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Culling Versus Density Effects in Management of a Deer Population

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Management and Conservation Article

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ABSTRACT Wildlife managers often manipulate hunting regulations to control deer populations. However, few empirical studies have examined the level of hunting effort (hunter-days) required to limit population growth and demographic effects through harvesting of females. Moreover, the relative importance of density effects on population growth has not been quantified. We reconstructed a sika deer [*Cervus nippon*] population over a period of 12 years (1990–2001) using age- and sex-specific harvest data. Using cohort analysis, we analyzed population dynamics, focusing on 1) the relationship between hunting effort and hunting-induced mortality rate, 2) relative contributions of hunting mortality and recruitment of yearlings to annual changes in population growth rate, and 3) annual variation in recruitment rate. Population size increased until 1998 and declined thereafter. The population growth rate changed more in response to annual changes in recruitment rate than hunting mortality rate. Temporal variation in recruitment rate was not controlled by birth rate alone; direct density dependence, intensities of hunting mortality for fawns, and for females (≥2 yr of age), which accounted for the fawn survival rate, were required as factors to explain temporal variation. Density effects on the recruitment rate were not strong enough to regulate the population within the study period; high hunting mortality, with intensive female harvesting, was necessary to prevent population growth. Hunting effort was a good predictor of the hunting mortality rate, and female harvest had a negative effect on the recruitment rate through fawn survival. We suggest that >3,500 hunter-days and prioritization of female harvesting are required to prevent increases in this deer population.

KEY WORDS *Cervus nippon*, cohort analysis, density dependence, female harvest, harvest-at-age, Japan, population growth, population reconstruction, recruitment, sika deer.

Many deer species have dramatically increased in abundance and expanded their distribution ranges in Europe, North America, and Japan over the last century (red deer [*Cervus elaphus*], Clutton-Brock and Albon 1992; white-tailed deer [*Odocoileus virginianus*], McShea et al. 1997; roe deer [*Capreolus capreolus*], Andersen and Linnell 2000; sika deer [*Cervus nippon*], Kaji et al. 2000). Dense populations can inflict major economic losses in forestry, agriculture, and transportation (Côté et al. 2004). Increases in grazing and browsing pressure also have strong impacts on natural ecosystems; sometimes less favorable plant species increase in abundance and density (Côté et al. 2004, Kaji et al. 2006). One solution to these problems is deer herd culling (Buckland et al. 1996, Brown et al. 2000, Gordon et al. 2004). Public hunting is the primary tool used to manage deer populations (Healy et al. 1997, Giles and Findlay 2004). Wildlife managers often manipulate the length of hunting seasons and bag limits to control populations (Diefenback et al. 1997, Healy et al. 1997). Because cervids are polygynous, killing females has been considered effective for limiting population growth; therefore, game laws have been amended to allow higher numbers of females and fawns to be harvested (Smith and Coggin 1984, Diefenback et al. 1997, Matsuda et al. 2002, Côté et al. 2004).

Although mortality caused by intensive hunting can be the dominant demographic factor affecting deer populations (Bowyer et al. 1999, Solberg et al. 1999, Bender et al. 2004, Lawrence et al. 2004, Uno and Kaji 2006), only a few examples have been reported in which deer numbers have been successfully reduced to favorable densities through hunting (e.g., Fryxell et al. 1991). Increases in harvest rates are apparently lower than the finite rate of population growth, indicating that present hunting pressure is not always sufficient to reduce population size (Milner et al. 2006). Because validity of the relationship and the level of hunting effort may be species- and population-specific, more empirical study will be required. The effect of female harvesting should also be tested. Although effectiveness of female-biased harvesting for reducing the proportion of fecund females in a population and, therefore, for lowering recruitment rates, is clear in ecological theory, few empirical studies have examined demographic consequences of intensive female harvesting (Caughley 1977, Solberg et al. 1999, Giles and Findlay 2004).

In addition, the extent to which density dependence limits population growth is important. Many studies have shown that density dependence works as a self-regulatory mechanism and detected density effects on recruitment rates for large mammals (Clutton-Brock et al. 1985, 1991; Bowyer et al. 1999; Solberg et al. 1999; reviewed in Fowler 1987). Nevertheless, few empirical studies have quantified density effects on population growth rates while considering hunting pressure. Although 3 studies have demonstrated an inverse relationship between recruitment rate and population density, which represents one potential regulatory process, this effect may be masked by demographic changes induced by high harvesting rates (white-tailed deer, Fryxell et al. 1991; moose [*Alces alces*], Bowyer et al. 1999, Solberg et al. 1999). Are effects of density on population growth rate negligible? If not, should density dependence be

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included when modeling dynamics of deer populations? Relative importance of hunting mortality and density dependence needs to be quantified.

Sika deer populations in Hokkaido, Japan, have erupted after recovering from a population bottleneck (1950s) and have caused serious damage to agricultural and forested areas (Kaji et al. 2000, Matsuda et al. 2002). To facilitate population control, regulations on sport hunting and pest control have been relaxed (Kaji et al. 2000, Matsuda et al. 2002). Because of uncertainty regarding abundance, growth, and the structure of deer populations, the government of Hokkaido relaxed regulations incrementally, following an adaptive management approach (Matsuda et al. 2002). Thus, the deer population in eastern Hokkaido has been subjected to considerable changes in hunting pressure during the 1990s, which can be regarded as a large-scale field-based experiment. These management activities have provided an excellent opportunity to examine the performance of relaxed hunting regulations on the growth rate of this deer population.

We analyzed dynamics of a sika deer population for 12 years. During this period, hunting pressure (sport hunting and pest control) changed through gradual relaxation of hunting regulations. We examined 1) the relationship between hunting effort and hunting mortality rate, 2) relative contributions of hunting mortality rate and recruitment rate on annual changes in the population growth rate, and 3) annual variation in recruitment rate.

STUDY AREA

We conducted our research in the town of Ashoro (1,408 km^2) in eastern Hokkaido, Japan (43°20′N, 143°50′E). During the study, mean daily temperature was 5.7° C, maximum temperature was 32.5° C in summer, and minimum temperature was −25.1° C in winter (Japan Meteorological Agency 2009). Snow accumulation typically persisted from late December to early April. Accumulated snowfall and maximum snow depth for each year were recorded at the weather station nearest to the town of Ashoro; average values during the study were 328 cm for accumulated snowfall and 43.7 cm for snow depth (Japan Meteorological Agency 2009).

