



Note

Optimum Density of Sika Deer for Tree Seedling Survival

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ABSTRACT Sika deer have both direct negative and indirect positive effects on tree seedlings because deer browse on seedlings themselves as well as the floor vegetation that suppresses their growth. As such, a non-zero optimum deer density may exist for tree seedling survival. We conducted a field experiment combining exclusion of deer and removal of floor vegetation to investigate possible conditions under which an optimum density of deer with respect to seedling survival could exist. We constructed a hierarchical Bayesian model and used it to predict the survival rate of tree seedlings under different deer densities and floor leaf biomass conditions. Results indicated that a non-zero optimum deer density existed when the following conditions were present: a negative relationship between deer density and floor leaf biomass, negative effects on seedling survival caused both by deer and by floor vegetation, positive interaction of deer and floor leaf biomass on seedling survival, and considerably large potential leaf biomass. We estimated optimum deer density was 9.5 deer/km² when floor leaf biomass of the dwarf bamboo was 0.15 kg/m². This optimum deer density may have been excessive because we examined only the initial stages of seedling development, in which seedlings were less vulnerable to deer browsing. These results suggested that in this system, managing deer density at moderate levels might be more effective from a forest regeneration perspective than the complete exclusion of deer. © 2014 The Wildlife Society.

KEY WORDS deer-plant interaction, floor vegetation, hierarchical Bayesian modeling, optimum density of deer, seedling survival, sika deer *Cervus nippon*.

Deer can be regarded as a keystone herbivore because they are capable of altering community structure in various ways (McShea and Rappole 1992, Waller and Alverson 1997). High deer densities, for example, affect regional biological communities and ecosystems in many areas of the world, and are capable of modifying species composition of plants and exerting cascading effects on animals (Fuller and Gill 2001, Côté et al. 2004, Takatsuki 2009). Itô and Hino (2005, 2008) previously demonstrated that sika deer (*Cervus nippon*) not only had direct negative effects on the survival of tree seedlings by browsing but also had indirect positive effects on seedling survival because of associated decreases in biomass of dwarf bamboo (*Sasa* spp.), a plant that suppresses tree seedling development through shading. Itô and Hino (2005, 2008) also showed that the indirect positive effects of sika deer on seedling survival were greater than the direct negative effects they exerted on the survival of *Fagus crenata* seedlings, which were severely affected by dwarf bamboo (Nakashizuka and Numata 1982). The indirect positive effects of sika deer on seedling survival became clearer after dwarf bamboo density had fully recovered from the browsing

pressure exerted by deer subsequent to the construction of exclosures.

It is not clear whether an optimal deer density exists that could sufficiently decrease floor vegetation to promote tree seedling survival while maintaining low enough associated effects of deer browsing so as not to inhibit regeneration. Nomiya et al. (2003) conducted an exclosure experiment in a riparian forest in central Japan to examine forest regeneration in relation to micro-topography (higher or lower terrace), canopy (closed or gap), and floor vegetation (with or without dwarf bamboo), and suggested that the existence of deer browsing would promote tree regeneration if the deer population was large enough to reduce dwarf bamboo but not so large as to result in the browsing of tree seedlings; however, their study did not quantitatively demonstrate an optimum deer density for tree regeneration. Results of other investigations into optimum deer density were limited in that they provided only 2 levels of density—presence and absence of deer. Suzuki et al. (2008) examined the relationship between characteristics of ground-level vegetation and variations in sika deer density in Japanese forests and found that vegetation species richness peaked at an intermediate deer density (5.5–7.2 deer/km²). Furthermore, Hegland et al. (2013) examined the relationship between browsing by red deer (*Cervus elaphus*) and plant species richness in old-growth Norwegian forest floors and determined that species richness increased along with increasing deer herbivory

Received: 8 April 2013; Accepted: 21 January 2014

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within natural levels, but it declined slightly under artificially high red deer densities. In both Suzuki et al. (2008) and Hegland et al. (2013), the increase in forest floor plant species richness due to deer herbivory was explained by the deer-induced reduction of dominant floor vegetation, which had previously suppressed the growth of other plant species.

The results of previously studies have indicated that the presence of dominant floor vegetation played a key role in the determination of whether or not an optimum deer density with respect to floor vegetation existed. We conducted a field experiment involving various deer densities and various states of floor vegetation to determine the conditions under which an optimum deer density with respect to tree seedlings survival existed.

STUDY AREA

We conducted our study within a forest on Mt. Ôdaigahara, Nara Prefecture, Japan (34.18°N, 136.10°E), which was a part of the Yoshino-Kumano National Park (Fig. 1). Elevations ranged from 1,400–1,600 m asl. The study site primarily consisted of 3 types of forest cover including coniferous forest of *Picea jezoensis* var. *hondoensis*, mixed forest type of *Abies homolepis*-*Fagus crenata*, and a regenerating mixed forest of *Abies homolepis*-*Fagus crenata* that included light-demanding species such as *Clethra barbinervis* in addition to late-successional *A. homolepis* and *F. crenata* (Kinki Regional Environment Office 2005).

