Wildlife Biology 2017: wlb.00329
doi: 10.2981/wlb.00329

Subject Editor: John Ball. Editor-in-Chief: Ilse Storch. Accepted 30 December 2016

The effects of landscape components, wildlife behavior and hunting methods on hunter effort and hunting efficiency of sika deer

Hayato Iijima

H. Iijima (hayato.iijima@gmail.com), Yamanashi Forest Research Inst., 2290-1, Saishoji, Fujikawa, JP-400-0502 Yamanashi, Japan

Population management of overabundant deer is essential in many countries. Hunting is one of the ways to manage such deer so it is important to understand how hunting affects deer and numbers caught. The number caught is the product of hunter effort and hunting efficiency. However, factors affecting effort and efficiency have rarely been properly investigated. I used a Bayesian state–space model to examine the effects of landscape components and deer behavior on the effort and efficiency of two hunting methods in hunting sika deer *Cervus nippon*. With shooting by gun, effort increased as the deer abundance of previous year increased and the percentages of wildlife protection areas and city areas decreased. With trapping, effort increased as the percentage of wildlife protection areas decreased. Efficiency of shooting decreased as the effort of the previous year increased. With trapping, efficiency was not affected by the effort of the previous year. Efficiency of trapping plateaued with the increase of deer abundance and the decrease of efficiency in relation to deer abundance was stronger with trapping than with shooting. In conclusion, effort and efficiency were affected by landscape components, deer behavior, and hunting methods. I recommend intensive shooting in the initial phase, and after deer abundance decreases and deer vigilance increases, trapping should be adopted for a sustainable hunting efficiency.

In recent years, the management of deer populations has become increasingly necessary (Côté et al. 2004, Takatsuki 2009). Population control by game hunting is one of the ways to manage overabundant deer (Decker and Connelly 1989, Simard et al. 2013). Successful management requires that the effects of hunting be understood in order to avoid unwanted population explosions or depletion of the targeted wildlife. A direct effect of hunting is the number of animals caught, and this number is determined by the product of hunter effort (hereafter, effort) and hunting efficiency (hereafter, efficiency). Therefore, to conduct effective population control of deer by hunting, factors affecting effort and efficiency should be clarified.

Many studies have examined the factors affecting effort and efficiency (Davidson and Fraser 1991, Harden et al. 2005, Ward and Myers 2005). Davidson and Fraser (1991) showed that deer hunter effort was high in places of high accessibility and good visibility. Harden et al. (2005) showed that deer hunters avoided urban areas. However, each of these studies has two major problems. First is the treatment of two type errors. In addition to demographic process error, effort and efficiency fluctuate greatly with each hunting event because of uncontrollable conditions like weather, the equipment for hunting, and the skill of hunters. A state–space model that can explicitly treat both stochastic and measurement errors (Calder et al. 2003) is probably the most useful way to analyze effort and efficiency, but state–space models have rarely been applied to effort and efficiency. The second problem is the difficulty in distinguishing between change in wildlife abundance and change in wildlife behavior caused by previous effort, although this problem is specific to efficiency. It is known that changes in efficiency correspond to changes in wildlife abundance (Bigelow et al. 2002, Haggarty and King 2006). However, at the same time, wildlife escape from hunters (Kilgo et al. 1998, Martin and Baltzinger 2002), which also decreases efficiency. Therefore, it is necessary to examine the factors affecting efficiency by discriminating between changes in abundance and changes in wildlife behavior (Harley et al. 2001). If the behavior of the target wildlife changes in response to the previous year's hunting effort, then hunting efficiency should not be used as an index of wildlife abundance.

Deer are a major target of game hunting, and data on effort and efficiency with respect to deer hunting have been collected from locations all over the world (e.g. Solberg et al. 1999 in Norway; Ueno et al. 2010 in Japan). Models to estimate deer abundance have been developed because of the demand for management of overabundant deer (Iijima et al. 2013). Thus, deer are a good study subject to use for examining the factors affecting effort and efficiency. Effort with respect to deer hunting is expected to vary depending on landscape characteristics like the type of land use (e.g. forest, farmland, and urban area), slope, and road density. The type of land use will affect outlook for hunters that would affect the hunters' selection of hunting point and the slope and road density will affect the accessibility for hunters. Hunters will select the place where deer abundance is high because they expect to hunt easily in such places. Furthermore, if the percentage of wildlife protection area and urban area is large, hunters will avoid hunting in such regions. Efficiency with respect to deer hunting is expected to vary depending on the degree of slope.

