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Original Investigation

Impact of anthropogenic disturbance on the density and activity pattern of deer evaluated with respect to spatial scale-dependency

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Abstract

This study examined the influence of anthropogenic disturbance (agriculture, forestry, hunting and feral domestic dogs) on the population density and daily activity pattern of deer. We quantified the effects of land use (broad-leaved forest, mixed coniferous/broad-leaved forest, natural grassland, subalpine vegetation, forestry area, and agricultural land), along with hunting pressure, and densities of feral domestic dogs and wild macaques on deer. The effects of land use were analyzed at various spatial scales and a model selection procedure (generalized mixed model) was used to examine the effects of factors on density and daily activity pattern of deer at each spatial scale. The combinations of influential factors differed between density and daily activity pattern and changed with spatial scale. The spatial scale with the smallest Akaike's Information Criterion value was defined as the effective spatial scale for each of density and daily activity pattern. Deer density was affected positively by the percentage of area covered by broad-leaved forest, natural grassland and macaque density, and negatively by percentage of area covered by agricultural land and mixed forest at the effective spatial scales. For the daily activity pattern of deer, agricultural land, forestry area, natural grassland, subalpine vegetation and dog density reduced diurnal and increased nocturnal activity. Crepuscular activity increased with hunting pressure and subalpine vegetation, and decreased with agricultural land. Thus, daily activity pattern was sensitive to more types of anthropogenic disturbance than density. Detecting the appropriate spatial scales at which significant anthropogenic disturbance should be managed is essential for effective wildlife conservation.

Keywords: *Cervus nippon yakushimae,* Hunting pressure, Land use, Macaque, Spatial scale

Introduction

Anthropogenic disturbance influences wildlife populations worldwide (Baillie et al., 2004) altering various aspects of their ecology, which may include population density (e.g.,

Blom et al., 2004; Hockin et al., 1992; Silva-Rodriguez and Sieving, 2012), activity pattern (e.g., Kilpatrick and Lima, 1999; Presley et al., 2009), habitat use (e.g., Coulon et al., 2008; Fletcher and Hutto, 2008; Hockin et al.,1992; Markovchick-Nicholls et al., 2008), reproductive success and energy budget (Hockin et al., 1992), depending on the type and magnitude of disturbance. A single type of disturbance may affect multiple aspects of wildlife ecology (Gill et al., 2001; Kilgo et al., 1998). Anthropogenic disturbance influences wildlife in complex ways, and may have both negative and positive effects (e.g., Fletcher and Hutto, 2008; Markovchick-Nicholls et al., 2008).

Habitat transformation is a major factor affecting wild populations by altering the availability of resources, including food and shelter sites. Examples of species whose populations have increased in response to such disturbance include raccoons (*Procyon lotor*), whose density has increased in urban and suburban areas (Riley et al., 1998) following considerable habitat modifications, and some species of New World fruit bats (Phyllostomidae), which are more abundant in farmland or secondary forests than in primary forests (Willig et al., 2007). However, in most cases the effects of habitat transformation on wildlife populations are negative. For example, the density of the Japanese macaque (*Macaca fuscata*) decreases in areas with coniferous plantations (Agetsuma et al., 2015; Hill et al., 1994) and ungulates may avoid artificially exposed areas without shelter sites (Mysterud and Ostbye, 1999).

Hunting and control measures also alter the population density, activity pattern and habitat use of some wildlife species. For example, white-tailed deer (*Odocoileus virginianus*) exhibited significant shifts in core area use and daily activity pattern between the pre-hunt and hunt periods (Kilpatrick and Lima, 1999). In addition, domestic dogs (*Canis familiaris*) induce alert and flight behaviors in some wildlife species (Hockin et al., 1992; Miller et al., 2001; Sweeney et al., 1971), and may decrease the population density of certain species (Silva-Rodriguez and Sieving, 2012).

To evaluate the effects of anthropogenic disturbance on wildlife populations, we should consider the extent of the effects across space, because the magnitude of the effects of disturbance on wildlife may vary with spatial scale (Coulon et al., 2008), and then responses of wildlife to anthropogenic disturbance and natural factors may depend on spatial scales (Anderson et al., 2005). Many studies have selected the spatial scales for analysis (buffer sizes) by referring to some ecological factor, such as the range size of individual animals (e.g., Boyce et al., 2003; Fletcher and Hutto, 2008; Zweifel-Schielly et al., 2009). However, we cannot accurately identify ecologically meaningful scales a priori (Zweifel-Schielly et al., 2009). Ideally, we should use the spatial scale at which the factors show the most significant effects on wildlife populations for analysis, otherwise significant factors may not be detected. Furthermore, for wildlife conservation, we should manage significant anthropogenic disturbances at the effective spatial scale.

This study examined the effects of anthropogenic disturbance on population density and daily activity pattern of Japanese sika deer (*Cervus nippon*). Forestry areas, agricultural land, hunting pressure and feral domestic dogs were regarded as forms of anthropogenic disturbance, and we quantified the effects of these factors, as well as those of natural factors.

