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Human disturbances increase vigilance levels in sika deer (*Cervus nippon*): A preliminary observation by camera-trapping

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ABSTRACT. Many deer species exhibit typical vigilance behavior as an anti-predator response to human disturbances. However, vigilance behavior in sika deer (*Cervus nippon*) has not previously been assessed. I explored whether human disturbances increase vigilance in sika deer by comparing their behaviors in two areas with different levels of human activity using camera-trapping techniques. The deer spent a significantly higher proportion of time exhibiting vigilance behavior in the site with higher levels of human activity, supporting my initial hypothesis. In addition, their vigilance increased in winter, possibly due to hunting by humans.

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KEY WORDS: hunting, landscape of fear, non-lethal effect, predation risk, ungulates.

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Антропогенное воздействие повышает уровень бдительности у пятнистого оленя (*Cervus nippon*): предварительные наблюдения с помощью фотоловушек

Х. Цунода

РЕЗЮМЕ. При беспокойстве со стороны человека, многие виды оленей проявляют типичное тревожное поведение, сходное с реакцией на хищников. Тревожное поведение пятнистого оленя (*Cervus nippon*) ранее не изучалось. Используя фотоловушки я исследовал, повышает ли беспокойство со стороны человека бдительность у пятнистых оленей, сравнивая их поведение в двух районах с различными уровнями человеческой активности. Олени проводили значительно больше времени в бдительном состоянии на участке с более высоким уровнем человеческой активности, что подтверждает первоначальную гипотезу. Кроме того, бдительность оленей зимой была выше, возможно, из-за сезонной охоты.

КЛЮЧЕВЫЕ СЛОВА: охота, ландшафт страха, нелетальный эффект, угроза хищника, копытные.

Introduction

Predators numerically affect prey populations through direct predation but also have indirect, non-lethal effects that lead to physiological, morphological, and/or behavioral responses in their prey (Lima, 1998). Both direct (lethal) and indirect (non-lethal) processes play a key role in shaping ecosystems via trophic cascades (Ripple *et al*., 2014). Through predator–prey coevolution, prey species have developed anti-predator behaviors, such as avoiding risky spaces that are often used by predators (Bongi *et al.*, 2008; Jarnemo & Wikenros, 2014) or increasing vigilance so that they can detect approaches or attacks by predators earlier (Lima & Bednekoff, 1999). However, these behaviors can also have a cost for prey animals, decreasing their food intake or increasing glucocorticoid stress responses and, thus, ultimately reducing their fecundity, growth, and/or survival (Lima, 1998; Creel *et al*., 2007; Creel, 2018).

Many species of deer (Cervidae, Cetartiodactyla) show typical vigilance behaviors as an anti-predator response to both large carnivores and human disturbances. For example, deer that inhabit the core area of a predator's home range or an area in which humans hunt exhibit greater vigilance than animals outside these areas (Lung & Childress, 2007; Winnie & Creel, 2007; Jayakody *et al*., 2008; Ciuti *et al*., 2012; Bonnot *et al*., 2015; Kuijper *et al*., 2015). Furthermore, deer also increase their vigilance at times of day or in seasons with higher risks of predation or hunting (Lung & Childress, 2007; Winnie & Creel, 2007; Pecorella *et al*., 2016).

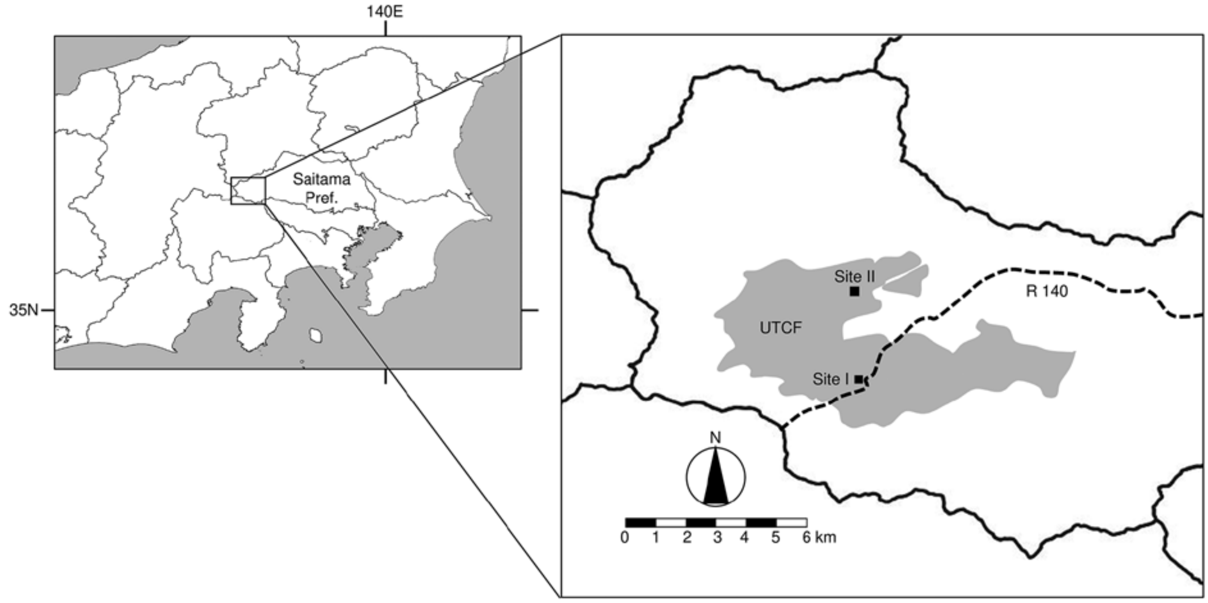

Fig. 1. Location of the study area, the University of Tokyo Chichibu Forest (UTCF).