Forest floor vegetation was dominated by *Sasa nipponica* in the eastern part of the study site, and by *Sasa borealis* in the western part of the study areas (Ando et al. 2003). *Skimmia japonica* var. *japonica* was distributed throughout the study area and was dominant in certain sections of forest floor, although the area in which this species was dominant was smaller than the area dominated by dwarf bamboo. *S. japonica* has been shown to be unpalatable to deer (Yokota et al. 2009). *S. borealis* is more vulnerable to deer browsing than *S. nipponica* and the majority of *S. borealis* culms at the study site had died prior to 2001 because of browsing by deer with remnants remaining at certain microsites such as steep slopes (Yokota 2011). Deer density within the study site was estimated to range between 4.8 deer/km² and 60.3 deer/km² with the wide range due in large part because of the distribution of their main forage item, *S. nipponica* (Maeki et al. 1999).

METHODS

Data Collection

In the spring of 2006, we established 9 plots (20 m × 20 m) at the study site (Table 1). Plots chosen across the study site were representative of forest floor vegetation types; dominant species within the forest floor were *S. nipponica* (Sn; plots 1, 2, 3, 5, and 7), *S. borealis* (Sb; plot 4), and *S. japonica* (Sj; plot 8). In plots 6 and 9, the previously dominant *S. borealis* had died out and no dominant species could be identified (dSb). In Sn and Sb plots, the forest floor was almost completely covered by vegetation; in Sj plots, vegetation covered >75% of the forest floor; and in dSb plots, we observed only sparse vegetation. We further divided plots into 4 subplots, each

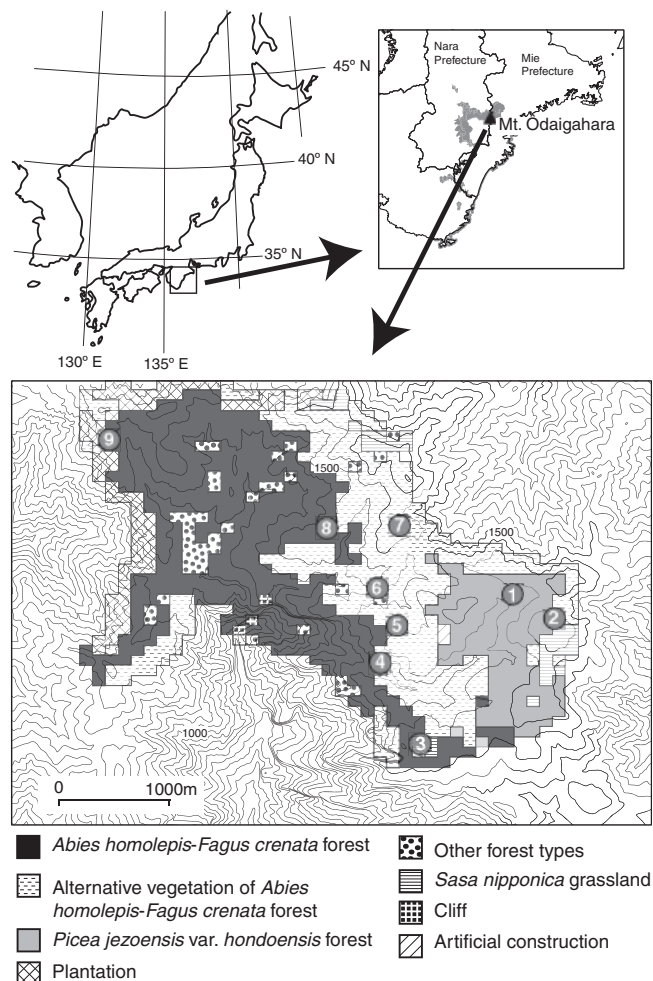


Figure 1. Map showing the study area and study plots where we investigated effects of sika deer browsing on seedling survival, 2006–2008. Gray area on the upper-right-hand side of the map indicates Yoshino-Kumano National Park. Circles indicate the study plots. Contour intervals indicate elevations of 50 m. Classification of vegetation on the lower map is based on information provided by the Kinki Regional Environment Office (2005).

containing 2 1-m × 1-m quadrats located in the corners of each plot (Fig. 2). We covered 1 quadrat in each subplot with a net supported by a wooden frame (1.2-m width × 1.2-m depth × 1.0-m height) to exclude deer, whereas the other quadrat remained uncovered. We placed 4 1-m × 20-m belts around each of the 9 study plots to monitor deer dung pellet groups (Fig. 2). We recorded dung pellet groups, define as 10 or more pellets produced during a single defecation (Goda et al. 2008), each month from April to December and from April to October in 2007 and 2008, respectively. When we found a dung pellet group on a belt edge, we recorded it if 10 or more pellets were located inside the belt, otherwise we ignored it. For plots 7 and 9, we extended the total length of the 4 belts used to 119 m during 2008 to collect more pellet groups. We estimated deer population density from dung pellet groups using the equation: deer density (deer/km²) = 8.9 ln(pellet group density (pellet groups/m²) × 100 + 1) (T. Hino, Meijo University, unpublished report).

During the first year of the study (2006), floor vegetation was intact and not subject to removal. During 2007, floor

Table 1. Study plot characteristics at sites in Mt. Ôdaigahara used to investigate the relationship between sika deer and seedling survival, 2006–2008.

