



Spatial heterogeneity in the carrying capacity of sika deer in Japan

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Carrying capacity is 1 driver of wildlife population dynamics. Although in previous studies carrying capacity was considered to be a fixed entity, it may differ among locations due to environmental variation. The factors underlying variability in carrying capacity, however, have rarely been examined. Here, we investigated spatial heterogeneity in the carrying capacity of Japanese sika deer (*Cervus nippon*) from 2005 to 2014 in Yamanashi Prefecture, central Japan (mesh with grid cells of 5.5 × 4.6 km) by state-space modeling. Both carrying capacity and density dependence differed greatly among cells. Estimated carrying capacities ranged from 1.34 to 98.4 deer/km². According to estimated population dynamics, grid cells with larger proportions of artificial grassland and deciduous forest were subject to lower density dependence and higher carrying capacity. We conclude that population dynamics of ungulates may vary spatially through spatial variation in carrying capacity and that the density level for controlling ungulate abundance should be based on the current density level relative to the carrying capacity for each area.

Key words: artificial grassland, Bayesian state-space model, deciduous forest, forage, integrated population model, intrinsic rate of natural increase, population regulation

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Population regulation is fundamental to ecology and related fields, such as conservation and wildlife management (Ratikainen et al. 2008). The negative feedback mechanism of density on reproduction and survival rates due to lack of food, space, cover, and other resources, known as the density effect, is essential to population regulation. The logistic model is a well-known basic model of population regulation (Hixon et al. 2002). When rates of reproduction and mortality are balanced, the population is stabilized at a certain density, called the carrying capacity, which is the equilibrium represented by K in the logistic model: $N_{t+1} = N_t \exp[r(1 - N_t/K)]$, where N_t is the number of individuals at time t and r is the population growth rate (e.g., Plumb et al. 2009). Thus, a population with more intensive density dependence has a lower carrying capacity.

Although it is questionable whether population density reaches carrying capacity or whether some individuals begin to disperse at this point (Plumb et al. 2009), the strength of density dependence and carrying capacity should differ among locations due to environmental variation, which would affect both reproduction and survival (Dempster and Pollard 1986; Pastor et al. 1997; Gaillard et al. 2000; Bonenfant et al. 2009). The strength of density dependence has been examined for various species, populations, and regions (e.g., Forchhammer et al.

1998; Coulson et al. 2005; Viljugrein et al. 2005), but few studies have investigated the effects of spatial heterogeneity on the strength of density dependence and its underlying factors (but see Sæther et al. 2008). Population size may show rapid growth in one area yet remain stable in another, due to regional variation in density dependence and carrying capacity. Combining these subpopulations at a larger scale without considering local population dynamics will result in inaccurate projections of future population size for informing conservation and management actions. Therefore, the spatial heterogeneity of carrying capacity must be quantified accurately to predict the future dynamics of animal populations.

Whereas small animals are more likely to be affected by density-independent factors, with populations only occasionally reaching carrying capacity, ungulate populations are often close to carrying capacity, due to their large size and long life spans (McCullough 1999; Bowyer et al. 2014). Ungulates exhibit strong competitive abilities, and their population dynamics can be greatly affected by intraspecific competition (Bowyer et al. 2014). Moreover, many ungulates in Europe and the United States have expanded their ranges and increased in density during the past few decades (McShea et al. 1997; Mysterud et al. 2002; Côté et al. 2004). Large-scale habitat

modification is sometimes associated with an overabundance of ungulates (Myrsterud et al. 2002; Côté et al. 2004; Iijima et al. 2013). Specifically, agricultural intensification or abandonment can provide good forage for deer during seasons with no snow, whereas coniferous plantations may be used for shelter during the day and in periods of severe winter weather (Kaji et al. 2010). Therefore, ungulates are important and suitable taxa for examining the role of carrying capacity in population dynamics associated with land use. We expect that carrying capacity in some regions may be lower than that in others due to habitat modification, although few studies have demonstrated an association between carrying capacity and landscape composition.

Therefore, we aimed to examine the effects of landscape components on the spatial heterogeneity of carrying capacity for a large ungulate. In this study, we analyzed the population dynamics of sika deer (*Cervus nippon*) from 2005 through 2014. We hypothesized that habitat modification would provide good forage for deer, resulting in regional variation in carrying

capacity. We predicted that carrying capacity would increase as the proportions of artificial meadow and/or evergreen coniferous forest increased. We applied a Bayesian state-space model that can explicitly treat the 2 types of error (i.e., error due to data sampling or stochastic population dynamics) and has been used in recent years for the estimation of population dynamics (e.g., Sæther et al. 2008; Colchero et al. 2009; Fukasawa et al. 2013). This modeling approach is superior to direct analysis of time-series abundance data using the autoregressive (AR) model, which is unable to distinguish between the 2 types of error in observed and latent population dynamics (Dennis and Taper 1994; Shenk et al. 1998; Calder et al. 2003; Wang et al. 2006).