In Japan, populations of sika deer (*Cervus nippon*) have increased since the 1980s, resulting in an increase and expansion of their ecological impacts (e.g., floral diversity losses) and conflicts with humans (e.g., crop raiding, forestry damage, and traffic collisions) (Takatsuki, 2009; Kaji *et al*., 2010; Sakurai, 2019; Tsunoda & Enari, 2020). Consequently, deer population control is currently a major task for wildlife management, with both the national and local governments reinforcing the regulated hunting and culling of deer. This has resulted in the total number of deer captured increasing over the past few decades (Kaji *et al*., 2010; Tsunoda & Enari, 2020). Previous studies have demonstrated that human disturbances (including hunting and culling) increased flight frequency by sika deer (Borkowski, 2001), alter their habitat uses (Kamei *et al*., 2010) and shift their diel activities from crepuscular to nocturnal (Doormaal *et al*., 2015; Ikeda *et al*., 2019). However, to date, there has been little detailed assessments of changes in the vigilance of the deer species in response to human disturbances (but see Borkowski, 2001).

Here, I explored whether human disturbances increase vigilance behavior in sika deer by observing the amounts of time deer spent exhibiting vigilance and foraging behaviors in two areas with different levels of human activity using camera-trapping techniques. I hypothesized that deer inhibiting the area with high levels of human activity would spend a greater proportion of time exhibiting vigilance behavior and a lower proportion of time foraging than those inhabiting the area with low levels of human activity, according to the "predation risk allocation hypothesis" (Lima & Bednekoff, 1999).

Materials and methods

Study area

This study was conducted in montane mixed forests in the University of Tokyo Chichibu Forest (hereafter UTCF; ca. 58.12 km^2), Saitama, Japan (Fig. 1). The UTCF is a research forest with 530–1980 m above sea level (a.s.l.), covered with both primeval/secondary deciduous (86% with dominated by *Fagus crenata*, *F. japonica*, *Fraxinus spaethiana* or *Pterocarya rhoifolia*) and artificial coniferous forests (13% with dominated by *Chamaecyparis obtuse*, *Larix kaempferi* or *Cryptomeria japonica*). Understory vegetations were degraded mostly and scarce annually in the UTCF owing to intense grazing pressures by sika deer since 2000s (Sakio *et al*., 2013), as exceptions in 30 deer-exclusive fences (30 × 30 m, 1.8 m high) located in the natural forests (see Appendix 1). The climate is a mountainous cooler-temperate zone with mean temperatures of ca. 0°C in January and 22.5°C in August, respectively. The annual precipitation is 1543 mm and the snow cover ranges typically 20–30 cm (Tochimoto Meteorological Observatory in the UTCF located at 740 m a.s.l.).

Two camera-trapping sites (I and II; ca. 150 m^2 each) were established ca. 3.6 km apart in areas with different levels of human disturbance and were separated by a deep, steep valley (Fig. 1). Site I (35°54′ N, 138°49′ E, 1050 m a.s.l.) was close to a small visitor center (named "Wasabi-zawa") and National Route 140, contained footpaths that were open to the public (e.g., tourists, hikers, and anglers), and was used by researchers and students from UTCF. While hunting was prohibited at this site, it is traditionally conducted in the surrounding forests from November 15 to February 15; indeed,

Table 1. Differences in human activities between the two camera trapping sites. CTD — a total number of videos taken by three camera-traps per 100 camera-trapping days.

		Spring–summer	Summer–autumn	Winter	Whole period
Site I	*n*	87	94	52	233
	Obs./100 CTD	11.2	7.5	3.3	6.5
Site II	*n*	7	13	12	32
	Obs./100 CTD	0.8	1.5	1.0	1.1