The town of Ashoro comprised primarily hilly terrain. Approximately 84% of the area was forested, and the remainder consisted of agricultural land and residential areas (Hokkaido 2006). Native deciduous broad-leaved and mixed forests comprised 55% of forested area. Broad-leaved forests were dominated by Erman's birch (*Betula ermanii*), Japanese elm (*Ulmus davidiana*), and Mongolian oak (*Quercus mongolica*), and mixed forests included Jezo spruce (*Picea jezoensis*) and Sachalin fir (*Abies sachalinensis*). The rest of forested areas were coniferous plantations including Japanese larch (*Larix leptolepis*), Jezo spruce, and Sachalin fir (Hokkaido 2006). Based on rumen analysis, deer in our study area consumed forbs and agricultural crops in spring and summer, sasa bamboo (*Sasa nipponica*) and browse in winter, and all of these plant foods in autumn (Yokoyama et al. 2000).

METHODS

During 1990–2001, 13,761 female and 22,108 male sika deer were killed through pest control (spring and summer) or sport hunting (autumn and winter). Pest control and hunter harvest were conducted continuously. As part of the sika deer monitoring project of the Hokkaido government, ages were determined for 12,186 culled females (88.6%) and 5,363 culled males (24.3%) either from tooth replacement or by counting number of layers of cementum annuli in the first incisor, following Ohtaishi (1980). To correct for missing individuals, the annual number of deer killed within an age class was multiplied by a factor correcting for the number of missing individuals in the data set. For instance, when y adults were killed and x were aged in a particular year, the number of individuals killed for each adult age-class for the year was obtained by multiplying the number of aged deer by y/x.

We used 2 quantitative values for mortality: mortality rate ($K_{a,y}$) and a mortality coefficient ($Z_{a,y}$). Mortality rate is equal to 1 minus the survival rate ($S_{a,y}$), whereas the mortality coefficient is equivalent to the negative logarithm of the survival rate, that is,

$$S_{a,y} = (1 - K_{a,y}) = \exp(-Z_{a,y}).$$

Larger mortality coefficient values indicate the survival rate is nonlinearly lower and closer to zero.

We assumed values of natural mortality for yearling and older deer, but not for fawns, because the natural mortality coefficient for adult deer is low and stable relative to density-independent and -dependent factors, whereas fawn natural mortality could vary annually subject to those factors (Sæther 1997, Gaillard et al. 2000). We assumed the natural mortality coefficient for prime-aged deer (F: 1–8 yr old, M: 1–9 yr old in our study) to be fixed at 0.03 based on adult female natural mortality estimates from radiotelemetry surveys in neighboring areas (Igota 2004, Uno and Kaji 2006). We assumed neither annual variation nor age-related differences in the natural mortality coefficient for those prime-aged individuals. The natural mortality coefficient for older-aged deer may be higher than for prime-aged deer due to senescence, which has been observed after 7–9 years of age in ungulate populations (Gaillard et al. 1993, Loison et al. 1999, Festa-Bianchet et al. 2003).

We assumed that natural mortality for older-aged deer was larger than prime-aged deer to prevent too many calves compared to adult females in the reconstructed population (Solberg et al. 1999). We defined composite-age classes of ≥9 years for females, and ≥10 years for males, as the older-aged class. We assumed that 999 out of 1,000 individuals should die before the age of 20 years. We also assumed that the age-specific natural mortality coefficient for deer 1–8 years old was fixed at 0.03; the total mortality coefficient for the older-aged class was computed to be high, 0.56 ([1 − 0.03]^8 × [1 − 0.56]^{12} = 0.001). We divided the total mortality coefficient into natural mortality and hunting mortality. As for females, we assumed 70% of total mortality was due to hunting during 1994–1997 and 84% during

Table 1. Sport hunting period and maximum number of kills by sex available per hunter per day, and hunting effort (hunter-days) for sika deer in the town of Ashoro, eastern Hokkaido, Japan, during 1990–2001.

Yr	Phase	M		F		Hunting effort (hunter-days)
		No./day	Period	No./day	Period	
1990	I	1	2 months	0	0	1,126
1991						1,735
1992						1,032
1993						362
1994	II	1	2 months	1	10 days	1,936
1995						2,771
1996						2,625
1997	III	1	1 month	1	1 month	2,452
1998	IV	1	3 months	2	3 months	3,294
1999						3,345
2000			4 months		4 months	3,097
2001	V	1	3 months	3	3 months	2,445

1998–2001 (see Standard value for Appendix A; Igota 2004, Uno and Kaji 2006). We lacked equivalent data during 1990–1993, a period with low hunting effort. Therefore, we assumed that the ratio of hunting mortality to total mortality was 0.05; the resulting sex ratio for the reconstructed population during that period was consistent with observation data (M:F = 1:1) from a spotlight survey (Hokkaido Institute of Environmental Science 1991; see Standard value for Appendix A). As for males, we assumed that the ratio of hunting mortality to total mortality was 0.70 during the whole period, because male hunting was as intensive as female hunting in 1998 and after (see Standard value for Appendix A).

Cohort Analysis

We reconstructed sex- and age-specific numbers of deer during 1990–2001 using sex-specific harvest-at-age data. We treated June as the start of a year because it corresponded with the period immediately following the birthing season. We assumed that hunting was a pulse-like event that occurred in the middle of the year and that animals were subjected to natural mortality throughout the year (Pope 1972). We used the following equations (1–4) to compute age-specific numbers for all age-classes. We computed age-specific numbers (except for both the oldest age class and all age classes for the final yr of the data set) as

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

where $N_{a,y}$ is the reconstructed number of deer at age a in year y, $C_{a,y}$ is number of deer killed at age a in year y, and M is the assumed natural mortality coefficient (Pope 1972, Yatsu et al. 2002).

We computed numbers of deer for the older-aged class in each sex ($p+$, $p = 9$ for F, $p = 10$ for M) in all periods as

$$\hat{N}_{p+,y} = C_{p+,y}(\hat{F}_{p+,y} + \hat{M}_{p+,y})/\hat{F}_{p+,y}/$$
$$\{1 - \exp[-(\hat{F}_{p+,y} + \hat{M}_{p+,y})]\}, \qquad (2)$$

where $\hat{N}_{p+,y}$ is estimated number of deer in $p+$, $\hat{F}_{p+,y}$ is the estimated hunting mortality coefficient for $p+$, and we computed $\hat{M}_{p+,y}$ and $\hat{F}_{p+,y}$ as described above (Ueno et al. 2009).