MATERIALS AND METHODS

Study site.—Our study was conducted in Yamanashi Prefecture in central Japan (Fig. 1); in a study area encompassing 4,465 km². The elevation of Yamanashi Prefecture ranges

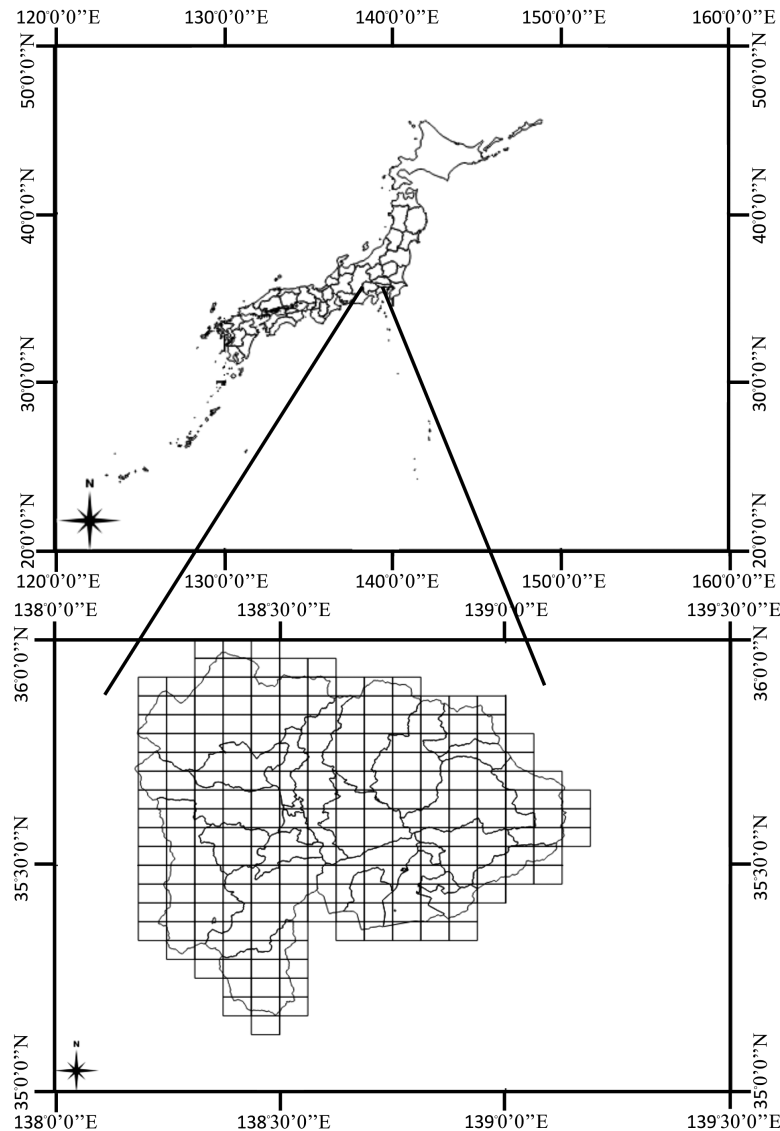


Fig. 1.—Location of Yamanashi Prefecture within Japan. A rectangular grid that covers Yamanashi Prefecture was established by the Ministry of the Environment of Japan, and each cell is 5.5 km × 4.6 km in size.

from 36 m to the peak of Mt. Fuji at 3,376 m. During our study period (2005–2014), 78% of the land was occupied by forests, and the remainder was occupied by artificial grassland and urban areas (Fig. 2). Forests included both deciduous (59%) and evergreen coniferous forest (41%). Deciduous forest comprised broad-leaved species (e.g., *Acer*, *Betula*, and *Quercus*) in 76% of area, and a coniferous species (*Larix kaempferi*) in 24% of the area (Iijima and Nagaïke 2015a). In Yamanashi Prefecture, the population density of *C. nippon* had increased in recent years (Iijima et al. 2013), resulting in extensive debarking of trees (Nagaïke and Hayashi 2003; Iijima and Nagaïke 2015b) and browsing of understory vegetation in forests (Iijima and Nagaïke 2015a) and subalpine grassland (Nagaïke 2012).

During the study period, the daily mean, annual maximum, and annual minimum temperatures at Kofu City, central Yamanashi Prefecture ranged from 14.8°C to 15.4°C, 37.0°C to 40.7°C, and –5.1°C to –9.0°C, respectively (Japan Meteorological Agency; <http://www.data.jma.go.jp/obd/stats/etrn/index.php>, accessed 20 April 2015). Snow cover typically persists from January to early March in most of our study area. Cumulative snowfall and maximum snow depth for each year ranged from 0 to 25 cm and from 0 to 14 cm at Kofu City, respectively (Japan Meteorological Agency; <http://www.data.jma.go.jp/obd/stats/etrn/index.php>, accessed 20 April 2015).

Data.—A rectangular grid (each cell was 5.5 × 4.6 km = 25.3 km²) was established to cover the entire prefecture (a total of 216 grid cells). The size and shape of the cell were set by the Ministry of the Environment of Japan and encompass all of Japan. All data were obtained at the scale of a cell. The data we used include deer sightings per unit effort (SPUE; the number of deer seen by hunters/total number of hunting days), pellet group density (number of pellet groups/length of census route), relative deer abundance based on block count survey (number of deer seen by researchers/census area), the total number of deer hunted for game and nuisance control during 2005–2014, and landscape composition.