In addition to landscape components, the method of hunting is also expected to affect effort and efficiency. In Japan, there are two major hunting methods: shooting and trapping. Shooting is the most common method, but it is expected that the use of guns may make deer extremely vigilant if the deer had previously been shot at and escaped. On the other hand, trapping is superior to shooting because a trapped deer will rarely escape. However, because hunters are legally required to check their traps every day in Japan, it is expected that hunting efficiency of trapping will be more rapidly saturate with the increase of deer abundance than the efficiency of shooting. In Japan, deer populations are managed both by nuisance control and by game hunting. Population control of deer in Japan is characterized by little participation of professional hunters, so both game hunting and nuisance control are conducted by amateur hunters, and nuisance control is conducted using the same methods of game hunting. Furthermore, Japanese hunters are aging and the number of active hunters is decreasing, which limits the number of hunted deer. For these reasons, examination of factors affecting effort and efficiency of game hunting is useful for population control of deer species.

To contribute to the effective management of overabundant deer populations, this study aimed to clarify the effects of landscape components, deer behavior, and hunting methods on variations in effort and efficiency of hunting deer. In this study, I analyzed effort and efficiency with respect to hunting sika deer *Cervus nippon*. I examined the hypotheses that 1) effort and efficiency of hunting are affected by landscape components, 2) efficiency of shooting, but not trapping, decreases with the increase of previous year's hunter effort, and 3) hunting efficiency of trapping will be more rapidly saturate with the increase of deer abundance than the efficiency of shooting.

Material and methods

Study site

The study site was the whole of Yamanashi Prefecture, central Japan. In Yamanashi Prefecture, the population density of sika deer has increased in recent years (Iijima and Ueno 2016), resulting in extensive debarking of trees (Nagaike and Hayashi 2003, Iijima and Nagaike 2015b) and browsing of understory vegetation in forests (Iijima and Nagaike 2015a) and herbaceous grasses in subalpine grasslands (Nagaike 2012). The hunting season in Yamanashi Prefecture is from November to March, and registered hunters hunt sika deer by shooting or trapping (snaring the legs). Furthermore, nuisance control of sika deer is conducted from April to November. The numbers of hunted deer by game hunting in 2005 was much higher than that of culled deer by nuisance control, but the number of hunted deer in 2010 was similar to that of culled deer (Fig. 1). Thus, game hunting also has important role in population control. Yamanashi Prefecture is characterized by complex topography. The elevation of Yamanashi Prefecture ranges from 36 m to the peak of Mt. Fuji at 3376 m.

Data

A rectangular grid (each cell was 5.5×4.6 km $= 25.3$ km^2) was established to cover the entire prefecture (a total of 216 grid cells). The size and shape of the cells was set by the Ministry of the Environment of Japan and is uniform all over Japan. All data were obtained at the scale of a cell.

The hunter effort (the number of hunting days multiplied by the number of shooters or the number of days that traps were set) and the number of caught deer from 2005 to 2010 in each cell were obtained from hunters' reports. Hunters (both shooters and trappers) voluntarily submit their efforts and the number of deer caught to the local government office at the end of the hunting season. The submission of hunters' reports is voluntary, but $>90\%$ of registered hunters submit their reports in Yamanashi Prefecture because public officers repeatedly and persistently request the submission of these reports through the Yamanashi branch of the Japan Hunting Association, and the Japan Hunting Association has a strong influence on hunters in Japan. Therefore, these reports can be regarded as unbiased. In contrast, there is no system to submit hunters' report in nuisance control in Yamanashi Prefecture. Then, I could not analyze effort and efficiency of nuisance control. However, as already stated, nuisance control is also conducted by amateur hunters who go to