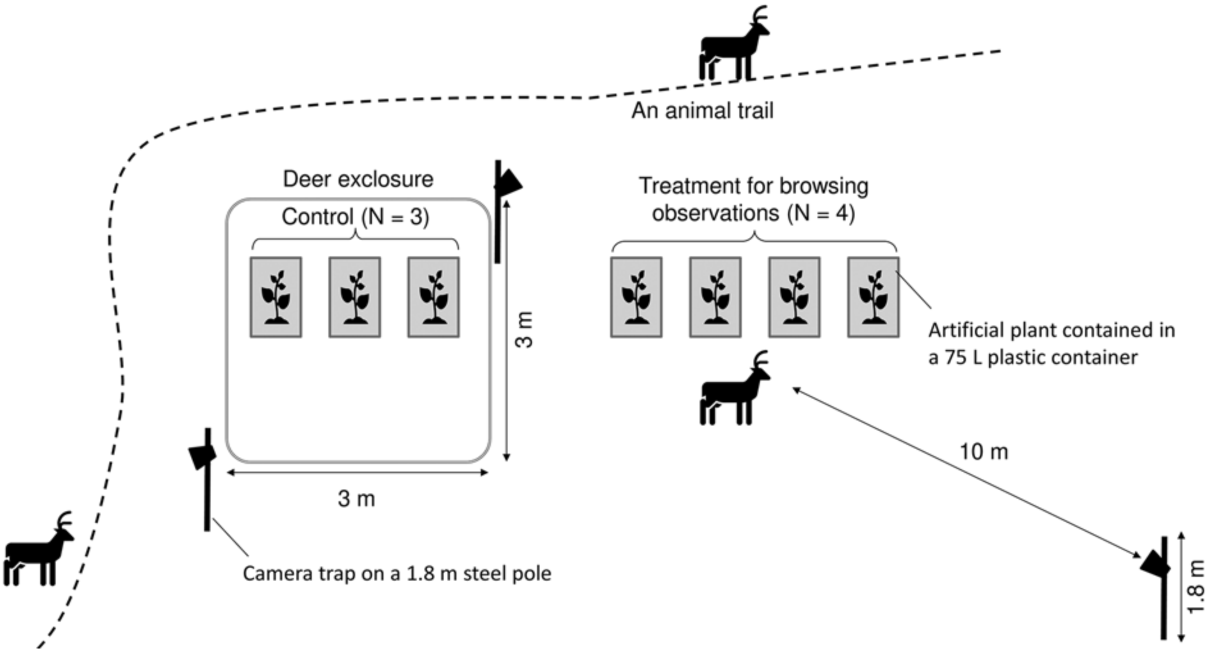

Fig. 2. Experimental design to observe deer-browsing effects on artificial plantings at camera-trapping site.

hunters and hunting dogs were observed passing in front of the camera traps. Site II (35°56′ N, 138°48′ E, 1148 m a.s.l.) had prohibited public access, only being accessible via a forestry road for academic and educational purposes with permission from UTCF. Although hunting was also restricted in this area, the culling of sika deer has been conducted for a few days each year (from February 16 to March 20) since 2014 as part of the prefectural population control program (UTCF, personal communication). Observations of humans by camera-trapping survey indicated that human activities were higher at Site I than at Site II (Tab. 1). In both areas, the hunting/culling methods typically involve drive hunting with dogs and beaters. Mean hunting efforts ranged 12.6–18.5 hunters/day during the studied periods (personal communication from Environmental Division of Saitama Prefecture).

Field survey

Three passive infrared cameras (TrophyCAM HD, Bushnell Inc., Kansas, USA) were installed at each site (Fig. 2). These cameras had a trigger speed of 0.6 s and were programmed to take 60-s videos with a 5-min delay. Each camera was mounted ca. 1.5 m above ground level on a 1.8-m-long steel pole and was angled to include the whole body of a sika deer in a frame. Artificial plantings of the evergreen shrub *Aucuba japonica* (0.8–1.5 m height) and a small deer exclosure (3 × 3 m, 1.8 m high) were also installed at each site to investigate deer browsing effects on vegetation as a separate research topic (Appendix 2). Each plant was placed in a 75-L plastic container (external dimensions: 60 × 40 × 30 cm) filled with horticultural soil, and four planted containers were put outside the exclosure as a treatment while three were placed inside the exclosure as a control (Appendix 2). The artificial plantings were replaced with other trees in August each year. One camera was set ca. 10 m from the plantings to observe deer browsing behavior, while the remaining two cameras were set pointing in different directions along an animal trail (Fig. 2).

Camera trapping was conducted between July 20, 2016 and March 10, 2020, with battery changes and memory card replacements occurring every 1–3 months. However, there were total of 401 non-trapped days at Site I and 555 non-trapped days at Site II, owing to camera failures or battery depletions. Moreover, Site II was not accessible after October 12, 2019 owing to degradation of a forestry road by a super typhoon; therefore, no data were available for this site after October 7, 2019 when I finally maintained the cameras there. All videos

Table 2. Total numbers of camera trapping days (CTD) and videos captured sika deer (*n*), and mean ± 95% confidence interval of total video lengths of deer captured using for behavioral analysis.

n		Spring–summer		Summer–autumn		Winter	
		Video length (s)	*n*	Video length (s)	*n*	Video length (s)	
Site I	CTD	776	–	1250	–	1560	–
	Female	89	54.3 ± 2.5	96	51.0 ± 2.5	130	49.7 ± 2.4
	Male	13	47.1 ± 8.8	55	49.1 ± 3.8	36	47.8 ± 4.7
Site II	CTD	885	–	850	–	1232	–
	Female	173	50.8 ± 2.0	181	48.1 ± 2.2	146	53.7 ± 2.0
	Male	55	49.4 ± 3.8	58	47.8 ± 4.0	205	51.4 ± 1.9

Table 3. Descriptions of the behavioral categories used for sika deer (*Cervus nippon*) observed during the camera-trapping survey.

Behavioral category	Description
«Foraging»	Grazing or searching for food on the ground while standing/walking slowly with the head positioned below the shoulders, or browsing on an artificial planting with the head positioned at/above the shoulders.
«Vigilance»	Scanning the surroundings with the head positioned above the shoulders, sometimes with ear movement.
«Mobile»	Walking or galloping with the head positioned at/above the shoulders.
«Others»	Lying down with rumination, sleeping, or grooming or scratching own body.
«Conspecific interaction»	Grooming, sniffing, paying attention to, or chasing other individual(s), or fighting (males only).

were reviewed to determine whether sika deer were detected, and the date, time, individual numbers, and sexes (male, female, or unknown) of all animals detected were recorded.

