primed ages due to senescence. Because it is unrealistic to refer to values obtained from different species (e.g., roe deer, bighorn sheep), we did not consider the senescence. Possible violation of this assumption was mentioned at the discussion section.

Age-class of juveniles (first year of life) was excluded from the present cohort analysis, because of the difficulty in estimating their number owing to potentially large variation in natural mortality caused by biotic and abiotic factors (Sæther 1997). Thus, the youngest age for which we reconstructed the number of deer was yearling (12-24th month). Total population size was defined as the sum of numbers of deer whose age was one year or older. We defined the number of yearlings as estimate of recruitment.

The numbers of deer for a composite age group beyond a particular age  $p$  ( $p+$ ) in all the

period and all age-classes in the most recent year (2001 in this study) were computed by Eq (2) (Hiramatsu 2001, Ueno in press):

$$\hat{N}_{a,y} = C_{a,y} \frac{(\hat{F}_{a,y} + M)}{\hat{F}_{a,y}} \cdot \frac{1}{1 - \exp(-(\hat{F}_{a,y} + M))} \dots\dots\dots(2).$$

where  $\hat{N}_{a,y}$  is the estimated number of deer at age  $a$  in year  $y$  and  $\hat{F}_{a,y}$  is the estimated harvesting mortality rate at age  $a$  in year  $y$ . Age of  $p$  in this study was set to 9 and 10 years old for males and females, respectively, because those ages were maximum beyond which the total number of deer harvested exceeded zero for every year.

We estimated age-specific harvesting mortality rate in the most recent year by assuming the same as the arithmetic mean of age-specific harvesting mortality rates during the precedent years. According to Ueno et al. (in press), it is appropriate to use the longest period with age-specific harvesting mortality rates when there is no trend in age-specific harvesting mortality rates over years. Hunting regulation in Hokkaido was greatly revised at 1998 and 2001. Hokkaido government allowed registered hunters to hunt up to the maximum of 2 deer (1 doe and 1 stag, or 2 does) per one day during hunting season (Nov-Jan) since 1998 (Hokkaido Institute of Environmental Sciences (HIES) 2006). To promote more intensive hunting, the maximum number was increased to 3 deer per one day in 2001 (HIES 2006). However, actual hunting effort (actual total number of days hunters went to the field) in 2001 was similar to those during 1998-2000. Thus, we assumed that age-specific harvesting mortality rate in 2001 is the same as arithmetic mean of age-specific harvesting mortality rates during precedent three years (Fig. 3-1-A). We assumed the same value as the age-specific harvesting mortality rate in 1998, which was highest among the three years (Fig. 3-1-B) or the same value as age-specific harvesting mortality rate in 2000, which was lowest among the three years (Fig. 3-1-C): annual trend and abundance of the total population were similar showing the robustness of the

estimation.

We estimated harvesting mortality rate of  $p+$  for all years using a regression relationship between observed harvesting mortality rates of the last two age-classes ( $p-1$  and  $p+$ ) (Ueno et al. in press). Observed harvesting mortality rates for the last two-age classes were calculable for some cohorts for which harvest-at-age are available until the oldest age-class (Ueno et al. in press).

Details of the computation for age-specific harvesting mortality rates in the most recent year and for age-class of  $p+$  in all years have been described in Ueno et al. (in press).

We estimated the number of deer at the age of  $p$  years assuming that the sum of number of individuals at ages  $\geq p$  years within a year ( $N_{p,y}, N_{p+1,y}, N_{p+2,y}, N_{p+3,y}, N_{p+4,y}, N_{p+5,y}$ ) is the same as the sum of number of individuals at ages  $\geq p$  within a cohort

( $N_{p,y}, N_{p+1,y+1}, N_{p+2,y+2}, N_{p+3,y+3}, N_{p+4,y+4}, N_{p+5,y+5}$ ). Then, the number of deer at age of  $p$  years old is analytically obtained (Hiramatsu 2001):

$$N_{p,y} = N_{p+,y} (1 - \exp(-(F_{p+,y} + M))) \dots\dots\dots(3).$$

The assumption is unlikely to be met, because the assumption requires the condition that age distribution of deer  $\geq p$  should be stationary stable. However, effect of this violation is of minor importance for the population estimation (Ueno et al. in press).

Cohort analysis assumes a closed population, i.e. neither immigration nor emigration occurred during the study period (Hilborn & Walters 1992). Because some radio-collared deer were migrating from this study area to the neighbor area in winter (Uno and Kaji 2000, Igota et al. 2004), it is clear that deer can freely immigrate to or emigrate from this study area. However, there is no evidence indicating that immigration (or emigration) dominated over emigration (immigration). Thus, this problem may also be of minor importance.

### Calculation of demographic variables

From a reconstructed population we calculated the following variables used in the subsequent analyses. Annual population size in year  $y$ :  $Z_{\geq 1,y} = \ln N_{\geq 1,y}$ . Population growth rate in year  $y$ :  $Z_{\geq 1,y+1} - Z_{\geq 1,y}$ . Recruitment rate in year  $y$ :  $\frac{N_{1,y+1}}{N_{\geq 1,y}}$ . The number of birth in year  $y$  ( $N_{0,y}$ ) was estimated as the number of females  $\geq 1$  year old at the end of year  $y-1$  multiplied by stage-specific fecundity rates in year  $y-1$ . The stage-specific fecundity rates classified by yearlings and individuals  $\geq 2$  years old during 1991-2001 were cited from Kaji et al. (2006). Because the survey on fecundity rates was not carried out in 1990 we used the fecundity rate in 1991 for that in 1990.

From the reconstructed population sizes and harvest-at-age data we calculated harvesting mortality rate in year  $y$ :  $\frac{C_{\geq 1,y}}{N_{\geq 1,y}}$  and harvesting mortality rate for female  $\geq 2$  years old in year  $y$ :

$$-\ln\left(1 - \frac{C_{female \geq 2,y} \exp(M/2)}{N_{female \geq 1,y}}\right).$$

### Data analysis

Because we reconstructed the population by assuming neither immigration nor emigration, and fixed natural mortality rate in this study, population growth rate is fractioned into three: annual changes in male- and female harvesting mortality rates and recruitment rate (*cf.* Fig. 3.5). Then, key-factor analysis following Yamamura (1999) was performed to evaluate the relative contribution of these three components to annual changes in population growth rates using SPSS 10.0. Next, factors accounting for variation in recruitment rate were examined.

Recruitment rate in year  $y$  is expressed as birth rate in year  $y$  multiplied by juvenile survival rate

in year  $y$  (*cf.* Fig. 3.5).

$$\frac{N_{1,y+1}}{N_{\geq 1,y}} = \frac{N_{0,y}}{N_{\geq 1,y}} \cdot \frac{N_{1,y+1}}{N_{0,y}} \dots\dots\dots (4).$$

We took off the term ‘ $N_{\geq 1,y}$ ’ from equation (4).

$$N_{1,y+1} = N_{0,y} \cdot \frac{N_{1,y+1}}{N_{0,y}}$$

$$\Leftrightarrow N_{1,y} = N_{0,y-1} \cdot \frac{N_{1,y}}{N_{0,y-1}} \dots\dots\dots (5).$$

Thus, number of recruitment in year  $y$  ( $N_{1,y}$ ), is expressed as number of birth in year  $y-1$

( $N_{0,y-1}$ ) multiplied by juvenile survival rate in year  $y-1$  ( $\frac{N_{1,y}}{N_{0,y-1}}$ ). We first examined if number

of recruitment in year  $y$  was correlated with number of birth in  $y-1$ . Second, variation of number of recruitment in year  $y$  was analyzed using models including factors affecting juvenile survival rate in year  $y-1$  as independent variables and number of birth in year  $y-1$  as covariate. The coefficients were derived from generalized linear model (GLM) assuming a negative binomial error distribution. Negative effects of population density, snow fall, and their interaction on juvenile survival rate have been reported (see a review paper by Sæther 1997). Female ( $\geq 2$  years old) culling was also included as a candidate factor, because Giuliano et al. (1999) reported lower survival rate for orphaned fawns than for unorphaned fawns suggesting negative effect of female culling on the number of recruitment. Thus, candidates of independent variables for the number of recruitment in year  $y$  were snow fall in year  $y-1$ , snow depth in year  $y-1$ , population size in year  $y-1$  (direct density-dependence) and in year  $y-2$  (delayed density-dependence), and harvesting mortality rate for female  $\geq 2$  years old in year  $y-1$ .

Statistics on snow fall was cited from Japan Meteorological Agency (<http://www.jma.go.jp/jma/index.html>). We used AIC to determine the best model. Deviance

which measures how close the model comes to perfection (observed data) was used to test whether the model is an adequate fit (goodness of fit test). We performed this statistical procedure using R 2.4.1.

### 3.3 Results

#### **Estimates of annual population size during 1990-2001**

The reconstructed population size ( $\geq 1$  year old) increased from 1990 to 1998, although the population growth decelerated after 1995 (Fig. 3.1-A). The population size decreased after 1998. The population size in 2001 was as many as population size in 1993 and 1994. Thus, the population size changed in a simple shape with one peak in 1998. Age- and sex-specific numbers are shown in Appendix II.

#### **Annual changes in population growth rate, harvesting rate and recruitment rate**

Population growth rate remained high with less variation (0.1-0.2) was during 1991-1995 and declined thereafter (Fig. 3.2). During 1996-1997 the rate was relatively stable between 0 and 0.1 and declined again. Population growth rate decreased to a negative value (-0.18) in 1998 and kept negative thereafter (Fig. 3.2).

Total harvesting mortality rate was high exceeding 0.30 in the first two years, and declined until 1994 (Fig. 3.2). The rate gradually climbed and recorded the highest value of 0.37 in 1998. Thereafter, total harvesting mortality rate kept the value above 0.30. Harvesting mortality rate was quite different by sexes (Fig. 3.2). Harvesting mortality rates for females was about one half for males every year. Annual trend in total harvesting mortality during 1990-1993 was consistent with that for males but not for females. Female harvesting mortality rate had been low before 1997. However, the rate greatly increased in 1998 (0.29) when hunting regulation for

females was relaxed. Thereafter, the rate kept as high as 0.2.

Recruitment rate was highest (0.54) in 1991 (Fig. 3.2). Thereafter, it declined until 1995 and became stable during 1995-1997. It decreased again showing annual variation until 2001.