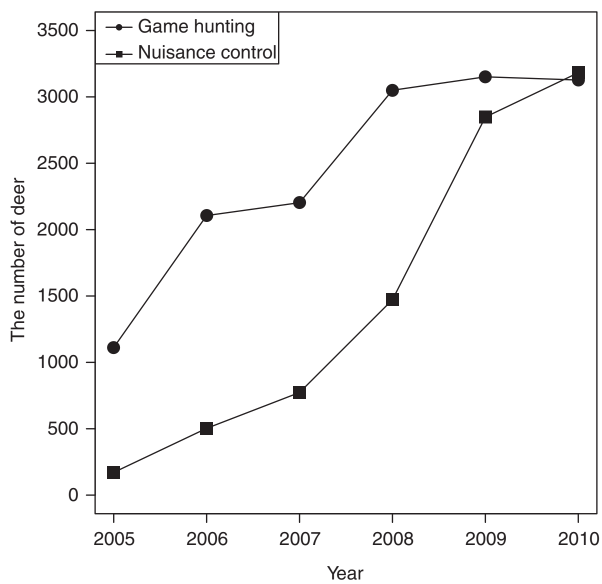

Figure 1. The numbers of hunted by game hunting and culled by nuisance control in Yamanashi Prefecture during study period.

hunting in the same region and the number of hunted deer by game hunting is similar or larger than that of culled deer by nuisance control. Then, in this study, I concentrate on the game hunting.

Deer abundance from 2005 to 2010 was obtained from Iijima et al. (2013), who estimated deer abundance in each cell (mean and standard deviation) from three types of monitoring data and took into consideration measurement error and spatial autocorrelation of deer abundance. Please refer to Iijima et al. (2013) for further details of the methods of estimation. In this study, I treat deer abundance in each cell as a random variable with a normal distribution with the estimated mean and standard deviation.

For each of the cells, the areas (to account for cells located at the boundary of Yamanashi Prefecture, km^2) and the percentages of the cell occupied by evergreen forests, deciduous forests, wildlife protection areas, artificial grassland (e.g. farmland and golf course) areas, city areas, the mean slope of the cell, and the forest road density (forest road length within a cell/area of the cell) were calculated by the QGIS software package (<http://qgis.osgeo.org/en/site/>, accessed 19 January 2016). The areas of the landscape components were obtained from the Natural Environment Information geographic information system (<www.biodic.go.jp/trialSystem/top.html>, accessed 19 January 2016) provided by the Biodiversity Center of Japan. A digital elevation model with 10-m mesh was used to calculate mean slope; this was obtained from the Geospatial Information Authority of Japan (<http://fgd.gsi.go.jp/download/>, accessed 19 January 2016). Forest road data were obtained from the Yamanashi prefectural government.

Statistical analysis

I adopted a state–space model (Calder et al. 2003) to examine the factors affecting effort and efficiency. The state–space model is composed of a process model, which describes latent processes like temporal changes in efficiency, and an observation model, which describes the relationship between latent processes and observed data. Thus, stochastic and observation errors could be incorporated explicitly. I analyzed effort and efficiency by hunting method (i.e. shooting and trapping).

Process model

The process model for hunter effort was as below:

$$\log\left(\mathrm{Effort}_{t,c}\right) \sim N\left(\log\left(\mathrm{Effort}_{t-1,c}\right)+\beta_{\mathrm{AB}}\log(\mathrm{D}_{t-1,c}),\sigma_1^2\right) \quad (1)$$

$$\begin{aligned}\log\left(\mathrm{Effort}_{1,c}\right) = {} & \alpha_1+\beta_{\mathrm{ER}}\,\mathrm{ER}_c+\beta_{\mathrm{DR}}\mathrm{DR}_c+\beta_{\mathrm{WR}}\mathrm{WR}_c+\beta_{\mathrm{SL1}}\mathrm{SL}_c \\ & +\beta_{\mathrm{AR}}\mathrm{AR}_c+\beta_{\mathrm{GR}}\mathrm{GR}_c+\beta_{\mathrm{CR}}\mathrm{CR}_c+\beta_{\mathrm{RD}}\mathrm{RD}_c+\varepsilon_1\end{aligned} \quad (2)$$