Behavioral analysis

In total, 1034 videos of sika deer were collected over 3586 trapping days at Site I and 1952 videos were collected over 2967 trapping days at Site II. These videos were screened for use in the behavioral analyses using the following criteria: 1) the whole body of a sika deer was recorded in a frame; 2) the animal was ca. 5–15 m from the camera; 3) the sex of the animal could be identified; and 4) the animal was recorded for 20 s or longer (i.e., for the judgement of just passing in front of the camera or staying at the observed venue). The fourth criteria (i.e., on video length) enabled me to estimate deer behavior precisely, as discussed in a previous study using camera-trapping (Kuijper *et al.*, 2015). When an animal was observed in two video sequences less than 6 min apart (i.e., a second video was recorded soon after the 5-min delay from the first video by the same camera or within the 5-min delay period by another camera), they were considered a single event by the same individual. When several animals were observed in a video frame, the behaviors of each individual were recorded. This screening resulted in a total of 419 videos of 291 independent events at Site I and 819 videos of 571 independent events at Site II.

The observed deer behaviors were separated into five categories, following Winnie & Creel (2007) and Jayakody *et al.* (2008): "foraging", "vigilance", "mobile", "others" and "conspecific interaction" (Tab. 3). The total time deer were observed exhibiting "vigilance" behavior or "foraging" in each video was then recorded.

Statistical analysis

The site differences in the lengths of vigilance and foraging behaviors in sika deer were assessed using zero-inflated generalized linear mixed models (Zi-GLMMs), as these models have robust statistical power for datasets that include many zero values (Zuur *et al.*, 2010). The Zi-GLMMs were two step procedures that include the first discriminating step for zero-inflations with Bernoulli distribution and logit link function and, then, the second count-process modelling with negative binomial distributions and log link functions (Zuur *et al.*, 2010; Brooks *et al.*, 2017). The total amount of time exhibiting vigilance (or foraging) behavior in a video was included as the response variable, using the total length of time the animal was recorded as an offset term. The camera-trapping sites (I/II), sex (male/female), season and their interaction terms were included as fixed effects, while the identification code for observation events and the studied year was included as a random effect. The study period was divided into three seasons that corresponded to the life history of sika deer (Nagata, 2015) and seasonal changes in human activities: spring to early summer (April 1 to July 31), late summer to fall (August 1 to November 14), and winter (November 15 to March 31; Tab. 1). The winter covered both hunting (from 15 Nov. to 15 Feb.) and culling (from 16 Feb. to 20 Mar.)

seasons in the study area (see "Study area"). Although the reproductive status (presence of fawns) and group size also affect the anti-predator behavior of cervids (e.g., Altendorf *et al.*, 2001; Borkowski, 2001; Lung & Childress, 2007), the available data for the analyses were mostly captured only one or two individuals in the frames, being difficult to observe the group sizes or animals out of the video frames correctly. Owing to this methodological limitation, the social status was not included in the statistical models. These analyses were performed using the "glmmTMB" package (Brooks *et al.*, 2017) with R ver. 3.5.1 (R Core Team, 2018). Then, to adopt models with higher explanatory power, I performed a multi-model inference approach based on Akaike"s information criterion (AIC) using all possible combinations of all the explanatory variables and their interactions (Burnham & Anderson, 2002; Burnham *et al.*, 2011). I selected the models with more than 10% values of the AIC weights of the best model (i.e., a model with the lowest AIC score) for model averaging approach to estimate coefficients of variables (Burnham and Anderson 2002). For these methods, I used the "dredge" function in the "MuMIn" package for R (Barton, 2015).

Results

From the Zi-GLMM analysis with multi-model inference on the proportion of vigilance behavior, all of the six top-ranked candidate models included site, season and site*season interaction term as common explanatory variables (Tab. 4). The proportion of time spent exhibiting vigilance behavior was significantly higher at Site I than at Site II (Wald test, $p<0.001$; Fig. 3A) and significantly increased in late summer–fall ($p<0.001$) and winter ($p<0.001$; Tab. 5). Furthermore, the

Table 4. The top-ranked candidate models (>10% AIC weights of the best model) on the results of a zero-inflated generalized linear mixed model analysis on the proportions of time sika deer (*Cervus nippon*) spent exhibiting vigilant behaviors (+, variable included in a model). Shaded rows represent top-ranked candidates for multi-model inference approach.

Rank	Explanatory variables (fixed effects)							*d.f.*	AIC	ΔAIC	Weight
	Site	Sex	Season	Site*Sex	Site*Season	Sex*Season	Site*Sex*Season				
1	+	+	+		+			11	6275.1	0.00	0.365
2	+		+		+			10	6276.2	1.13	0.207
3	+	+	+	+	+			12	6276.6	1.49	0.173
4	+	+	+	+	+	+	+	16	6276.9	1.84	0.146
5	+	+	+		+	+		13	6278.3	3.25	0.072
6	+	+	+	+	+	+		14	6279.8	4.76	0.034
7	+	+	+					9	6286.7	11.66	0.001
8	+		+					8	6287.0	11.91	0.001
9	+	+	+	+				10	6287.3	12.25	0.001
10	+	+	+			+		11	6290.7	15.60	0
11	+	+	+	+		+		12	6291.3	16.21	0
12	+	+						7	6291.4	16.34	0
13	+	+		+				8	6292.1	16.98	0
14	+							6	6292.9	17.85	0
15			+					7	6296.2	21.17	0
16		+	+					8	6297.4	22.32	0
17		+	+			+		10	6300.4	25.36	0
18								5	6303.0	27.96	0
19		+						6	6303.5	28.45	0
20	+	+	+		+			11	6407.8	132.69	0
21	+	+	+	+	+			12	6409.6	134.55	0
22	+		+		+			10	6410.2	135.12	0
23	+	+	+	+	+	+	+	16	6410.2	135.15	0
24	+	+	+		+	+		13	6410.3	135.24	0
25	+	+	+	+	+	+		14	6412.3	137.18	0
26	+	+	+					9	6419.4	144.37	0
27	+		+					8	6420.1	144.99	0
28	+	+	+	+				10	6420.9	145.79	0
29	+	+	+			+		11	6422.5	147.46	0
30			+					7	6422.8	147.68	0
31		+	+					8	6423.4	148.32	0
32	+	+						7	6424.0	148.91	0
33	+	+	+	+		+		12	6424.1	149.00	0
34	+	+		+				8	6425.5	150.45	0
35		+	+			+		10	6426.1	151.04	0
36	+							6	6427.1	151.98	0
37		+						6	6429.4	154.28	0
38								5	6430.7	155.66	0