We computed the number of deer of the youngest age (p) in the older-aged class by assuming a stationary stable age distribution in the older-aged class. Then, we analytically computed deer age (p yr old) as follows (Ueno et al. 2009):

$$N_{p,y} = N_{p+,y}\{1 - \exp[-(F_{p+,y} + M_{p+,y})]\}. \qquad (3)$$

We computed age-specific numbers of deer in the final year of the data set (2001) as follows (Ueno et al. 2009):

$$\hat{N}_{a,2001} = C_{a,2001}(\hat{F}_{a,2001} + M)/\hat{F}_{a,2001}/$$
$$\{1 - \exp[-(\hat{F}_{a,2001} + M)]\}. \qquad (4)$$

We obtained the age-specific hunting mortality coefficient in 2001 ($\hat{F}_{a,2001}$) by referring to hunting mortality coefficients for the corresponding age-classes in preceding years. Hunting regulations in eastern Hokkaido were gradually relaxed starting in 1994 (Table 1), and substantial changes were made in 1998, when the maximum number of females that could be killed was doubled to 2 deer/day and the hunting season was prolonged (Table 1). Although the maximum harvest number was further increased in 2001 (phase V), hunting effort (hunter-days) in 2001 was similar to that during 1998–2000 (phase IV). Therefore, we assumed that the age-specific hunting mortality coefficient in 2001 was the arithmetic mean of the corresponding age-specific hunting mortality coefficients from 1998 to 2000 (see Yamaguchi and Matsuishi 2007 and Ueno et al. 2009 for details). We obtained the range of estimations by assuming a ±10% variation in hunting mortality coefficients for the oldest age class and for the final year of data (Fig. 1).

Because we did not use assumed values for fawn natural mortality in the present cohort analysis as stated in the previous section, age-classes of population we reconstructed were yearling and older. After we reconstructed numbers of deer by sex, we combined numbers for both sexes and defined the sum of deer yearling and older as the total population size ($N_{\geq 1,y}$). We defined the number of yearlings in year ($y + 1$) as the number of recruits at the end of year y.

Cohort analysis assumes a closed population, meaning that neither immigration nor emigration occurred during the study period (Hilborn and Walters 1992). However, this assumption was not satisfied in our study, because some
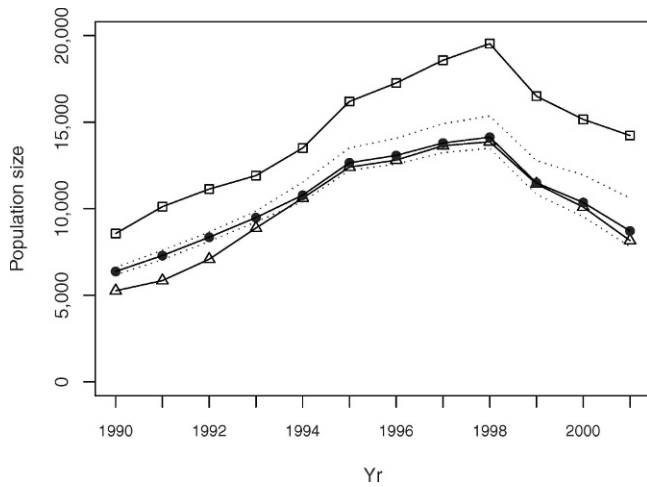
Figure 1. Annual changes in population size (sika deer ≥1 yr old; solid circle) during 1990–2001 reconstructed using harvest-at-age data in the town of Ashoro, eastern Hokkaido, Japan. We assumed that hunting mortality coefficients for the older-aged class in all periods followed the ratio of hunting mortality to total mortality based on Uno and Kaji (2006) and Igota (2004) and that hunting mortality coefficients for all age-classes in the final year of the data set corresponded to values from the preceding 3 years (1998–2000). We obtained interval estimates (dotted lines) by assuming ±10% variation in the hunting mortality coefficients for the older-aged class and for 2001. The 2 lines show reconstructed populations given higher (triangles) and lower (squares) hunting mortality coefficients than we assumed in our study.

radiocollared deer emigrated from the study area to a neighboring area in the winter (Uno and Kaji 2000, Igota et al. 2004). Assumption of a stationary stable age distribution for the older-aged class may cause an underestimation of the population size when a population is growing and an overestimation during periods of decrease (Millspaugh et al. 2009); the actual annual trend in population growth may be moderated by such dynamics. Nevertheless, the reconstructed population showed a trend consistent with a population index that was independently observed in eastern Hokkaido. A population index based on a spotlight survey showed increases from 1992 to 1998 followed by stability after some reductions (Uno et al. 2006, Yamamura et al. 2008). Thus, our estimates of the population through cohort analysis are reliable.

The reconstructed population may also depend on assumptions regarding intensity of both hunting mortality for the older-aged class in all periods and age-specific hunting mortality during the final year of data (Davis et al. 2007). We examined effects of violations of these assumptions by reconstructing the population under different assumptions. Regarding hunting mortality for the older-aged class, we examined conditions when the ratio of hunting mortality to total mortality was higher by using a value of 1, which would mean that all deer die from hunting, and lower by using a value that was half of the standard ratio (Appendix A). As for age-specific hunting mortalities in 2001, we used values equivalent to 1998 for higher conditions and values comparable to 2000 for lower values (Appendix B). The size of the reconstructed population

doubled when we assumed a lower ratio of hunting mortality to total mortality for the older-aged class and under the lower hunting mortality intensities of 2001 (Fig. 1; Appendices A, B). Nevertheless, the population showed the same trend regardless of assumptions, demonstrating robustness of our conclusions (Fig. 1).

