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Seasonal variation of activity pattern in sika deer (*Cervus nippon*) as assessed by camera trap survey

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Abstract. Ungulate populations such as deer and wild boars have been expanding in range and increasing in number throughout many areas of the world. Regulation of these overabundant populations is urgently needed. For an effective culling program addressing these overabundant populations, it is essential to have information on the activity pattern of animals. To determine the factors affecting seasonality of daily activity pattern in sika deer, we studied deer activity through camera traps on Nakanoshima Island, Lake Toya in Hokkaido, Japan, where human disturbance is low. We estimated activity pattern during four time periods (dawn, dusk, day, and night), and evaluated the effects of weather conditions on activity pattern (camera trap rate) for each period. Deer activity at dawn, dusk and night showed clear seasonal patterns, with peaks in September, while the activity pattern during the day was constant in all seasons. The activity at dawn and dusk tended to be higher than that at day during July–October and July–November, respectively. Although the activity of sika deer may be influenced by weather condition, there was no seasonal consistency. Our study reveals that human disturbance might decrease diurnal activity and increase nocturnal activity.

Key words: daily activity pattern, human disturbance, seasonality, weather conditions.

Ungulate populations such as deer and wild boar have been expanding in range and increasing in number in many areas of the world, which has caused serious damage to agriculture (Kaji et al. 2010) and forestry (Côté et al. 2004), as well as their own habitats. In Japan, as in other regions, there is urgent need to regulate these overabundant ungulate populations. Currently, the major method of population control is culling animals. However, for these programs to be effective, seasonal change in daily activity pattern of ungulates in overabundant populations should be considered.

It is known that ungulate activity patterns are influenced by human disturbance such as recreation (George and Crooks 2006; Sibbald et al. 2011) and hunting (Kilgo et al. 1998; Ikeda 2001; Di Bitetti et al. 2008; Kamei et al. 2010; Karns et al. 2012). Probably owing to habituation to humans, it is difficult to find clear and consistent patterns of how deer avoid areas of human recreation (George and Crooks 2006; Sibbald et al. 2011). On the other hand, hunting might have a stronger effect on deer behavior. White-tailed deer on the Osceola National Forest in Florida respond to human hunting by decreasing diurnal activity, and increasing nocturnal activity (Kilgo et al. 1998), while at Chesapeake Farms in Virginia, they decrease in overall activity from the pre-hunt to hunt period during Maryland's 2-week firearms season (Karns et al. 2012). Studies on the activity pattern of sika deer as a result of hunting also differ in their findings; Kamei

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et al. (2010) reported that a GPS-collared female deer showed diurnal activity in pastures during the non-hunting season; on the other hand, a camera trap survey by Takahashi et al. (2012) revealed that sika deer were predominantly active at dusk and night in summer, and suggested that deer activity might be influenced by human activity rather than hunting. In addition, recent camera trap studies examining the relationship between human disturbance (hunting and settlement) and activity patterns of both sika deer (van Doormaal et al. 2015) and wild boar (Ohashi et al. 2013; van Doormaal et al. 2015) in central Japan revealed that both species were most active at night during the non-hunting season and hunting activities significantly reduced their overall activity patterns. In the non-hunting season, nocturnal activity of both sika deer and wild boar increased with decreasing distance to settlements, suggesting that they avoid humans and human-dominated areas by being nocturnal. These studies have shown that ungulate activity pattern is influenced by human disturbance, which causes complex and inconsistent activity patterns. Because sika deer and wild boar are primarily nocturnal, night hunting appear to be effective for culling (van Doormaal et al. 2015). Nonetheless, the effectiveness of night hunting may vary depending upon localities and seasons according to the variation in activity patterns, which are partly influenced by human disturbance. To design effective culling program for overabundant deer in Japan, we need more detailed information on the seasonality of daily activity pattern and what factors influence it.