Plot	Dominant species in the crown layer	Basal area (m ² /ha)	Floor type
1	<i>Abies homolepis</i>	33.3	Sn
2	<i>Acer shirasawanum</i> , <i>Picea jezoensis</i> var. <i>bondoensis</i>	27.6	Sn
3	<i>Fagus crenata</i>	22.3	Sn
4	<i>Fagus crenata</i> , <i>Stewartia monadelphica</i>	45.4	Sb
5	<i>Quercus crispula</i> , <i>Abies homolepis</i>	35.8	Sn
6	<i>Quercus crispula</i> , <i>Abies homolepis</i>	76.6	dSb
7	<i>Fagus crenata</i> , <i>Acer shirasawanum</i>	37.8	Sn
8	<i>Fagus crenata</i> , <i>Abies homolepis</i>	43.1	Sj
9	<i>Abies homolepis</i> , <i>Fagus crenata</i>	38.5	dSb

Sn, *Sasa nipponica*; Sb, *Sasa borealis*; dSb, dead *Sasa borealis*; Sj, *Skimia japonica*.

vegetation within Sn, Sb, and Sj quadrats was subjected to experimental manipulation, whereas vegetation in dSb plots was not because vegetation was too sparse. Manipulations consisted of removing aboveground parts of dominant floor species, *Sasa* spp. and *S. japonica*, from half the area of each quadrat, whereas the other half was left intact. During 2008, we removed aboveground parts of dominant species from the remaining half of each 1-m² quadrat. We cut floor species at ground level using scissors in either May 2007 or April 2008. We collected removed plants and desiccated them with an electric oven (95°C, 72 hr) to determine leaf biomass (kg/m²) of the 3 dominant species. We removed newly emerged plants from quadrats during the third year of the study; however, they were not taken into account during calculations of floor leaf biomass.

We marked all seedlings that existed at the beginning of the study and emerged over the course of the study within the quadrats and monitored their survival from the spring of 2006 to the spring of 2009. We defined seedlings as small plants of tree species (height <50 cm) that appeared to have germinated from a seed, as opposed to having derived from the root system of another plant. We estimated ages of existing seedlings based on numbers of bud scars (Cao 2001).

Statistical Analysis

We adapted a hierarchical Bayesian modeling approach to determine how the interaction between deer and dwarf bamboo affected the survival of tree seedlings. In this model, annual survival (Apr–Mar) of seedlings (l ; dead = 0, alive = 1) was as follows:

$$l \sim \text{Bernoulli}(P),$$

where the parameter P denoted the probability of survival. We modeled the probability of survival to be affected by deer density, floor leaf biomass, interaction of deer density and floor leaf biomass, seedling age, and yearly fluctuation. We assumed random effects by species would influence all factors except yearly fluctuation. Therefore, we determined logit of P as follows:

$$\begin{aligned} \text{logit}(P) = & \beta + (\beta_D + \varepsilon_{D_s})dx_p + (\beta_F + \varepsilon_{F_s})f\omega_{pqd} \\ & + (\beta_{DF} + \varepsilon_{DF_s})dfx_p\omega_{pqd} + (\beta_G + \varepsilon_{G_s})g \\ & + \beta_{07}y_{07} + \beta_{08}y_{08} + \varepsilon_s + \varepsilon_{P_p} + \varepsilon_{Q_{pq}} + \varepsilon_{V_{pqv}}, \end{aligned}$$

where variables d , f , and g denoted treatment of deer exclusion (exclusion: 0, control: 1), floor vegetation (removal: 0, control: 1), and seedling age, respectively. The parameter x_p denoted latent deer density of plot p ; x_p was estimated in relation to floor leaf biomass and density of dung pellets groups as described

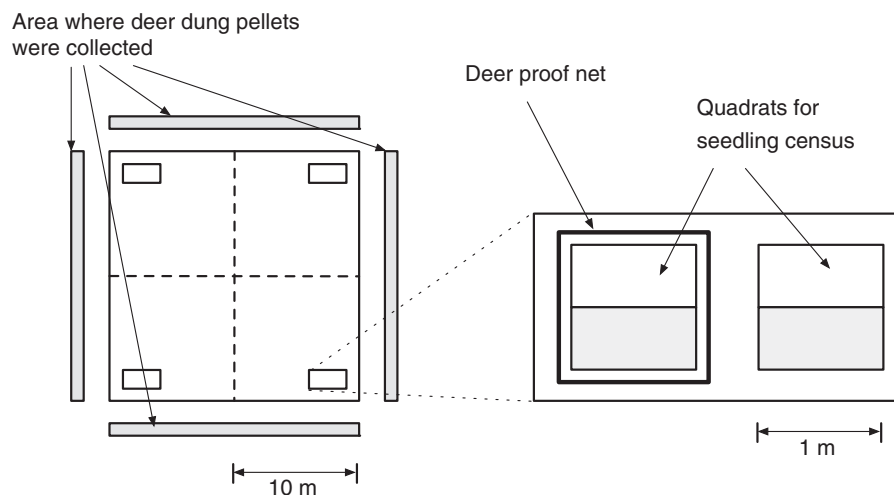


Figure 2. Schematic view of a study plot we used to investigate effects of sika deer browsing on seedling survival in Mt. Ôdaigahara, 2006–2008. We removed aboveground floor vegetation from half of each quadrat (as indicated by the gray rectangles on the right-hand side of the diagram) in 2007, and we removed floor vegetation from the other half (as indicated by the white rectangles) in 2008.