where $\mathrm{Effort}_{t,c}$ is latent (true) effort in year t in cell c; β_{AB} is the coefficient of $D_{t-1,c}$; $D_{t-1,c}$ is deer abundance in year t–1 in cell c; σ_1 is an variance parameter; α_1 is an intercept term; β_{ER} is the coefficient of the percentage of evergreen forest within cell c (ER_c); β_{DR} is the coefficient of the percentage of deciduous forest within cell c (DR_c); β_{WR} is the coefficient of the percentage of wildlife protection area within cell c (WR_c); β_{SL1} is the coefficient of mean slope within cell c (SL_c); β_{AR} is the coefficient of area within cell c (AR_c); β_{GR} is the coefficient of artificial grassland area within cell c (GR_c); β_{CR} is the coefficient of city area within cell c (CR_c); β_{RD1} is the coefficient of forest road density within cell c (RD_c); and ε_1 is the random effect of cell c. Prior distributions of β_{AB}, α_1, β_{ER}, β_{DR}, β_{WR}, β_{SL1}, β_{AR}, β_{GR}, β_{CR}, and β_{RD} were a vague Gaussian distribution with mean 0 and variance 1000. Prior distribution of ε_1 was a Gaussian distribution with mean 0 and variance σ_2^2. Prior distributions of σ_1 and σ_2 were a uniform distribution from 0 to 100 (Gelman 2006).

The process model for efficiency was as below:

$$\begin{aligned}\log\left(\mathrm{Efficiency}_{t,c}\right) \sim \mathrm{Normal}\Big(\Big(&\log\left(\mathrm{Efficiency}_{t-1,c}\right) \\ &+\beta_{\mathrm{EF}}\log \mathrm{Effort}_{t-1,c},\sigma_3^2\Big)\end{aligned} \quad (3)$$

$$\log\left(\mathrm{Efficiency}_{1,c}\right)=\alpha_2+\beta_{\mathrm{SL2}}\mathrm{SL}_c+\varepsilon_2 \quad (4)$$

where $\mathrm{Efficiency}_{t,c}$ is latent (true) efficiency in year t in cell c; β_{EF} is the coefficient of effort in the previous year; σ_3 is an variance parameter; α_2 is an intercept term; β_{SL2} is the coefficient of SL_c; and ε_2 is the random effect of cell c. A negative value of β_{EF} indicates that effort in the previous year decreased efficiency. In previous studies, efficiency has been determined as a mixture of target wildlife abundance, wildlife behavior, and landscape components, as noted in the Introduction. However, in this study, deer abundance was already known. Therefore, deer abundance was not included in the process model for efficiency and was treated in the observation model. Prior distributions of β_{EF}, α_2 and β_{SL2} were a vague Gaussian distribution with mean 0 and variance 1000. Prior distribution of ε_2 was a Gaussian distribution with mean 0 and variance σ_4^2. Prior distributions of σ_3 and σ_4 were a uniform distribution from 0 to 100 (Gelman 2006).

Observation model

The observation model for effort was as below:

$$\mathrm{E}_{t,c} \sim \mathrm{Poisson}(\mathrm{Effort}_{t,c}) \quad (5)$$

The observation model for efficiency was as below:

$$\mathrm{C}_{t,c} \sim \mathrm{Poisson}\left(\mathrm{Efficiency}_{t,c}\mathrm{D}_{t,c}^{\beta_D}\mathrm{E}_{t,c}\right) \quad (6)$$

where $E_{t,c}$ is the observed effort (the number of hunting days multiplied by the number of shooters or the number of days that traps were set) in year t in cell c; $C_{t,c}$ is the number of deer caught in year t in cell c; and β_D is the strength of the deer abundance dependence of hunting efficiency (shape parameter; Tsuboi and Endou 2008). Prior distribution of β_D was a uniform distribution from 0 to 2. If β_D is smaller than 1, the number of deer caught will not increase linearly with an increase in deer abundance. As stated above, I treat deer abundance of each cell as a random variable with normal distribution with the estimated mean ($\mu_{t,c}$) and variance ($\sigma_{t,c}^2$) in year t in cell c as below:

$$\mathrm{D}_{t,c} \sim \mathrm{Normal}\left(\mu_{t,c},\sigma_{t,c}^2\right) \quad (7)$$

