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SHORT COMMUNICATION

Freezing behavior of the Japanese serow (*Capricornis crispus*) in relation to habitat and group size

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Abstract Freezing behavior is frequently observed among forest-dwelling ungulates and is thought to function as a method of concealment from predators. However, because of the difficulty of observing such behaviors, detailed observations have not previously been conducted to provide evidence for this interpretation. Therefore, we have examined the response to human observers of the Japanese serow (*Capricornis crispus*), a typical forest dweller, in relation to visibility and group size based on direct observations conducted over 3 years. From a total of 221 sightings, freezing behavior was observed more frequently in the closed habitat (14.3% of 196 sightings) and during the growing season (22.8% of 92 sightings) than in the open habitat (0% of 25 sightings) and during the non-growing season (5.2% of 129 sightings). Freezing behavior was also frequently observed in solitary animals (15.2% of 184 sightings) than in groups (0% of 37 sightings). These results suggest that the function of this freezing behavior is concealment from predators. Japanese serows fled more frequently in the open habitat (72%) and during the non-growing season (58.7%) than in the closed habitat (18%) and during the growing season (41.3%). Japanese serows selected closed habitat significantly more often regardless of the season. These results suggest that Japanese serow adopt cryptic anti-predator strategy to avoid detection by predators in the dense forest habitat, and their strategy changes according to visibility.

Keywords Anti-predator behavior · Crypsis · Forest dweller · Habitat selection · Solitary ungulate · Visibility

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Introduction

The Japanese serow (*Capricornis crispus*) is a typical forest-dwelling ungulate (Ochiai 2015), which belongs to the tribe Rupicaprinae (Schaller 1977). The general behavior and sociality of the Japanese serow have been studied in detail in past studies. The Japanese serow is mainly a solitary and monogamous species, and exhibits intra-sexual territoriality (Kishimoto and Kawamichi 1996; Ochiai and Susaki 2002). However, little is known about anti-predator behaviors.

Anti-predator behaviors differ between open-habitat-dwelling ungulates and closed-forest-dwelling ungulates (Estes 1974; Jarman 1974). Open-habitat dwellers employ individual visual signals such as stotting (FitzGibbon and Fanshwe 1988) and tail-flicking (Stankowich 2008), and group behaviors such as bunching (Lingle 2001) and group attacking (Estes 1991). In contrast, forest dwellers adopt inconspicuous anti-predator behaviors such as freezing and fleeing into bushes (Estes 1974). Forest dwellers are thought to use crypsis as a strategy to reduce exposure to predators (Jarman 1974; Brashares et al. 2000; Caro et al. 2004), and crypsis is enhanced by using closed habitats, small body size, and solitary habits (Jarman 1974; Ydenberg and Dill 1986; Caro et al. 2004). The functions of anti-predator behaviors in open-habitat dwellers have been well studied by observing the behavior and surrounding environment (e.g., Lagory 1987; FitzGibbon and Fanshawe 1988; FitzGibbon 1994; Stankowich and Coss 2007). However, little is known about

such behaviors among forest dwellers such as the Japanese serow because of the greater difficulty of conducting observations in closed habitats.

Freezing behavior is thought to function as a method of concealment from predators by the animal remaining motionless by either standing still or by lying low when predators approach (Smythe 1977; Caro et al. 2004). This behavior is frequently observed in small bovids and small cervids such as blue duiker (*Cephalophus monticola*, Estes 1991), Kirk's dikdiks (*Madoqua kirkii*, Hendrichs and Hendrichs 1971), fourhorned antelopes (*Tetracerus quadricornis*, Sharma et al. 2009), and muntjacs (*Muntiacus reevesi*, Eisenberg 1974). Hendrichs and Hendrichs (1971) reported that Kirk's dikdiks show different anti-predator behavior according to predator type. When the predator is a courser such as a spotted hyena (*Crocuta crocuta*) or wild dog (*Lycaon pictus*), dik-diks frequently freeze; however, dik-diks immediately flee when the predator is a stalker such as a caracal (*Felis caracal*) or leopard (*Panthera pardus*) (Hendrichs and Hendrichs 1971). Croes et al. (2007) also reported that the occurrence of freezing behavior in blue duikers differ based on the effects of human hunting. Although studies on freezing behavior according to potential danger have been conducted (Hendrichs and Hendrichs 1971; Croes et al. 2007), few studies have focused on freezing behavior relative to the surrounding environment and group size. If the function of freezing is concealment, it is expected that animals will freeze more frequently in conditions where it will be more difficult for predators to detect them. Therefore, forest dwellers would be more likely to freeze in solitude and/or in closed environments. Alternatively, forest dwellers may immediately flee into bushes when they are in open habitats (Jarman 1974) because it is easier for them to be detected by predators. Moreover, predation risk may be reduced by the selection of environments with poor visibility (Ydenberg and Dill 1986).