### **Key-factor for the population growth rate**

Population growth rate was correlated with recruitment rate rather than male- or female harvesting mortality rate (Fig. 3.2). Key-factor analysis divided variation in population growth rate into three components: male- and female harvesting mortality rate and recruitment rate. Covariance for recruitment rate (0.34) was much higher than covariance for harvesting mortality rate for males (0.15) and females (0.07). Thus, the key-factor was recruitment rate contributing 60% to annual change in population growth rate.

### **Factors accounting for the variation in number of recruitment.**

Number of recruitment in year  $y$  did not show a clear relationship only with number of birth in year  $y-1$  (Fig. 3.3; Pearson's correlation coefficient  $r = 0.075$ ,  $n = 10$ ,  $p = 0.826$ ) indicating that temporal variation in number of recruitment was not explained by variation in number of birth alone.

The model with the lowest AIC contained population size in year  $y-2$  and the harvesting mortality rate in year  $y$  for females  $\geq 2$  years old in year  $y-1$  as explanatory variables, and number of birth in year  $y-1$  as covariate (Table 3.2-a). Coefficients of these two explanatory variables were negative (Table 3.2-b). Goodness of fit test revealed that the model fitted observed data statistically well (Table 3.2-a). Null model including only intercept had high AIC and did not fit observed data (Table 3.2-a).

Relative importance of each factor accounting for the variation in the number of recruitment

for year  $y$  was different between early and late periods. Juvenile survival rate during 1991-1998 was correlated with population size in the precedent one year but not with the harvesting mortality rate for female  $\geq 2$  years old in that year (Fig. 3.4). On the other hand, juvenile survival rate during 1998-2000 was correlated with the harvesting mortality rate for female  $\geq 2$  years old in that year rather than population size in the precedent one year (Fig. 3.4).

### 3.4 Discussion

#### **A demographic parameter dominating population growth rate.**

Adult female harvesting mortality had been low before 1998 due to restricted opportunities for female hunting showing high adult female survival rate with small temporal variation overall. According to Gaillard et al. (2000), recruitment rates with low elasticity but with high temporal variability is more important to the changes in population growth rate than adult female survival rate with high elasticity but with low temporal variability. Thus, annual change in recruitment rate can become reflected on the population growth rate, unless intensive adult female hunting is carried out.

#### **Mechanism for variation in numbers of recruitment.**

The most realistic model for number of recruitment included number of birth as a covariate and several factors accounting for juvenile survival rate (Table 3.2-a). Negative effect of population size on juvenile survival rate indicates the presence of density-dependence in juvenile mortality rate. The density-dependent increase in juvenile natural mortality has been reported in many ungulate species (Bartmann RM et al. 1992 for mule deer; Clutton-Brock et al. 1987 for red deer; Clutton-Brock et al. 1992 for Soay sheep; Houston DB et al. 1988 for mountain goats; Portier et al. 1998 for bighorn sheep; Singer et al. 1997 for elk; but see Sæther et al. 1996 for

moose). Juvenile natural mortality rate in roe deer was higher for individuals with smaller body size during winter through food availability (Gaillard et al. 1996). Kaji et al. (2006) reported density-dependent decrease in mean body size of sika deer in this study area. Thus, density-dependent increase in juvenile natural mortality rate in this study may have occurred through food limitation. Body mass of juveniles during winter is influenced by (1) body mass during the summer at juveniles, (2) body mass of their mother in pregnancy, or (3) both (Sæther and Heim 1993). Following this, density-dependent decrease in body size is caused either by (1) direct density-dependence, (2) delayed density-dependence, or (3) both (Fryxell et al. 1991). In this study, we detected delayed density-dependence in juvenile natural mortality supporting a mechanism of (2). However, because there was a strong positive relationship between population sizes in neighboring two years, we could not rule out another mechanism of (1) or (3).

Neither snow fall nor snow depth were not included in the parsimonious model (Table 3.2-a). This is contrary to the prediction that snow accumulation makes deer difficult to access to food, which in turn reduces body condition and subsequently, lower juvenile survival rate (Mech et al. 1987, Post and Stenseth 1998). Maximum depth at the study area was calculated as 43.7cm in average during the study period (Japan Meteorological Agency). Uno et al. (personal communication) detected negative effect of snow depth on the percentage of females with their fawn in the neighbor area named Akan, where maximum snow depth in Akan was 135 cm in average (cited from website of Japan Meteorological Agency). Takatsuki (1992) demonstrated that the distribution of sika deer in Honshu Island is limited to areas of  $> 50$  cm of snow. Because deer in Hokkaido was larger in the length of hind foot than deer in Honshu Island (Takatsuki 1992), the snow depth limiting deer survival in Hokkaido may be higher than 50 cm in Honshu. Kaji et al. (2000) suggested that sika deer dispersal into areas with  $\leq 100$  cm of snow

depth enabled deer to access large amounts of bamboo grass forage, which could lead to successful range expansion. Therefore, snow accumulation in this study might have not been critical for deer survival.

We revealed that female harvesting mortality rate for females  $\geq 2$  years old negatively affected juvenile survival rate (Table 3.2-a, Fig. 3.4). Giuliano et al. (1999) reported lower survival rate for orphaned fawns than for unorphaned fawns, and they suggested the negative effect of female culling on recruitment. On the other hand, other studies have reported that orphaning had either no adverse effects on fawns (Woodson et al 1980), or had the positive effect of increasing survival (Holzenbein and Marchinton 1992). Although there is no study to explain these conflicting results, our result is consistent with the demographic effect suggested by Giuliano et al. (1999). We first demonstrated that female culling can reduce the population growth rate not only by direct negative effect on birth rate (Caughley 1977) but also indirect negative effect on juvenile survival rate.

### **Quantifying effect of self-regulatory mechanism on population growth.**

Relative importance of factors accounting for juvenile survival rate was different between early (1991-1998) and late (1998-2000) phases. Variation in juvenile survival rate during the early phase was well explained by density dependence, while in the late phase harvesting mortality rate for females  $\geq 2$  years old (Fig. 4). Although density-dependence reduced population growth rate through negative effect of juvenile survival rate, population growth rate was still positive in 1997 (Fig. 3.1, 3.2). In other words, self-regulatory mechanism reduced population growth rate, but not the population size.

Density-dependent responses in life history traits begin with juvenile survival, age at maturity and adult survival (Eberhardet 1977). In this study, we detected density-dependent

decrease in juvenile survival rate only. If the population continued to increase after 1998, we might have detected density-dependent delay in age at maturity resulting in even further lower rate in the population growth rate. Actually, an island deer population at high density shows delay in the age at maturity by two years old (Kaji et al. 1988, Kaji et al. 2001), making great impact on their habitat; forest structure has been greatly changed by grazing pressure (Kaji et al. 2006). Therefore, the population in this study area would destroy the local systems of environments and agriculture if the population were permitted to increase until the high density level at which self-regulatory mechanism would be realized. Moreover, the level of crop damage by deer grazing pressure has been already unacceptable by the end of 1990s in eastern Hokkaido; Damage on Agriculture recorded five billion yen and generation of forests is delayed (Kaji et al. 2001, Terasawa and Akashi 2006). Therefore, self-regulatory mechanism by density-dependence may be not strong enough to prevent the overabundance: culling is necessary.

Population reconstruction using cohort analysis requires a number of assumptions, some of which were not clearly justified in this study. During 1990-1995, there were too few females rather than many calves, and too few females rather than many males in the reconstructed population (Appendix II), which resulted in extremely high recruitment rate and male-biased sex ratio during the period. This discrepancy is probably caused by the violation of assumption that natural mortality is 0.03 for both sexes without age-related difference. During 1990-1995 when female leisure hunting was banned, adult females were subjected to natural mortality and low pressure hunting by pest control. Then, 0.03 of annual natural mortality rate for females seems too low to end considering their physiological life span of 20 years. Therefore, if physiological life span assumed to be the same between years and the sexes, natural mortality for old age-classes of females during 1990-1995 must have been higher. Nevertheless, the

reconstructed population showed the consistent trend with the observed population index in Eastern Hokkaido; the relative population index calculated using spotlight counts increased from 1992 to 1998 and decreased thereafter (Uno et al. 2006; Fig. 3.1-A). Thus, we suggest that annual estimates of the population by cohort analysis are robust against a number of assumptions and are reliable.

To summarize, we revealed the dynamics of a population with changing culling from low to high intensity. The population with low intense adult female harvesting continued to increase and subsequently, the population growth rate was density-dependently lowered through juvenile survival rate. Nevertheless, the population size was not reduced by self-regulatory mechanism: population size was finally reduced when intensive adult female harvesting was started. Female harvesting affected recruitment rate not only via birth rate but also via juvenile natural mortality rate. Thus, we conclude that female harvesting is a powerful mechanism to prevent deer overabundance.

Tables

Table 3.1.

Hunting season and the maximum number of hunts available per one hunting day by sexes in Ashoro town, eastern Hokkaido during 1990-2001. In Japan, hunting is not regulated by the number of quota but the length of hunting season and the number of hunts permissible per one hunter per one hunting day. All registered hunters are obliged to report when they went hunting and how many deer they observe and hunt during the entire hunting season.

Fiscal year (begins on Apr.1)	Hunting regulation phase	Males		Females	
		number/day	period	number/day	period
1990	I	1	Nov.15-Jan.15		
1991	I	1	Nov.15-Jan.15		
1992	I	1	Nov.15-Jan.15		
1993	I	1	Nov.15-Jan.15		
1994	II	1	Nov.15-Jan.15	1	Jan.6-Jan.15
1995	II	1	Nov.15-Jan.15	1	Jan.6-Jan.15
1996	II	1	Nov.15-Jan.15	1	Jan.6-Jan.15
1997	III	1	Nov.15-Jan.15	1	Nov.15-Dec.15
1998	IV	1	Nov.1-Jan.31	2	Nov.1-Jan.31
1999	IV	1	Nov.1-Jan.31	2	Nov.1-Jan.31
2000	IV	1	Nov.1-Feb.28	2	Nov.1-Feb.28
2001	V	1	Nov.1-Jan.31	3	Nov.1-Jan.31

Table 3.2-a. Model selection for the logarithmic number of recruitment (yearlings) in year  $y$  ( $n = 11$ ) taking logarithmic number of birth in year  $y-1$  as a covariate. Explanatory variables accounting for the variation in juvenile survival rate included population size in year  $y-2$  ( $\text{pop.size}(y-2)$ ), the culling mortality rate for females  $\geq 2$  years old in year  $y-1$  ( $\text{Hadf}_{\geq 2}_{y-1}$ ), and snow fall in year  $y-1$ . The deviance was used to test whether a model is an adequate fit (goodness of fit test).