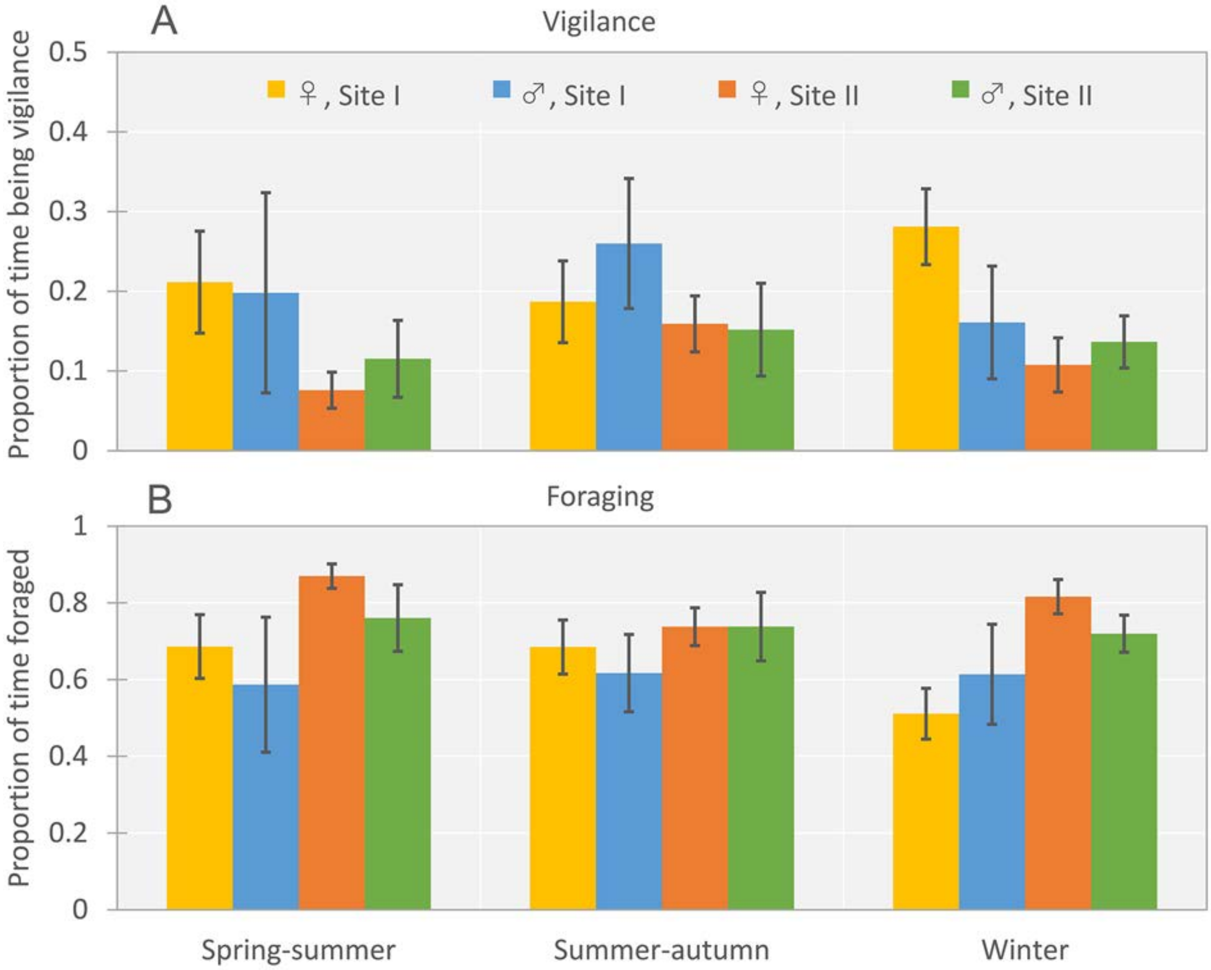

Fig. 3. Seasonal changes in the proportions of time sika deer (*Cervus nippon*) spent exhibiting (A) vigilance and (B) foraging behaviors at two camera-trapping sites with different levels of human disturbance (Site I > Site II; see Tab. 2. for details)

Table 5. Results of the zero-inflated generalized linear mixed model with model averaging in the top-ranked candidate models (>10% AIC weights of the best model) on the proportions of time sika deer (*Cervus nippon*) spent exhibiting vigilant behavior.