below and may have reflected habitat utilization intensity of deer rather than apparent deer density. The variable w_{pqd} denoted observed leaf biomass of floor vegetation for plot p , quadrat q , and deer treatment d . Variables y_{07} and y_{08} were dummy variables that denoted observation years (2006: $y_{07} = 0$ and $y_{08} = 0$, 2007: $y_{07} = 1$ and $y_{08} = 0$, and 2008: $y_{07} = 0$ and $y_{08} = 1$). The parameter β denoted the intercept, and parameters β_D , β_F , β_{DF} , and β_G denoted coefficients of deer (dx_p), floor vegetation ($f\omega_{pqd}$), interaction of deer and floor vegetation ($dfx_p\omega_{pqd}$), and seedling age (g), respectively. Parameters β_{07} and β_{08} were coefficients of yearly fluctuation in terms of y_{07} and y_{08} , respectively. Priors of the intercept and coefficients were all non-informative, $\text{Normal}(0, 10^4)$. Parameters $\varepsilon_{D,s}$, $\varepsilon_{F,s}$, $\varepsilon_{DF,s}$, and $\varepsilon_{G,s}$ denoted random effects of various seedling species on slopes of deer, floor vegetation, interaction of deer and floor vegetation, and seedling age, respectively, whereas parameters $\varepsilon_{S,s}$, $\varepsilon_{P,p}$, $\varepsilon_{Q,q}$, and $\varepsilon_{V,v}$ denoted random effects on the intercept by species of seedlings (s), plots (p), subplots (q), and individuals (v), respectively. Priors of the random effect parameters ($\varepsilon_{D,s}$, $\varepsilon_{F,s}$, $\varepsilon_{DF,s}$, $\varepsilon_{G,s}$, $\varepsilon_{S,s}$, $\varepsilon_{P,p}$, $\varepsilon_{Q,q}$, and $\varepsilon_{V,v}$) were dependent on normal distributions with mean values of 0 and standard deviations that were hyper-parameters (σ_D , σ_F , σ_{DF} , σ_G , σ_S , σ_P , σ_Q , and σ_V , respectively). Priors of the hyper-parameters were all non-informative, $1/\text{Gamma}(10^{-3}, 10^{-3})$.

Observed Leaf Biomass of Floor Vegetation (w_{pqd}) for plot p , subplot q , and deer treatment d was

$$\begin{aligned} w_{pqd} &\sim \text{Normal}(\mu_{W_{pqd}}, \sigma_W^2) \\ \mu_{W_{pqd}} &= z_p \exp(\beta_{WX} t_p dx_p + \varepsilon_{WQ_{pq}}) \\ \varepsilon_{WQ_{pq}} &\sim \text{Normal}(0, \sigma_{WQ}^2), \end{aligned}$$

where $\mu_{W_{pqd}}$ denoted latent mean leaf biomass, z_p denoted potential leaf biomass of the forest floor 1–2 years after exposure to deer browsing, β_{WX} represented a coefficient of $t_p \times d \times x_p$, and t_p denoted the type of plot p (0 for Sb, dSb or Sj, and 1 for Sn). For simplicity, this model assumed that only *S. nipponica* had been subjected to deer browsing. We made this assumption because *S. borealis*, although known to be palatable to sika deer, was located only in plots too steep to be regularly accessed by deer. Furthermore, dSb plots possessed little floor vegetation, and *Skimmia japonica* was known to be unpalatable to sika deer. If t_p or d was equal to 0, $\mu_{W_{pqd}}$ was approximately equal to z_p , which represented potential leaf biomass. The parameter $\varepsilon_{WQ_{pq}}$ denoted a random effect by quadrats, and parameters σ_W and σ_{WQ} denoted standard deviations. Priors of these parameters were non-informative, $\text{Normal}(0, 10^4)$ for β_{WX} and $1/\text{Gamma}(10^{-3}, 10^{-3})$ for σ_W and σ_{WQ} . Potential leaf biomass z_p was dependent on a gamma distribution because of its positive value,

$$z_p \sim \text{Gamma}(\kappa_Z, \lambda_Z),$$

where parameters κ_Z and λ_Z denoted shape and rate parameters, respectively. The priors of these parameters were non-informative $\text{Gamma}(10^{-3}, 10^{-3})$. We defined observed deer density h_{pyi} (deer/km²) for the i -th observation during year y in plot p , estimated from number of dung pellet groups,

using the unobserved true density x_p which we determined as follows,

$$\begin{aligned} h_{pyi} &\sim \text{Normal}(\mu_{H_{py}}, \sigma_H^2) \\ \mu_{H_{py}} &= x_p + \beta_{H8} y_{08} \end{aligned}$$

where, $\mu_{H_{py}}$ denoted mean deer density, σ_H denoted standard deviation, and β_{H8} denoted a coefficient of y_{08} incorporating yearly fluctuation. Priors of β_{H8} and σ_H were $\text{Normal}(0, 10^4)$ and $1/\text{Gamma}(10^{-3}, 10^{-3})$, respectively. We defined the unobserved true deer density x_p as dependent on a gamma distribution assuming a positive and unimodal distribution,

$$x_p \sim \text{Gamma}(\kappa_X, \lambda_X),$$

where parameters κ_X and λ_X denoted shape and rate parameters, respectively. The priors of these parameters were non-informative $\text{Gamma}(10^{-3}, 10^{-3})$.