We analyzed the effects of land use at various spatial scales to determine the effective spatial scale. We then made three predictions concerning anthropogenic disturbance. Prediction 1: deer density will be negatively affected by forestry areas, hunting pressure and dog density, and positively affected by agricultural land. This is based on findings that the availability of natural resources for deer is much reduced in coniferous plantations (Agetsuma, 2007; Gill et al., 1996), that hunting and dogs can directly and indirectly decrease deer numbers, respectively (Kilpatrick and Lima, 1999; Silva-Rodriguez and Sieving, 2012), while agricultural crops may attract deer. Prediction 2: hunting pressure, agricultural land and forestry area will modify the daily activity pattern of deer because human activity is likely to restrict diurnal activity of the deer (Mysterud and Ostbye, 1999). As a result, diurnal activity will decrease, while crepuscular and nocturnal activity will increase under these types of disturbance. In addition, dog density also will modify the daily activity pattern of deer, because the presence of predators may influence deer activity (Kamler et al., 2007). Prediction 3: at the effective spatial scale, influential factors will differ between deer density and daily activity pattern because density and activity may be modified through different mechanisms.

Material and methods

Study area and subjects

Yakushima is a roughly circular, mountainous island (peak elevation 1936 m) of 505 km^2 located in Kagoshima Prefecture, southern Japan (30◦N, 130◦E). Approximately 13,500 residents live in more than 20 villages around the coast. Most of the settled areas are at less than 100 m above sea level (a.s.l.). Agricultural fields including orange orchards, rice paddies, vegetable fields and pastures lie below approximately 200 m a.s.l. The natural vegetation shows zonation (Fig. 1) with elevation (Ohsawa et al., 2006; Tagawa, 1994). Below approximately 800 m a.s.l. the predominant vegetation is evergreen broad-leaved forest, which was extensively logged from the 1960s to 1970s. Following logging, many areas were replanted with coniferous trees (*Cryptomeria japonica*) (Agetsuma, 2007). Mixed forests including coniferous, and evergreen and deciduous broad-leaved trees dominate the area from approximately 800 to 1700 m a.s.l. In the subalpine region (above1800 m a.s.l.), vegetation is mainly comprised of rhododendron shrubs (*Rhododendron yakushimanum*) and dwarf bamboo (*Pseudosasa owatarii*) grasslands.

The annual precipitation ranges from 2500 to 8700 mm across the island depending on location (Environment Agency, 1984). Along the coast, the annual mean temperature is approximately 20 ℃, which corresponds to the margin between subtropical and warm temperate zones (Tagawa, 1994). However, above 1000 m a.s.l., the climate is much cooler, with snowfall in winter and a mean annual temperature of approximately 10 ℃ (Ohsawa et al., 2006).

The subject of this study was a subspecies of the Japanese sika deer (*Cervus nippon yakushimae*) that is endemic to Yakushima and Kuchinoerabujima, an island of 36 km^2 located 12 km northwest of Yakushima. *C. n. yakushimae* has the smallest body size of all subspecies of Japanese sika deer (Izawa et al., 1996). Habitat modification by logging and

replacement with coniferous plantations caused the deer population to decline greatly from the 1960s to1970s. However, it has been recovering since the 1990s (Agetsuma, 2007) and the population size was estimated to be around 17,000 in 2008 (Koda et al., 2010). The deer inhabit most regions of the island, ranging from the coast to the subalpine zone. However, population density varies considerably with location (Agetsuma, 2007; Koda et al., 2011).