Data Analysis

We calculated the following variables for use in subsequent analyses. Population growth rate in year y: $(N_{\geq 1,y+1}/N_{\geq 1,y}) - 1$. Recruitment rate in year y: $N_{1,y+1}/N_{\geq 1,y}$. From the reconstructed population sizes and harvest-at-age numbers we calculated hunting mortality rate in year y: $C_{\geq 1,y}/N_{\geq 1,y}$, male hunting mortality rate in year y: $C_{males \geq 1,y}/N_{males \geq 1,y}$, female hunting mortality rate in year y: $C_{females \geq 1,y}/N_{females \geq 1,y}$, the hunting mortality coefficient for females ≥2 years old in year y: $-\ln(N_{females \geq 3,y+1}/N_{females \geq 2,y}) - M$, and the hunting mortality coefficient for fawns in year y: $-\ln[1 - (C_{0,y}/N_{0,y})]$. We computed number of births ($N_{0,y}$) using the reconstructed number of females (≥1 yr old) after hunting in year ($y - 1$), multiplied by stage-specific fecundity rates for year ($y - 1$), classified by yearlings and individuals ≥2 years old. We cited stage-specific fecundity rates from Kaji et al. (2006). Because a survey of fecundity rates was not conducted in 1990, we assumed fecundity rates were consistent between 1991 and 1990.

We first examined a simple linear regression for hunting mortality rate against hunting effort (hunter-days). Secondly, to quantify relative contributions of the hunting mortality rate and the recruitment rate to annual changes in population growth rates, we compared covariances between those values and population growth rate. Thirdly, to analyze the demographic processes of annual variation in the recruitment rate, we decomposed the recruitment rate in year y into the birth rate in year y and the fawn survival rate in year y (eq. 5; Fig. 2),

$$N_{1,y+1}/N_{\geq 1,y} = (N_{0,y}/N_{\geq 1,y})(N_{1,y+1}/N_{0,y}). \quad (5)$$

We first examined whether variation in the recruitment rate ($N_{1,y+1}/N_{\geq 1,y}$) could be explained by variation in the birth rate ($N_{0,y}/N_{\geq 1,y}$) alone, apart from the fawn survival rate ($N_{1,y+1}/N_{0,y}$). We divided the number of births into 2 demographic variables: proportion of fecund females after hunting and fecundity rate in the previous year (F_{y-1}):

$$N_{1,y+1}/N_{\geq 1,y} = (N_{fecundfemalesafterkill,y-1}/N_{\geq 1,y})$$
$$F_{y-1}(N_{1,y+1}/N_{0,y}). \quad (6)$$

We then examined whether variation in the recruitment rate could be explained by variation in the proportion of fecund females in the population after hunting and the fecundity rate in the previous year. Age at primiparity in sika deer is at the yearling stage (Kaji et al. 1988). We examined the correlation between the recruitment rate and 1) the proportion of females (≥1 yr old) in the population after hunting, and 2) the stage-specific fecundity rates in the previous year. We also compared the proportion of females (≥1 yr old) in the population before and after hunting to
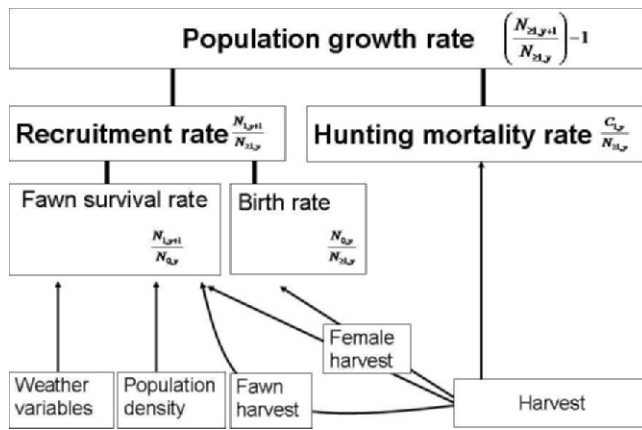
Figure 2. Demographic constituents of population growth rates and related factors for sika deer in the town of Ashoro, eastern Hokkaido, Japan, during 1990–2001.

examine whether the proportion was influenced by sex-biased harvesting.

We removed the term $N_{\geq 1,y}$ from equation 5,

$$N_{1,y+1} = N_{0,y}(N_{1,y+1}/N_{0,y})$$

$$\Leftrightarrow N_{1,y} = N_{0,y-1}(N_{1,y}/N_{0,y-1}). \qquad (7)$$

We expected the number of recruits ($N_{1,y}$) to be correlated with number of births ($N_{0,y-1}$) in the previous year, which is the product of the number of females (≥ 1 yr old) after hunting and the fecundity rate in the previous year. We examined the correlation between these factors.

If annual variation in the recruitment rate was not explained by variation in the birth rate alone, fawn survival rates should also be considered when analyzing variation in recruitment. We examined the impact of different factors on annual variation in the fawn survival rate. Following equation 7, the number of recruits in year y is expressed as the number of births in year ($y - 1$) multiplied by the fawn survival rate in year ($y - 1$). We then analyzed variation in the number of recruits in year y using models including the number of births in year ($y - 1$) as an offset and factors affecting the fawn survival rate in year ($y - 1$) as independent variables. We derived coefficients from generalized linear models assuming a negative binomial error distribution. Effects of population density and winter weather on fawn survival rates have been reported (Sæther 1997), and the intensity of hunting mortality on fawns also affects the fawn survival rate. Giuliano et al. (1999) reported lower survival rates for orphaned fawns than for fawns accompanied by their mother; therefore, the intensity of harvest for females aged ≥ 2 years old negatively affects the fawn survival rate. Thus, candidate-independent variables for the fawn survival rate in year ($y - 1$) were 1) population size (logarithmic form) in year ($y - 1$; direct density-dependence), and 2) population size (logarithmic form) in year ($y - 2$; delayed density dependence), 3) maximum snow depth (snow depth) in year ($y - 1$), 4) hunting mortality coefficient for fawns (fawn harvest) in year ($y - 1$), and 5) hunting mortality coefficient for females ≥ 2 years old (F

harvest) in year ($y - 1$). We used Akaike's Information Criteria (AIC) and Akaike weight to determine the best model (Burnham and Anderson 1998). We did not use AIC_c in spite of small sample size because usage of AIC_c is proved only with a normal error distribution (Burnham and Anderson 1998). We conducted statistical procedures using statistical software R (R Version 2.8.1, <http://www.R-project.org/>, accessed 27 Oct 2009).

RESULTS

### Estimates of Population Size and Demographic Parameters

The reconstructed population (≥ 1 yr old) increased from 6,000 in 1990 to 14,000 in 1998 and declined to 8,000 thereafter (Fig. 1). The population in 2001 was as high as the population between 1993 and 1994. The population growth rate was consistently high (0.1–0.2) during 1991–1994 and declined thereafter (Fig. 3). During 1995–1997 the rate decreased to nearly zero and decreased again to negative values after 1998 (Fig. 3).