The activity patterns of ruminants respond to environmental conditions such as weather conditions (Hofmann 1989). For example, Bourgoin et al. (2008, 2011) suggested that mouflon might modify their behavior, physiological states (e.g., reproductive status, hormonal state, and body reserves), and thermoregulations in response to seasonal weather conditions. In addition, Beier and McCullough (1990) showed that activity of white-tailed deer decreased at both higher and lower temperatures. Further, Mysterud and Ostbye (1999) indicated that activity periods of ungulates shifted to more favorable conditions. However, these studies evaluating the relationship between activity pattern and weather conditions were conducted using radio telemetry or GPS collars, which means that surveys occurred at designated times before the activity (e.g., 30-min, 1-hr, 3-hr intervals). Camera trap surveys, on the other hand, can record events continuously throughout the day, and obtain date and time of deer photographed. Therefore, we used a camera traps to collect detailed information about weather conditions and seasonality of daily activity pattern in sika deer.

To clarify the influence of human disturbance and weather condition on the seasonality of daily activity pattern in sika deer, we monitored animals using camera traps, and evaluated the seasonality of daily activity pattern (camera trap rate) on Nakanoshima Island in the Shikotsu-Toya National Park in Hokkaido, Japan, where human disturbance is low. We predicted that (i) sika deer showed higher diurnal activity than nocturnal one under low human disturbance, and (ii) seasonality of daily activity pattern was influenced by weather conditions.

Materials and methods

Study area

The camera trap survey was conducted on Nakanoshima Island in Lake Toya (42°36'N, 140°51'E), Shikotsu-Toya National Park, Hokkaido, Japan. As the island is located about 4 km offshore, emigration and immigration of sika deer is negligible. There are no predators and hunting is prohibited on the island. Nakanoshima Island is composed of one main island and two adjacent islets (total area is 524.6 ha) and rises from 80 m to 460 m above sea level. In the winter of 1983–1984, the number of sika deer on the island peaked at 273 deer (52.0 deer/km^2; Kaji et al. 1988) and has since exhibited repeated irruptions and crashes (Kaji et al. 2006, 2009). Current estimates of population size obtained by drive counts were 236 deer in March 2011 (44.5 deer/km^2) and 277 deer in March 2012 (52.8 deer/km^2). From 2010 to 2011, the mean annual precipitation in the study area was 1,075 mm (Japan Meteorological Agency 2010, 2011), and the mean annual temperature was 10.2°C (range of –1.3°C in January to 24.0°C in August; Toya Lake Station, Field Science Center for Northern Biosphere, Hokkaido University). Vegetation on the island comprises deciduous broad-leaved trees (91.8%), coniferous plantations (6.3%), and open grassland (1.6%). In the deciduous forest, the major canopy species are Japanese oak (*Quercus crispula*), castor-aralia (*Kalopanax pictus*), Japanese bigleaf magnolia (*Magnolia obovata*), painted maple (*Acer mono*), and Japanese linden (*Tilia japonica*) (Kaji et al. 1991).

Camera-trap survey

We placed 12 camera traps (Moultrie Game Spy I-40 Infrared Flash Game Cameras; Cabelas Inc., U.S.A.) throughout the main island (Fig. 1). For herd composition