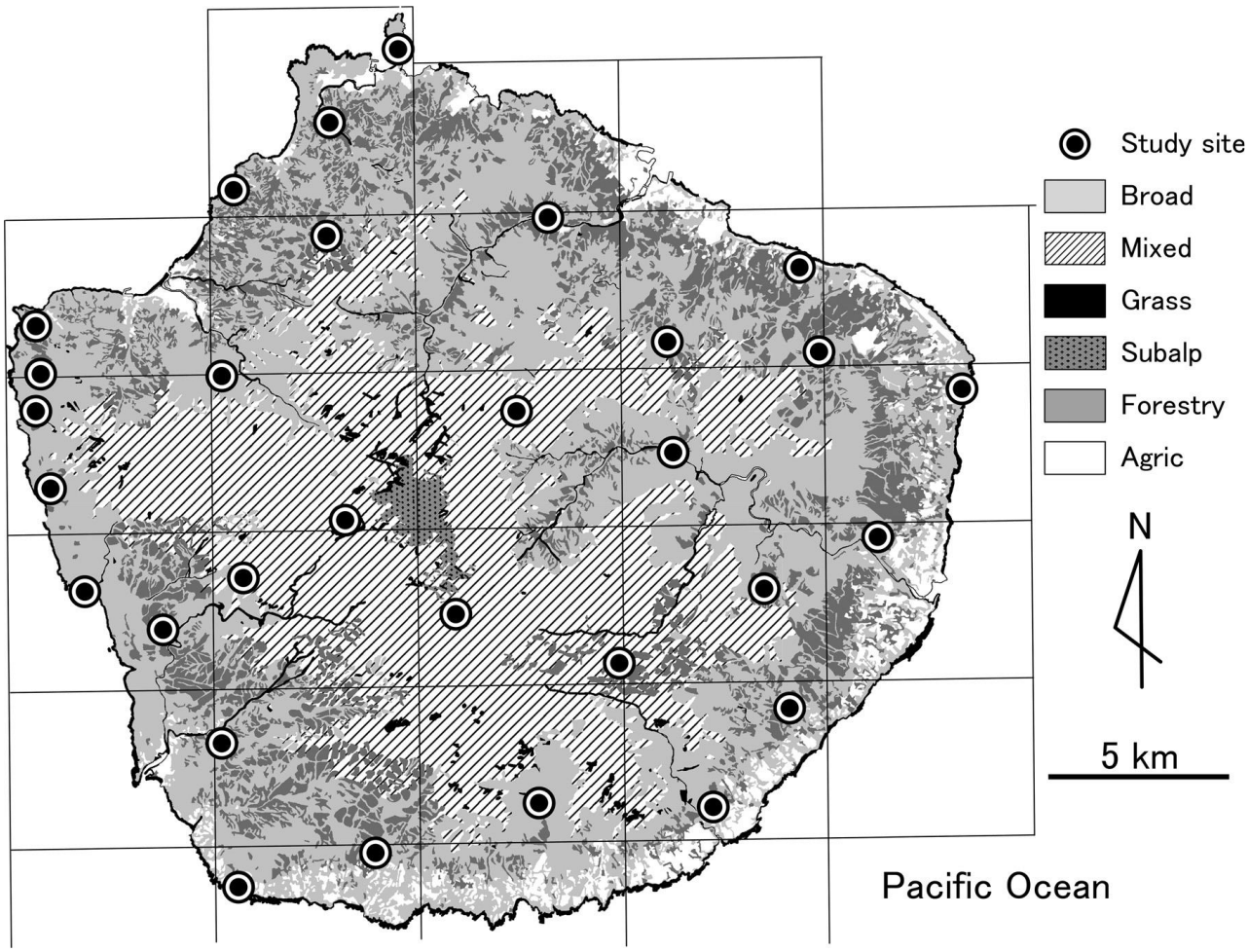

Fig. 1. Land use and study sites on the island of Yakushima. Symbols for study sites indicate gravity points of analyzed camera locations at the sites. Broad, broad-leaved forest, Mixed, mixed coniferous/broad-leaved forest; Grass, natural grassland; Subalp, subalpine vegetation; Forestry, forestry area; Agric, agricultural land. Natural grassland occurred in very narrow strips near the coast, rivers and cliffs. The number of hunted deer was summarized using cells of about 4.6 km × 6 km shown on this map.

Leaves, fruits and seeds of woody plants make up the typical staple diet of the deer (Takatsuki, 1990). These foods are obtained largely from the forest litter (Agetsuma et al., 2011). The deer also feed on food dropped from trees by Japanese macaques (*Macaca fuscata yakui*) that also inhabit most regions of the island. Food obtained in this way accounts for 7% of time spent feeding by deer in broad-leaved forest (Agetsuma et al., 2011). Because the foods dropped by the macaques from the trees are relatively high quality foods (fruits and seeds) compared with other foods (Agetsuma et al., 2011), the presence of macaques attracts deer in

the forest (Koda, 2012). A previous study showed that the density of macaques was positively affected by broad-leaved forest area and negatively by forestry area within a radius of 400 m (Agetsuma et al., 2015).

The mean annual range size of an individual of deer in a broad-leaved forest, expressed as a 90 % fixed kernel, is 12 ha (7–17 ha, n = 4) for adult females and 36 ha (4–78 ha, n = 4) for adult males (Agetsuma et al., 2005). The deer have very stable ranges which last for years, however, some adult males occasionally emigrate 4–8 km from their former ranges regardless of the season (Agetsuma et al., 2005; Agetsuma et al., unpublished data).

The only wild carnivores in Yakushima are a small weasel (*Mustela itatsi sho*), which is native, and the raccoon dog (*Nyctereutes procyonoides*), which was introduced to the island around1990 (Tsujino and Agetsuma-Yanagihara, 2006). So the deer have no natural predators, although feral domestic dogs (*C. familiaris*) also inhabit the island, and local people and researchers (Tsujino and Agetsuma-Yanagihara, 2006) have observed predation of deer by both solitary individuals and groups of feral dogs.