The hunting mortality rate was <0.25, with little annual variation, until 1994, and it gradually increased between 1995 and 1997 (Fig. 3). The hunting mortality rate increased considerably to 0.35 in 1998 and remained >0.30. Female hunting mortality rates were <0.1 before 1994, slowly rose up to 0.1 during 1995–1997 (phases II and III), increased considerably to 0.28 in 1998 (phase IV), and remained >0.2 thereafter. Hunting mortality rates for females were about one-third as low as those for males. Hunting effort (hunter-days) increased as hunting regulations were relaxed from phases I to IV (Table 1). The hunting mortality rate was positively regressed by hunting effort ($Y = 0.000054X + 0.11$, $r^2 = 0.70$, $t = 4.93$, df = 9, $P < 0.001$).

The recruitment rate was >0.3 during the first 4 years (1991–1994) and declined in 1995 (Fig. 3). After being stable during 1995–1997, the recruitment rate subsequently decreased <0.25 again, as did annual variation. Covariance of the recruitment rate and the population growth rate (0.008) was higher than that between the hunting mortality rate and the population growth rate (−0.007); the recruitment rate explained 54% of variation in the population growth rate. In other words, the population growth rate changed in response to annual changes in the recruitment rate rather than to changes in the hunting mortality rate.

Processes of Annual Variation in Recruitment Rate

We detected a negative correlation between recruitment rate and proportion of females after hunting in the previous year ($r_s = -0.73$, $S = 379.73$, $P = 0.011$). The proportion of females in the population after hunting increased regularly after 1993, which showed a trend opposite to that observed for recruitment rate (Fig. 4). The proportion of female deer after hunting was 14% larger than that before hunting throughout the period even after intensive-female harvesting (phase IV) was introduced in 1998. The proportion of females in the hunting data did not exceed 0.5, which was
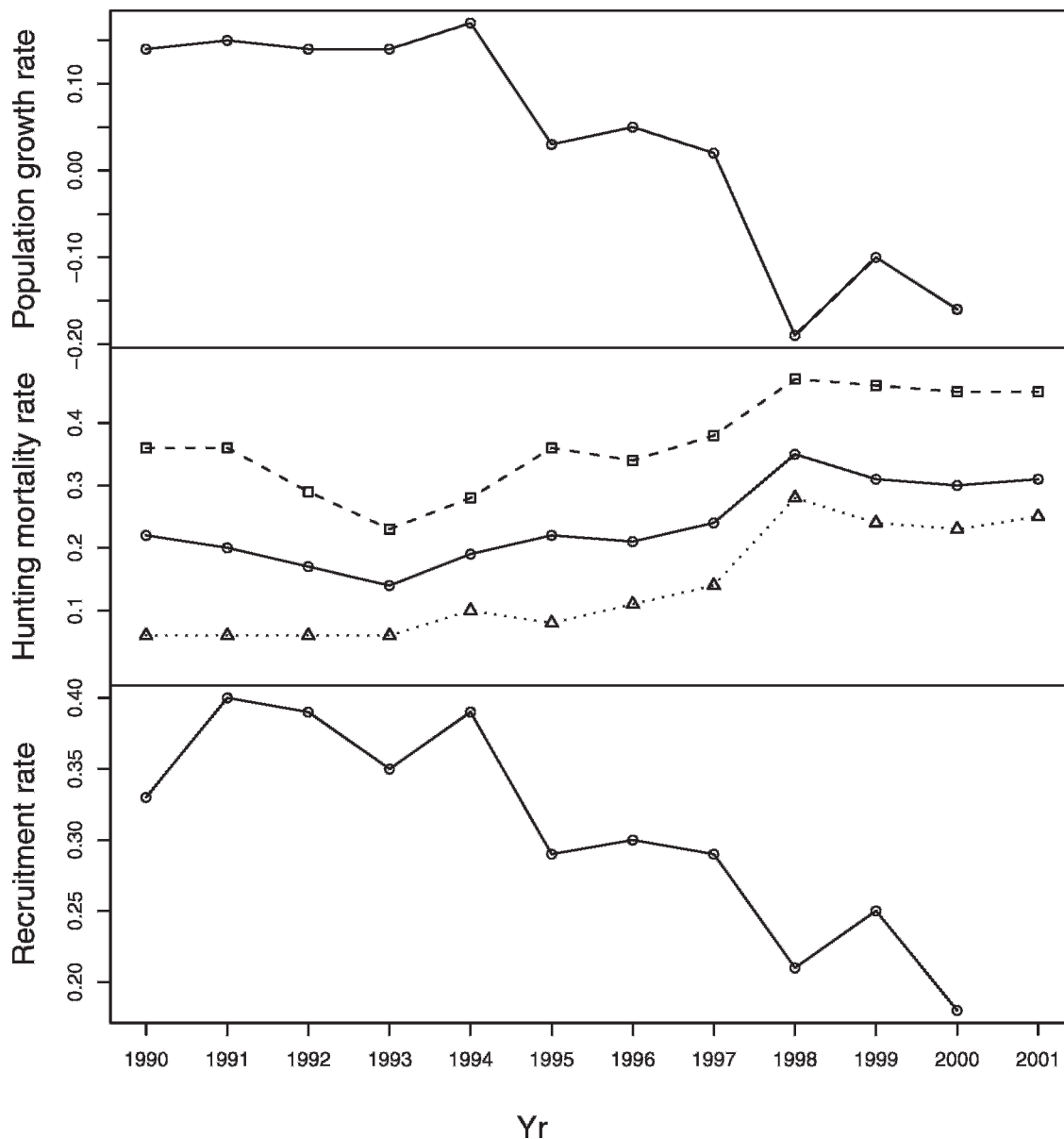
Figure 3. Annual changes in the population growth rate (upper), hunting mortality rates (middle; solid: total; dashed: M; dotted: F), and the recruitment rate (lower) for sika deer in the town of Ashoro, eastern Hokkaido, Japan, during 1990–2000 (1990–2001 for hunting mortality rates).

considerably lower than the proportion of females in the population before hunting throughout the period (Fig. 4). Therefore, the proportion of females in the population may have been elevated because a smaller proportion of females were removed through hunting. The recruitment rate was not correlated with stage-specific fecundity rates in the previous year (fecundity of yearlings, $r_s = 0.47$, $S = 116.64$, $P = 0.14$, fecundity of ad, $r_s = -0.32$, $S = 290.61$, $P = 0.36$). The fecundity rate was as high as 90% with little annual variation for both yearlings and older females (≥ 2; Fig. 5). Number of recruits was not correlated with number of births in the previous year ($r_s = 0.26$, $S = 162$, $P = 0.43$). Whereas the number of recruits in year (y) increased from 2,100 in 1990 to 4,200 in 1995 and then declined since 1998 to as many as in 1990, the number of births in the prior year ($y - 1$) increased linearly from 1,800 in 1990 to 6,300 in 1999 and then declined thereafter to 4,700 (Fig. 6).