We calculated SPUE from hunters' reports submitted to the prefectural government each year. Of the total, about 180 grid cells had SPUE data for each year. The pellet group count

survey was conducted in November of each year in only 40 grid cells. During the survey, a researcher counted the number of pellet groups (a pellet group was defined as > 10 pellets, which was regarded as 1 excretion) within a width of 50 cm along a 5-km census route in each grid cell. The block count survey was conducted in November of each year in 10 grid cells (except in 2011, when it was conducted in 40 cells). About 10 researchers searched for sika deer for 2 h within an approximately 1-km² area in each grid cell. Duplicate counts of deer were avoided by using radio communication. The prefectural government summarized the number of sika deer killed each year. As a measure of landscape composition, the percentages of deciduous forest, evergreen coniferous forest, and artificial grassland within each cell in 2003 were calculated by QGIS (QGIS Development Team 2014) using Natural Environment Information geographic information system data provided by the Biodiversity Center of Japan (GIS; <http://www.biodic.go.jp/trialSystem/top.html>, accessed 20 April 2015). There might have been minor changes in landscape composition after 2003, but there were no reports of large-scale habitat modifications in Yamanashi Prefecture between 2003 and 2014.

Population model.—A state-space model (Calder et al. 2003; Sæther et al. 2008; Iijima et al. 2013) was adopted to estimate population dynamics and the strength of density dependence for sika deer in our study area. We estimated the time series of deer abundance by cells by considering process error and measurement error explicitly. For practical reasons, we chose the cell as the spatial scale for comparing population dynamics among locations. Our estimates were limited to the 204 cells among the 216 in which SPUE, pellet group survey, and/or block count survey data were available for at least 3 years. The sika deer population in Yamanashi Prefecture is subject to both game hunting from November through March and nuisance control intermittently throughout the year except summer (hereafter, we use “hunting” to represent both), and young are born in May (Table 1).

Process model.—We modeled the annual population dynamics of sika deer from 2005 to 2014, setting October as the start of a year. The annual change in population size without hunting is modeled as shown below (Case 2000):

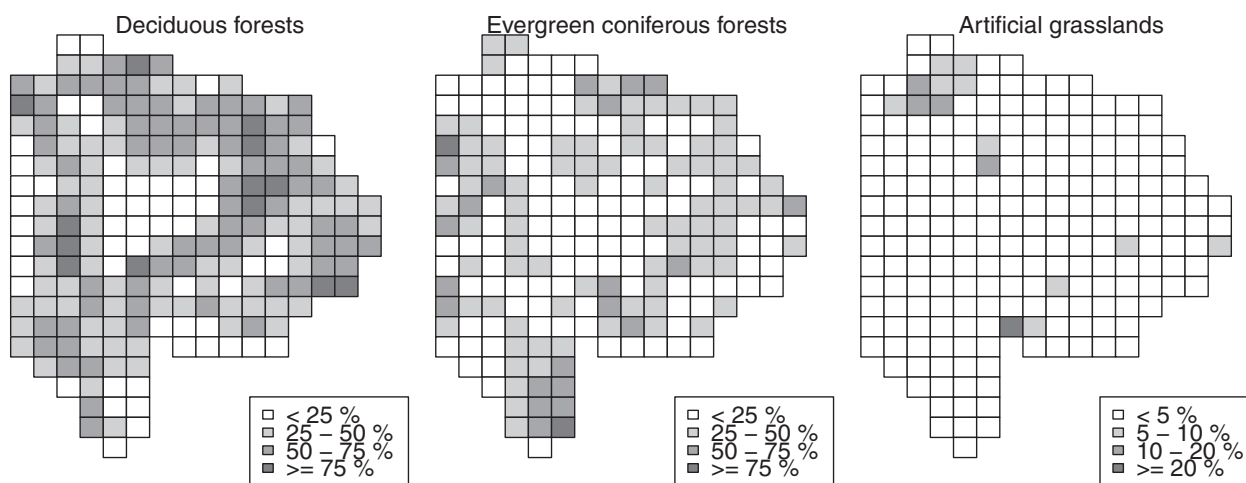


Fig. 2.—Percentages of deciduous forest, evergreen coniferous forest, and artificial grassland in the 216 cells in Yamanashi Prefecture, Japan.

Table 1.—Timing of life-history events for sika deer (*Cervus nippon*) in Yamanashi Prefecture, Japan. Solid arrows indicate the annual period for each life-history event. Most (ca. 90 %) nuisance control was conducted within the period covered by the solid arrow, and the rest was done during the period with the dashed arrow.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.
Game Hunting	←—————→											
Nuisance control	←—————→								- - - - -			
Natural Mortality	←—————→											
Birth	←—————→											
Lactation/Breeding	←—————→											
Mating	←————→										←————→	

$$N_{t+1,c} = N_t \exp[r(1 - N_{t,c} / K_c)] \quad (1)$$

where $N_{t,c}$ is the number of sika deer in year t ($t = 2005, 2006, \dots, 2014$) in cell c ($c = 1, 2, \dots, 204$); r is the intrinsic rate of natural increase including survival, reproduction, and migration between cells; and K_c is the carrying capacity in cell c . We assumed that r was fixed across cells because it is determined by the life history of the species, but we expected K_c to differ among cells (equation 8). In Ontario, maximum rates of population growth for moose (*Alces alces*) did not vary predictably with any of the landscape covariates tested, whereas carrying capacity was affected by landscape composition (Street et al. 2015). Thus, we consider these assumptions to be justified.

