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Effects of the physical and social environment on flight response and habitat use in a solitary ungulate, the Japanese serow (*Capricornis crispus*)

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ABSTRACT

Observations of the flight response of ungulates are commonly used to test behavioral responses to predation risk. In gregarious ungulates with sexual body-size dimorphism such responses are likely to be stronger in situations where individuals have perceptions of less security as well as among more-sensitive individuals, such as female groups or female groups with offspring which are understood to use safety habitats more often than males do. However, little is known about these behaviors in solitary ungulates with little sexual dimorphism. Therefore, we examined the flight response to human presence and the habitat use of Japanese serow (*Capricornis crispus*), a solitary ungulate with little sexual dimorphism, in relation to its physical and social environments, based on direct observations conducted over approximately four years. Based on a total of 335 sightings, serows took flight less often when in steep terrain, in closed habitat, or in low-visibility seasons, and they selectively used steep–closed habitat. These findings suggest that steep slopes and low-visibility conditions provide the species with greater security, and that serows select safer habitats to decrease predation risk. There were no significant differences in the flight responses and habitat use of solitary males and solitary females; the absence of differences is likely related to the serow's habit of monogamy and its underdeveloped sexual dimorphism. Females with kids more frequently fled than other group types; this difference is thought to be linked to females' priority to secure the survival of their offspring. This result shows the key role of offspring presence in affecting flight response in the serow. Conversely, there were no differences in habitat use between females with kids and other group types; here, the absence of such differences may be associated with intra-sexual territoriality of the serow, since all types of territory holders (including females with kids) need to continuously use the entire home range to maintain a territory.

1. Introduction

Flight is a common anti-predator behavior among wild ungulates when confronted with a potential danger, particularly wild predators and human interference, and is a vital factor in enhancing individual fitness (Stankowich and Reimers, 2015). Factors influencing the escape decisions of wild ungulates has gained much research attention in the past, signifying a surge of interest in the potential contribution of behavioral ecology to wildlife conservation and management, and a greater recognition of predation as a key evolutionary force (Stankowich, 2008).

Previous studies have shown that a range of factors influence the decision of an ungulate to flee from perceived danger, especially those related to the species' physical and social environments (Stankowich, 2008). As physical environmental factors, the availability of escape terrain, such as dense vegetation cover and steep cliffs, is thought to affect the flight response of some ungulates. Animals in close proximity to escape terrain may flee less often because of the potential security it provides (Rowe-Rowe, 1974; MacArthur et al., 1982; Tyler, 1991; Bleich, 1999; de Boer et al., 2004). As social environmental factors, sex and the presence of young offspring have large and consistent effects on the flight response in ungulates (Stankowich, 2008). Groups of females took flight more often than groups of males (Recarte et al., 1998), confirming the reports of many studies showing that females with offspring are generally more easily disturbed than males (Horejsi, 1981; McLaren and Green, 1985; Thompson, 1989; Langbein and Putman, 1992; Bullock et al., 1993; Vandenheede and Bouissou, 1993; Aastrup, 2000; Ciuti et al., 2008). Sexual dimorphism is associated with the

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polygynous mating system in most ungulates (Weckerly, 1998; Loison et al., 1999; Pérez-Barbería et al., 2002) and is thought to be a key factor in favoring behavioral responses to predation risk which differ according to sex (Ciuti et al., 2008). Smaller females and young offspring seem to be more vulnerable than larger males (Ruckstuhl and Neuhaus, 2002), and males and females pursue different strategies to maximize their reproductive success, with a tendency for males to maximize their body condition while females will maximize offspring survival (Main et al., 1996; Ruckstuhl and Neuhaus, 2002; Mooring et al., 2003). Such sexual differences in vulnerability and the given reproductive strategy are thought to cause differences in the flight response according to sex (Ciuti et al., 2008). In addition, some studies have shown that sexual differences in perceived predation risk also cause differences in habitat use according to the sex, whereby adult females or females with young offspring more often utilize safety habitats than do males (Berger, 1991; Mysterud, 2000; Mooring et al., 2003).

The effects of these physical and social factors on flight response has been well studied in gregarious ungulate species that live in open land rather than in closed forests, and in species with sexual dimorphism (Berger, 1991; Recarte et al., 1998; Bleich, 1999; Aastrup, 2000; Taraborelli et al., 2012; Holmern et al., 2016). However, little is known about the behavioral responses of solitary ungulates that live in dense forests and display little sexual dimorphism, because of the greater difficulty of conducting observations in closed habitats. In solitary ungulate species with little sexual dimorphism, predation risk may not differ between the sexes, unlike in gregarious ungulates; thus, this may amount to no differences in flight response and habitat use between the sexes.