explanatory variables	AIC	deviance	d.f.	$p$
$\text{Pop.size}(y-2) + \text{Hadf}_{\geq 2}_{y-1}$	152	10	7	0.185
$\text{Pop.size}(y-2)$	172	32	8	<0.001
$\text{Hadf}_{\geq 2}_{y-1}$	202	42	8	<0.001
Null	226	244	9	<0.001

Table 3.2-b. Rates of explanatory variables for the best model derived from generalized linear model assuming the negative binomial error distribution. Explanatory variables accounting for the variation in juvenile survival rate included population size in year  $y-1$  (pop.size ( $y-1$ )) and the culling mortality rate for female  $\geq 2$  years old in year  $y-1$  (Hadf\_ $\geq 2$ \_y-1).

coefficients		
intercept	slope	
	pop.size( $y-1$ )	Hadf_ $\geq 2$ _y-1
1.43E+00	-1.11E-04	-3.04E+00

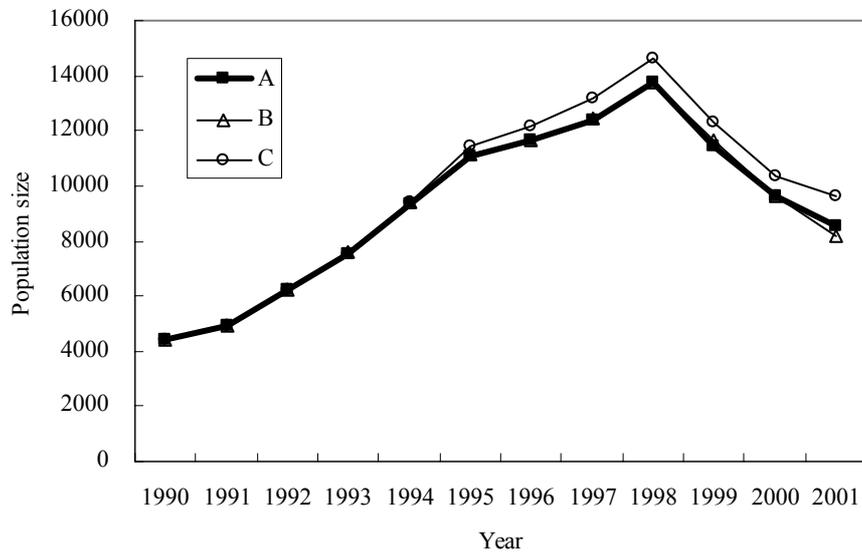


Fig. 3.1. Annual population size ( $\geq 1$  year old) during 1990-2001 reconstructed using cohort analysis by assuming that the age-specific harvesting mortality rate in the most recent year (i.e., 2001) is the same as arithmetic mean of age-specific harvesting mortality rates during 1998-2000 (A), the same as age-specific harvesting mortality rates 1998 (B) or the same as age-specific harvesting mortality rates in 2000.

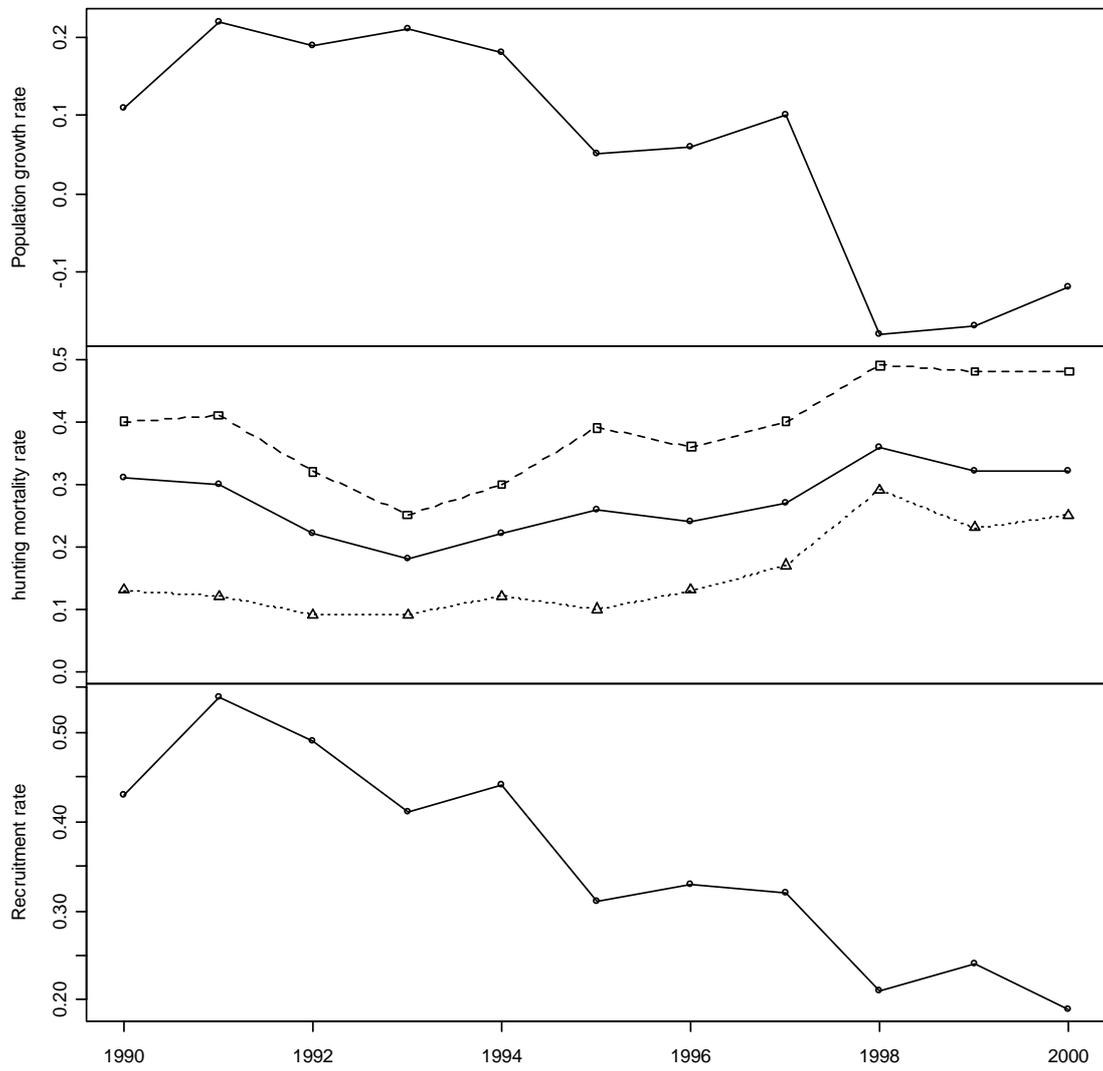


Fig. 3.2. Annual changes in population growth rate, harvesting mortality rate in total (solid) and by sexes (male, dashed; female, dotted), and recruitment rate.

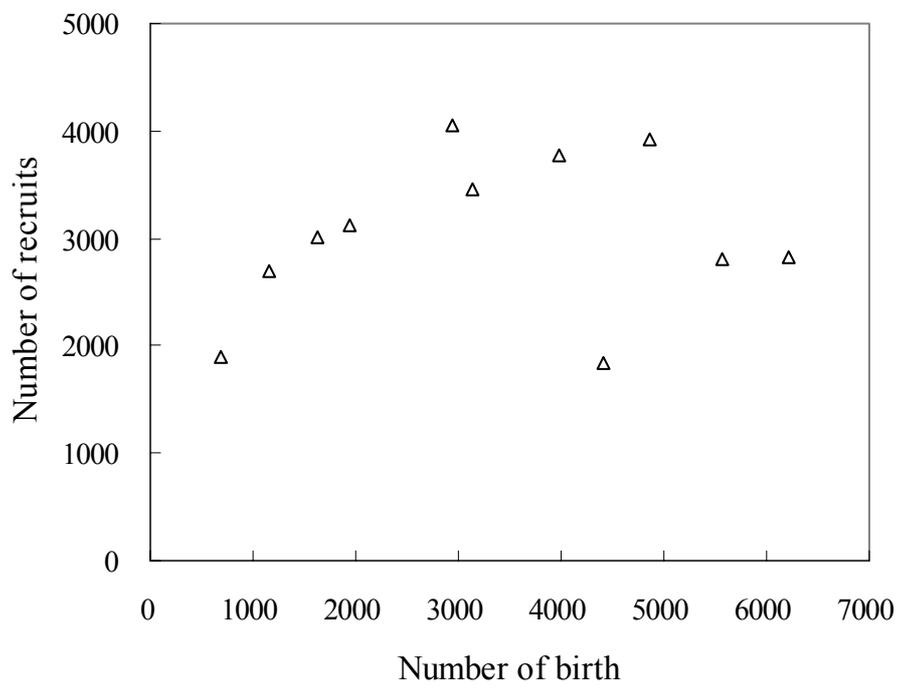


Fig. 3.3. Annual changes in number of recruits (yearlings) in year  $y$  and the number of birth in year  $y-1$ .