We estimated posterior probability distributions of parameters using the Markov Chain Monte Carlo (MCMC) method. We employed 12,000 iterations with a thinning interval of 100 and the first 2,000 iterations discarded as a burn-in. We calculated 3 chains with different random number series and initial values yielding a total of 3,000 samples. We coded the model using BUGS language (Spiegelhalter et al. 1996; List S1, available online at www.onlinelibrary.wiley.com). We carried out calculations using JAGS version 3.3.0 (<http://mcmc-jags.sourceforge.net>, accessed 28 Feb 2013).

We predicted the yearly survival rate of tree seedlings in relation to deer density and leaf biomass using estimated parameter values assuming average status (without any random effects), current-year seedlings ($g = 0$), and year 2006 ($y_{07} = 0$ and $y_{08} = 0$).

RESULTS

We identified 3,533 seedlings of 31 species during the present study (Table 2), which meant that each of the random effects of species variation ($\varepsilon_{D,s}$, $\varepsilon_{F,s}$, $\varepsilon_{DF,s}$, $\varepsilon_{G,s}$, and $\varepsilon_{S,s}$) were modeled to include 31 levels. Deer density and floor leaf biomass were not significantly correlated, and differences in leaf biomass between deer-excluded quadrats and control quadrats were greater in Sn plots than in other plot types (Fig. 3). Deer density ranged from 4 deer/km² to 31 deer/km². The minimum value of leaf biomass (dry weight) was 0.00 kg/m² (observed in dSb), whereas maximum values of 0.14 kg/m² and 0.18 kg/m² were obtained from Sj control quadrats and Sn deer-proof quadrats, respectively (Fig. 3). Seedling density was higher in dSb plots with deer exclusion and some plots with no or small leaf biomass showed the highest seedling survival (Fig. 4).

The MCMC calculations for the Bayesian model successfully converged, and values of Gelman-Rubin's convergence diagnostic (Gelman and Rubin 1992) did not exceed 1.03 for any of the parameters (Table 3). The effects of deer (β_D) and leaf biomass (β_F) on seedling survival were both negative, whereas the effect of the interaction of deer and leaf biomass (β_{DF}) on seedling survival was positive

Table 2. Number of seedlings of each species in the 36 quadrats (36 m²) at sites in Mt. Ōdaigahara used to investigate the relationship between sika deer and seedling survival, 2006–2008.

Species	Number of seedlings found over 3 years	Number of seedlings surviving until 2009
<i>Abies homolepis</i>	1,203	349
<i>Acer</i> spp. ^a	1,063	392
<i>Fraxinus lanuginosa</i> f. <i>serrata</i>	545	316
<i>Chamaecyparis obtusa</i>	188	6
<i>Rhododendron quinquefolium</i>	109	57
<i>Pourthiaea villosa</i> var. <i>villosa</i>	100	49
<i>Fagus crenata</i>	55	29
<i>Clethra barbinervis</i>	52	16
<i>Carpinus japonica</i>	38	4
<i>Symplocos coreana</i>	35	17
<i>Stewartia monadelphica</i>	28	3
<i>Chengioanax sciadophylloides</i>	24	5
<i>Kalopanax septemlobus</i>	23	2
<i>Ilex geniculata</i>	20	7
<i>Aralia elata</i>	8	4
<i>Styrax japonica</i>	6	0
<i>Phellodendron amurense</i>	5	3
<i>Viburnum dilatatum</i>	5	3
<i>Betula corylifolia</i>	4	1
<i>Quercus crispula</i>	4	2
<i>Ilex macrospora</i>	3	2
<i>Picea jezoensis</i> var. <i>hondoensis</i>	3	2
<i>Cornus controversa</i>	3	1
<i>Cornus macrophylla</i>	3	3
<i>Enkianthus campanulatus</i>	2	1
<i>Sorbus commixta</i>	2	0
<i>Tilia japonica</i>	2	0

^a We found 5 *Acer* species, *A. argutum*, *A. micranthum*, *A. shirasawanum*, *A. sieboldianum*, and *A. tenuifolium*, but we unified them into *Acer* spp. because we could not clearly distinguish them in their initial stages of emergence.