Next, we incorporated the effect of hunting, which mainly occurs in autumn and winter (Table 1), into equation 1. Adult females that were not hunted can give birth. The annual population dynamics incorporating hunting was calculated as follows:

$$S_{t,c} = N_{t,c} (1 - HR_{t,c}) \quad (2)$$

$$N_{t+1,c} = S_{t,c} \exp[r(1 - S_{t,c} / K_c)] \quad (3)$$

where $S_{t,c}$ is the number of sika deer not hunted in year t in cell c , and $HR_{t,c}$ is the fraction of hunted sika deer in year t in cell c (see observation model). The right side of equation 3 was transformed as

$$N_{t+1,c} = S_{t,c} \exp[r - (r / K_c) S_{t,c}] \quad (4)$$

In equation 4, r/K_c is the strength of density dependence (hereafter, s_c) because $r - (r/K_c)S_{t,c}$ decreases with the increase of r/K_c at the same $S_{t,c}$.

Equations 2 and 3 were expressed in logarithmic scale as

$$\log(S_{t,c}) = x_{t,c} + \log(1 - HR_{t,c}) \quad (5)$$

$$x_{t+1,c} = \log(S_{t,c}) + r(1 - S_{t,c} / K_c) \quad (6)$$

where $x_{t,c}$ is the number of sika deer in logarithmic scale in year t in cell c [$x_{t,c} = \log(N_{t,c})$]. Because there may be stochastic error

in population dynamics, a stochastic error term was incorporated into equation 6 as follows:

$$x_{t+1,c} = \log(S_{t,c}) + r(1 - S_{t,c} / K_c) + \epsilon_{t,c} \quad (7)$$

where $\epsilon_{t,c}$ is stochastic error with a normal distribution of mean 0. We adopted a vague prior of $x_{t,c}$ with a normal distribution of mean x_{init} and variance σ_{init} . The prior of σ_{init} was a uniform prior ranging from 0 to 100 (Gelman 2006). In this study, deer density (per km²) in year t in grid cell c was calculated as $N_{t,c} / 25.3$ (i.e., each grid cell = 25.3 km²).

The prior of the intrinsic rate of natural increase (r) was a vague normal distribution of mean 0 and variance 1,000. To reduce calculation time, however, we assumed that r never exceeded $\log(2)$ (0.693), because sika deer are monotoxic, so abundance never doubles in a year, even if all were female with a 100% pregnancy rate. This assumption is justified because the posterior distribution of r was below $\log(2)$ without truncation.

Carrying capacity (K_c) was modeled as

$$K_c = \exp(\alpha + \beta_{DF} DF_c + \beta_{EF} EF_c + \beta_{AG} AG_c + \epsilon_c) \quad (8)$$

where α is the intercept, β terms are the coefficients of landscape composition, DF_c is the percentage of deciduous forest in cell c , EF_c is the percentage of evergreen coniferous forest in cell c , AG_c is the percentage of artificial grassland in cell c , and ϵ_c is stochastic error whose prior is a vague normal distribution of mean 0 and variance σ_K . The prior of σ_K was a uniform prior ranging from 0 to 100 (Gelman 2006). Priors of α , β_{DF} , β_{EF} , and β_{AG} were vague normal priors of mean 0 and variance 1,000. To save calculation time, we assumed that K_c never falls below 25.3 (= 1 deer/km²) nor exceeds 5,060 (= 200 deer/km²) because the highest reported density for sika deer in Japan was 118 deer/km² (Kaji et al. 2004). The assumption is justified because the posterior distributions of K_c ranged between 25.3 and 5,060 without truncation. We attempted to include spatial autocorrelation for carrying capacity in our model, but the estimate of carrying capacity was unrealistically low, so we excluded it from our analyses.

Observation model.—The observation model of SPUE was as follows (Iijima et al. 2013):

$$SD_{t,c} \sim \text{Poisson}(\exp(b_{\text{SPUE}} + x_{t,c} + \varepsilon_{\text{SPUE};t,c}) \text{Effort}_{t,c}) \quad (9)$$

where $SD_{t,c}$ is the number of deer seen in year t in cell c , b_{SPUE} is the rate parameter, $\varepsilon_{\text{SPUE};t,c}$ is observation error of SPUE, and $\text{Effort}_{t,c}$ is the product of the number of hunters and days for game hunting in year t in cell c .