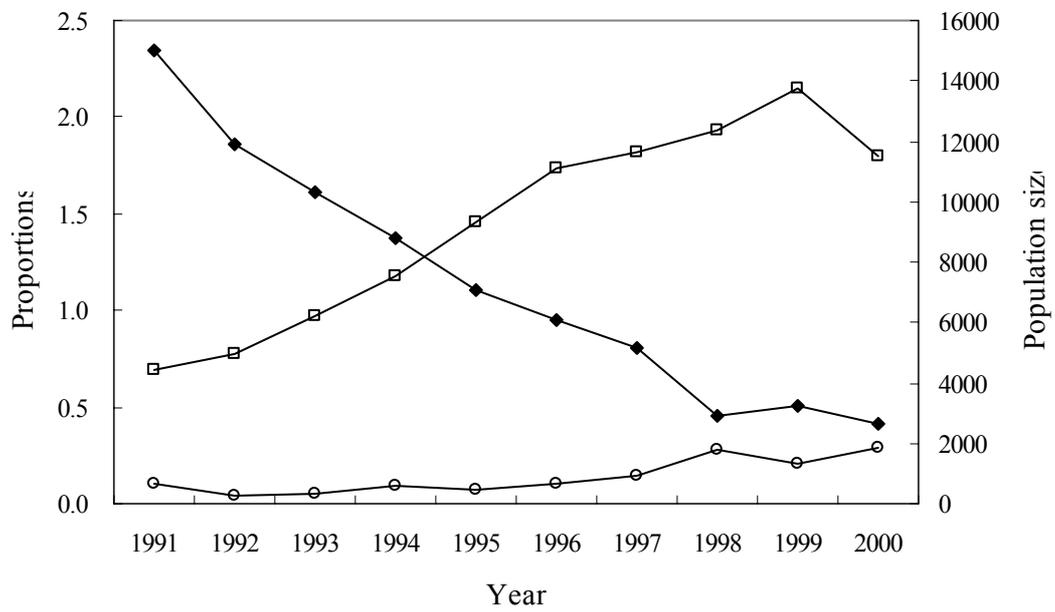
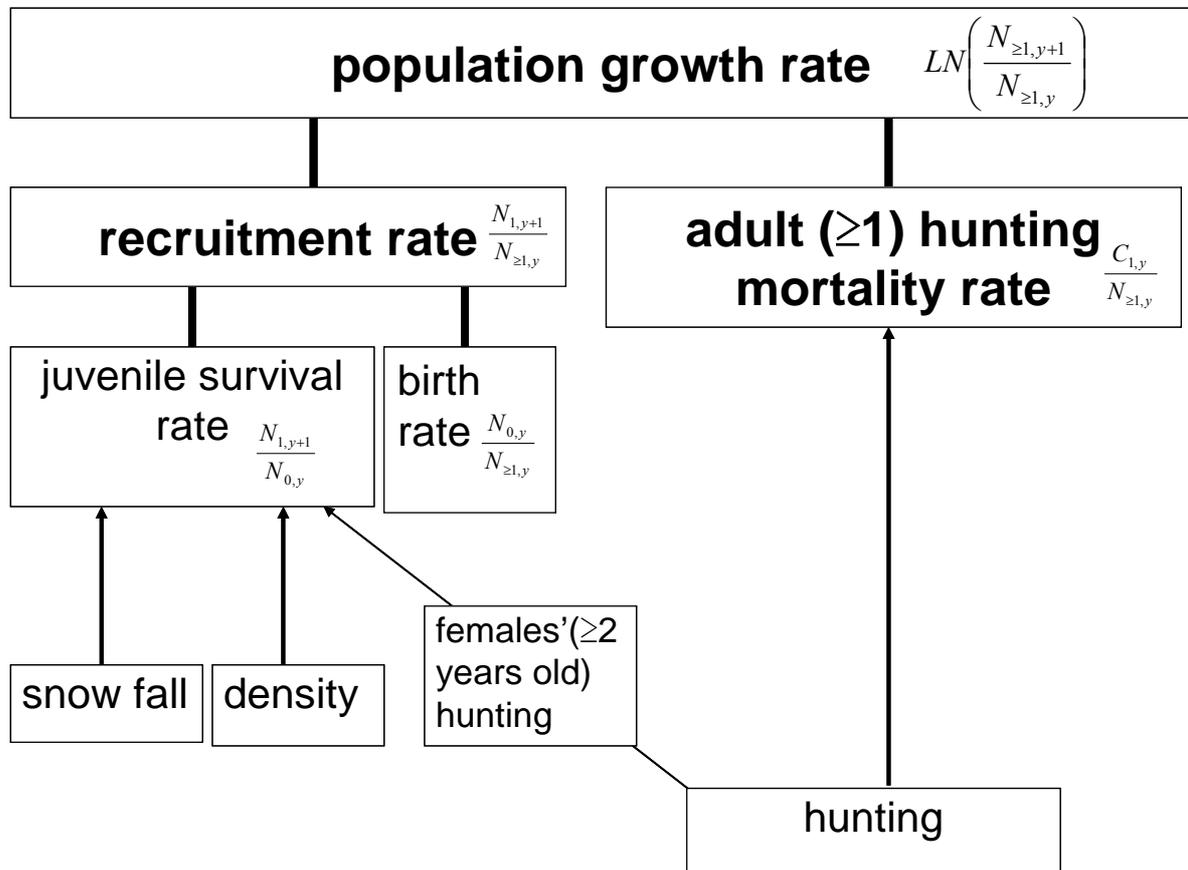


Fig. 3.4. Annual change in juvenile survival rate in year  $y$  (◆, left axis), and population size in year  $y-1$  (□, right axis) and harvesting mortality rate for females  $\geq 2$  years old in year  $y$  (○, left axis).

Fig. 3.5.

A diagram showing demographic constituents of population growth rate and related factors.



### Appendix 3.I. Harvest-at-age data of sika deer during 1990-2001

male

Age	Year											
	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
0	230	299	115	85	54	201	239	216	151	256	426	275
1	855	550	711	441	857	1221	722	868	1106	738	534	422
2	224	325	133	354	351	229	431	523	534	275	277	296
3	57	251	128	135	165	449	332	316	306	302	305	151
4	4	7	79	57	61	234	240	143	217	166	117	110
5	2	2	29	20	46	84	65	110	107	127	89	41
6	53	18	3	12	10	45	63	52	72	86	58	33
7	1	0	13	13	7	1	43	52	45	62	44	27
8	0	28	23	13	8	0	25	17	46	24	30	18
9	0	11	7	1	1	11	12	22	9	19	18	18
10+	2	37	6	10	24	42	38	47	60	43	35	27
Total	1428	1529	1248	1140	1585	2518	2210	2367	2652	2097	1933	1418

female

Age	Year											
	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
0	38	68	40	24	61	104	163	175	416	414	484	459
1	63	86	127	120	149	171	202	328	707	486	287	294
2	73	65	37	70	104	74	171	268	503	298	308	376
3	10	38	24	26	75	77	106	189	291	279	398	233
4	16	8	17	23	52	54	95	107	291	168	167	134
5	3	7	10	16	34	39	59	69	145	159	107	103
6	3	10	7	7	29	28	35	54	145	80	93	79
7	1	5	6	8	16	17	32	32	112	91	78	78
8	13	6	5	5	9	13	17	29	47	64	34	58
9+	1	15	19	11	42	41	68	84	215	151	154	174
Total	224	309	293	311	572	619	948	1335	2872	2191	2111	1989

Appendix 3.II. Age- and sex-specific numbers of sika deer during 1990-2001 reconstructed using cohort analysis

males

Age	Year											
	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
1	1636	1255	1784	1939	1939	2527	1961	1968	1958	1323	1228	819
2	740	758	684	1041	1454	1049	1267	1202	1068	826	568	673
3	191	501	420	536	666	1071	796	811	659	518	535	282
4	94	130	243	283	389	486	604	450	481	343	210	223
5	101	87	119	158	219	318	244	353	299	256	172	89
6	108	96	82	87	134	168	227	174	235	186	126	80
7	48	53	76	77	73	120	119	160	119	159	97	65
8	17	46	52	61	62	64	116	74	104	71	94	51
9	39	17	18	27	47	52	62	88	55	56	46	62
10+	8	58	12	32	81	107	100	113	165	93	71	60
Total	2982	3002	3489	4241	5065	5964	5497	5393	5142	3832	3146	2406

females

Age	Year											
	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
1	654	642	909	1078	1176	1526	1500	1811	1958	1507	1582	1019
2	339	573	540	759	930	996	1314	1260	1439	1214	991	1257
3	166	258	493	489	668	801	895	1109	963	908	889	662
4	106	151	213	454	449	576	703	766	892	652	610	476
5	82	87	139	191	419	385	506	590	639	584	470	430
6	28	77	77	125	170	374	336	434	506	480	413	352
7	36	25	64	68	114	137	335	292	368	350	388	310
8	32	34	19	56	58	95	117	294	253	249	251	301
9+	1	106	261	60	265	247	422	446	1562	1698	916	1318
Total	1444	1952	2716	3280	4249	5137	6128	7001	8581	7641	6510	6125

## Chapter 4

Harvest-based estimation of a sika deer population incorporating a model for the rate of population growth.

### 4.1 Introduction

One of the main challenges wildlife managers face are how to estimate population sizes, demography and trends (Mysterud et al. 2007). Previous studies have shown that capture-mark-recapture methods and cohort analysis (known as virtual population analysis, VPA) are reliable methods for population estimation (Novak et al. 1991, Lebreton et al. 1992). Those methods are labor consuming and have, therefore, been applied to population estimation at a relatively small geographical scale (e.g. Chapter 3). On the other hand, estimation methods applied to population size at a large scale, alternatively are lower-cost methods such as fecal pellet counts (review in Neff 1968), number of catch per unit effort (CPUE; Noss et al. 2005), seen per unit effort (SPUE; Solberg and Sæther 1999), thermal imaging (Wiggers and Backerman 1993) or indirect methods based on performance indices such as body weight or size (Hewison et al. 1996). While population indices are useful in indicating the population trend, we need to estimate absolute population size to know how many deer we should cull to control them. The absolute population size estimated using a regression equation of absolute number of individuals by a population index in a specific area is often underestimated, possibly because complete counts treated as true values are often impossible in the dense forest (Kaji 2006, Uno et al. 2007). Moreover, because detection rate (sightability) can vary across time and space, correction using the detection rate estimated in a specific area may produce biased estimates for other areas.

Matsuda et al. (2002) proposed a method for estimating the total number of individuals from a population index. In this method, called harvest-based estimation, the total number of individuals is estimated by examining the response of the population index to the known number of individuals that have been artificially removed (Yamamura et al. 2008). The harvest-based estimation of Matsuda et al. (2002), however, did not explicitly incorporate the observation errors into their estimation of the population (Yamamura et al. 2008). To circumvent the problem, Yamamura et al. (2008) estimated the population by explicitly assuming the observation errors in the population index. They divided the process of estimation of populations into two parts; the ‘observed population index,’ which contained observation errors and the ‘true population,’ which did not contain observation errors. Thus, harvest-based estimation combined with state-space modeling (Yamamura et al. 2008) is promising for population estimation at a larger scale.

Their method requires the rate of population growth with which deer increase in number subjecting to mortality factors except for harvest (hunting and pest control). Yamamura et al. (2008) referred to one of values estimated in two local areas (Kaji et al. 2004), and assumed no annual variation in the rate during the study period except for stochastic variation. However, the assumption may not be met, since many studies have reported that the rate of population growth is influenced by biotic and abiotic factors such as density and weather variables (Sæther 1997, Chapter 3). Even if the assumption was met, we have no idea which values of population growth would be most appropriate for a target population among some different values: two different values for the rate of population growth resulted in different consequences in the population size estimation (Yamamura et al. 2008). Unrealistic assumption or referring to a biased value in a specific area for the rate of population growth may cause biased population estimates.

If we construct a universal model for the rate of population growth that is applicable to various populations, the problems with the unrealistic assumption and a biased value of population growth can be disappeared. Reliable population estimates based on data intensively surveyed at a small scale within a large scale may provide good material to model the rate of population growth with which deer increase in number subjecting to mortality factors except for harvest (hunting and pest control).