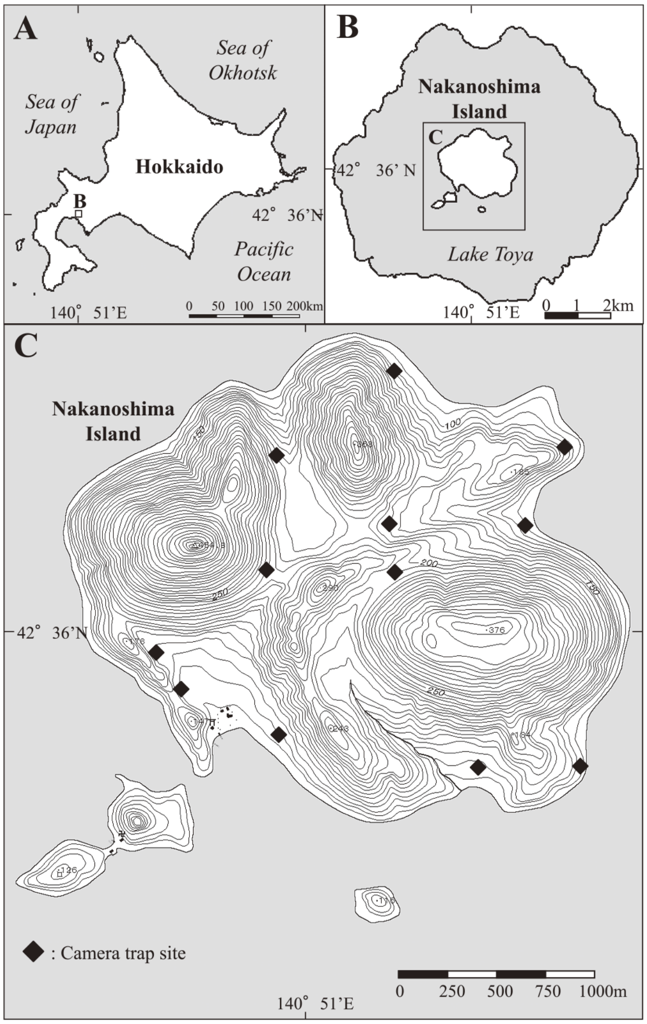

Fig. 1. Map of Nakanoshima Island, Lake Toya, Hokkaido, showing 12 camera trap sites (modified from Ikeda 2013).

count of sika deer, we set cameras along two fixed routes, covering representative habitats in this study area, which successfully monitored sex and age ratios reflecting life history by season (Kaji et al. 2005; Ikeda et al. 2013). Cameras were strapped to trees approximately 1 m above the ground and oriented parallel to sika deer trails. They were set to take three photos per 13 sec with a 5-min interval between consecutive groups of photos. The cameras were active from August 2010 to November 2011, excluding between December 2010 and April 2011 to avoid the risk of equipment malfunction when sika deer were concentrated in their wintering areas. During October 2009 and July 2010, five adult females were equipped with GPS telemetry in this study area, which revealed no seasonal differences in each individual home range size (e.g., foraging activity) during spring–autumn (C. Takeda, unpublished data). Thus, we thought that daily activity pattern in these seasons would not be influenced by seasonal home range size differences.

All photos taken by the cameras recorded date and time, and we estimated daily activity pattern for four time periods: dawn (1 hr before and after sunrise), dusk (1 hr before and after sunset), the day (from 1 hr after sunrise to 1 hr before sunset), and night (from 1 hr after sunset to 1 hr before sunrise), according to Pepin et al. (2006). We estimated daily activity pattern as the total number of deer photographed per hour for each period and the mean monthly activity pattern by pooling daily activity pattern.

Data analysis

To determine the influence of weather conditions on seasonality of daily activity pattern of sika deer, we used daily weather data (temperature, precipitation, and wind speed) and camera trap data (the total number of deer photographed for each day and camera) and analyzed each month. To analyze the influence of weather conditions on activity pattern of sika deer, we used generalized linear mixed model with a Poisson distribution. We set camera trap data as the response variable and weather condition data and time period as explanatory variables. The location of each camera was included as a random intercept. Further, we included the length of each time period (hours) as an offset term. Then, all possible models were compared using Akaike's information criterion (AIC) to select a minimum adequate model. Alternative models with indistinguishable AIC values (ΔAIC < 2) were considered to be competing models (Burnham and Anderson 2002). Records of daily weather conditions were obtained from the Toya Lake Station, Field Science Center for Northern Biosphere, Hokkaido University. Daily mean temperature, daily total precipitation, and wind speed at 10 a.m. were included in the weather condition data. All analyses were conducted in R version 3.1.0 (R Core Team 2014) with the lme4 package (Bates et al. 2014) and the MuMIn package (Barton 2014).