Variable	β	*s.e.*	Wald test *p*
(Intercept)	−1.879	0.120	<0.001
(Effect of zero inflation)	−0.123	0.061	0.044
Site[a]	0.871	0.181	<0.001
Sex[b]	0.233	0.177	0.190
Season (sum.-aut.)	0.623	0.147	<0.001
Season (win.)	0.535	0.144	<0.001
Site * Sex	−0.373	0.413	0.367
Site * Season (sum.-aut.)	−0.862	0.248	<0.001
Site * Season (win.)	−0.631	0.220	0.004
Sex * Season (sum.-aut.)	−0.513	0.302	0.090
Sex * Season (win.)	−0.210	0.280	0.452
Site * Sex * Season (sum.-aut.)	1.094	0.513	0.033
Site * Sex * Season (win.)	0.161	0.517	0.755

[a] A positive coefficient (β) indicates that the value was higher at Site I than at Site II, while a negative value indicates the opposite

[b] A positive coefficient (β) indicates that the value was higher in males than in females, while a negative value indicates the opposite

Table 6. The top-ranked candidate models (>10% AIC weights of the best model) on the results of a zero-inflated generalized linear mixed model analysis on the proportions of time sika deer (*Cervus nippon*) spent exhibiting foraging behaviors (+, variable included in a model). Shaded rows represent top-ranked candidates for multi-model inference approach.

Rank	Explanatory variables (fixed effects)							*d.f.*	AIC	ΔAIC	Weight
	Site	Sex	Season	Site*Sex	Site*-Season	Sex*-Season	Site*Sex*-Season				
1	+	+	+			+		11	10278.4	0.00	0.190
2	+	+	+					9	10278.9	0.51	0.147
3	+	+						7	10279.2	0.84	0.125
4	+	+	+		+			11	10279.4	1.01	0.115
5	+	+	+		+	+		13	10279.7	1.36	0.096
6	+	+	+	+		+		12	10280.3	1.94	0.072
7	+	+	+	+				10	10280.8	2.47	0.055
8	+	+		+				8	10281.2	2.83	0.046
9	+	+	+	+	+			12	10281.4	3.00	0.042
10	+	+	+	+	+	+		14	10281.7	3.36	0.035
11	+	+	+	+	+	+	+	16	10282.2	3.87	0.027
12	+		+					8	10282.4	4.08	0.025
13	+		+		+			10	10283.6	5.27	0.014
14	+							6	10286.7	8.30	0.003
15		+	+			+		10	10287.1	8.77	0.002
16		+						6	10287.3	8.93	0.002
17		+	+					8	10287.6	9.28	0.002
18			+					7	10290.5	12.17	0
19								5	10293.4	15.02	0
20	+		+					8	10512.3	233.94	0
21	+	+	+					9	10514.2	235.81	0
22	+	+	+			+		11	10515.1	236.76	0
23	+	+	+	+				10	10515.2	236.84	0
24	+		+		+			10	10516.1	237.71	0
25	+	+	+	+		+		12	10516.4	238.06	0
26	+	+	+		+			11	10517.9	239.54	0
27	+	+	+		+	+		13	10518.8	240.46	0
28	+	+	+	+	+			12	10518.9	240.56	0
29	+	+	+	+	+	+		14	10520.2	241.81	0
30	+	+	+	+	+	+	+	16	10521.4	243.08	0
31			+					7	10523.7	245.36	0
32	+	+						7	10524.5	246.12	0
33	+	+		+				8	10524.7	246.35	0
34	+							6	10524.9	246.55	0
35		+	+					8	10525.6	247.28	0
36		+	+			+		10	10527.1	248.75	0
37								5	10533.2	254.82	0
38		+						6	10533.3	254.96	0

proportion of vigilance behavior were also associated with site*season (both in summer–autumn and in winter; $p<0.01$ for both) and site*sex*season (only in summer-autumn; $p=0.033$) interaction terms (Tab. 5).

All of the 12 top-ranked candidate models on the proportion of foraging behavior included only site as a common explanatory variable (Tab. 6). The proportion of time spent foraging was significantly lower at Site I than at Site II (Wald test, $p=0.049$; Tab. 7 and Fig. 3).

Both the Zi-GLMM analyses also processed potential overdispersions by zero-inflation (Tabs. 5 and 7).

Discussion

Sika deer at Site I spent more time exhibiting vigilance behavior and less time foraging than deer at Site II, supporting my initial hypothesis. This indicates that human disturbances may provoke a behavioral response (i.e., increased vigilance and decreased foraging) in sika deer that is similar to observations in other cervids (Benhaiem *et al.*, 2008; Jayakody *et al.*, 2008). However, multivariate analysis also indicated that sika deer vigilance changed through the year, increasing

Table 7. Results of the zero-inflated generalized linear mixed model with model averaging in the top-ranked candidate models (>10% AIC weights of the best model) on the proportions of time sika deer (*Cervus nippon*) spent exhibiting foraging behavior.