The model for recruits in year y with the lowest AIC included direct density dependence ($y - 1$), fawn harvest ($y - 1$), and female harvest in year ($y - 1$) as explanatory variables for the fawn survival rate (Table 2). Parameter estimates for all 3 variables were negative (Table 2).

DISCUSSION

Quantifying Effects of Density Dependence on Population Growth

Relative importance of hunting mortality and density dependence needs to be quantified to consider density dependence when managing deer populations. The size of our study population fluctuated in response to annual changes in the recruitment rate rather than in the hunting mortality rate, contrary to previous studies in which hunting mortality rates dominated other factors affecting population fluctuations (Fryxell et al. 1991, Bowyer et al. 1999, Solberg
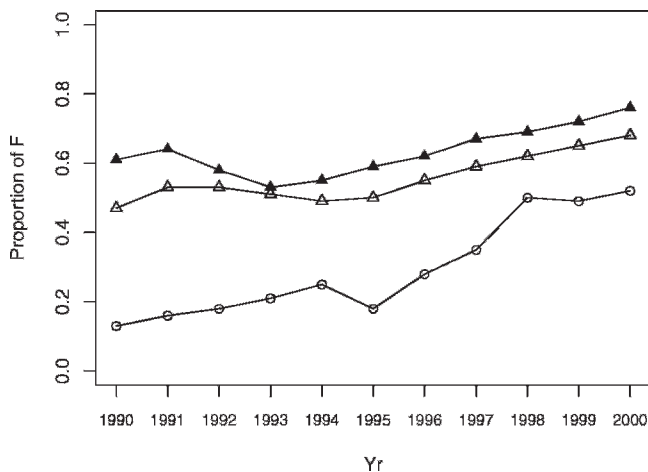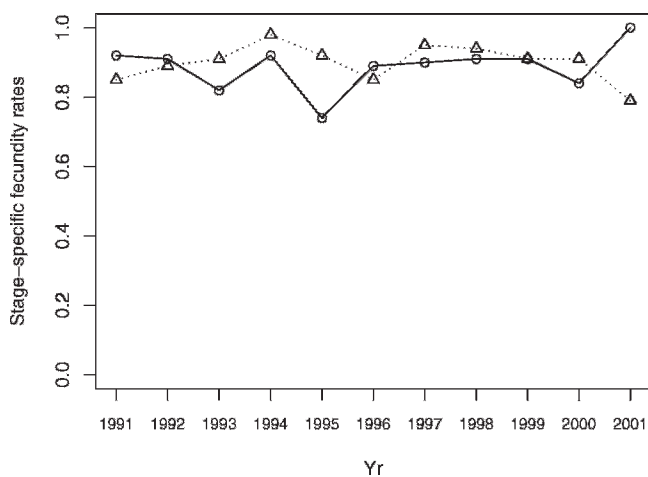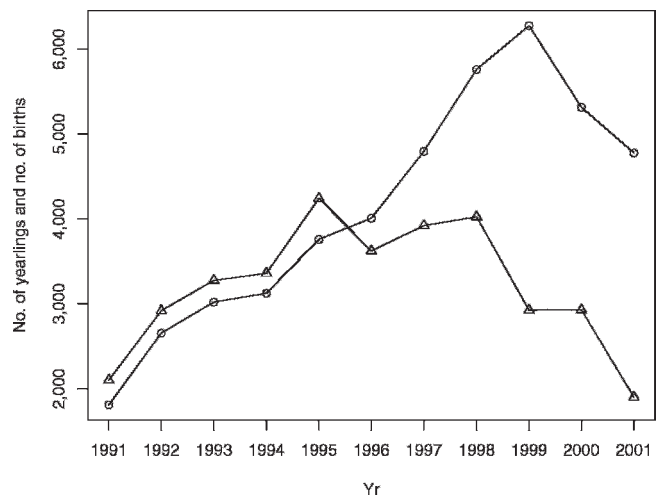
Figure 4. Annual changes in the proportion of females (≥1 yr old) in the population before (open triangles) and after (solid triangles) hunting, and in the hunting data (open circles) for sika deer in the town of Ashoro, eastern Hokkaido, Japan, during 1991–2001.

Figure 6. Annual changes in number of yearlings (triangles) in year (y) and number of births (circles) in the previous year ($y - 1$) for sika deer in the town of Ashoro, eastern Hokkaido, Japan, during 1991–2001.

et al. 1999). According to Gaillard et al. (2000), the recruitment rate is more important for changes in population growth rates because of higher temporal variability, compared to the adult survival rate, despite its lower elasticity. However, in previously hunted populations, survival rates with high elasticity were variable and fluctuated with hunting intensity (Fryxell et al. 1991, Ferguson and Messier 1996, Bowyer et al. 1999, Solberg et al. 1999). On the other hand, in our study population, hunting mortality rates were low and less variable throughout most of the study period (until 1997) because of restricted hunting opportunities. As a result, recruitment rates may have dominated the population growth rate; thus, recruitment rates should be monitored to predict population growth.

Given that one mature male is capable of inseminating multiple females, the recruitment rate would increase in a population with a higher proportion of females (Caughley 1977). Male-biased hunting regimes have created female-biased populations (reviewed in Milner et al. 2007). Therefore, we expected that the proportion of females in the population would decrease after hunting in phase IV when female-intensive hunting was introduced. However, because of lasting male-biased hunting prior to the phase, the population had already become female-biased. Even in phase IV, the proportion of females in the hunting data did not exceed 0.5, which was far below the proportion of females in the population during that phase (Fig. 4). As a result, the proportion of females in the population did not decrease, but rather increased, after hunting throughout the study period. Therefore, female-biased hunting regulations introduced during our study period did not significantly affect the sex ratio of the population.