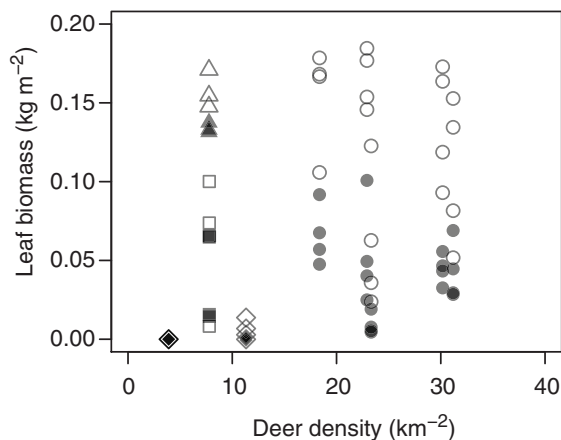


Figure 3. Relationships between sika deer density and leaf biomass of floor vegetation in Mt. Ōdaigahara, 2006–2008. Circles indicate quadrats dominated by *Sasa nipponica*. Squares indicate quadrats dominated by *S. borealis*. Diamonds indicate quadrats previously dominated by *S. borealis* now lacking a dominant ground cover species. Triangles indicate quadrats dominated by *Skimmia japonica*. Open shapes indicate quadrats subjected to deer exclusion treatment (effective deer density of these quadrats should be 0), and closed shapes indicate control quadrats.

(Table 3). The effect of deer density on leaf biomass (β_{wx}) was negative (Table 3).

Deer presence and leaf biomass were negatively related (negative β_{wx} ; dashed lines in Fig. 5). Seedling survival rate declined with increasing leaf biomass in the absence of deer, but in areas with no leaf biomass, survival rate declined with increasing deer density (Fig. 5). If potential leaf biomass was less than approximately 0.06 kg/m², survival rate was predicted to decline monotonically without any peaks as deer density increased (lower dashed line in Fig. 5); however, if potential leaf biomass was 0.15 kg/m², a value equivalent to the estimates obtained for plots 2 and 3 (Table 3), survival rate was predicted to peak when deer density was approximately 9.5 deer/km² (upper dashed line in Fig. 5).

DISCUSSION

Suzuki et al. (2008) and Hegland et al. (2013) reported maximal floor plant species richness at an intermediate deer density and attributed this observation to reductions in dominant plant species as a result of deer herbivory. Although the present study dealt with seedling survival rate and not species richness, greater average seedling survival rate could contribute to the establishment of more species within the forest floor environment.

In the present study, 3 major factors that affected seedling survival were incorporated into the model: deer density, leaf biomass of dominant floor species, and an interaction between these 2 variables. Based on the results of this study, we inferred that the following 4 conditions needed to be present for an optimum curve to be observed: 1) a negative relationship between deer density and leaf biomass, 2) a negative effect of deer and floor leaf biomass on seedling survival, 3) a positive effect of the interaction of deer and floor leaf biomass on seedling survival, and 4) a considerably large potential leaf biomass (approx. ≥ 0.07 kg/m²; Fig. 5). These conditions were not inconsistent with previous studies that determined that the greatest species richness would be achieved at intermediate deer densities, as the presence of some deer allowed many shade-intolerant species to thrive because of the reduction of dominant floor species (Suzuki et al. 2008, Hegland et al. 2013). In the present study, although we found a negative relationship between deer density and leaf biomass in Sn plots (the condition 3; negative value of β_{wx}), this was not true in plots with unpalatable floor vegetation ($t_p = 0$: Sj), plots that were located on a steep slope (Sb), and plots with sparse floor vegetation (dSb). Based on the data obtained, the model used in the present study assumed that areas with these 3 types of forest floor would exhibit no relationship between deer density and leaf biomass ($t_p = 0$; Fig. 3). In Sj, Sb, and dSb plots, our model defined that floor leaf biomass was not affected by deer density (the curve representing the relationship should be horizontal in Fig. 5), and the seedling survival was highest when deer were absent (Fig. 4). The positive interaction between deer and leaf biomass on seedling survival may result from either deer decreasing floor vegetation or floor vegetation protecting seedlings from deer browsing. This relationship may be even more apparent