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). I ran three parallel MCMC chains and retained 200 000 iterations after an initial burn-in of 50 000 iterations. I thinned the sampled values to 0.5% (i.e. obtained 1000 samples as posterior distributions

Table 1. Posterior summary of estimated parameters for latent effort. β_{AB} is the coefficient of $D_{t,c}$; $D_{t,c}$ is deer abundance in year t in cell c; β_{ER} is the coefficient of the percentage of evergreen forest within cell c (ER_c); β_{DR} is the coefficient of the percentage of deciduous forest within cell c (DR_c); β_{WR} is the coefficient of the percentage of wildlife protection area within cell c (WR_c); β_{SL1} is the coefficient of mean slope within cell c (SL_c); β_{AR} is the coefficient of area within cell c (AR_c); β_{GR} is the coefficient of artificial grassland area within cell c (GR_c); β_{CR} is the coefficient of city area within cell c (CR_c); and β_{RD1} is the coefficient of forest road density within cell c (RD_c). A parameter was considered significant if the 95% credible intervals of the parameter did not overlap 0.

	Shooting			Trapping		
		95% credible interval			95% credible interval	
	Mean	Lower bound	Upper bound	Mean	Lower bound	Upper bound
β_{AB}	0.02	0.01	0.03	−0.02	−0.12	0.07
β_{ER}	0.57	−0.53	1.71	−1.34	−9.72	6.78
β_{DR}	0.31	−0.44	1.08	−0.63	−5.60	4.28
β_{WR}	−2.92	−3.53	−2.32	−12.64	−18.66	−7.18
β_{SL1}	0.01	−0.04	0.02	−0.17	−0.34	0.01
β_{AR}	0.11	0.09	0.13	0.50	0.32	0.69
β_{GR}	1.58	−1.62	4.83	3.22	−17.05	23.41
β_{CR}	−10.37	−14.17	−6.68	−12.44	−35.51	8.62
β_{RD}	−2.75	−62.71	58.20	1.81	−58.22	62.46

for each chain). Convergence of MCMC sampling was judged by the criterion that $\hat{R}$ was smaller than 1.1 (Gelman et al. 2004). To conduct MCMC sampling, I used JAGS (Plummer 2003) in the "rjags" package in R (<www.r-project.org>). I also used the package 'snow' to conduct multi-thread MCMC sampling. I concluded that a parameter was significant if the 95% credible intervals of the parameter did not overlap 0.

Results

$Effort_{t,c}$ for shooting significantly increased with the increase in $D_{t,c}$ and AR_c and the decrease in WR_c and CR_c (Table 1). We failed to detect any significant difference in $Effort_{t,c}$ for shooting with the differences in ER_c, DR_c, SL_c, GR_c and RD_c (Table 1). $Effort_{t,c}$ for trapping significantly increased with the increase in AR_c and the decrease in WR_c but was not affected by other factors (Table 1).

$Efficiency_{t,c}$ for shooting in a certain year significantly decreased following a high hunter effort in the previous year (Table 2, Fig. 2). During the study period (six years), $Efficiency_{t,c}$ for shooting of the cell where the sum of effort during six years was maximum among cells decreased more than 40%. Mean (95% credible interval) of β_D for shooting was 0.79 (0.69–0.89; Table 2, Fig. 3). $Efficiency_{t,c}$ for trapping was not affected by any factors including hunter effort in the previous year (Table 2, Fig. 2). Mean (95% credible interval) of β_D for trapping was 0.46 (0.22–0.74; Table 2, Fig. 3).

Discussion

The factors affecting effort differed between shooting and trapping. Effort for shooting was high under high deer abundance, low percentages of wildlife protection area, and low percentages of city area (Table 1). The increase of effort by high deer abundance and the suppression of effort by wildlife protection areas and city area (Table 1) has been reported in other areas (Davidson and Fraser 1991, Harden et al. 2005). Contrary to my prediction, effort of shooting was not affected by forest, artificial grassland, slope and road density (Table 1). It is common in Yamanashi Prefecture to use dogs to flush out deer for shooting, so it is not necessary for hunters to walk long distances to find deer. The general usage of dogs in shooting might also have contributed to why I did not detect an effect of forest, artificial grassland, slope and road density on effort. Increased percentage of wildlife protection areas decreased effort for trapping as well (Table 1). However, city area did not affect effort for trapping (Table 1). Trap hunters would like to set their traps near their home because hunters must patrol set traps every day in Japan. Hunters live in both city and rural areas. Then, there was no relationship between the city area and effort for trapping.