Results

We obtained a total of 4,046 photos of 4,809 deer in 4,032 camera trap-days (12 cameras × 336 days). The number of deer photographed was 2,164 (45.0%) during the day, 1,325 (27.6%) at night, 626 (13.0%) at dawn and 694 (14.4%) at dusk. Activity pattern (number of photographed deer per hour) at dawn, dusk and night peaked in September, while activity pattern in the day was stable

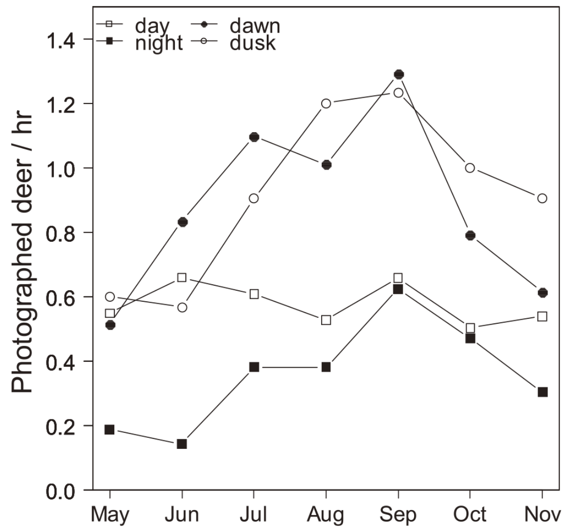

Fig. 2. Number of deer photographed per hour at dawn (1 hr before and after sunrise), dusk (1 hr before and after sunset), the day (from 1 hr after sunrise to 1 hr before sunset), and night (from 1 hr after sunset to 1 hr before sunrise) in Nakanoshima Island, Japan, during May–November. Filled circles, open circles, open squares, and filled squares show dawn, dusk, the day, and night, respectively.

across all months (Fig. 2).

For time period, parameter estimates of the day were not included in Table 1, because we set the day as counterparts of other periods (dawn, dusk, and night). The positive values indicate that these periods had a positive influence on increasing number of photographs in comparison to the day periods. Therefore, we found that fewer deer were photographed at night than the day, except for during September and October (Table 1). On the other hand, the number of deer photographed at dawn and dusk tended to be higher than in the day during July–October and July–November, respectively. However, there were no differences among number of deer photographed in the day, dawn, and dusk during May–June (Table 1).

Temperature showed negative effects on the number of deer photographed during September–October. On the other hand, precipitation was positively correlated with the number of deer photographed in May. Further, wind speed also showed positive effects on the number of deer photographed in July and October (Table 1).

Discussion

Seasonality of daily activity pattern in sika deer

The activity patterns of ruminants are related to feeding rhythm, which is characterized by morphology of the stomach and physiology of digestion, and responds to environmental conditions (Hofmann 1989). This rhythm of ruminants mainly includes feeding, ruminating, and resting behaviors, and a daily peak in activity at dawn and dusk has been widely reported for deer (white-tailed deer, Beier and McCullough 1990; elk, Green and Bear 1990; moose, Gillingham and Klein 1992).

We found that activity at dawn and dusk tended to be higher than that at day and night from July. On the other hand, our study indicated that deer activity was lowest at night, except for during September and October, when the activity pattern was nearly the same as in the day. In Białowieża National Park, Eastern Poland, activity patterns of red deer tend to be more diurnal in areas with restricted tourism and where hunting had been prohibited for several years (Kamler et al. 2007). Under low human disturbance, red deer activity peaks throughout the day and night in summer and autumn (Kamler et al. 2007). Our results in September and October are consistent with this finding. Further, sika deer in Nara Park, where hunting and logging is prohibited and deer are artificially fed by tourists and local people, display diurnal activity as a result of human contact (Torii and Tatsuzawa 2009). In our study of a wild population with low human disturbance, it is therefore noteworthy that daytime activity pattern was stable in all months and predominantly diurnal.

Relationship between activity pattern of sika deer and weather conditions

We found that activity of sika deer was influenced by weather conditions; however, there was no seasonal consistency in the relationship between weather and activity pattern. This might be due to the relatively mild weather conditions in the study area compared with those in previous studies.