In this study, we illustrate a harvest-based estimation method incorporating a model for the rate of population growth. Deer population in eastern Hokkaido, Japan was taken as an example. First, we constructed a model for the rate of population growth based on part of a population in Ashoro, one of towns in eastern Hokkaido, where the subpopulation can be reconstructed from age-specific harvest data using cohort analysis. Next, we applied the model to harvest-based population estimation to test the accuracy of the estimates. Finally, we applied the model to harvest-based estimation of eastern Hokkaido population.

## 4.2 Materials and methods

Historical change in hunting regulations in Eastern Hokkaido (Table 4.1).

Sika deer population in Hokkaido gradually recovered in abundance and distribution from the bottleneck (-1950s) under government protection, and by the mid-1970s the population occupied most available habitats in eastern Hokkaido (Kaji et al. 2000). More recently, deer population has irrupted in eastern Hokkaido and has caused severe damage to agricultural and forested areas (Kaji et al. 2000, Matsuda et al. 2002). To reduce the damages, hunting regulations were relaxed (Kaji et al. 2000, Matsuda et al. 2002) to expect increase in hunting effort (number of days for hunting multiplied by number of hunters). In Japan, hunting is regulated by manipulating the length of hunting season and the number of hunts permissible per

one hunting day. Table 4.1 shows changes in hunting season and the maximum number of hunts available per one hunter per one hunting day by sexes in Ashoro town, eastern Hokkaido during 1990-2007. Although there is little difference in the regulations between towns in eastern Hokkaido, the regulations in Ashoro town represent the majority taken in most towns of Eastern Hokkaido. Although there has also been some change in the way of pest control since 1990, no sex-specific regulation has been built. All registered hunters are obliged to report when they went hunting and how many deer they observe and hunt during the entire hunting season.

A-I : Modeling the finite rate of population growth

**1. Population reconstruction using cohort analysis**

To construct a model for the finite rate of population growth, we reconstructed a deer subpopulation in Ashoro using cohort analysis. Cohort analysis is a method applied to age-specific harvest data. This method produces unbiased results if input data are unbiased and assumptions are satisfied (Hiramatsu 2001, Chapter 2).

We used the age-specific number of harvest, 22630 female and 14040 male sika deer during 1990-2001. Age was determined for 12,186 females (86.8%) and 5,363 males (23.7%) either from tooth replacement or by counting the number of layers of cementum of annuli of the first incisor following Ohtaishi (1980). We corrected for the number of missing individuals in the data set.

Let November be the start of a year. We assumed that the harvest is a pulse-like event that occurs in the middle of the year and that animals are subjected to natural mortality throughout the year (Pope 1972).

$$N_{a,y} = N_{a+1,y+1} \exp(M_{a,y}) + K_{a,y} \exp\left(\frac{M_{a,y}}{2}\right) \dots\dots\dots(1)$$

where  $M_{a,y}$  is natural mortality rate,  $K_{a,y}$  is number of individuals harvest at the age of  $a$  in

year  $y$ . With this equation, number of individuals within a cohort can be calculated backward in a recursive way. On the other hand, the number of deer in the oldest age-class which includes ages beyond  $p$  years ( $p+$ ), and all age-classes in the most recent year was obtained by a following equation.

$$\hat{N}_{a,y} = C_{a,y} \frac{(\hat{F}_{a,y} + M)}{\hat{F}_{a,y}} \cdot \frac{1}{1 - \exp(-(\hat{F}_{a,y} + M))} \dots\dots\dots(2)$$

where  $\hat{N}_{a,y}$  is the number of deer at age  $a$  in year  $y$  and  $\hat{F}_{a,y}$  is the estimated harvesting mortality rate at age  $a$  in year  $y$ . We set following assumptions for harvesting mortality rates: (1) the harvesting mortality rates for every age-class in the most recent year is the same as the arithmetic mean of the rates of age-specific harvesting mortality for the counter age during the precedent 3 years, and (2) the rate of harvesting mortality at age-class  $p+$  is regressed by the rate of harvesting mortality at age  $p-1$  following a simple linear-regression based on the original cohort analysis (Chapter 2, Chapter 3).

We obtained a following equation for the number of  $p$  year-old-deer from the number of deer at the age-class of  $p+$  by assuming the stationary stable age distribution for the population beyond  $p$  years old (Hiramatsu 2001).

$$N_{p,y} = C_{p+,y} \frac{F_{p+,y}}{F_{p+,y} + M_{p+,y}} \dots\dots\dots(3).$$

In this study, we set 9 on  $p$ . We assumed that natural mortality rates for 1-5, 6-8, and 9+-year-old deer for both sexes are 0.03, 0.1, 0.5, respectively. Values for 1-5 and 6-8 year-old-deer were set based on observed values in radio telemetry surveys in eastern Hokkaido (Igota 2004, Uno and Kaji 2006). The high value for natural mortality for 9+ year-old deer was set to adjust the numbers of yearlings between the sexes. We assumed no annual variation for natural mortality. This effect may be of minor importance in large mammals, because adult

survival rates are generally high and stable (Fowler 1987, Sæther 1997, Gaillard et al. 1998, Gaillard et al. 2000, Igota 2004). Because the natural mortality rate for juveniles (first year of life) is affected by biotic and abiotic factors (Sæther 1997), juvenile natural mortality can not be assumed stable. Therefore, the age-class of juvenile was excluded from the present cohort analysis and defined the total number of deer beyond 1 year old as population size.

## 2. Model for the rate of natural population increase

Density accounted for annual variation in the rate of population growth, while weather variables such as snow depth or snow fall did not (Chapter 3). Thus, the finite rate of population growth in year  $t$ , which is a numerical proportion between the number of individuals alive at start of year  $t+1$  and the number of individuals at start of year  $t$ , was modeled using population density as an explanatory variable,

Density Dependent (DD) model: 
$$R_t = \frac{R_{\max}}{(1 + b(D_t))} \dots\dots\dots(4)$$

where  $R_t$  is the finite rate of population growth in year  $t$ ,  $R_{\max}$  is the maximized rate of  $R_t$ , i.e., the rate without density effect,  $b$  is the coefficient for density-dependence and  $D_t$  is population density (deer / km<sup>2</sup>) in year  $t$ . We estimated  $R_{\max}$  and  $b$  by maximum likelihood estimation (MLE).

A-II : Harvest-based estimation of Ashoro population using state-space modeling.

### 1. Population index

A spotlight survey was conducted annually for 8 years from 1991 to 1998 at a fixed route by Hokkaido government. The survey was performed between late October and early November, before the start of the hunting season. Each survey route was about 10 km in length. Two observers holding spotlights (Q-beam 160,000 candle-power; Brinkmann, Dallas, TX), riding

in a vehicle at a speed ranging from 20 to 40 km/h), searched for deer on both sides of the survey route from about 1900 to 2000 in the night. The total number of deer detected along the route was recorded. We defined those numbers as observed population index for Ashoro population (Fig. 4.1).

## 2. Population density dynamics model

We constructed a univariate model by simplifying the stage-structured model, because the estimates based on the univariate model was similar to those obtained by the stage-structured model (Yamamura et al. 2008). Let  $H_t$  be density of harvested deer ( $\geq 1$ ) by hunting (number of harvests by hunting / total area) from late October in year  $t$  to February in year  $t+1$ . Let  $C_t$  be density of harvested deer ( $\geq 1$ ) by pest control (number of harvests by pest control / total area) from March to late October in the year  $t+1$ . Let  $\lambda$  be the finite rate of population growth subject to mortality factors except for hunting and pest control. Then, we constructed a population density ( $D_{t+1}$ ) dynamics model as follows,

$$D_{t+1} = (D_t - H_t)\lambda - C_t \dots\dots\dots(5).$$

Harvest data in Ashoro used here was the same as described in the section of population reconstruction using cohort analysis, though age information for harvested deer was masked (Fig. 4.2). As for  $\lambda$ , we applied a model for the finite rate of population growth considering density-dependence (DD model: Eq. 4), and models assuming constant growth rate of 1.15 and 1.21 (CON models).

## 3. State-space model

We estimated population density ( $D_t$ ) from the population index ( $I_t$ ) using the population density dynamics model described above (Eq. 5). Two equations appear in states-space modeling: a

state equation and an observation equation. A state equation describes the dynamics of the true population density, while an observation equation describes the relation between the observed population density and the true number of individuals. The ‘true population index’,  $U_t$  is defined by,

$$U_t = \alpha D_t \dots\dots\dots(6)$$

where alpha is the conversion factor. Let  $\log_e(\mathbf{I}_t)$  be the vector of the logarithm of the observed population index from 1991 to 1998, and let  $\log_e(\mathbf{U}_t)$  be the vector of the logarithm of the true population index. We then have

$$\log_e(\mathbf{I}_t) = \log_e(\mathbf{U}_t) + \mathbf{e}_{It} \dots\dots\dots(7)$$

where  $\mathbf{e}_{It}$  is the vector of errors. Eq. 5 is a state equation, while Eq. 7 is an observation equation. See Yamamura et al. (2008) for further information in details.

The probability that a given set of estimated indices  $I_t$  ( $t = 1991, 1992, \dots, 1998$ ) was obtained was expressed by

$$\Pr(I_{1991}, I_{1992}, \dots, I_{1998}) = \int_{D_{1991}} \int_{D_{1992}} \dots \int_{D_{1998}} \Pr(I_{1991}, I_{1992}, \dots, I_{1998} | D_{1991}, D_{1992}, \dots, D_{1998}) \cdot \Pr(D_{1991}, D_{1992}, \dots, D_{1998}) dD_{1991} dD_{1992} \dots dD_{1998}$$

where  $\Pr(D_{1991}, D_{1992}, \dots, D_{1998})$  is the probability that the set of  $D_t$  is generated. This probability was calculated using state equations.  $\Pr(I_{1991}, I_{1992}, \dots, I_{1998} | D_{1991}, D_{1992}, \dots, D_{1998})$  is the conditional probability that the set of  $I_t$  is obtained under a given set of  $D_t$ . This probability was calculated using observation equations. The integration was performed over the entire range of  $D_t$ . We used the Bayesian estimate as an approximation of maximum likelihood estimate (cf. Yamamura et al. 2008).

B : Example: Harvest-based estimation of eastern Hokkaido deer population using state-space modeling.