The factors affecting efficiency also differed between shooting and trapping. Effort of the previous year decreased efficiency of shooting of the current year (Table 2, Fig. 2). Because deer abundance was incorporated into my model (Eq. 6) and considered estimation error (Eq. 7), the decrease in hunting efficiency by the previous year's high hunter effort

Table 2. Posterior summary of estimated parameters for latent efficiency. β_{EF} is the coefficient of effort in the previous year; β_{SL2} is the coefficient of SL_c; and β_D is the strength of density dependence of hunting efficiency (shape parameter; Tsuboi and Endou 2008). A parameter was considered significant if the 95% credible intervals of the parameter did not overlap 0.

	Shooting			Trapping		
		95% credible interval			95% credible interval	
	Mean	Lower bound	Upper bound	Mean	Lower bound	Upper bound
β_{EF}	-1.48×10^{-2}	-2.25×10^{-2}	-0.70×10^{-2}	-0.23×10^{-2}	-1.65×10^{-2}	1.21×10^{-2}
β_{SL2}	-0.02×10^{-2}	-1.02×10^{-2}	0.95×10^{-2}	0.92×10^{-2}	-1.84×10^{-2}	3.92×10^{-2}
β_D	0.79	0.69	0.89	0.46	0.22	0.74

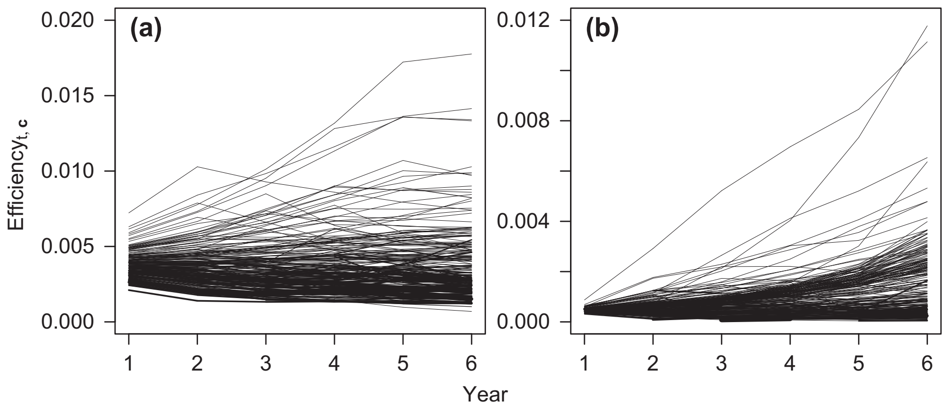

Figure 2. Effect of previous hunter effort on the change in hunting efficiency. (a) shooting; (b) trapping. The darker lines indicate high effort of previous years. Hunter effort was defined as the number of hunting days multiplied by the number of shooters or the number of days that traps were set. Efficiency$_{t,c}$ is hunting efficiency in year *t* in cell *c*.

indicates a change in the behavior of deer. To the best of my knowledge, this is the first study to show directly a change in deer behavior as a result of human behavior (previous year's effort) although such a possibility has been suggested from ethological studies or the change in vegetation after hunting (Martin and Baltzinger 2002). In Yamanashi Prefecture, shooters use dogs to flush out deer, and it is known that the percentage of hunting failure per unit effort (where hunters encounter their quarry, but the quarry escapes) increases when using dogs (Godwin et al. 2013). Thus, the increase of effort increased the number of high-vigilance deer scared by dogs, resulting in lower efficiency the following year. In contrast to shooting, efficiency for trapping was not affected by the previous year's hunting effort (Table 2, Fig. 2). Basically, trapped deer cannot escape and so a change in deer behavior as a result of the previous year's effort would rarely occur. From this point of view, trapping is superior to shooting. However, the decrease of efficiency in relation to deer abundance (β_D) was stronger with trapping than with shooting (Table 2, Fig. 3). The number of traps that can be set is limited by law in Japan, and patrolling of set traps is difficult if too many traps are set. Therefore, trapping is not suitable for taking large numbers of deer.