Variable	*β*	*s.e.*	Wald test *p*
(Intercept)	−0.184	0.060	0.002
(Effect of zero inflation)	−2.309	0.099	<0.001
Site[a]	−0.087	0.044	0.049
Sex[b]	−0.119	0.068	0.078
Season (sum.-aut.)	−0.052	0.043	0.228
Season (win.)	−0.084	0.050	0.092
Site * Sex	−0.021	0.086	0.807
Site * Season (sum.-aut.)	0.005	0.076	0.945
Site * Season (win.)	−0.121	0.084	0.152
Sex * Season (sum.-aut.)	0.117	0.081	0.150
Sex * Season (win.)	0.145	0.076	0.055
Site * Sex * Season (sum.-aut.)	0.034	0.188	0.856
Site * Sex * Season (win.)	0.268	0.184	0.144

[a] A positive coefficient (*β*) indicates that the value was higher at Site I than at Site II, while a negative value indicates the opposite
[b] A positive coefficient (*β*) indicates that the value was higher in males than in females, while a negative value indicates the opposite

in summer–fall and winter, but those seasonal patterns differed between the two studied sites, resulted from statistic significant associations of the site*season interaction term (Tab. 5). Vigilance levels in cervids typically increased in autumn, when it is the mating season, despite presence/absence of human disturbances (Eccard *et al.*, 2017; Schuttler *et al.*, 2017). The results of this study indicated that vigilances by deer in Site II also increased slightly and were the highest in this season (Fig. 3). In winter, however, the increased vigilances, specifically observed in females in Site I, might be associated with types of human activities, because the human activities were the lowest among the studied seasons (Tab. 1). Previous studies demonstrated that hunting by humans had a stronger effect than other types of human disturbance (e.g., outdoor recreations or presences of automobile) on the vigilance of ungulates in human-modified habitats (Jayakody *et al.*, 2008; Ciuti *et al.*, 2012). Therefore, it is possible that the anti-predator behaviors at Site I were substantially in response to human hunting rather than other types of human activities (e.g., hiking or academic research).

The results from multivariate analysis indicated that seasonal patterns in the deer vigilance were different between the sexes (Tab. 5). At Site I, females significantly spent the least time foraging and showed the highest vigilance in winter. Males were most vigilant in summer–fall but no seasonal changes in their foraging (Fig. 3). However, these patterns were inconsistent with seasonal changes in human activities (decreased from spring-summer to winter; Tab. 1), indicating that their behavioral responses were unlikely to be directly influenced by increased human activities.

Previous studies on other cervids have demonstrated that females (specifically accompanied with their fawns) are more sensitive to the presence of predator (including human hunters) than males, showing remarkably increased vigilance and decreased foraging (Lung & Childress, 2007; Winnie & Creel, 2007; Benoist *et al.*, 2013; Pecorella *et al.*, 2016; Eccard *et al.*, 2017). Although human activities were relatively lower in winter than in other seasons (Tab. 1), intrusions of hunters and hunting dogs into surrounding forests (see "Study area") might provoke the behavioral responses in female deer as reacting to the risk of their presences (e.g., Eccard *et al.*, 2017). Male deer had the greatest vigilance in summer–fall when human activities were the moderate level (Tab. 1), which may be partly caused by conspecific interactions (fighting for the dominance in the harem) during the mating season (Nagata, 2015), as observed in previous studies (Lung & Childress, 2007; Winnie & Creel, 2007; Benoist *et al.*, 2013). Further studies associating with the reproductive status as well as group sizes of the observed animals need to assess these assumptions, according to previous studies on other cervids (e.g., Lung & Childress, 2007; Winnie & Creel, 2007).

Conclusion

The findings of the present study indicate that human disturbances (specifically hunting) may provoke increased vigilance as an anti-predator behavioral response and a concurrent decline in food consumption in sika deer. Non-lethal effects by human hunting modifying deer behavior may be applicable for deer management through effects of "landscape of fear" (Cromsigt *et al.*, 2013), in depopulating rural areas of Japan (Tsunoda & Enari, 2020). However, this observation was made at only one site, so further research is required at the population level to generalize this result.

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References

Altendorf K.B., Laundre J.W., Lopez Gonzalez C.A. & Brown J.S. 2001. Assessing effects of predation risk on foraging behavior of mule deer // Journal of Mammalogy. Vol.82. No.2. P.430–439.

Barton K. 2015. MuMIn: multi-model Inference // R package version 1.15.1. https://cran.r-project.org/web/packages/MuMIn/index.html

Benhaiem S., Delon M., Lourtet B., Cargnelutti B., Aulagnier S., Hewison A.J.M., Morellet N. & Verheyden H. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection // Animal Behaviour. Vol.76. No.3. P.611–618.

Benoist S., Garel M., Cugnasse J.-M. & Blanchard P. 2013. Human disturbances, habitat characteristics and social environment generate sex-specific responses in vigilance of Mediterranean mouflon // PLoS ONE. Vol.8. No.12. e82960.

Bongi P., Ciuti S., Grignolio S., Del Frate M., Gandelli D. & Apollonio M. 2008. Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area // Journal of Zoology. Vol.276. No.3. P.242–251.

Bonnot N., Verheyden H., Blanchard P., Cote J., Debeffe L., Cargnelutti B., Klein F., Hewison A.J.M. & Morellet N. 2015. Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? // Behavioral Ecology. Vol.26. No.1. P.105–114.

Borkowski J. 2001. Flight behaviour and observability in human-disturbed sika deer // Acta Theriologica. Vol.46. No.2. P.195–206.

Brooks M.E., Kristensen K., van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Maechler M. & Bolker B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling // R Journal. Vol.9. No.2. P.378–400.

Burnham K.P. & Anderson D.R. 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. 2nd ed. New York: Springer. 488 p.

Burnham K.P., Anderson D.R. & Huyvaert K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons // Behavioral Ecology and Sociobiology. Vol.65. P.23–35.