We applied the model for the rate of natural population increase from Ashoro data to the estimation of eastern Hokkaido population. We defined here deer management units 9-12 (20461 km<sup>2</sup>) as Eastern Hokkaido (Fig. 4.3). For the estimation of population index, we used data on a spotlight survey which was conducted annually for 15 years, from 1993 to 2007, at 46 survey routes over those units. Result of the estimates was shown in Fig. 4.4 (see Yamamura et al. (2008) for further information about the estimation of population index in eastern Hokkaido).

We estimated population density ( $D_t$ ) from the estimated population index ( $\hat{I}_t$ ) using the population dynamics model described above (Eq. 5). Procedures for the eastern Hokkaido population are the same as described in the estimation Ashoro population. The number of killed deer by hunting and pest control was shown in Fig. 4.5. As for  $\lambda$ , we applied a model for the finite rate of population growth considering density-dependence (DD model), and models assuming constant growth rate of 1.15 and 1.21 (CON models). CON model represents the assumption on the finite rate of population growth used in Yamamura et al. (2008). We obtained estimates based on the same model at the density level in this study.

### 4.3 Results

A-I: Estimating a density-dependent model for the finite rate of population growth (DD model). The population size ( $\geq 1$ ) reconstructed by cohort analysis increased from 6335 (5.4 deer / km<sup>2</sup>) in 1990 to 14239 (12.2 deer / km<sup>2</sup>) in 1996, although the population growth decelerated after 1996 (Fig. 4.6). The population decreased after 1998: population size in 2001 was 5721 (4.9 deer / km<sup>2</sup>).

Our estimates of  $R_{\max}$  and  $b$  were 1.41 and 0.017, respectively.

A-II: Applying DD model to harvest-based estimation of Ashoro subpopulation.

The population density in Ashoro, as estimated using DD model increased from 7.2 deer / km<sup>2</sup> in 1990 to 10.9 deer / km<sup>2</sup> in 1995. The population decreased to 6.8 deer / km<sup>2</sup> in 2001. The results on population growth using DD model was consistent with the reconstructed population (Fig. 4.6).

On the other hand, estimates of population density using CON models showed different population abundance and trends by assuming 1.15 and 1.21 for the finite rate of population growth (Fig. 4.6). The population abundance was higher than that of the reconstructed population and continued to increase during the study period. Nevertheless, with assumed value of 1.32, the population estimates using CON model showed fairly consistent abundance and its trend with the reconstructed population.

B: Applying DD model into harvest-based estimation of Eastern Hokkaido population.

The population density in eastern Hokkaido, as estimated using DD model gradually increased from  $14.6 \pm 3.9$  deer / km<sup>2</sup> in 1993 to  $15.8 \pm 3.1$  deer / km<sup>2</sup> in 1995 (Fig. 4.7). The population decreased to  $13.9 \pm 2.0$  deer / km<sup>2</sup> in 2007. Trend in the estimates was consistent with those using Con models either by assuming 1.15 or 1.21 for the finite rate of population growth. However, estimated density was close to estimates by assuming 1.15 for the rate (Fig. 4.7). Estimated rate of population growth using DD model was lower in the early study period than later study period (Fig.4.8).

#### 4.4 Discussion

Our estimate of  $R_{max}$  indicates high potential for population increase of sika deer in Hokkaido. This is supported by previous observations on their reproduction and survival. In Hokkaido, age at primiparity for most female deer is the third year of life (two year-old females) and the oldest

deer showing pregnancy was 16 years old (Kaji et al. 2006). Natural mortality rates for adult females are very low with little annual variation (Igota 2004, Uno and Kaji 2007); some deer survive to over 20 years (Hokkaido Institute for Environmental Sciences 1997, Chapter 3). However, our estimate of  $R_{max}$  (1.41) exceeded the value (1.36), which is expected from stage-matrix model assuming 100% birth rate and 100% survival under 1:1 sex ratio condition in the population. Deer populations that have been subject to male-biased hunting like our study population may violate the assumption of 1:1 sex ratio. In 1957, Hokkaido deer hunting ban was lifted and only buck hunting was allowed. On the other hand, female hunting has been banned until 1978 when female pest control was only permitted. Female leisure hunting was finally permitted in 1994. Thus, male-biased hunting for a long period might have resulted in female-biased population, which caused high  $R_{max}$ .

Our estimate of Ashoro population density using DD model was consistent in the abundance and its trend with the reconstructed population indicating that rate of population growth obtained by the model was valid. Density-dependent increase in juvenile natural mortality has been reported in many cervids (e.g. Bartmann RM et al. 1992 for mule deer; Clutton-Brock et al. 1987 for red deer; Singer et al. 1997 for elk) and recently in sika deer as well (Chapter 3). Finite rates of population growth have been estimated with sika deer populations in Lake Toya (1.15) and Shiretoko Peninsula (1.21; Kaji et al. 2004). These values are lower than our estimate (1.41). Time-series data included the period at high population density just before the population crash in both areas. Estimates of population growth rates both in Shiretoko and Nakanoshima Island may be higher if we limit the period of data for the estimation.

Similar estimates of Ashoro population density were obtained without applying DD model but by assuming the constant value of 1.32. This suggests that the effect of density

dependence by itself may not be very influential on the annual variation in the population growth rate. However, because 1.32 was not obtained from empirical data and we would never know the appropriate value applied to the constant growth model for the rate of population growth, it is meaningful that a model for the rate of population growth can be obtained from intensively surveyed population.

The finite rate for population growth in Ashoro was higher than 1.15, whereas that in eastern Hokkaido was close to 1.15. This suggests that there is spatial variation in rates of population growth. Thus, our model succeeded in estimating different growth rate for each area using the universal model. Therefore, intensive survey focusing on a model area within the entire area will enable us to make a model for finite rate of population growth and estimate absolute population size in a large scale.

Table 4.1.

Chronology of the length of hunting season and the maximum number of hunts permissible per one hunter per hunting day by sexes in Ashoro town, eastern Hokkaido during 1990-2007.

Fiscal year (begins on Apr.1)	Hunting regulation phase	Males		Females	
		number/day	period	number/day	period
1990	I	1	Nov.15-Jan.15		
1991	I	1	Nov.15-Jan.15		
1992	I	1	Nov.15-Jan.15		
1993	I	1	Nov.15-Jan.15		
1994	II	1	Nov.15-Jan.15	1	Jan.6-Jan.15
1995	II	1	Nov.15-Jan.15	1	Jan.6-Jan.15
1996	II	1	Nov.15-Jan.15	1	Jan.6-Jan.15
1997	III	1	Nov.15-Jan.15	1	Nov.15-Dec.15
1998	IV	1	Nov.1-Jan.31	2	Nov.1-Jan.31
1999	IV	1	Nov.1-Jan.31	2	Nov.1-Jan.31
2000	IV	1	Nov.1-Feb.28	2	Nov.1-Feb.28
2001	V	1	Nov.1-Jan.31	3	Nov.1-Jan.31
2002	V	1	Nov.1-Jan.31	3	Nov.1-Jan.31
2003	V	1	Nov.1-Jan.31	3	Nov.1-Jan.31
2004	VI	1	Nov.1-Feb.13	no limit	Nov.1-Feb.13
2005	VI	1	Oct.25-Jan.31	no limit	Oct.25-Jan.31
2006	VI	1	Oct.25-Jan.31	no limit	Oct.25-Jan.31
2007	VI	1	Oct.25-Feb.29	no limit	Oct.25-Feb.29
2008	VI	1	Oct.25-Mar.1	no limit	Oct.25-Mar.1

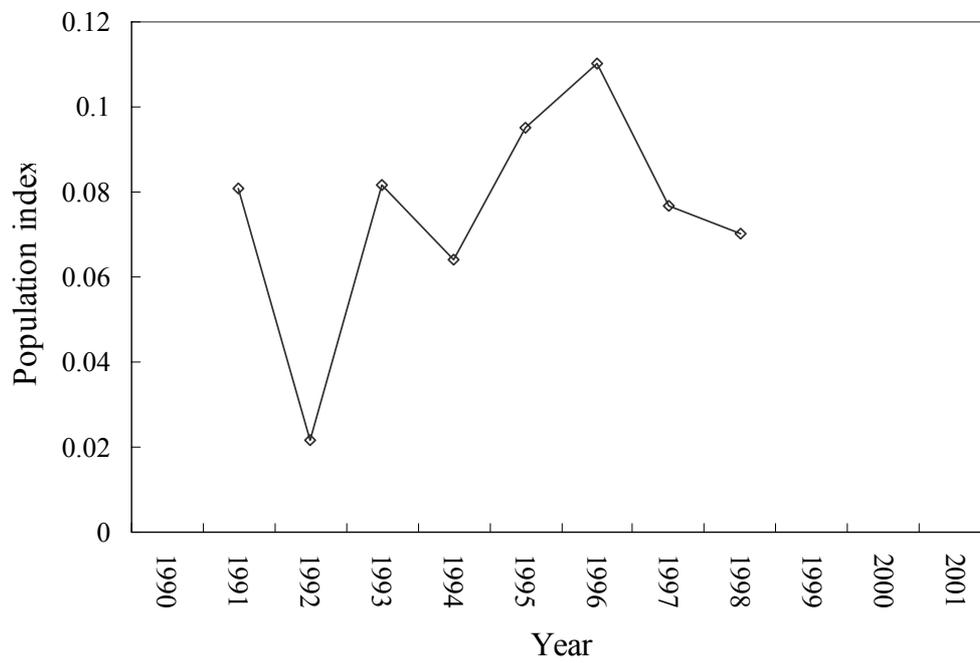


Fig. 4.1. Population index based on spotlight counts on a suvey route during 1991-1998 in Ashoro town.

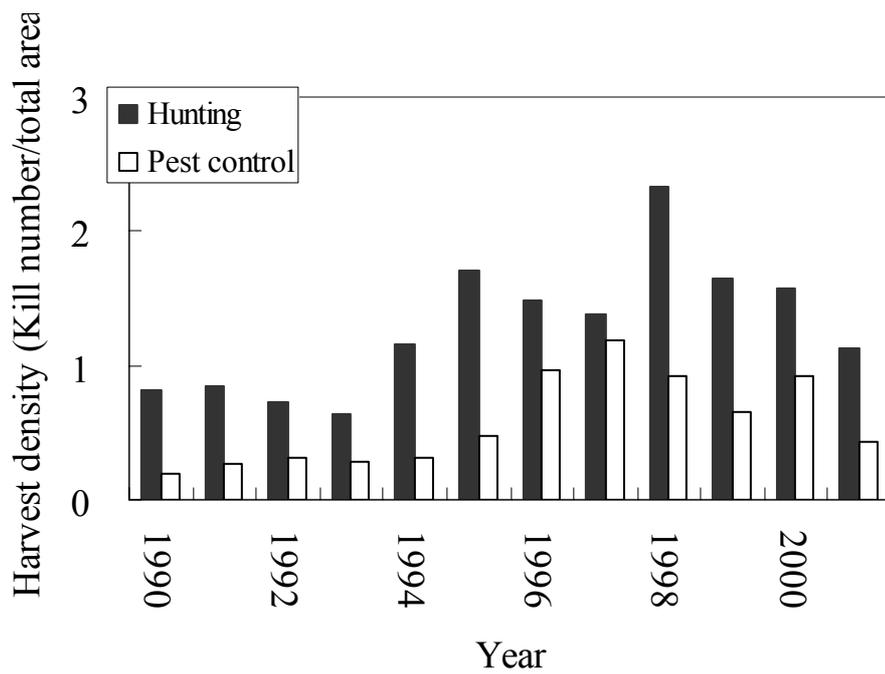


Fig. 4.2. Annual number of harvested deer by hunting and pest control in Ashoro town during 1990-2001.