The observation model of the pellet group survey was calculated as

$$PG_{t,c} \sim \text{Poisson}(\exp(b_{\text{PD}} + x_{t,c} + \varepsilon_{\text{PD};t,c}) \text{RL}_{t,c}) \quad (10)$$

where $PG_{t,c}$ is the number of pellet groups in year t in cell c , b_{PD} is the rate parameter, $\varepsilon_{\text{PD};t,c}$ is observation error from the pellet group survey, and $\text{RL}_{t,c}$ is the length of the census route in year t in cell c .

The observation model of the block count survey was calculated as

$$BC_{t,c} \sim \text{Poisson}(\exp(x_{t,c} + \varepsilon_{\text{BC};t,c}) \text{AREA}_{t,c}) \quad (11)$$

where $BC_{t,c}$ is the number of deer seen in year t in cell c , $\varepsilon_{\text{BC};t,c}$ is observation error of the block count survey, and $\text{AREA}_{t,c}$ is the area of the block count survey in year t in cell c .

The observation model of the fraction of hunted deer was as follows:

$$C_{t,c} \sim \text{Binomial}(HR_{t,c}, N_{t,c}) \quad (12)$$

$$HR_{t,c} = \frac{1}{1 + \exp(-(\text{HRLOGIT}_{t,c}))} \quad (13)$$

$$\text{HRLOGIT}_{t,c} \sim N(\mu_t, \sigma_{hr1}) \quad (14)$$

$$\mu_t \sim N(\mu_{t-1}, \sigma_{hr2}) \quad (15)$$

where $C_{t,c}$ is the number of deer hunted in year t in cell c . The prior of μ_1 was a vague normal distribution of mean 0 and variance 1,000.

Parameter estimation.—Parameter estimation of the state-space model was conducted using a Bayesian framework. Posterior samples of parameters were obtained by the Markov Chain Monte Carlo (MCMC) method (Calder et al. 2003). We ran 3 parallel MCMC chains and retained 1,000,000 iterations after an initial burn-in of 500,000 iterations. We thinned sampled values to 0.1% (i.e., obtained 1,000 samples as posterior distributions for each chain). Convergence of MCMC sampling was judged by the criterion that \hat{R} was smaller than 1.1 (Gelman et al. 2004). We also checked how well the model fit the data by using Bayesian P -values calculated from χ^2 -discrepancy statistics (Kéry and Schaub 2012). If the model completely reproduces the data, the Bayesian P -value will be 0.5. However, it is unclear what Bayesian P -value represents a “good fit,” so the Bayesian P -values are used as a descriptive technique only (Kéry

and Schaub 2012). To conduct MCMC sampling, we used JAGS (Plummer 2003) in the package “rjags” in R (R Core Team 2015). We also used the package “snow” to conduct multi-thread MCMC sampling. We concluded that landscape composition significantly affected K_c if the 95% credible intervals of the estimated coefficients (i.e., β_{DF} , β_{EP} or β_{AG}) did not overlap 0. The model code is available as [Supporting Information S1](#).

RESULTS

Summary of population dynamics.—The Bayesian P -values of SPUE, pellet group survey, and block count survey were 0.008, 0.454, and 0.385, respectively, and that for all data were 0.283. The estimated deer density averaged across Yamanashi Prefecture increased from 5.9 deer/km² in 2005 to 13.2 deer/km² in 2014 (Fig. 3a). Deer density in the prefecture increased linearly from 2005 to 2010 and then began to plateau. In contrast to the prefectural trends, deer densities varied spatially and temporally among cells (Fig. 3b). In 2005, the minimum density was 0.11 deer/km² and the maximum was 49.6 deer/km². Spatial heterogeneity was greater in 2014, when the minimum density was 1.3 deer/km² and the maximum was 70.5 deer/km². Temporal trends of estimated deer density differed among cells. Many cells showed low population growth (< 1.1) and became saturated at a density level of ~20 deer/km², whereas other cells showed steady population increases (Fig. 3b).

Estimated population dynamics.—As deer density approached carrying capacity and the fraction of hunted deer increased, deer density grew more slowly (Fig. 4). The estimated fraction of hunted deer ($HR_{t,c}$) ranged from 0.006 to 0.264 in 2005 and from 0.011 to 0.633 in 2013. Estimated carrying capacity (K_c) ranged from 1.34 to 98.4 deer/km² (mean = 17.11 deer/km²), and the strength of density dependence (s_c) ranged from -1.77×10^{-2} to -0.03×10^{-2} among grid cells (Fig. 5). Means (95% credible intervals) of β_{DF} , β_{EP} and β_{AG} were 0.92 (0.17 to 1.62), 0.74 (−0.17 to 1.69), and 9.79 (4.31 to 15.77), respectively. Thus, higher percentages of deciduous forest and artificial grassland increased K_c and lowered s_c (Figs. 2 and 6), whereas evergreen coniferous forest did not significantly affect K_c and s_c , having only a marginally positive effect. The mean (95% credible interval) for the intrinsic rate of natural increase (r) was 0.57 (0.49–0.66).