Although deer damage crops and planted trees, the amount of damage appears to have stabilized since 1990 (Agetsuma, 2007). Deer hunting has been traditionally conducted in Yakushima, and in addition, pest control of deer started in 1978 (Agetsuma, 2007). Since 1998, hunting and controlling have only been permitted around agricultural lands. Therefore, the hunting pressure is high in agricultural areas and declines with distance from them. By 2009, local people were culling around 250–500 deer for hunting and pest control every year (data from Kagoshima Prefecture).

Density of wildlife and activity pattern

Field surveys were conducted during periods when there is no snow cover (from November to December 2007, from February to June and from November to December 2008) at 30 sites across the island that were chosen to represent various types of land use and topographies (Fig. 1). The mean minimum interval between sites was 2.7 km (range: 0.5–4.5 km). We surveyed the density and daily activity pattern of deer, macaques and dogs using automatic cameras with infrared sensors that could detect animal movement, as used in a previous study (Okabe and Agetsuma, 2007). At each site, 11–15 cameras (Yoyshot, Umezawa Musen Denki Co. Ltd., Sapporo, Japan) were set arbitrarily at ~100 m intervals for approximately one month. We recorded the locations of these cameras using Global Positioning System receivers (GPSmap 60CSx, Garmin Ltd., Olathe, KS, USA). We loaded each camera with a 36-exposure film and fixed it ~1.4 m above the ground. The camera's flash was set in poor lighting conditions and the lens was pointed downward at an angle of ~30° toward the ground surface (Okabe and Agetsuma, 2007). Each camera could photograph animals entering an area of approximately 15 m^2. The date and time were superimposed on each photograph. Some cameras were damaged by wind and rain, but data were obtained from 8 to 15 cameras at each site (403 cameras in total). The mean area of the minimum convex polygons surrounding the camera locations at each site was 21 ha.

We identified the species of photographed animals and counted them. Where there were more than one image of the same individual (as identified by sex, body size, fur color,

antler shape and other physical characteristics) taken within 1 h by the same camera, only one was counted to prevent repetitive photographing of the same individual during a single visit to the camera. We then counted the number of deer, macaques and dogs in the photographs. Because the cameras did not always function for the complete duration of the study, either as a result of malfunction or completion of the film roll, we determined the number of hours that each camera was functioning from date and time stamps on the photographs, and the operating condition of the camera when collected.

The rate at which animals are photographed by automatic cameras can be used as an index of the population density (e.g., Rovero and Marshall, 2009). The photographic rate for each camera was calculated by dividing the number of photographed animals by the number of days (24 h) for which the camera operated. Then the density index of each species at each site was obtained by averaging the photographic rates for cameras at each site. The density index of macaques and dogs at each site was assigned to each camera location within the same site (Table 1).

We assessed the daily activity pattern of animals by counting the number of animals photographed by each camera during daytime (08:00–16:00), nighttime (20:00–04:00), and crepuscular periods(04:00–08:00 and 16:00–20:00).

Land use

To analyze land use on Yakushima, we used data from the 6th and 7th National Surveys of the Natural Environment conducted in 2004 by the Biodiversity Center of Japan, Ministry of the Environment. The data were generated by analyzing aerial photographs and provided in shape files that could be manipulated in a Geographic Information System (GIS). The spatial resolution was approximately 20 m, which was sufficient for this study. We classified the land use of the island into six types (Fig. 1): (1) broad-leaved forest; (2) mixed coniferous/broad-leaved forest; (3) natural grass-land (mainly riverside, coastal and cliff vegetation); (4) subalpine vegetation (dwarf bamboo and rhododendron shrubs); (5) forestry area (coniferous plantations and logged areas); (6) agricultural land(orchards, rice paddies, vegetable fields, pastures, previously-used arable land and human residential areas).

Buffer zones were created within a radius of 200 m of each camera using ArcGIS (ver. 9.3, ESRI, Redlands, CA, USA). Then we calculated the percentage of total land area covered by each land use type within each buffer zone. We repeated this procedure, increasing the radius of the buffer at 50-m intervals from 250 m up to 1500 m. These buffers were then used to determine the spatial scale at which the deer density and daily activity pattern were most affected. The mean terrestrial area of buffer zones with 200 m radius was 12.4 ha, which is approximately equal to the mean annual range of a female deer.

Some climatic factors such as temperature, precipitation and wind strength may affect deer density and activity patterns. In Yakushima, variations in elevation influence both climatic factors (i.e. higher elevations tend to have lower temperatures and greater amounts of precipitation), as well as vegetation zonation (Ohsawa et al., 2006; Tagawa, 1994). Therefore, in this study, we considered that climatic factors could be reflected in the differing types of natural vegetation in the land use types (1–4), described above.