Summer activity levels of mouflon are influenced by climatic conditions (high temperature, low wind speed, and little precipitation) and demonstrated that the negative influence of heat on activity resulted in decreasing overall activity and the switch towards nocturnal activity in summer (Bourgoin et al. 2008). In this study, sika deer tended to decrease activity pattern with increasing temperature in September and October. Similarly, temperature and relative humidity is known to negatively influence white-tailed deer activity in autumn (Beier and McCullough 1990).

For black-tailed deer, heat loss due to rain is greater than heat or cold stress (Parker 1988). Further, precipitation may decrease habitat use of ungulates (Mysterud and Ostbye 1999). However, our result found that the number

Table 1. Selected models (ΔAIC < 2) and estimates (± *SE*) of each explanatory variable for the relationship between total number of deer photographed and four time periods (dawn = 1 hr before and 1 hr after sunrise, dusk = 1 hr before and 1 hr after sunset, day = from 1 hr after sunrise to 1 hr before sunset and night = from 1 hr after sunset to 1 hr before sunrise) or weather conditions (temperature, precipitation and wind speed) using generalized linear mixed model with a Poisson distribution. Parameter estimates of day period were not shown included in table, because we set day period as counterparts of other periods (dawn, dusk and night period). Daily mean temperature, daily total precipitation and wind speed at 10 a.m. were used as weather condition data. Data are from 12 camera traps on Nakanoshima Island, Hokkaido, Japan.