To evaluate the freezing behavior in the Japanese serow, multiple factors must be considered. Trees in the deciduous broad-leaved forests that the Japanese serow inhabits sheds their leaves in winter. As a result of this phenomenon, the degree of visibility in the Japanese serow's habitat changes throughout the year. This makes it possible to examine the effects of visibility on its anti-predator behaviors. Furthermore, the Japanese serow is typically a solitary species, but sometimes may form groups of two to four (Kishimoto and Kawamichi 1996). This affords the opportunity to examine the effects of group sizes on anti-predator behaviors. Habitat selection is thought to be related to anti-predator strategy as well (Sih 1992). Therefore, this study examined anti-predator behaviors among different visibility conditions and different group sizes, and examined habitat selections focusing on habitat visibility.

The Asian black bear (*Ursus thibetanus*) is a potential predator of the Japanese serow (Ochiai 2015). In fact, attacks by bears against Japanese serows have been observed at Mt. Asama (H. Takada unpublished data). In our study area, Japanese serows apparently regarded humans as dangerous; they oriented toward humans and monitored human behaviors, or fled immediately, as they do when they encounter bears (H. Takada unpublished data). Humans pose a similar perceived predation risk to the serows as their natural predators. Thus, we assume that the response of serows toward predators can be predicted from the response toward human observers. Humans have also been used as "presumed predators" in several other studies on anti-predator behaviors of ungulates (e.g., LaGory 1987; Caro 1994; Reby et al. 1999; Stankowich and Coss 2006; Stankowich 2008).

Methods

Study area

The study area (36° 38′ N, 138° 47′ E) is located on the south-facing slope of Mt. Asama in Nagano Prefecture, central Japan. The elevation ranges from 1200 to 1600 m above sea level. The area is covered in snow (10–100 cm in depth) for approximately 3 months of the year, between late December and March. The vegetation consists of plantations of Japanese larch (*Larix kaempferi*), secondary deciduous forests of mongolian oak (*Quercus crispula*) and white birch (*Betula platyphylla*), and evergreen coniferous forests of Japanese red pine (*Pinus densiflora*). During our observations, patches of clear-cut logging areas occupied one fifth of the study area. The understory vegetation is dominated by dwarf bamboo (*Sasa nipponica*) and shrubs. We divided the habitat into the open habitat, i.e., the clear-cut logging areas and dwarf bamboo communities, and the closed habitat, i.e., the shrub communities. Open habitat and closed habitat accounted for 48.1 and 51.9%, respectively, of the study area. Because leaves fall from trees in November and do not regrow until March (referred to as the "non-growing season" hereafter), visibility in this habitat is greater during this season than in the "growing season" from April to October.

Observation of the Japanese serow

We conducted field observations for 68 days from September to June during 2011–2014. We walked throughout the study area in the daytime, and recorded trail length for each habitat type. The observation time and trail length per day were arbitrary. We expressed each season's and habitat's observation effort in terms of walking distance. Observations were conducted mainly from 10 am to 4 pm and did not include dawn and dusk. When we found Japanese serows, we recorded the habitat type, group size, group composition, individual name (IDs), distance between the serow and the observer, behavior

pattern, and duration of alert posture. We observed serows using binocular telescopes (× 10) and spotting scopes (× 25–50), and observation distance was approximately 15 to 80 m. A group was defined as when individuals were within 30 m of each other. Distance between Japanese serows and observer, and between individual Japanese serows were recorded by eye and a digital distance meter. Individual recognition was carried out based on the variation of natural features in the serow such as horn shape, torn ears, facial scars, and body colors. When the individuals were unidentified or could not be identified, they were recorded as unknown individuals. The definition of freezing behavior of ungulates in previous studies is ambiguous (Caro et al. 2004; Croes et al. 2007; Sharma et al. 2009), so we defined behavior patterns based on the duration of the alert posture and behavior after the alert posture. When detected by observers, serows first assumed an alert posture. Behavior patterns toward the observer were classified as fleeing from the observer (termed "fleeing"), walking or feeding without alert to the observer ("normal behavior"), and sustaining the alert posture ("freezing").