The decrease in efficiency of shooting by the previous year's high effort also indicates the difficulty in using catch per unit effort (CPUE) as a deer abundance index. In previous studies about deer population dynamics, CPUE was sometimes used as the index of deer abundance (Noss et al. 2005, Uno et al. 2006). However, efficiency decreased by the increase in the previous year's effort even though the change of deer abundance was considered (Fig. 2). Thus, if the managers of deer abundance only monitor CPUE as the index of deer abundance, they can overestimate the effect of hunting which will lead to the failure of population control.

These characteristics of each hunting method clarified by my analysis indicate the most effective method of managing populations of overabundant deer. Intensive hunting by gun is recommended in the initial phase because the decrease of efficiency of shooting in relation to deer abundance was not strong (Table 2, Fig. 3). After deer abundance decreases and deer vigilance increases (Table 2, Fig. 2), trapping should be adopted for a sustainable hunting efficiency (Table 2,

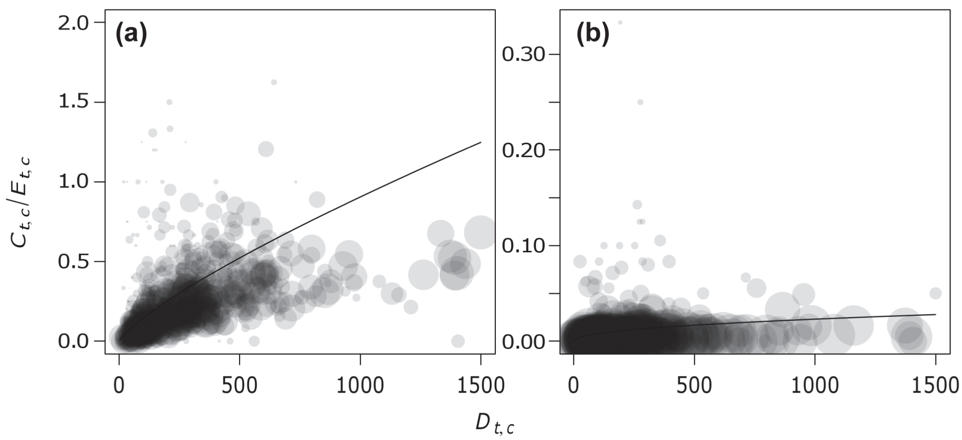

Figure 3. Relationship between deer abundance and hunting efficiency. (a) shooting, (b) trapping. The difference in color strength indicates the number of overlapping circles. The difference in symbol size indicates the difference in effort. The solid line indicates the predicted curve of efficiency from the state–space model. The shape of curve was determined by β_D that was the strength of density dependence of hunting efficiency (shape parameter; Tsuboi and Endou 2008). Zeroes of hunting efficiency indicate no success of hunting given some effort. $E_{t,c}$ is the observed hunter effort in year *t* in cell *c*; $C_{t,c}$ is the number of deer caught in year *t* in cell *c*; $D_{t,c}$ is deer abundance in year *t* in cell *c*.

Fig. 2). However, hunting efforts of shooting and trapping were low around wildlife protection area (Table 1). Then, control of nuisance deer around wildlife protection areas should be actively introduced. The combination of game hunting and nuisance control is an effective way of managing overabundant deer (Kaji et al. 2010). In conclusion, effort and efficiency were affected by landscape components, deer behavior, and hunting methods. For best results, it may be necessary to use of a variety of methods to control overabundant wildlife.

Acknowledgements – I thank the public officers and hunters in Yamanashi Prefecture for data collection.
Funding – This work was supported by Japanese Society for Promotion of Science (JSPS) KAKENHI grant number 26450221.