Ciuti S., Northrup J.M., Muhly T.B., Simi S., Musiani M., Pit J.A. & Boyce M.S. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear // PLoS ONE. Vol.7. No.11. e50611.

Creel S. 2018. The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response // Ecology Letters. Vol.21. No.7. P.947–956.

Creel S., Christianson D., Liley S. & Winnie J.A. 2007. Predation risk affects reproductive physiology and demography of elk // Science. Vol.315. No.5814. P.960.

Cromsigt J.P.G.M., Kujiper D.P.J., Adam M., Beschta R.L., Churski M., Eycott A., Kerley G.I.H., Mysterud A., Schmidt K. & West K. 2013. Hunting for fear: innovating management of human–wildlife conflicts // Journal of Applied Ecology. Vol.50. No.3. P.544–549.

Doormaal N. van, Ohashi H., Koike S. & Kaji K. 2015. Influence of human activities on the activity patterns of Japanese sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) in Central Japan // European Journal of Wildlife Research. Vol.61. P.517–527.

Eccard J.A., Meißner J.K. & Heurich M. 2017. European roe deer increase vigilance when faced with immediate predation risk by Eurasian lynx // Ethology. Vol.123. No.1. P.30–40.

Ikeda T., Takahashi H., Igota H., Matsuura Y., Azumaya M., Yoshida T. & Kaji K. 2019. Effects of culling intensity on diel and seasonal activity patterns of sika deer (*Cervus nippon*) // Scientific Reports. Vol.9. P.17205.

Jayakody S., Sibbald A.M., Gordon I.J. & Lambin X. 2008. Red deer *Cervus elaphus* vigilance behaviour differs with habitat and type of human disturbance // Wildlife Biology. Vol.14. No.1. P.81–91.

Jarnemo A. & Wikenros C. 2014. Movement pattern of red deer during drive hunts in Sweden // European Journal of Wildlife Research. Vol.60. No.1. P.77–84.

Kaji K., Saitoh T., Uno H., Matsuda H. & Yamamura K. 2010. Adaptive management of sika deer populations in Hokkaido, Japan: Theory and practice // Population Ecology. Vol.52. P.373–387.

Kamei T., Takeda K., Izumiyama S. & Ohshima K. 2010. The effect of hunting on the behavior and habitat utilization of sika deer (*Cervus nippon*) // Mammal Study. Vol.35. No.4. P.235–241.

Kuijper D.P.J., Bubnicki J.W., Churski M., Mols B. & van Hooft P. 2015. Context dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest // Behavioral Ecology. Vol.26. No.6. P.1558–1568.

Lima S.L. 1998. Nonlethal effects in the ecology of predator–prey interactions // Bioscience. Vol.48. No.1. P.25–34.

Lima S.L. & Bednekoff P.A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis // American Naturalist. Vol.153. No.6. P.649–659.

Lung M.A. & Childress M.J. 2007. The influence of conspecific and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park // Behavioral Ecology. Vol.18. No.1. P.12–20.

Nagata J. 2015. *Cervus nippon* Temminck, 1836 // Ohdachi S.D., Ishibashi Y., Iwasa M.A., Fukui D. & Saitoh T. (eds.) The Wild Mammals of Japan. 2nd ed. Kyoto: Shoukadoh. P.304–306.

Pecorella I., Ferreti F., Sforzi A. & Macchi E. 2016. Effects of culling on vigilance behaviour and endogenous stress response of female fallow deer // Wildlife Research Vol.43. No.3. P.189–196.

R Core Team. 2018. R: A Language and Environment for Statistical Computing // Vienna: R Foundation for Statistical Computing. Available at https://www.R-project.org/ (Accessed 25 January 2017).

Ripple W.J., Estes J.A., Beschta R.L., Wilmers C.C., Ritchie E.G., Hebblewhite M., Berger J., Elmhagen B., Letnic M., Nelson M.P., Schmitz O.J., Smith D.W., Wallach A.D. & Wirsing A.J. 2014. Status and ecological effects of the world's largest carnivores // Science. Vol.343. No.6167. P.1241484.

Sakio H., Kubo M., Kawanishi M. & Higa M. 2013. Effects of deer feeding on forest floor vegetation in the Chichibu Mountains, Japan // Journal of the Japanese Society of Revegetation Technology. Vol.39. No.2. P.226–231.

Sakurai R. 2019. Human Dimensions of Wildlife Management in Japan: From Asia to the World. Singapore: Springer. 139 p.

Schuttler S.G., Parsons A.W., Forrester T.D., Baker M.C., McShea W.J., Costello R. & Kays R. 2017. Deer on the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance // Journal of Zoology. Vol.301. No.4. P.320–327.

Takatsuki S. 2009. Effects of sika deer on vegetation in Japan: a review // Biological Conservation. Vol.142. No.9. P.1922–1929.

Tsunoda H. & Enari H. 2020. A strategy of wildlife management in the depopulating rural society of Japan // Conservation Biology. Vol.34. No.4. P.819–828.

Winnie J.J. & Creel S. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation // Animal Behaviour. Vol.73. No.1. P.215–225.

Zuur A.F., Ieno E.N. & Elphick C.S. 2010. A protocol for data exploration to avoid common statistical problems // Methods in Ecology and Evolution. Vol.1. No.1. P.3–14.

Appendix 1. A photo of a deer-exclusive fence in a natural forest of the University of Tokyo Chichibu Forest.

Appendix 2. Photos taken at each camera-trapping Sites I (left) and II (right).