Statistical analyses

We completed the following analyses in R. 3.4.1 (R Core Team 2017). To test the effects of season, habitat type, group size, and interactions of these variables on freezing, we used the probability of freezing as our dependent variable (1 = freezing, 0 = no freezing) and fit generalized linear mixed models (GLMMs) with a logit-link function and binomial error distribution with the package lme4 (Bates et al. 2015). Fixed effects included season, habitat type, group size, and their interactions (season × habitat type, season × group size, habitat type × group size, and season × habitat type × group size). IDs and group compositions were used as a random effect to minimize the influence of variation among individuals and group members. Unknown individuals and unknown groups were treated as one ID. Analysis of variance was used to test differences in the probability of freezing between seasons (growing versus non-growing), habitat types (closed versus open) and group sizes (solitary versus grouped), and their interactions. All significance tests referred to the type 2 analysis with the package car (Fox and Weisberg 2011). To test the effects of season, habitat type, group size, and interactions of these variables on fleeing, we used the probability of fleeing as our dependent variable (1 = fleeing, 0 = no fleeing) and fit GLMMs with a logit-link function and binomial error distribution with the package lme4 (Bates et al. 2015). Fixed effects included season, habitat type, group size, and their interactions (season × habitat type, season × group size, habitat type × group size, and season × habitat type × group size). Analysis of variance was also used to test differences in the probability of fleeing between seasons (growing versus non-growing), habitat types (closed versus open) and group sizes (solitary versus grouped), and their interactions.

All significance tests referred to the type 2 analysis with the package car (Fox and Weisberg 2011).

Habitat selection was calculated by measuring the relationship between habitat use and habitat availability. Although there is no general agreement in the literature about which of the several existing indices is the best measure for selection, the Manly et al. (2007) selection index appears to be one of the best indices for selection in most situations (Murase et al. 2007). Confidence intervals of the selection index were estimated as described below to statistically test whether the serow used the habitat randomly.

Manly's selection indices (w_i) are

$$w_i = r_i/n_i$$

Where r_i is ratio of habitat i sighted serows and n_i is ratio of habitat i we walked.

Bonferroni confidence interval of w_i is given by

$$w_i \pm Z_{\alpha/2} \times \mathrm{SE}\,(w_i).$$

Confidence intervals of 1 indicate that the serow used that terrain type randomly. Confidence intervals of more than 1 and less than 1 indicate significant selection and avoidance, respectively (Manly et al. 2002). The value of $Z_{\alpha/2}$ was set at 2.58.

Results

Sightings of Japanese serow

In total, 367.2 km was the distance walked throughout the study period, and Table 1 shows the walking distance during each season and each habitat. A total of 221 sightings were recorded. We identified 13 individuals and six group compositions, and were able to identify individuals and groups for 90.0% of all sightings. The serows were mostly solitary (83.3%). In the remaining 16.7% sightings, 15.4% of the sightings consisted of groups from two animals, which were typically one mother with one fawn or a pair of one adult male and one adult female; 1.3% of the sightings were of three animals, which typically consisted of one adult male-female

Table 1 Walking distances (km) of each habitat and season on Mt. Asama, central Japan, between October 2011 and December 2014

Season	Growing	Non-growing	Total
Habitat			
Open	51.5	73.1	124.6
Close	111.6	131	242.6
Total	163.1	204.1	367.2

pair with one fawn. Serows were found in both the non-growing (58.3%) and growing (41.7%) seasons.

Response to the observer

Of the 221 total sightings, freezing, fleeing, and normal behavior were observed 28 times, 134 times, and 59 times, respectively. Table 2 shows the behavior patterns of serows during each season, habitat, group type, and ID. When a serow showed a fleeing response after assuming an alert posture toward the observer, fleeing was immediate in many cases. The longest alert duration was 52 s (mean ± SD = 6.4 ± 7.9 s, $N = 134$). When a serow showed normal behavior after assuming an alert posture toward the observer, the longest alert duration was 38 s (mean ± SD = 4.2 ± 6.7 s, $N = 59$). When the serow showed a freezing response, they were immobilized for over 5 min and observations were aborted. The longest alert duration was 2 h and 15 s (mean ± SD = 1680.8 ± 2047.9 s, $N = 28$).