Hunting pressure

Kagoshima Prefecture summarized the number of deer hunted from 2006 to 2008 using a systematic grid system, with cells of about 4.6 km × 6 km (Fig. 1). Because the cells included water bodies, total land area varied between cells. Therefore, we estimated hunting pressure for each cell by dividing the number of deer hunted in each cell by the total land area. For each study site hunting pressure was determined by that of the cell in which the site was located, and the same hunting pressure value was attributed to every camera at that site. When a study site included parts of two adjacent cells, we calculated the hunting pressure as the mean hunting pressure of the two cells. Hunting pressure was only evaluated at one spatial scale, and the spatial resolution was lower than that of land use.

Statistical analyses

Statistical analyses were performed using the R statistical computing environment, version 3.2.0 (R Core Team, 2015). To quantify the factors affecting deer density and daily activity pattern (diurnal, crepuscular and nocturnal activities) we used generalized linear mixed models (GLMM). For multivariate analyses, including GLMM, multicollinearity among explanatory variables needs to be resolved in advance. Because high multicollinearity among the nine explanatory variables was expected, we created two explanatory variable groups each including eight of the nine variables (broad-leaved forest and mixed forest were each excluded from one group; see Table 1). We checked the variance inflation factors (VIF) and correlation coefficients (r) between all variables in the two variable groups at each spatial scale. From scales of 200 m to 1500 m, VIF remained less than 4.0 and absolute values of r were less than 0.7 within each variable group. As the degree of the multicollinearity was acceptable (Dormann et al., 2013; Sergent et al., 1995) using the two variable groups up to the 1500-m scale, we focused on these spatial scales for further analyses. The 1500 m radius buffer from each camera was quite large (on average 616 ha excluding areas of sea and rivers) in relation to the annual range size of most deer.

GLMMs were created using the “glmmadmb” function in the glmmADMB package of R (Skaug et al., 2014). For the analysis of deer density, we set the number of deer photographed by each camera as a response variable, the two groups of variables alternately as explanatory variables, and the log-transformed number of days the camera operated as an offset term at each spatial scale (Table 1). As data were collected from multiple cameras at each site, there was a risk of pseudoreplication (Hurlbert, 1984). To control for this the study site at which the camera was located was set as a random effect term on the intercept in the GLMM. For the analysis of daily activity pattern, we set the number of deer photographed during each time window as a response variable (Table 1). Then we set the two groups of variables alternately as explanatory variables, the log-transformed total number of deer photographed by each camera as an offset term, and the study site as a random effect term on the intercept. We assumed that the response variables follow a negative binomial distribution with a log link function for GLMM.

Table 1

Information of response variables, explanatory variables, offset terms and a random effect term for the negative binomial generalized linear mixed models.

Ecological trait	Response variable	Explanatory variable			N	Offset	Random effect
		Land use and vegetation	Densities of macaque and dog	Hunting risk			
Deer density	No. deer photographed by each camera	1) Rates of areas of agricultural land, 2) natural grassland, 3) subalpine vegetation, 4) forestry area, and 5-1) broad-leaved forest OR 5-2) mixed forest in each buffer area around each camera location	6) Macaque density and 7) dog density of each site	8) hunting pressure of each site	403	No. days each camera operating	Site
Diurnal activity	No. deer photographed between 8:00 and 16:00 by each camera				348	No. deer photographed by each camera	
Crepuscular activity	No. deer photographed between 4:00 and 8:00, and 16:00 and 20:00 by each camera				348	No. deer photographed by each camera	
Nocturnal activity	No. deer photographed between 20:00 and 4:00 by each camera				348	No. deer photographed by each camera	

First, we made 384 models with all possible combinations of variables, including the null model, at each spatial scale for deer density and daily activity pattern, and calculated Akaike's Information Criterion (AIC) of the models. Then a 95 % confidence set of models was identified by cumulatively summing the Akaike weights from highest to lowest until ≥ 0.95 (Burnham and Anderson, 2002) using the "model.sel" and "model.avg" functions in the MuMIn package of R (Barton, 2015). We calculated confidence intervals for each model-averaged coefficient of variable using unconditional standard errors of the coefficient. We excluded variables having 85 % confidence intervals of the coefficients including zero as uninformative variables (Arnold, 2010). Next, we selected models among possible combinations of variables without the uninformative variables at each spatial scale. We selected variables included in the models with ΔAIC < 2 at each spatial scale. To test the significance of the model with the smallest AIC value at each spatial scale, a likelihood ratio test to the null model was performed using the "anova" function in the glmmADMB package.

We assumed that the smallest AIC value found among the models at each spatial scale represented the effectiveness of the scale for explaining deer density and activity pattern. We identified the points at which the AIC values dipped as the effective spatial scales. At the effective spatial scales, we selected models having ΔAIC < 2.

Results

Deer density

The mean number of cameras used for wildlife density estimation was 13.4 per site (total 403 cameras) and the mean operating period of each camera was 503.7 h (20.9 days). We obtained 3322 images of deer, 1046 of macaques and 65 of dogs for density estimations. The mean deer density varied widely between sites and the maximum was 19.5 times the minimum. Even between the two closest sites, which were 0.5 km apart, there was a difference of 9.5 times in mean deer density.