The recruitment rate was not correlated with the proportion of females in the population after hunting, stage-specific fecundity rates in the previous year, or parameters created through a combination of these factors, such as the birth rate (Figs. 4–6). Therefore, annual variation in the recruitment rate was not controlled by birth rate alone. Revealing factors that account for the fawn survival rate is important for understanding annual variation in recruitment rates.

The negative effect of population size in the preceding year on the fawn survival rate indicates a density-dependent decrease in fawn survival, as has been reported for many ungulate species (red deer, Clutton-Brock et al. 1987; mountain goats [*Oreamnos americanus*], Houston and Stevens 1988; mule deer [*Odocoileus hemionus*], Bartmann et al. 1992; Soay sheep [*Ovis aries*], Clutton-Brock et al. 1992; elk, Singer et al. 1997; bighorn sheep [*Ovis canadensis*], Portier et al. 1998; but see Sæther et al. 1996 for moose). Fawn survival in the roe deer was lower for individuals with smaller body sizes during winter (Gaillard et al. 1996). Density-dependent decreases in body size in sika deer were also reported on an island with an introduced population in Hokkaido (Kaji et al. 1988). Thus, during our study, density-dependent decreases in fawn survival may

Figure 5. Annual changes in the fecundity rate of yearlings (circles) and older females (≥2 yr; triangles) for sika deer in the town of Ashoro, eastern Hokkaido, Japan during 1991–2001 (from Kaji et al. 2006).

Table 2. Candidate models accounting for variation in fawn survival rate with the difference in Akaike's Information Criterion values (ΔAIC) from the lowest model and with Akaike weights (w_i) for sika deer in the town of Ashoro, eastern Hokkaido, Japan, during 1990–2001. Explanatory variables accounting for fawn survival rate in year ($y - 1$) included direct density dependence (logarithm of population size in yr [$y - 1$]), delayed density dependence (logarithm of population size in yr [$y - 2$]), maximum snow depth, and levels of hunting mortality for fawn (fawn harvest) and hunting mortality for females $\geq$2 years old (F harvest) in year ($y - 1$).

Model	ΔAIC	w_i	Explanatory variables					
			Intercept	Density	Delayed density	Snow depth	Fawn harvest	F harvest
A	0.00	0.14	3.14**	−0.30*			−1.87***	−2.77***
B	0.66	0.10	0.45***			−0.003	−0.86	−3.30***
C	0.70	0.10	2.60		−0.25		−1.59***	−2.67***
D	0.78	0.10	2.28		−0.20	−0.003	−1.31**	−2.76***
E	0.90	0.09	0.44***			−0.004**		−3.53***

* $P = 0.53$ (marginally significant), ** $P < 0.05$, *** $P < 0.01$.

have occurred through food limitation. Body mass of fawns during winter is influenced by body growth during the preceding summer after birth, body mass at birth (maternal effects), or both of these factors (Sæther and Heim 1993). Following this, density-dependent decreases in fawn body size can be caused by direct density dependence, delayed density dependence, or both (Fryxell et al. 1991). We detected direct density dependence in fawn survival, suggesting body growth during the preceding summer was critical for winter survival (Gaillard et al. 1996).

Although the female-biased relaxation of hunting regulations did not result in a decrease in the female proportion of the population, the level of hunting mortality in females $\geq$2 years old (F harvest) negatively affected fawn survival (Table 2). Giuliano et al. (1999) reported lower survival rates for orphaned fawns compared to fawns accompanied by their mother. However, other studies have reported that orphaning either had no adverse effects on fawns or led to increased survival (Woodson et al. 1980, Hölzenbein and Marchinton 1992). Although no study currently explains these conflicting results, our result supports Giuliano et al. (1999).

Previous studies have predicted that snow accumulation makes access to food difficult for deer, which in turn reduces body condition and subsequently lowers fawn survival rate (Mech et al. 1987, Post and Stenseth 1998). However, snow depth was not included as an explanatory variable in the model with lowest AIC value in our study (Table 2), suggesting snow depth was not necessarily an important explanatory variable to predict fawn survival to the next year. Maximum depth at the study area averaged 43.7 cm during our study (Japan Meteorological Agency 2009). Less than 100 cm of snow depth is the maximum level for distribution of sika deer in Hokkaido (Kaji et al. 2000, but see Takatsuki 1992 for sika deer in Honshu island). Snow depth had a negative effect on percentage of females accompanied by their fawn in another town of eastern Hokkaido where maximum snow depth averaged 135 cm (Uno 2006, Japan Meteorological Agency 2009). Therefore, the impact of snow on fawn survival may locally differ.

Density dependence had a negative effect on the recruitment rate through its negative effect on fawn survival (Table 2). Density dependence should, therefore, be included when modeling dynamics of deer populations. If we ignore effects of density dependence on the population growth rate, we risk overestimating the growth rate or abundance of the population. Nevertheless, the population was still growing in 1997 and finally decreased in 1998 when hunting regulations were relaxed (Fig. 3), which casts doubt about whether self-regulatory mechanisms for density dependence could prevent population increases. Using our recruitment model (first model of Table 2), we projected recruitment rate of yearlings if level of hunting mortality in 1998 and after had been the same as in 1997; recruitment rate (0.33) would have been high enough to overcome the level of hunting mortality of 1997 (0.24; Fig. 3) and let the population grow in 1998. Therefore, population reduction in 1998 would not have been possible without relaxed hunting regulations. In other words, density dependence alone could regulate the population growth rate but not the population size. Although we detected density-dependent effects on fawn survival alone, density-dependent responses include fawn survival, age at maturity, and adult survival (Eberhardt 1977). If the population had continued to increase after 1998, we might have detected density-dependent delays in age at maturity, resulting in even further reductions in the population growth rate (Kaji et al. 1988, 2000, 2006). However, at the end of the 1990s in eastern Hokkaido the cost of damage to agriculture was reported to be 5 billion Japanese yen (US$50 million) and regeneration of forests has been prevented (Kaji et al. 2000, Terasawa and Akashi 2006). Therefore, self-regulatory mechanisms for density dependence may not be strong enough to prevent population increases.