Season	Model structure	Intercept	1-1. Dawn	1-2. Dusk	1-3. Night	2. Temperature	3. Precipitation	4. Wind speed	*df*	AIC	ΔAIC
May	13	–3.243 ± 0.159†	–0.081 ± 0.169	0.037 ± 0.160	–1.115 ± 0.148†		0.008 ± 0.004*		6	1954.8	0
	134	–3.200 ± 0.161†	–0.081 ± 0.169	0.037 ± 0.160	–1.115 ± 0.148†		0.009 ± 0.004*	–0.043 ± 0.035	7	1955.3	0.52
	123	–3.108 ± 0.228†	–0.081 ± 0.169	0.037 ± 0.160	–1.115 ± 0.148†	–0.009 ± 0.010	0.009 ± 0.004*		7	1956.1	1.34
	1234	–3.018 ± 0.235†	–0.081 ± 0.169	0.037 ± 0.160	–1.115 ± 0.148†	–0.011 ± 0.011	0.009 ± 0.004*	–0.049 ± 0.036	8	1956.2	1.46
June	1	–3.071 ± 0.169†	0.267 ± 0.154	–0.148 ± 0.184	–1.498 ± 0.195†				5	1543.7	0
	13	–3.091 ± 0.169†	0.267 ± 0.154	–0.148 ± 0.184	–1.498 ± 0.195†		0.004 ± 0.004		6	1544.7	1.00
	12	–2.869 ± 0.283†	0.267 ± 0.154	–0.148 ± 0.184	–1.498 ± 0.195†	–0.013 ± 0.014			6	1544.9	1.17
	14	–3.079 ± 0.176†	0.267 ± 0.154	–0.148 ± 0.184	–1.498 ± 0.195†			0.007 ± 0.040	6	1545.7	1.97
July	14	–3.256 ± 0.178†	0.546 ± 0.141†	0.428 ± 0.148**	–0.360 ± 0.123**			0.073 ± 0.034*	6	1927.9	0
	124	–2.990 ± 0.296†	0.546 ± 0.141†	0.428 ± 0.148**	–0.361 ± 0.123**	–0.016 ± 0.014		0.066 ± 0.035	7	1928.5	0.63
	134	–3.248 ± 0.179†	0.546 ± 0.141†	0.428 ± 0.148**	–0.360 ± 0.123**		–0.003 ± 0.005	0.074 ± 0.034*	7	1929.6	1.71
August	1	–3.454 ± 0.243†	0.634 ± 0.112†	0.850 ± 0.104†	–0.283 ± 0.094**				5	3239.9	0
	14	–3.418 ± 0.246†	0.634 ± 0.112†	0.850 ± 0.104†	–0.283 ± 0.094**			–0.034 ± 0.027	6	3240.4	0.46
	13	–3.447 ± 0.244†	0.634 ± 0.112†	0.850 ± 0.104†	–0.283 ± 0.094**		–0.002 ± 0.003		6	3241.7	1.73
September	123	–2.550 ± 0.271†	0.631 ± 0.100†	0.661 ± 0.099†	–0.038 ± 0.076	–0.028 ± 0.009**	–0.004 ± 0.003		7	4094.7	0
	12	–2.558 ± 0.271†	0.632 ± 0.100†	0.661 ± 0.099†	–0.038 ± 0.076	–0.029 ± 0.009**			6	4094.8	0.08
	124	–2.517 ± 0.273†	0.632 ± 0.100†	0.661 ± 0.099†	–0.038 ± 0.076	–0.029 ± 0.010**		–0.033 ± 0.027	7	4095.3	0.57
	1234	–2.524 ± 0.273†	0.631 ± 0.100†	0.661 ± 0.099†	–0.038 ± 0.076	–0.029 ± 0.010**	–0.003 ± 0.003	–0.021 ± 0.028	8	4096.2	1.42
October	124	–2.932 ± 0.290†	0.477 ± 0.119†	0.694 ± 0.110†	–0.043 ± 0.083	–0.051 ± 0.010†		0.094 ± 0.019†	7	3730.0	0
	1234	–2.934 ± 0.290†	0.477 ± 0.119†	0.694 ± 0.110†	–0.043 ± 0.083	–0.051 ± 0.010†	0.004 ± 0.004	0.093 ± 0.019†	8	3731.0	1.09
November	12	–3.398 ± 0.249†	0.167 ± 0.129	0.375 ± 0.119**	–0.432 ± 0.088†	0.015 ± 0.009			6	3297.2	0
	1	–3.289 ± 0.239†	0.166 ± 0.129	0.374 ± 0.119**	–0.434 ± 0.088†				5	3297.6	0.41
	123	–3.394 ± 0.251†	0.167 ± 0.129	0.375 ± 0.119**	–0.432 ± 0.088†	0.014 ± 0.009	–0.001 ± 0.010		7	3299.2	1.98
	124	–3.404 ± 0.253†	0.167 ± 0.129	0.375 ± 0.119**	–0.432 ± 0.088†	0.015 ± 0.009		0.003 ± 0.024	7	3299.2	1.99

*: $P < 0.05$, **: $P < 0.01$, †: $P < 0.001$.

of sika deer photographed seemed to increase as a result of precipitation in May.

White-tailed deer in winter shift to closed forests and swamps to escape cold wind, while the effect of temperature on deer varies with wind speed during spring–autumn (Beier and McCullough 1990). Their result indicated that activity of white-tailed deer increased under strong wind speed when temperatures were warm (Beier and McCullough 1990). Further, activity pattern of mouflon is strongly influenced by temperature and wind speed during summer (Bourgoin et al. 2011). In this study, we also found that wind speed positively influenced sika deer activity pattern in July (though there was no effect of temperature), and that deer were more active during strong winds in October.

Conclusions

Our study conducted in the Nakanoshima Island characterized by low human disturbance revealed that the activity pattern of sika deer peaked at dawn and dusk, and activity pattern in the day was stable in all months and was predominantly diurnal. This finding strongly suggests that human disturbance, including hunting, might decrease diurnal activity and increase nocturnal activity. Further study is required to determine the factors affecting seasonality of daily activity pattern depending on the level of human disturbance.

Although there was no seasonal consistency in the relationship between weather condition and activity pattern of deer, we nevertheless found that activity tended to be influenced by weather. This might be due to the relatively moderate weather conditions in the study area and the short duration of the research. Further studies are required to elucidate the relationship between weather conditions and activity pattern of sika deer.

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