For all spatial scales, the models with the smallest AIC were highly significantly different from the null model (likelihood ratio test, for all spatial scales, $p < 0.0001$). In total, six factors were selected across the scales for deer density (Fig. 2A). Combinations of the selected factors changed with spatial scale, although macaque density was consistently selected. The AIC value was smallest at the 250-m scale, and a dip of AIC was also observed at the 600-m scale, so these were identified as the effective spatial scales for deer density. At both of these scales, broad-leaved forest and macaque density were positive factors and agricultural land was a negative factor affecting deer density (Table 2). In addition, mixed coniferous/broad-leaved forest was a negative factor at a scale of 250 m and natural grassland was a positive factor at a scale of 600 m. The mean buffer areas at the spatial scales of 250 m and 600 m, excluding sea and rivers, were 19.2 ha and 105.8 ha, respectively.

Among the models without macaque density in the explanatory variables, the smallest AIC model also appeared at the 250-m scale (AIC: 2550.6, likelihood ratio test to the null model; $p < 0.001$) and included agricultural land as a negative factor and broad-leaved forest as a positive factor affecting deer density. However, the model had a significantly lower likelihood than the model including macaque density (likelihood ratio test: $p < 0.001$).

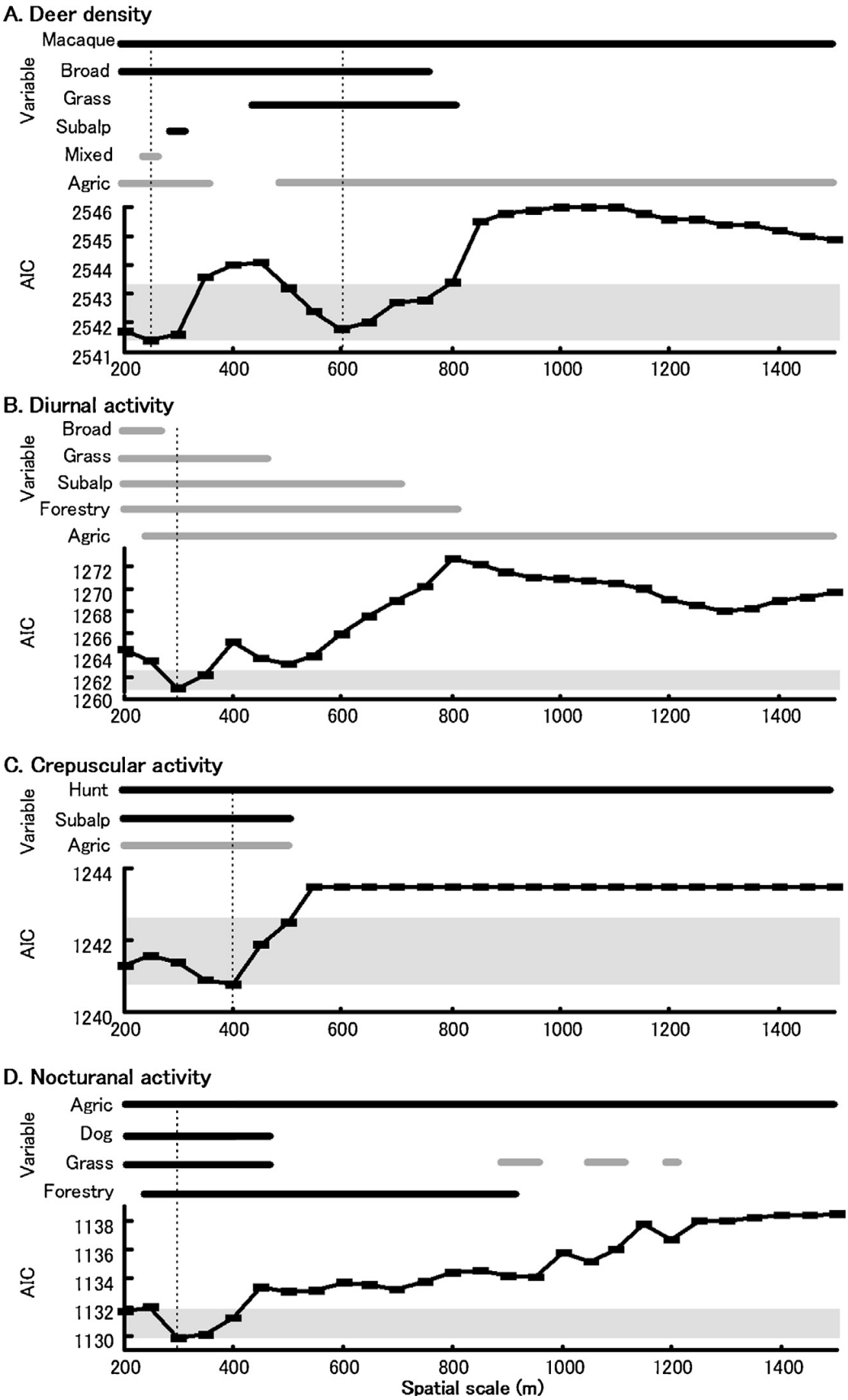

Fig. 2. Selected variables and the smallest Akaike's Information Criterion (AIC) value among models at each spatial scale for deer density (A), diurnal activity (B), crepuscular activity (C) and nocturnal activity (D). Abbreviations of land use types are the same as Fig. 1. Macaque, macaque density; Dog, dog density; Hunt, hunting pressure; black and gray horizontal lines above the graphs indicate positive and negative factors, respectively; a dotted vertical line indicates the effective spatial scale; the gray area indicates the difference of AIC < 2.0 from the smallest AIC model across the scales.

Table 2

The effective spatial scales, the selected models and the coefficients of variables at the effective spatial scales.

Ecological trait	The effective spatial scale (m)	Buffer area[a] (ha)	Selected model					AIC	ΔAIC[b]	Weight[c]
Deer density	250	19.2	-1.64***	-1.99 Agric*	+0.62 Broad†		+2.81 Macaque***	2541.4	-	0.42
			-1.40***	-2.20 Agric*			+3.52 Macaque***	2542.8	1.46	0.20
			-1.26***	-2.38 Agric*		-0.44 Mixed	+3.14 Macaque***	2543.0	1.66	0.18
	600	105.8	-1.67***	-2.69 Agric*	+0.61 Broad†	+5.39 Grass*	+2.52 Macaque***	2541.8	-	0.36