Tactics to Prevent Deer Population Increases

Hunting effort increased as hunting regulations were relaxed from phases I to IV. Nevertheless, during phases II and III, deer population growth was not prevented. The population finally decreased in 1998, when phase IV was introduced. Hunting regulations in phase IV provided hunting effort sufficient to induce a high intensity of hunting mortality as well as opportunities that enabled intensive female harvest. During phase IV, approximately 30% of the total population was removed, including a 25% removal of females. Because the hunting mortality rate was statistically associated with hunting effort, hunting effort exceeding 3,500 days in this population can serve as a baseline to obtain a 30% hunting

mortality rate. However, a 30% hunting rate may not apply to all populations for 2 reasons. First, the level of hunting effort necessary to limit population growth may be species- and population-specific. We compared our regression relationship of hunting mortality rate against hunting effort for sika deer with those for white-tailed deer by Fryxell et al. (1991) and found that higher hunter effort is needed for sika deer than for white-tailed deer, relative to level of hunting mortality. Moreover, the level of hunting effort necessary to limit population growth may also vary according to harvest techniques. Weckerly et al. (2005) demonstrated that hunter effort required to sustain a given level of hunting pressure varied among multiple types of hunts. Weckerly et al. (2005) found that hunts with shotguns and center-fired rifles had the lowest hunter effort relative to harvest sizes among several hunting methods. In our study area, shotguns and center-fired rifles were the only available methods for harvesting sika deer, so we suggest that our result is a minimum estimate of hunting effort necessary to decrease sika deer in this population.

Second, the relationship between hunting mortality rate and hunter effort may not be constant and may also depend on population density. In some situations, harvest of animals may stay high even though the population is in decline, a situation that is known as hyperstability (Hilborn and Walters 1992, Solberg et al. 1999, Harley et al. 2001, but see Tsuboi and Endou 2008). Therefore, if we consider the possibility of hyperstability of sika deer, hunter effort estimated by the regression equation in our study may be an overestimate for another sika deer population with higher density.

Female harvest negatively affected the recruitment rate through impacts on the fawn survival rate. Although female harvest during sport hunting was permitted during phases II and III, the length of the season for hunting females was limited, which resulted in little increase to the female hunting mortality rate. In phase IV, on the other hand, length of the season for hunting of female deer was prolonged and was the same length as the season for males; furthermore, more permits were available per day for female deer than for males, and the female hunting mortality rate subsequently increased. Because we do not have data on hunting effort by deer sex, we could not examine the relationship between the female hunting mortality rate and hunting effort. Despite prioritization of hunting female deer in the hunting regulations, the proportion of females in the harvest was still 0.5 and a strongly female-biased harvest was not induced. Therefore, we suggest that hunting regulations prioritizing hunting of female deer will be necessary to enhance hunting mortality in female deer.

To conclude, we demonstrated that population growth decelerated as population size increased. However, density-dependent effects were not strong enough to achieve population regulation within the study period. A high level of hunting mortality including intensive female harvesting would be necessary to prevent population growth. Female harvesting had indirect negative effects on the recruitment rate through fawn survival, and hunting effort (hunter-days) was a good predictor of the hunting mortality rate.

Therefore, >3,500 hunter-days, and hunting regulations prioritizing female harvesting, will be required to prevent increases in this sika deer population. However, level of hunting effort shown here may apply to other sika deer populations inhabiting forests with agricultural land and hunted with shotgun or center-fired rifles.

MANAGEMENT IMPLICATIONS

During the early 1990s, a debate occurred over whether hunting regulations should be relaxed to control sika deer populations in Hokkaido (Kaji et al. 2006). Considering uncertainty regarding abundance, growth, and population structure, stakeholders were concerned that sika deer populations would again face a high risk of extinction if female-intensive harvesting were permitted. Because of these concerns, the government of Hokkaido relaxed the hunting regulations gradually using several phases to test the regulations' performance. However, the slow relaxation of regulations and the lasting bias in favor of hunting males combined to allow the population to grow and have resulted in a female-biased population structure. As a result, agricultural damages in 1998 were the highest recorded in Japan (Kaji et al. 2006). Therefore, a quick shift to high-intensity hunting that prioritizes harvesting of females is required to avoid catastrophic impacts from an overabundance of deer.

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Appendix A. Coefficients for hunting mortality and natural mortality for older-aged class (p+) for sika deer in the town of Ashoro, eastern Hokkaido, Japan, during 1990–2001. "Standard" shows values we assumed in our study; that is, we computed the hunting mortality coefficient for the older-aged class from the total mortality coefficient (0.56) multiplied by the ratio of hunting mortality to total mortality determined in independent studies. To examine robustness of the population estimation against our assumptions we assumed the ratio of hunting mortality to total mortality to be 1, which means all deer die from hunting (Higher) and the ratio that is half of the Standard ratio (Lower).

Sex	Ratio	Yr 1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Hunting mortality													
M	Standard	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	Higher	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56
	Lower	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23
F	Standard	0.03	0.03	0.03	0.03	0.40	0.40	0.40	0.50	0.50	0.50	0.50	0.50
	Higher	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56	0.56
	Lower	0.01	0.01	0.01	0.01	0.20	0.20	0.20	0.23	0.23	0.23	0.23	0.23
Natural mortality													
M	Standard	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
	Higher	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.33
F	Standard	0.53	0.53	0.53	0.53	0.16	0.16	0.16	0.06	0.06	0.06	0.06	0.06
	Higher	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.55	0.55	0.55	0.55	0.36	0.36	0.36	0.33	0.33	0.33	0.33	0.33

Appendix B. Age-specific hunting mortality coefficients in 2001 for sika deer in the town of Ashoro, eastern Hokkaido, Japan. "Standard" shows values we assumed in our study; that is, the age-specific hunting mortality coefficients in 2001 are the same as the mean of the age-specific hunting mortality coefficients during 1998–2001. To examine robustness of the population estimation against our assumptions we assumed that the age-specific hunting mortality coefficient in 2001 is the same as in 1998 (Higher) and that the age-specific hunting mortality coefficient in 2001 is the same as in 2000 (Lower).

Sex	Ratio	Age (yr) 1	2	3	4	5	6	7	8	9
M	Standard	0.74	0.58	0.76	0.66	0.56	0.45	0.40	0.30	0.19
	Higher	0.81	0.67	0.50	0.56	0.43	0.20	0.37	0.40	0.09
	Lower	0.64	0.73	0.94	0.88	0.72	0.51	0.38	0.22	0.18
F	Standard	0.32	0.33	0.38	0.27	0.21	0.18	0.19	0.13	
	Higher	0.46	0.38	0.35	0.37	0.20	0.25	0.25	0.14	
	Lower	0.16	0.27	0.27	0.12	0.08	0.07	0.07	0.05	