Freezing behavior occurred when the distance between the serow and the observer was more than 20 m (mean ± SD = 29 ± 10.3 m, $N = 28$). Serows froze while concealing parts of their body behind woody plants. This behavior was observed in both non-growing and growing seasons, but was seen more often in the growing seasons (22.8% of 92 sightings) than in the non-growing seasons (5.2% of 129 sightings). This difference was statistically significant [GLMMs, likelihood ratio test (LRT), $\chi^2 = 13.99$, df = 1, $P < 0.001$]. Although not a statistically significant difference (GLMMs, LRT, $\chi^2 = 0.00$, df = 1, $P = 0.99$), freezing behavior was only seen in closed habitats (14.3% of 196 sightings). In addition, although not statistically significant (GLMMs, LRT, $\chi^2 = 0.00$, df = 1, $P = 0.99$), freezing behavior was only observed in solitary individuals (15.2% of 184 sightings). Interactions between the effects of season, habitat type, and group size were not significant (GLMMs, LRT, season × habitat × group size: $\chi^2 = 0$, df = 1, $P = 0.99$; season × habitat: $\chi^2 = 0$, df = 1, $P = 0.99$; season × group size: $\chi^2 = 0$, df = 1, $P = 0.99$; habitat × group size: $\chi^2 = 0$, df = 1, $P = 0.99$).

Japanese serows fled significantly more often in the non-growing season (GLMMs, LRT, $\chi^2 = 36.54$, df = 1, $P < 0.001$) and when they were in open habitats (GLMMs, LRT, $\chi^2 = 5.84$, df = 1, $P < 0.05$). Effects of group sizes and interactions between the effects of season, habitat type, and group

Table 2 Behavior patterns of Japanese serows (*Capricornis crispus*) observed on Mt. Asama, central Japan for each season, habitat type, group type, and individual (IDs) between October 2011 and December 2014

	Season	Growing						Non-growing					
	Habitat	Close			Open			Close			Open		
	Behavior pattern IDs	Freeze	Flee	Normal	Freeze	Flee	Normal	Freeze	Flee	Normal	Freeze	Flee	Normal
Solitary	a	0	0	9	0	0	1	0	0	12	0	0	0
	b	1	0	5	0	1	2	0	0	8	0	3	1
	c	1	1	4	0	1	2	1	12	1	0	1	0
	d	4	2	0	0	0	0	1	7	0	0	0	0
	e	3	3	2	0	1	0	0	9	1	0	3	0
	f	4	3	1	0	0	0	2	18	0	0	1	0
	g	0	0	2	0	0	0	0	0	2	0	1	1
	h	3	3	0	0	0	0	0	6	0	0	0	0
	i	2	1	1	0	0	0	0	2	0	0	0	0
	j	0	0	2	0	0	0	0	0	0	0	0	0
	k	0	0	1	0	0	0	1	1	0	0	0	0
	l	0	0	0	0	0	0	1	0	0	0	1	0
	m	0	0	0	0	0	0	1	3	0	0	0	0
	Unknown	3	6	1	0	0	0	0	6	0	0	1	0
Groups	o	0	0	0	0	0	0	0	6	0	0	0	0
	p	0	2	0	0	1	0	0	4	0	0	1	0
	q	0	2	0	0	0	0	0	5	0	0	0	0
	r	0	1	0	0	1	0	0	0	0	0	0	0
	s	0	3	0	0	0	0	0	2	0	0	1	0
	t	0	2	0	0	0	0	0	1	0	0	0	0
	Unknown	0	4	0	0	0	0	0	1	0	0	0	0

size were not significant (GLMMs, LRT, group size: $\chi^2 = 0$, df = 1, $P = 0.99$; season × habitat × group size: $\chi^2 = 0$, df = 1, $P = 0.99$; season × habitat: $\chi^2 = 1.314$, df = 1, $P = 0.25$; season × group size: $\chi^2 = 0$, df = 1, $P = 0.99$; habitat × group size: $\chi^2 = 0$, df = 1, $P = 0.99$).

Habitat selection

Selection indices indicated that the Japanese serow selected the closed habitat significantly more often regardless of season. Furthermore, they showed a significant tendency to avoid open habitat (Table 3).