DISCUSSION

Relationship between the model and the data.—The Bayesian P -value for SPUE was very low (0.008). This result indicates that our model was not appropriate to simulate SPUE data, despite the fact that it considered observation error (equation 9). SPUE differed from other data (i.e., pellet group survey and block count survey) because the sample size was huge, and the data were collected by an array of hunters with different skill levels during autumn and winter, whereas pellet group surveys and block count surveys were conducted by well-trained researchers in November. In this study, differences in effort were explicitly considered by adding effort in the model (see equations 9–11).

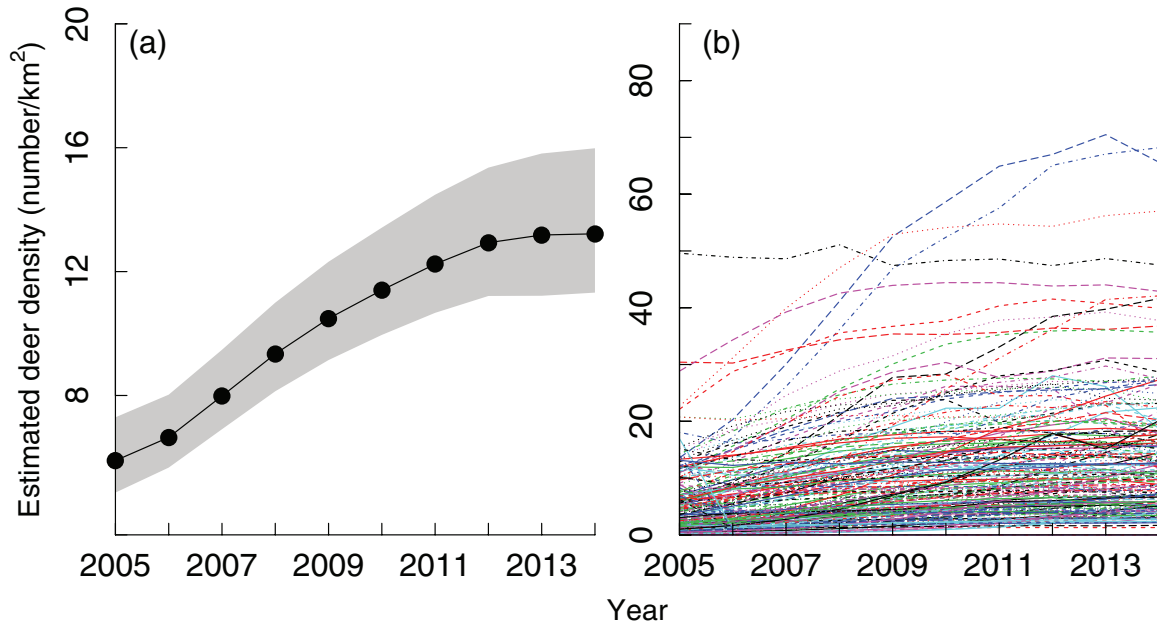


Fig. 3.—Temporal trend of sika deer (*Cervus nippon*) density in Yamanashi Prefecture during 2005–2014. a) Trend of the entire prefecture. Gray zone indicates 95% credible intervals. b) Trend of each cell.

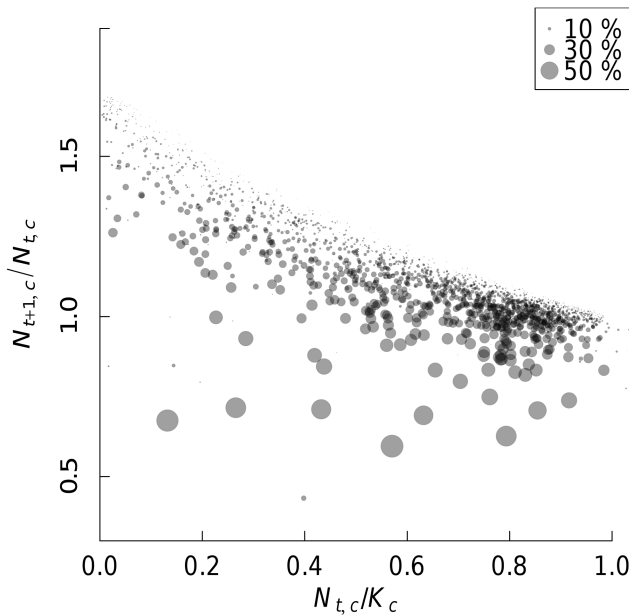


Fig. 4.—Population growth ($N_{t+1,c}/N_{t,c}$) of sika deer (*Cervus nippon*) in relation to carrying capacity ($N_{t,c}/K_c$) and the fraction of hunted deer (10%, 30%, or 50%, represented by the size of circles) for 204 cells in Yamanashi Prefecture, Japan, during 2005–2014.

Role of landscape composition in the variability of carrying capacity.—In this study, we demonstrated a tight link between land use and carrying capacity. Habitats with larger proportions of artificial grassland and deciduous forest were less subject to food limitation for sika deer. This is consistent with findings from previous studies. The main factor contributing to the rapid growth of deer populations is increased forage (Côté et al. 2004). Increases in openings or grassland increases forage for deer during seasons with no snow, whereas forest area provides good cover for wintering (Diefenbach et al. 1997; Honda 2009).