References

Bigelow, K. A. et al. 2002. Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). – Fish Oceanogr. 11: 143–155.
Calder, C. et al. 2003. Incorporating multiple sources of stochasticity into dynamic population models. – Ecology 84: 1395–1402.
Côté, S. D. et al. 2004. Ecological impacts of deer overabundance. – Annu. Rev. Ecol. Evol. Syst. 35: 113–147.
Davidson, M. M. and Fraser, K. W. 1991. Official hunting pattern, and trends in proportions of sika (*Cervus nippon*) and red deer (*C. elaphus scoticus*) in the Kaweka range, New Zealand, 1958–1988. – N. Zeal. J. Ecol. 15: 31–40.
Decker, D. J. and Connelly, N. A. 1989. Motivations for deer hunting: implications for antlerless deer harvest as a management tool. – Wildl. Soc. Bull. 17: 455–463.
Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. – Bayes. Anal. 1: 515–533.
Gelman, A. et al. 2004. Bayesian data analysis. – Chapman & Hall/CRC.
Godwin, C. et al. 2013. Contribution of dogs to white-tailed deer hunting success. – J. Wildl. Manage. 77: 290–296.
Haggarty, D. R. and King, J. R. 2006. CPUE as an index of relative abundance for nearshore reef fishes. – Fish. Res. 81: 89–93.
Harden, C. D. et al. 2005. Influence of exurban development on hunting opportunity, hunter distribution, and harvest efficiency of white-tailed deer. – Wildl. Soc. Bull. 33: 233–242.
Harley, S. J. et al. 2001. Is catch-per-unit-effort proportional to abundance? – Can. J. Fish. Aquatic Sci. 58: 1760–1772.
Iijima, H. and Nagaike, T. 2015a. Appropriate vegetation indices for measuring the impacts of deer on forest ecosystems. – Ecol. Ind. 48: 457–463.
Iijima, H. and Nagaike, T. 2015b. Susceptible conditions for debarking by deer in subalpine coniferous forests in central Japan. – For. Ecosyst. 2: 33.
Iijima, H. and Ueno, M. 2016. Spatial heterogeneity in the carrying capacity of sika deer in Japan. – J. Mamm. 97: 734–743.
Iijima, H. et al. 2013. Estimation of deer population dynamics using a Bayesian state-space model with multiple abundance indices. – J. Wildl. Manage. 77: 1038–1047.
Kaji, K. et al. 2010. Adaptive management of sika deer populations in Hokkaido, Japan: theory and practice. – Popul. Ecol. 52: 373–387.
Kilgo, J. C. et al. 1998. Influences of hunting on the behavior of white-tailed deer: implication for conservation of the Florida panther. – Conserv. Biol. 12: 1359–1364.
Martin, J. L. and Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. – Can. J. For. Res. 32: 1254–1264.
Nagaike, T. 2012. Effects of browsing by sika deer (*Cervus nippon*) on subalpine vegetation at Mt. Kita, central Japan. – Ecol. Res. 24: 467–473.
Nagaike, T. and Hayashi, A. 2003. Bark-stripping by sika deer (*Cervus nippon*) in *Larix kaempferi* plantations in central Japan. – For. Ecol. Manage. 175: 563–572.
Noss, A. J. et al. 2005. Hunter self-monitoring by the Isoseño-Guaraní in the Bolivian Chaco. – Biodivers. Conserv. 14: 2679–2693.
Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. – In: Proc. 3rd Int. Workshop on Distributed Statistical Computing, Vienna, Austria, pp. 20–22.
Simard, M. A. et al. 2013. Is hunting an effective tool to control overabundant deer? A test using an experimental approach. – J. Wildl. Manage. 77: 254–269.
Solberg, E. J. et al. 1999. Dynamics of a harvested moose population in a variable environment. – J. Ani. Ecol. 68: 186–204.
Takatsuki, S. 2009. Effects of sika deer on vegetation in Japan: a review. – Biol. Conserv. 142: 1922–1929.
Tsuboi, J. and Endou, S. 2008. Relationship between catch per unit effort, catchability, and abundance based on actual measurements of Salmonids in a mountain stream. – Trans. Am. Fish. Soc. 137: 496–502.
Ueno, M. et al. 2010. Culling versus density effects in management of a deer population. – J. Wildl. Manage. 74: 1472–1483.
Uno, H. et al. 2006. Evaluation of relative density indices for sika deer in eastern Hokkaido, Japan. – Ecol. Res. 21: 624–632.
Ward, P. and Myers, R. A. 2005. Inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. – Can. J. Fish. Aquatic Sci. 62: 1130–1142.