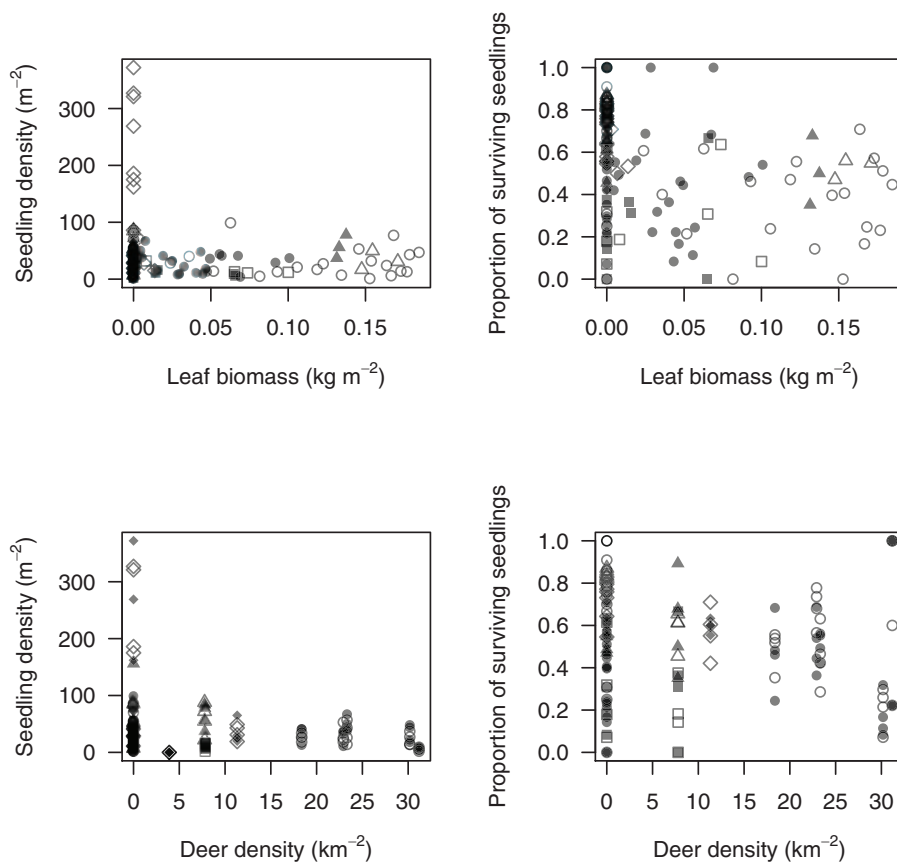


Figure 4. Relationships between leaf biomass of floor vegetation and seedling density that emerged between 2006 and 2008 (upper left), leaf biomass and proportion of surviving seedlings prior to spring 2009 (upper right), sika deer density and seedling density (lower left), and deer density and proportion of surviving seedlings (lower right) in Mt. Ōdaigahara. Circles indicate quadrats dominated by *Sasa nipponica*. Squares indicate quadrats dominated by *S. borealis*. Diamonds indicate quadrats previously dominated by *S. borealis* now lacking a dominant ground cover species. Triangles indicate quadrats dominated by *Skimmia japonica*. Open shapes indicate quadrats subjected to deer exclusion treatment (upper) or floor removal treatment (lower), and closed shapes indicate control quadrats.

when considerable floor leaf biomass exists. When deer were more abundant and floor vegetation was even denser, seedling survival would also improve (Fig. 5); however, these conditions were not likely to occur in any natural environment.

We estimated optimum deer density leading to the highest stem survival to be approximately 9.5 individuals/km² when potential leaf biomass of *S. nipponica* in the first or second year subsequent to release from deer browsing was 0.15 kg/m². This value seemed excessive compared to the deer density of 3–5 deer/km² proposed by Japanese prefectural governments (Suzuki et al. 2008) and the Ministry of the Environment (2010), for incurring little effect on natural vegetation. One reason for this discrepancy may have been that, although tall seedlings are more likely to be browsed by deer, only initial seedling survival was considered in the present model. For example, *Abies homolepis* seedlings were severely affected by deer browsing after 24 months when dense *Sasa* floor coverage was not present (Itô and Hino 2005). If the value of the deer effect on seedling survival, β_D , had been -0.22 , twofold more severe than the estimated value estimated in the present data and model (Table 3), optimal deer density would have been 1.8 deer/km² when potential leaf biomass of dwarf bamboo was 0.15 kg/m².

Optimum deer density to maximize seedling survival rate in a specific forest community would not necessarily be ideal for other types of plants and animals even within the same community. The severity of the impact of both deer and floor vegetation on seedling survival differs among tree species in Japanese forests (Nomiya et al. 2003, Itô and Hino 2007). Hegland et al. (2013) demonstrated in an old-growth Norwegian pine forest that relationships between the intensity of red deer herbivory and plant species richness differed between low-growing functional groups (forbs, graminoids, and mosses) and taller growing woody species (dwarf-shrubs and young trees). Differences in response to deer densities were known in birds. For example, Hino et al. (2003) demonstrated that bird species that used tree stems or hollows such as woodpeckers (Picidae) and the Eurasian nuthatch (*Sitta europaea*) were abundant in areas with high densities of sika deer, whereas species that used the understory, such as the Japanese bush warbler (*Cettia diphone*), were abundant in areas of low deer density, which reflected the changes in vegetation caused by deer activity. Management standards other than tree seedling survival, such as the diversity of plants and animals, should also be considered when determining optimum deer densities for a given site.

Table 3. Means and 95% credible intervals (CI) of posterior distributions for each parameter used to model the relationship between sika deer and seedling survival in Mt. Ōdaigahara, 2006–2008.