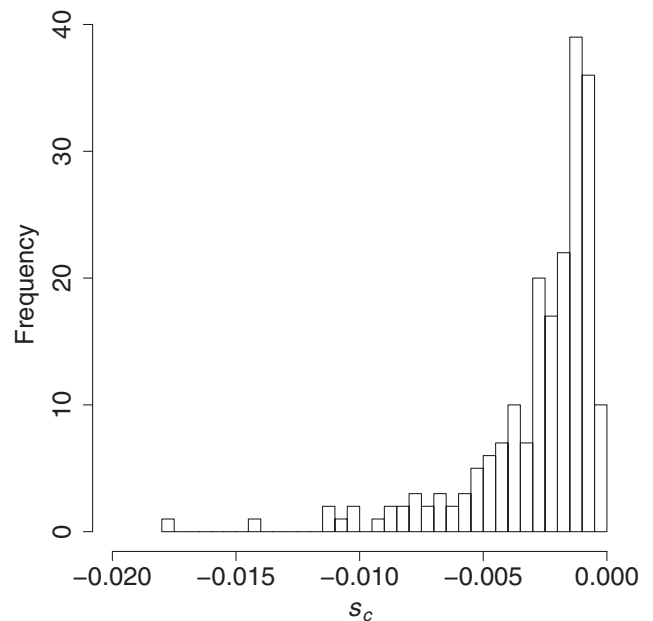


Fig. 5.—Histogram of the strength of density dependence in each cell.

Diet analyses of rumen contents also showed that artificial grasslands provide good forage during seasons with no snow, whereas the twigs and bark of deciduous broad-leaved trees are the main constituents of the winter diet of sika deer (Yokoyama et al. 2000; Ueno et al. 2007). As reported in Europe and the United States (Côté et al. 2004), Kaji et al. (2000) also suggested that widespread agricultural and silvicultural activities in Japan enhance the quality of deer habitat, which would, in turn, increase carrying capacity.

Contrary to our prediction, we did not detect an obvious effect of evergreen coniferous forest on carrying capacity. Because a nearby mature conifer canopy may provide protection from

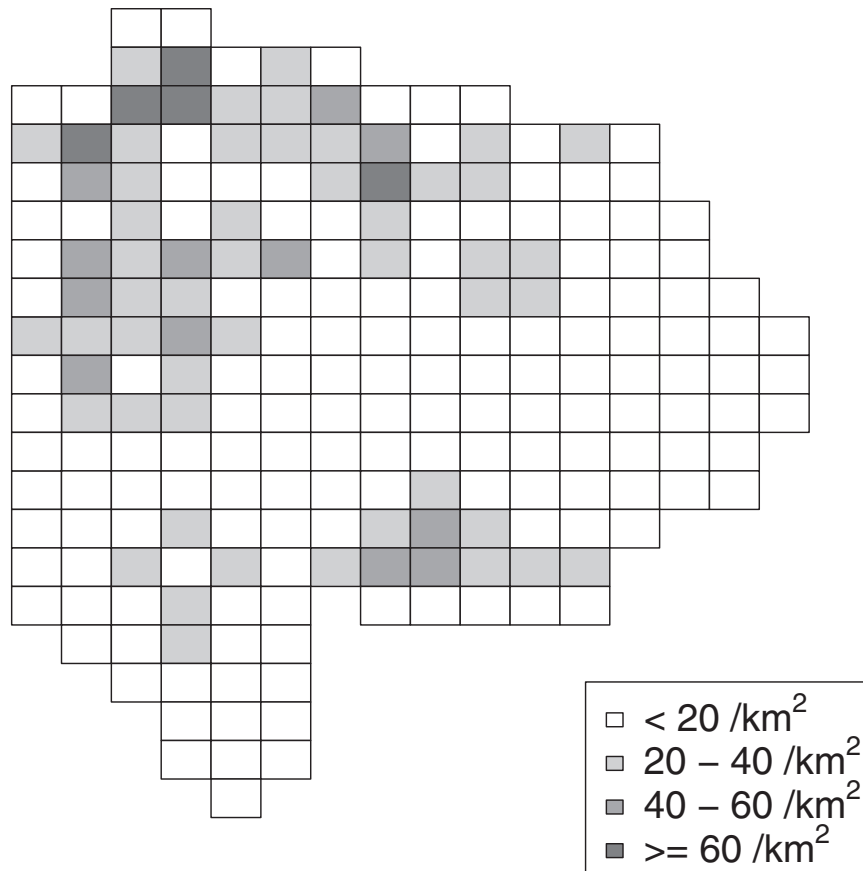


Fig. 6.—Estimated values of sika deer (*Cervus nippon*) carrying capacity (K_c) for 204 cells in Yamanashi Prefecture, Japan. K_c of each cell was estimated from the percentages of evergreen forest, deciduous forest, and artificial grassland; darker cells indicate higher K_c .

snow (Gill 1992a, 1992b), evergreen coniferous forest could be beneficial to winter survival. However, Portier et al. (1998) observed no correlation between snowfall or winter temperature and winter lamb survival in bighorn sheep (*Ovis canadensis*), suggesting that only exceptionally cold and long winters affect survival. In our study area, annual cumulative snowfall and maximum snow depth ranged from 0 to 25 cm and from 0 to 14 cm, far less than the 50 cm of snow that Takatsuki (1992) reported for areas preferred by sika deer on Honshu Island. Moreover, snow only covers the ground from January to early March in most of our study area. Our findings suggest that forests affect the dynamics of our deer population by providing winter forage, rather than as cover for wintering. Thus, the extent of the benefit of evergreen coniferous forest may depend on the severity of winter conditions. The relative importance of the effect of evergreen coniferous forest on carrying capacity may be small compared to the roles of grassland and deciduous broad-leaved forest.