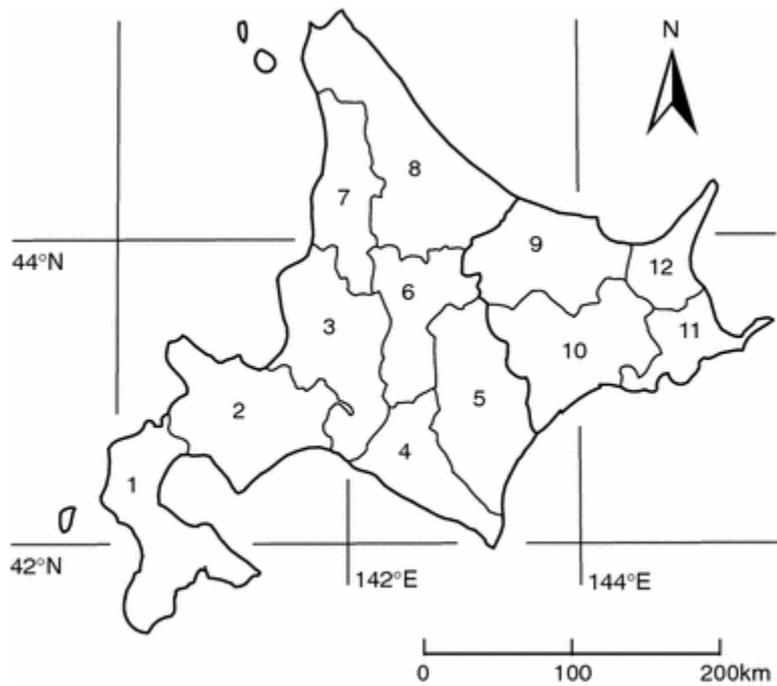


Fig. 4.3. Map of Hokkaido Island. Numbers inside the map indicate the sika deer management unit (Hokkaido Institute of Environmental Sciences 1994). Hokkaido is divided into two areas-the eastern area (units 9-12) focused in this study and western area (units 1-8). Ashoro town is included in unit 10.

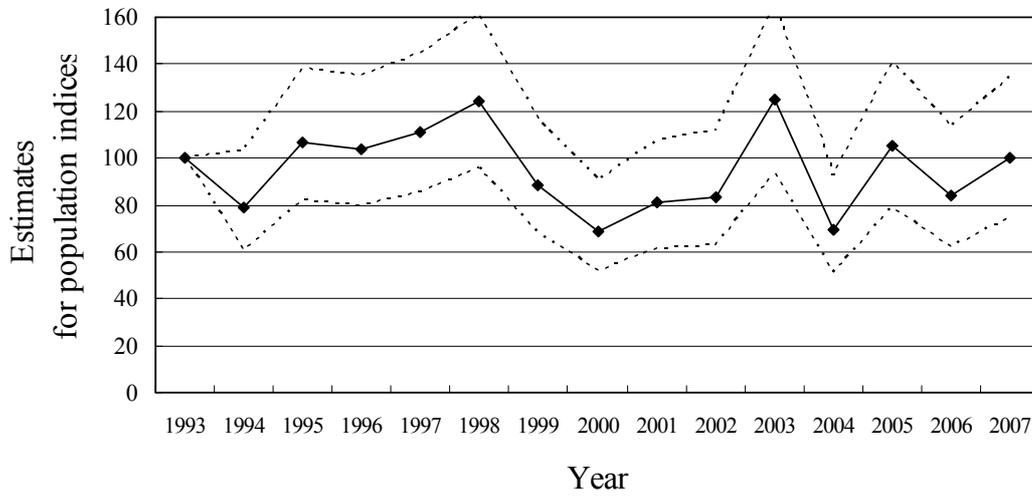


Fig. 4.4. Population indices in eastern Hokkaido during 1993-2007 that were estimated by the function `glmmPQL` in R. Dotted lines indicate the 95% Wald confidence intervals.

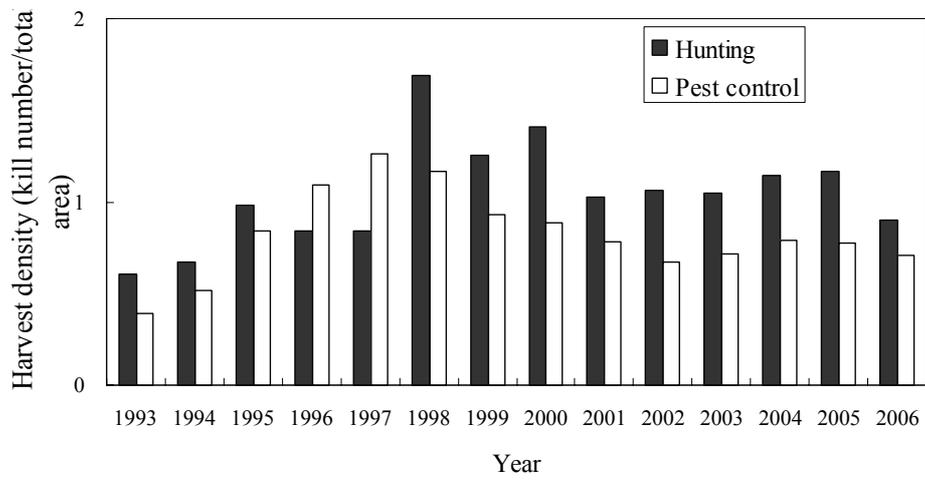


Fig. 4.5. Annual number of harvested deer by hunting and pest control in eastern Hokkaido during 1993-2006.

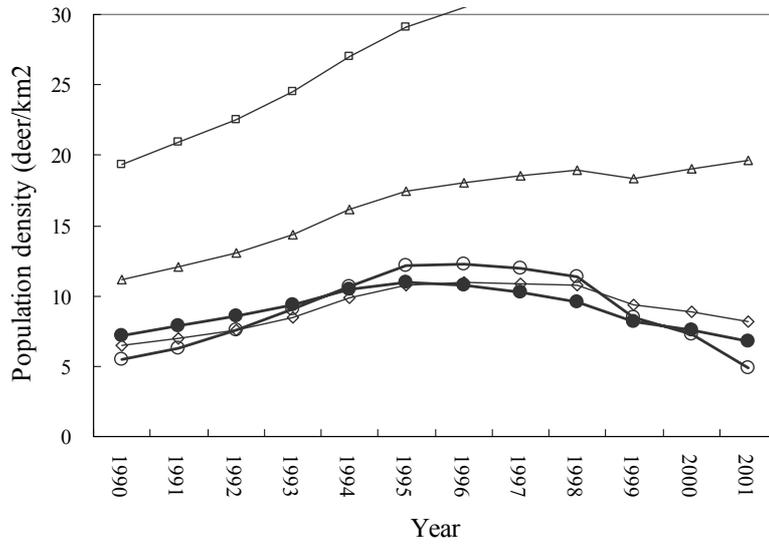


Fig. 4.6. Estimates of density of Ashoro population during 1990-2001 using DD model (●) and CON models with 1.15 (□), 1.21 (△) and 1.32(◇). Ashoro population reconstructed using cohort analysis (○) was shown to compare with.

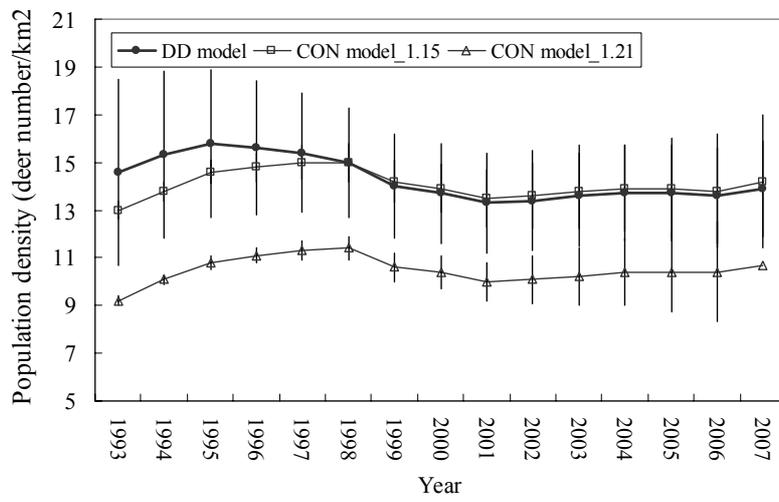


Fig. 4.7. Estimates of population density in Eastern Hokkaido during 1993-2007 using DD model (●) and CON models with 1.15 (□) and 1.21 (△).

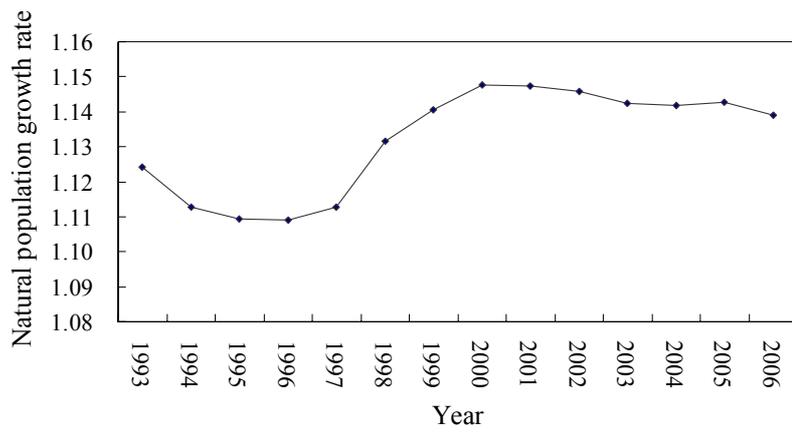


Fig. 4.8. Estimated rates of natural population increase using DD model in eastern Hokkaido during 1993-2006.