Discussion

Freezing behavior is thought to function as a method of concealment from predators because it is associated with dense vegetation, small body size, solitary habits (Brashares et al. 2000; Caro et al. 2004), and cryptic coloration (Stoner et al. 2003). The results in this study strongly support this presumption. The significant occurrence of freezing behavior in the growing season indicates the possibility of low visibility leading to this behavior in the Japanese serow. Although no statistically significant differences could be seen between habitat types due to the small number of observations, freezing behavior was seen only in closed habitats. This result demonstrates the possibility of freezing behaviors occurring in environments with poor visibility as well. There was no significant difference between group sizes relative to freezing behavior, but solitary individuals had a higher tendency showoff showing freezing responses compared with responses from individuals in groups. This may be due to serows being less detectable by predators when they are alone compared with when they are in groups. These results indicate that the purpose of Japanese serow freezing behavior is to avoid detection by predators. Thus, this finding supports the interpretation that concealment from predators is a function of freezing behaviors (Caro et al. 2004).

Frequent fleeing behavior was seen during the non-growing seasons and in open habitats. These results indicate

Table 3 Selection index (w_i) and statistical results of Japanese serow presence in each habitat and season between 2011 and 2014 surveys

Season	Growing		Non-growing	
Habitat	Close	Open	Close	Open
w_i	1.30	0.34	1.38	0.32
se (w_i)	0.05	0.10	0.02	0.01
Bonferroni (low)	1.42	0.61	1.42	0.35
Bonferroni (high)	1.18	0.08	1.33	0.30

that the fleeing behavior of the Japanese serow is associated with good visibility. In other forest-dwelling ungulates such as the roe deer (*Capreolus capreolus*), strong flight response has been reported in open habitats rather than in closed habitats (de Boer et al. 2004). Because forest dwellers are easily detected by predators in open habitats, it is considered that the anti-predator strategy of fleeing quickly into bushes leads to lower predation risks.

Crypsis is thought to be an important anti-predator strategy to reduce exposure to predators in forest-dwelling ungulates (Jarman 1974; Brashares et al. 2000; Caro et al. 2004). It is enhanced by increasing the usage of cover and it minimizes detection by predators (Sih 1992; Luttbeg and Trussell 2013). Like other ungulates that show freezing behavior, the Japanese serow selected covered habitats over non-covered habitats as well (Teng et al. 2004; Brodie and Brockelman 2009). This result may support the assumption that the Japanese serow enhances crypsis by frequent usage of cover (Sih 1992; Luttbeg and Trussell 2013). However, since habitat selection depends not only on avoidance of predation but on multiple factors such as the amount and/or quality of food (Albon and Langvatn 1992; Mysterud et al. 1999) and climatic conditions (Schmitz 1991; Mysterud and Østbye 1995), further examination is necessary. The Japanese serow is considered a browser (Ochiai 1999; Kobayashi and Takatsuki 2012) and feeds mainly on leaves and twigs of deciduous broad-leaved trees in the study area (H. Takada unpublished data). Deciduous broad-leaved trees are more abundant in closed habitats than in open habitats and therefore food conditions may also be associated with the preference for closed habitats in the Japanese serow.

The findings in this study contain some potential limitations regarding methodology. First, the number of freezing behaviors that could be confirmed were as low as 12.7% of all sightings. Compared with non-growing seasons and open habitats where there is good visibility, growing seasons and closed habitats offer poor visibility and make detection of serows difficult. Furthermore, the difficulty of finding serows increases if the animal is freezing. Therefore, the counts of serow sightings and freezing behavior may be underestimated in the poor-visibility environments. Second, the low number of sighting in open habitat may result from an earlier detection of observer by Japanese serows and thus, the part of Japanese serows may flee before observer detect them. However, there were many vestiges such as faces and hair of the Japanese serow in closed habitat, and rarely in open habitats (H. Takada unpublished data). Thus, there is a possibility that Japanese serows actually avoided the open habitat. To clarify accurate habitat selection, investigation using GPS collars should be conducted. Third, there were some individuals (IDs a, b, g, and j) that showed little wariness toward the observers. It is possible that those individuals did not recognize the observers as predators. To more accurately observe

anti-predator behaviors, it is necessary to observe behaviors in response to wild predators such as black bears.

In conclusion, freezing behavior in the Japanese serow functions as mode of concealment from predators, and the Japanese serow adopts cryptic anti-predator strategy. These strategies are considered to have developed in the closed-forest habitat of the Japanese archipelago, and differ according to visibility.

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