Forsyth and Caley (2006) reported the widespread existence of irruptive dynamics of large herbivores. Irruption is a phenomenon in which a herbivore population increases to peak abundance, crashes to a lower abundance, and then increases to a carrying capacity lower than the peak abundance. Although their study focused on temporal dynamics in 7 populations that had reached carrying capacity, a key issue in irruptive dynamics is that deer are subject to variations in food supply. This

temporal heterogeneity may be analogous to spatial heterogeneity in the food supply of our study population. Fragmentation of forests into small patches surrounded by highly nutritious croplands provides the conditions for increased carrying capacity for deer, but this idea remains largely hypothetical and needs to be tested (Sinclair 1997). Some theoretical studies here examined the spatial heterogeneity of carrying capacity and its effects on movement and population dynamics (Roughgarden 1974; Pastor et al. 1997). In the current study, estimates of carrying capacity differed markedly, ranging between 1.34 and 98.4 deer/km² among cells. This is the 1st study to suggest that there is spatial heterogeneity in carrying capacity for sika deer on a continuous scale.

Importance of spatial heterogeneity in management.—As noted above, spatial heterogeneity in carrying capacity may be caused by differences in the quality and quantity of forage. Projected abundance and population trends at the same density levels may diverge due to environmental variation. This demonstrates the fact that density relative to the carrying capacity is more important than absolute density for population projections (Kjellander et al. 2006; Bowyer et al. 2014).

Administrative borders are often used to divide management units. For example, Yamanashi Prefecture is a single unit for deer management. However, our findings revealed that sika deer population dynamics were spatially structured at narrow spatial scales of 5.5 km × 4.6 km. More specifically, we found

that population density continued to increase in one area with high proportions of grassland and deciduous forest, yet became saturated in another area due to density dependence. Based on our findings, we recommend that spatial heterogeneity in carrying capacity be considered to improve deer management.

Our results were obtained at the scale of the cell we used (5.5 × 4.6 km), which may not be the best spatial scale to reveal spatial variation in population dynamics within our study area. In and around Yamanashi Prefecture, sika deer were shown to migrate seasonally between summer and winter habitats that are 2.5 to 31.9 km apart (Takii et al. 2012). Thus, estimates of the annual rate of population growth (annual growth rate of sika deer number under no density effect) may have been affected by immigration or emigration. However, deer exhibit high fidelity to annual migration routes (Sakuragi et al. 2004), and sika deer home range size is less than the area of a cell in both seasons (Miyashita et al. 2008). Therefore, we believe spatial differences in population dynamics among cells would be not change substantially if immigration and emigration were included in the models.

The use of this cell size and shape may also have affected our estimate of the intrinsic rate of natural increase (r) of sika deer. Hone et al. (2010) estimated the maximum annual population growth rate (r_m) of 55 mammal species using theoretical models and observational data, and showed that r_m of sika deer was 0.38. Matsuda et al. (1999) estimated the theoretical intrinsic rate of natural increase at 0.31. According to Kaji et al. (2004), r_m of a naturally colonizing sika deer population at Cape Shiretoko in northeastern Hokkaido was 0.19 (95% confidence interval was 0.16–0.22). On the other hand, our empirical estimate of natural increase was 0.57, which was within the 95% credible interval of Hone et al. (2010), but much higher than previously expected. This discrepancy is due to whether immigration and emigration are considered. In this study, deer density differed greatly among cells (Fig. 3b). At low density, it is likely that deer would increase by more than 1.46 [= exp(0.38)] times due to immigration from surrounding cells. Because Hone et al. (2010) and Matsuda et al. (1999) assumed a closed population, they only considered demographic parameters such as age at 1st reproduction, sex ratio, pregnancy rate, and natural mortality rate, but not immigration rate. Therefore, at smaller spatial scales, deer density may increase more rapidly than expected in an open system.

Researchers have criticized the logistic model we applied because it contains a simple and linear relationship between density dependence and carrying capacity (McCullough 1999; Kaji et al. 2010). Future studies are needed to test whether other factors influence the relationship and to test its linearity. However, our modeling approach elucidated the effects of landscape components on spatial variation in carrying capacity and revealed spatial heterogeneity in the strength of density dependence and carrying capacity in a sika deer population. As in Europe and the United States, grassland areas have increased the carrying capacity of deer populations in Japan. Consequently, projected abundance and population trends diverge into different patterns among locations, and density relative to carrying

capacity—rather than absolute density—can be expected to influence population projections.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—JAGS code of model.

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