			-1.43***	-2.80 Agric*		+5.58 Grass*	+3.10 Macaque***	2542.6	0.84	0.24
Diurnal activity	300	27.4	-0.87***	-3.12 Agric**	-0.87 Forestry**	-3.64 Grass**	-8.10 Subalp*	1261.0	-	0.76
Crepuscular activity	400	48.1	-0.96***	-0.87 Agric†	+2.49 Subalp†	+4.20 Hunt***		1240.8	-	0.41
			-0.95***	-0.89 Agric†		+3.99 Hunt***		1241.3	0.52	0.32
			-0.97***		+2.59 Subalp†	+3.97 Hunt***		1242.8	1.99	0.15
Nocturnal activity	300	27.4	-1.94***	+2.94 Agric***	+0.66 Forestry	+3.79 Grass**	+8.60 Dog	1129.9	-	0.33
			-1.91***	+3.00 Agric***	+0.83 Forestry*	+3.76 Grass**		1130.0	0.18	0.30
			-1.82***	+2.80 Agric**		+3.69 Grass**	+11.64 Dog*	1130.4	0.55	0.25

Abbreviations of variables are the same as Fig. 2. † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. [a] The mean buffer area excluding sea and rivers at the spatial scale. [b] ΔAIC within the spatial scale. [c] Akaike weight within the spatial scale.

Daily activity patterns

We obtained 3264 images of deer with time stamps from 348 cameras for analysis of daily activity patterns. Of these, 35 %, 42 %and 23 % of deer were photographed during daytime (08:00–16:00), crepuscular periods (4:00–8:00 and 16:00–20:00) and nighttime (20:00–04:00), respectively. However, percentages of operating hours of the cameras in these time windows were almost the same (daytime, 33.4 ± 1.2 % (mean ± SD); crepuscular periods 33.3 ± 1.5 % and nighttime, 33.3 ± 0.7 %). Photographs of dogs were taken by 31cameras, 72 % of which were taken during the daytime.

For all spatial scales of activities in the three time windows (diurnal, nocturnal and crepuscular), the smallest AIC models were significantly different from the null models

(likelihood ratio test, for all spatial scales for all activities; $p < 0.01$). Five factors were selected for diurnal activity, but the combinations of the factors shifted with spatial scale (Fig. 2B). The effective spatial scale (i.e. the one with the smallest AIC value) was found at 300 m. Agricultural land, forestry area, natural grassland and subalpine vegetation were negative factors for diurnal activity at the effective spatial scale (Table 2). For crepuscular activity, hunting pressure was constantly selected as a positive factor, although two other factors were selected up to the 500-m scale (Fig. 2C). At the effective spatial scale of 400 m, hunting pressure and subalpine vegetation were positive, and agricultural land was a negative factor (Table 2). Four factors were selected for nocturnal activity, and among them agricultural land was consistently selected (Fig. 2D). The effective spatial scale was 300 m at which agricultural land, forestry area, natural grassland and dog density had positive effects (Table 2).