Parameter	Explanation	Mean	95% CI	
			Lower	Upper
β	Intercept of seedling survival	0.91	0.03	1.86
β_D	Coefficient of deer density to seedling survival	-0.11	-0.16	-0.07
β_F	Coefficient of leaf biomass to seedling survival	-9.80	-15.36	-5.88
β_{DF}	Coefficient of interaction between deer density and leaf biomass to seedling survival	1.24	0.80	1.80
β_G	Coefficient of seedling age to seedling survival	0.18	0.04	0.33
β_{HY8}	Coefficient of year = 2008 to deer density	-0.82	-3.10	1.46
β_{WX}	Coefficient of deer density to leaf biomass	-0.046	-0.059	-0.037
β_{Y7}	Coefficient of year = 2007 to seedling survival	0.08	-0.23	0.35
β_{Y8}	Coefficient of year = 2008 to seedling survival	-0.82	-1.33	-0.37
κ_X	Shape parameters of deer density	2.98	0.92	6.53
κ_Z	Shape parameters of leaf biomass	1.00	0.25	2.50
λ_X	Rate parameters of deer density	0.17	0.04	0.38
λ_Z	Rate parameters of leaf biomass	10.62	1.27	28.60
σ_H	Standard deviation of deer density	6.91	6.03	7.91
σ_P	Standard deviation of plot-level random effects on seedling survival	0.83	0.36	1.61
σ_Q	Standard deviation of quadrat-level random effect on seedling survival	0.58	0.34	0.91
σ_S	Standard deviation of species-level random effect on seedling survival	1.00	0.57	1.61
σ_V	Standard deviation of individual-level random effect on seedling survival	1.36	0.78	1.98
σ_W	Standard deviation of leaf biomass	0.023	0.017	0.031
σ_{WQ}	Standard deviation of quadrat-level random effect on leaf biomass	0.20	0.03	0.39
x_1	Estimated deer density in plot 1	28.91	25.34	32.28
x_2	Estimated deer density in plot 2	21.02	17.97	24.13
x_3	Estimated deer density in plot 3	25.11	22.03	28.18
x_4	Estimated deer density in plot 4	7.35	4.20	10.59
x_5	Estimated deer density in plot 5	19.56	16.18	22.81
x_6	Estimated deer density in plot 6	8.36	5.37	11.52
x_7	Estimated deer density in plot 7	30.21	26.53	33.80
x_8	Estimated deer density in plot 8	13.13	10.44	16.15
x_9	Estimated deer density in plot 9	5.79	3.51	8.28
z_1	Estimated potential leaf biomass in plot 1	0.14	0.11	0.18
z_2	Estimated potential leaf biomass in plot 2	0.15	0.12	0.20
z_3	Estimated potential leaf biomass in plot 3	0.15	0.12	0.20
z_4	Estimated potential leaf biomass in plot 4	0.05	0.03	0.07
z_5	Estimated potential leaf biomass in plot 5	0.07	0.05	0.10
z_6	Estimated potential leaf biomass in plot 6	0.01	0.00	0.02
z_7	Estimated potential leaf biomass in plot 7	0.11	0.08	0.15
z_8	Estimated potential leaf biomass in plot 8	0.14	0.10	0.19
z_9	Estimated potential leaf biomass in plot 9	0.01	0.00	0.02

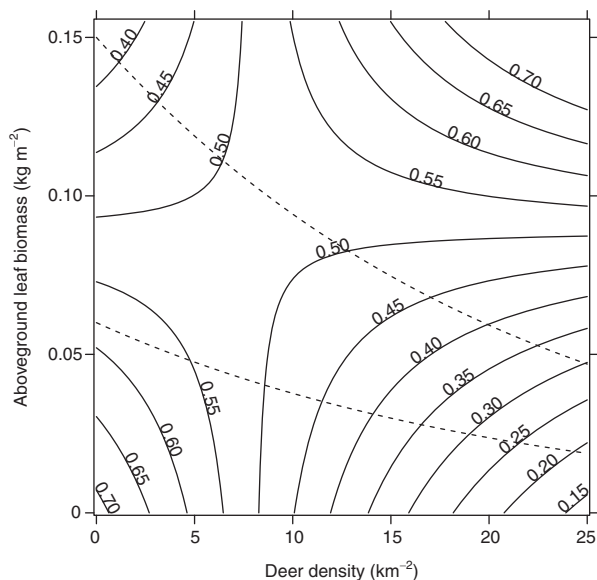


Figure 5. Seedling survival in relation to deer density and leaf biomass in Mt. Ōdaigahara, 2006–2008. Contours indicate yearly survival rate of seedlings. Dashed lines indicate relationships between deer density and leaf biomass where potential leaf biomass (deer density = 0) is 0.15 kg/m² (upper line) and 0.06 kg/m² (lower line). The estimated leaf biomass for study plots dominated by *Sasa nipponica* was 0.15 kg/m², the upper limit for which survival rates exhibited monotonic decline without any peaks alongside increasing deer density was 0.06 kg/m².

The modeling framework developed in the present study could potentially be used to detect optimum deer densities for target species in other communities.

MANAGEMENT IMPLICATIONS

The model developed in the present study determined that sparse deer populations could potentially be more favorable for tree seedling survival than a complete absence of deer. This indicated that deer may contribute to forest regeneration by controlling floor vegetation that suppresses seedlings. Forest managers typically consider deer density on a regional scale; however, results of the present study suggested that monitoring both the status of deer density and floor vegetation on a smaller scale in correspondence to vegetation type as well as a regional scale might be advantageous to planned forest regeneration.

ACKNOWLEDGMENTS

We would like to thank T. Chikaguchi and S. Narayama of the Forestry and Forest Products Research Institute, the staff of the Ōdaigahara Visitors' Center (Ministry of Environment), S. and S. Tagaito, and Dr. E. Shibata for their cooperation and support. This study was supported by grants from the Ministry of Environment (Environmental Research by the National Research Institutes of Government

Ministries and Agencies, 2007–2009) and the Ministry of Education, Culture, Sports, Science and Technology of Japan (No. 18380097).

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Associate Editor: Graham Hall.

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