## Chapter 5

### General Discussion

In this chapter, I discussed application of harvest-based population estimation methods examined in this thesis for sika deer management in Japan.

#### *Utility of cohort analysis as a method for reconstruction of a local population*

Harvest information for game species is often collected by age and sex as part of management programs by wildlife agencies (Skalski and Millspaugh 2002; Conn et al. 2008, Davis et al. 2007); consequently, under many circumstances, harvest data can be available for the population estimation. Because with cohort analysis we assume a certain value for natural mortality, violation of the assumption may bias accuracy in the estimates. However, it is well known that natural mortality rates for adults are low with small annual variation (Gaillard et al. 1998). Therefore, assuming natural mortality would not have great impact on accuracy in population estimates, i.e., population dynamics. Thus, cohort analysis shown in Chapter 2 is a reliable method to estimate absolute population size and to quantify effects of sex- and age-specific hunting on the population (Chapter 3).

Although Capture-Mark-Recapture methods (CMR) have been known as a promising method for reliable estimates (Lebreton et al. 1992), the condition preparing sufficient number of marked individuals is problematic: sample size must exceed 100 for adult survival rate and more for juvenile survival rate in ungulates (Gaillard et al. 1998), which will be almost impossible to be implemented. There are only five areas in Japan where live capture has been implemented (Uno et al. 2007) and the maximum sample size of marked adult individuals was 43 (Sakuragi et al. 2002, Igota et al. 2003). In addition, CMR methods require assumptions such

as independent sightings and homogeneity of individual sighting probabilities (Neal et al. 1993, see Bender and Spencer 1999), which are difficult to be met. Therefore, in population management, cohort analysis is more beneficial in estimating absolute population size compared to CMR methods.

Note that we need some conditions when applying age-specific harvest data to cohort analysis. First, we have to grasp total number of harvests. Second, aged individuals must be randomly sampled from the total harvests, and the proportion of harvested animals with known age in the total harvest requires being quantified to correct for the number of missing individuals in the data set. Third, data need to be collected relatively large scale enough to cover home range of a single individual or to exceed about 100 harvested animals, because demographic stochasticity caused by small sample size in harvests would degrade the precision of reconstructed population. Moreover, population estimates during early periods of data will be more robust as harvest data has been accumulated longer thereafter (Shimoda et al. 2006). In brown sole *Pleuronectes herzensteini* populations, robust population estimate in a single year required following 7 years of age-specific harvest data (Shimoda et al. 2006). Therefore, more robust population reconstruction will be possible, as longer-term data has been collected.

#### *Subpopulation as a model of a whole population*

Estimates based on observation surveys such as aerial and spotlight surveys have been evaluated as reflecting trends in population abundance. Therefore, monitoring the population trend is useful to know if the current management action is working. Nevertheless, indices wouldn't tell us how much the population decreased or increased in number. To prevent overabundance or extinction, we yet need to know the abundance to quantify how much effort we should pay for our management objectives. Especially, we have to keep in mind that estimates of absolute

population size based on observation surveys such as aerial and spotlight surveys are often underestimated, because overestimation of sightability or underestimation of decaying rate. Harvest-based population estimation combining observation data with harvest data examined in Chapter 4 is relatively low cost and easily applied to large-scale population by preparing intensive data sets in a model area. Population estimation methods targeting two hierarchal scales we established here are sound both in light of cost and robustness of estimates, and therefore will be most practical methods to achieve absolute population estimation and evaluating culling as a population control in population management.

*Can double-scale sampling be applied in current deer management system?*

Combining intensive data at small scale with low-cost data at large scale made it possible to estimate absolute population size in a large scale. I discuss application of harvest-based population estimation methods examined in this thesis to population management in other nations or regions. In Norway, moose populations have been monitored annually since 1991 as part of the National Moose-Monitoring Program (Solberg et al. 2002). Harvest-at-age data are collected in eight different populations along a north-south gradient covering the most important regions where moose are harvested. Cohort analysis has been applied to population estimation of moose and red deer in Norway (Solberg and Sæther 1999, Solberg et al. 1999, Solberg et al. 2000, Mysterud et al. 2004). Reporting moose observations is compulsory for the leader of hunting team in state forests, with which SPUE is calculated and has been an important index of moose density (Solberg and Sæther 1999). Therefore, design of data collection of moose in Norway is ready for estimating absolute population size at large scale. On the other hand, in Scotland there is no national leadership to collect data systematically because most of areas are private land managed by landowners (Milner et al. 2006a). Therefore, it is difficult to perform

population management in a large scale integrating private lands.

In Japan, 22 prefectures out of 36 prefectures where deer occur have made Specified Wildlife Conservation and Management Plans (SWCMP) mainly to reduce damage on agriculture and forestry (Tokita 2006, Uno et al. 2007). Plans are implemented by administrative compartments (i.e., prefectures). However, deer populations in Honshu, Shikoku and Kyushu Islands may be distributed across several prefectures (The Ministry of the Environment). If we integrate data-sets in neighboring prefectures, it may be possible to estimate absolute population size at the large scale. To date, however, there are only a few prefectures (Hokkaido, Chiba, Kyoto prefectures) that have collected harvest-at-age data (Ueno personal communication). Moreover, quality of data and periods of data collection are disjointed between prefectures. We call for utilizing data collection system by prefectures to apply an estimation method for absolute population size at large scale based on double-scale sampling.

The Ministry of the Environment has declared establishing science-based population management system for wildlife in a document of the National Biodiversity Strategy (see HP of the Ministry of the Environment). The Ministry emphasizes the significance of the monitoring and feedback management system in sika deer population management, which evaluate the effect of a particular management action on the population and examines if target goal and the management tactic are appropriate. Whereas a large number of long-term surveys have been conducted on health-related information dedicated to the maintenance of health and safety for the people of Japan across the country based on laws, there are only a few attempts related on wildlife (see HP of the Ministry of the Environment, Akasaka 2006, Kaji 2006). Monitoring wildlife populations is as important as monitoring pollution (Akasaka 2006). Integrating prefecture-based system for data collection into a national-based system ensuring a long-term research is required for wildlife management hereafter.

## Summary

シカ類は世界各地で激増し、人間社会との軋轢を高めているため、駆除や狩猟による捕獲（以下、捕獲）を通じた個体数コントロールが試みられている。しかし、いまだに個体数を目標レベルにまで減少させた例はなく、捕獲の個体数削減効果の検証と個体数管理に必要な分析手法の確立が求められている。本研究は、捕獲効果の検証と捕獲数を用いた個体数推定法の確立を目的に、以下の3つの課題に取り組んだものである。課題1：年齢別捕獲数を用いた個体数復元法を確立（2章）。課題2：ニホンジカ個体群の動態分析と捕獲効果の検証（3章）。課題3：大規模スケールでの個体数推定法の確立（4章）。また、総合討論として、4章で検討した手法を実施する場合の問題点を議論している（5章）。

2章では、年齢別捕獲数を出生年ごとに集計することで、過去の個体数を復元する手法であるコホート解析法の改良を行っている。原理に忠実な方法（以下、オリジナルコホート解析）は、ある年の個体数復元のために寿命と同じ年数の年齢別捕獲数が必要なため、寿命の長い陸棲大型哺乳類ではほとんど適用されていない。水産資源管理学では、捕獲データと同期間の個体数復元を可能にする方法が開発されているが、捕獲率にいくつかの仮定を置くため、陸棲大型哺乳類に適用するためには、それらの仮定の妥当性やより適切な仮定の探索が必要である。この章では、ノルウェーのヘラジカの長期間にわたる年齢別捕獲数を用いて、オリジナルコホート解析によって算出した年齢別個体数を真に近い値と考え、仮定の妥当性を検討した。その結果、データの最終年における年齢別捕獲率は、捕獲率の年変化に一定の傾向が見られない限り、過去数年間の平均捕獲率に等しいと仮定することが、後半の復元個体数の正確性を著しく高めることを明らかにした。このように、より適切な仮定を得ることで、陸棲大型哺乳類における個体数復元法の改良に貢献した。

3章では、2章で検討した手法を用いて、1990-2001年における北海道足寄町ニホンジカ個体群の動態を分析し、個体数コントロールに対する捕獲の効果を検証した。90年代前半において、メスの捕獲率は低い値で推移し、個体数は増加し続けた。一方、個体群成長率への密度効果が検出され、個体群自己制御機構の存在が示唆された。しかし、密度が最も高い時でさえ個体群成長率は正であり、密度効果によって個体数は減少しなかった。個体数が初めて減少したのは、積極的なメスジカ捕獲が開始された1998年の翌年で、捕獲率の上昇だけでなく1歳個体の加入率の低下がこの減少に寄与していた。加入率の低下には、子の母親にあたる2歳以上メスの捕獲率の上昇が作用していた。2歳以上メスの捕獲が加入率を低下させた理由には、母親を失った孤児は生存に不利であることが考えられた。以上の分析から、個体数が過剰な状態にあるニホンジカを減少させるためにはメスジカの大量捕獲が不可欠であることが立証された。

4章では、3章で復元した個体数を使って自然増加率の推定モデルを作成し、大規模スケールでの新たな個体数推定法を検討した。Matsuda et al. (2002)やYamamura et al. (2008)は、ライトセンサスで得られた個体数指数の動向を参照しながら、捕獲実績に基

づいて個体数を推定する手法を開発した。しかし、仮定する自然増加率の大きさによって推定個体数が大きく異なるという問題があった。3章の分析に基づき、密度効果を考慮した自然増加率の時間的変化をモデル化することによって、この問題を解決し、より確度の高い個体数推定が可能になると考えられた。足寄町の復元個体数から自然増加率の推定モデル（以下、足寄モデル）を作成し、その上位個体群にあたる道東個体群の個体数推定法を検討した。その結果、新しい推定値の年変化は妥当で、個体数は自然増加率に1.15を仮定した場合に近い値が得られた。このように、本章ではモデル個体群から得た詳細な情報を取り入れた個体数推定法を確立し、確度の高い個体数推定を可能にした。

5章では4章で検討した手法を実施する場合の問題点を議論し、個体群動態に関する詳細な情報を得ることができるモデル個体群の重要性を指摘し、モデル地区からのデータ収集システムの確立を提言した。

以上のように本研究は、シカ類の個体数コントロールに不可欠な捕獲の個体数削減効果を検証し、個体数管理に必要な個体数推定法の確立に貢献した。

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### **General discussion**

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