Discussion

We predicted that forestry area, hunting pressure and dog density would have negative effects, and agricultural land a positive effect, on deer density (Prediction 1). In fact, our results indicated that forestry area did not have a significant negative effect on deer density (Table 2). However, forestry area may have an indirect negative effect by displacing areas of broad-leaved forest, which had a positive effect on deer density. Contrary to Prediction 1, agricultural land had a negative effect on deer density. Crop raiding by deer has occurred in Yakushima (Agetsuma, 2007), which demonstrates that agricultural lands provide food resources for deer. However, agricultural land tends to have high levels of human activity and a lack of cover. In addition, the local government and individual farmers have been constructing fences around agricultural land to prevent intrusion by deer. These factors may combine to reduce deer density around agricultural land. For hunting pressure, we could not detect a negative effect on deer density. Deer do not always move away from areas where hunting pressure has increased (Kufeld et al., 1988). The low spatial resolution of hunting pressure data in this study may have restricted the detection of a possible negative effect on deer density. However, the effect of hunting was clearly demonstrated in an increase in crepuscular activity. Although some studies have reported negative effects of dogs on ungulate populations (Corti et al., 2010; Silva-Rodriguez and Sieving, 2012), we did not find a negative effect on deer density in Yakushima.

Among natural factors, deer density was affected positively by broad-leaved forest and macaque density, and negatively by mixed forest (Table 2). Deer on this island mainly depend on leaves, fruits and seeds of broad-leaved plants for food (Takatsuki, 1990), which they obtain largely from the forest litter (Agetsuma et al., 2011). In Yakushima, productivity of litter fall and fruits in broad-leaved forests are higher than those in mixed forests or coniferous plantations (Aiba et al., 2007; Hanya and Aiba, 2010; Hanya et al., 2005). Thus, broad-leaved forest should primarily support the deer population in this island. Macaques will supply relatively higher quality food from the tree canopies for deer (Agetsuma et al., 2011). Deer tend to gather where macaques emit food calls (Koda, 2012) to obtain macaque-supplied

foods efficiently. The positive effect of macaque density on deer density might also be influenced by the fact that both species tend to select similar habitats, as the macaques show a preference for broad-leaved forest where their food resources are abundant (Agetsuma et al., 2015).

The mean buffer areas at the effective spatial scales for daily activity pattern (Table 2) roughly corresponded to the mean annual range size of an individual deer. In accordance with Prediction 2, the daily activity pattern of deer changed with anthropogenic disturbance. Agricultural land, forestry area and dog density shifted daily activity pattern of deer from diurnal to nocturnal (Table 2). The greater human disturbance and visibility in agricultural land and forestry area may restrict diurnal activity of deer (Mysterud and Ostbye, 1999). In addition, deer also seemed to increase activity during the nighttime when the activity of dogs was relatively low in the study area. Hunting pressure increased deer activity in the crepuscular period. Hunting pressure restricts diurnal activity of deer (Kilgo et al., 1998; Nixon et al., 1991), which may lead them to increase foraging activity just before daylight, and just after daylight to satisfy their hunger quickly.

Although agricultural land was selected as a significant factor for both deer density and daily activity pattern, other types of anthropogenic disturbance (forestry area, hunting pressure and dog density) only affected the daily activity pattern of deer (Table 2), as per Prediction 3. Thus, deer behavior appeared to be more sensitive to various types of disturbance than the population density.

Managing a broad range of habitats and controlling the various kinds of anthropogenic disturbances would promote wildlife conservation. However, in reality, human economic activities and deficiencies in conservation funds make this level of control impossible to achieve. Therefore, we are forced to select types of disturbances and limit the areas that can be managed efficiently and effectively to reduce the impact on wildlife. The types and magnitudes of factors influencing wildlife ecology change with spatial scales (Boyce et al., 2003) as demonstrating in this study (Fig. 2). Thus, it is important to detect the most effective spatial scale to show the greatest effects on wildlife (Agetsuma et al., 2015). We must analyze various factors at appropriate spatial scales to prevent overlooking significant types of anthropogenic disturbances that should be managed.

The protection of natural vegetation (broad-leaved forest and natural grassland) and the restriction of human land use (agricultural land) may be essential for maintaining the deer population size in the study area. The effective spatial scale for deer density suggested that a buffer width of 600 m will be required for deer habitat management; 750 m is desirable where the AIC difference from the smallest AIC model across the scales was < 2.0 (Fig. 2A). The mean buffer areas at 750-m scale excluding sea and rivers (162.9 ha) was five to 14 times wider than the mean annual range size of an individual deer. In this study, we could not examine anthropogenic effects on deer ecology at scales greater than1500 m. Additional studies will be needed on larger spatial scales to complete an evaluation of these effects. Macaques were also positively associated with deer density, which suggests that conservation of sympatric species may benefit the conservation of a target species through interspecies interaction.

Even if a type of anthropogenic disturbance does not have a significant effect on population density, the effect may emerge as the modification of behaviors (Gill et al., 2001) as found in this study. Thus, although most studies to date have focused on only a single aspect of wildlife ecology, such as population density or habitat use (e.g., Anderson et al., 2005; Coulon et al., 2008; Markovchick-Nicholls et al., 2008), detecting the effects on multiple aspects of the ecology is essential.

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