With these assumptions in mind, we investigated the habitat use and flight response to human presence exhibited in a population of Japanese serow (*Capricornis crispus*). The Japanese serow is a typical mountainous forest-dwelling ungulate (Ochiai et al., 2015) belonging to the subfamily Caprinae (Gentry, 1992). Japanese serow are mainly solitary (Kishimoto and Kawamichi, 1996; Takada et al., 2018), territorial (Kishimoto and Kawamichi, 1996; Ochiai and Susaki, 2002), and monogamous (Ochiai and Susaki, 2002; Kishimoto, 2003), with little sexual dimorphism (Ochiai et al., 2015). Escape terrains for Japanese serow are thought to be vegetation cover (Takada et al., 2018) and steep slopes (Akasaka, 1974). Therefore, our predictions were as follows:

(i) Serows were expected to flee less often when in close proximity to escape terrain, such as dense vegetation and steep slopes, and during low-visibility seasons, because these physical environments provide greater security against predators.
(ii) Given the little sexual dimorphism of this species, barren females and adult males were expected to flee with similar probability and to display no difference in habitat use.
(iii) As a direct consequence of kid presence and thus an increased perception of predation risk, females with a kid were expected to flee more often than other group types, and were also expected to utilize safety habitat more often than other group types.

2. Materials and methods

2.1. Study area

The study was performed on the south-facing slope of Mount Asama, Nagano Prefecture, central Japan (36°38′N, 138°47′E); the area covered approximately 210 ha at an elevation of 1200–1600 m. The area is covered with snow (10–100 cm deep) for three months of the year, from late December to March. Vegetation in the study area primarily consists of plantations of Japanese larch (*Larix kaempferi*), evergreen forests of Japanese red pine (*Pinus densiflora*), and, to a lesser extent, secondary deciduous forests of Mongolian oak (*Quercus crispula*) and white birch (*Betula platyphylla*). Cutover areas were patchily distributed and comprised approximately one-fifth of the study area. The understory mostly consisted of dwarf bamboo (*Sasa nipponica*) and shrub thickets. We divided the habitat structure into open (i.e., areas of clearcut logging or dwarf bamboos) and closed (areas of shrub thickets) communities. The open and closed habitats, respectively, accounted for 48.1% and 51.9% of the study area. Slope obliquity of the area ranged from 0° to 39.2° (average slope 12.1°). We drew a slope map of the study area and conducted analyses with Geographic Information System (GIS) software (Environmental Systems Research Institute, 1992); for the analysis, a 50-m digital elevation model was resampled to a 250-m grid cell size to delineate three terrain types: obliquity < 10° (“flat area”), 10–20° (“mid-slope area”), and > 20° (“steep-slope area”). The flat, mid-slope, and steep-slope areas accounted for 23.4%, 63.8%, and 12.8% of the study area, respectively. Because leaves fall in October and do not regrow until April (here, referred to as the non-growing season), visibility is greater during this season than in the growing season, from May to September. The growing season is consistent with periods of parturition and lactation in the serows (nursery season), and the non-growing season is consistent with periods of rut and pregnancy (non-nursery season).

2.2. Japanese serow population

To identify individual serows in the population, we used variations in natural features such as shapes of the horns, torn ears, facial scars, and body colors. Sexing was mainly by observation of the external genitalia (Kishimoto, 1988). We classified individuals into four age classes by horn shape (Kishimoto, 1988): kids, yearlings, subadults (in their 2nd year), and adults (age 3 years or more). We recorded 9 adult and 6 juvenile (< 2 years old) serows during the approximately four-year study period. All of the identified juveniles disappeared from our study areas before aging into adults, either by dispersion or death. The average population density ± SD was 4.5 ± 0.5 individuals km^{-2}, and the average sex ratio of adult males to adult females in the population was 1.0 ± 0.3.

2.3. Data correction and definition of variables

We conducted field observations for 163 days, from October 2011 to May 2015. We walked throughout the study area in the daytime, and recorded our trail length in each habitat structure and terrain type. The observation time and trail length per day were arbitrary. We expressed observation effort in each habitat structure and terrain type in terms of walking distance. Observations were conducted mainly from 10 a.m. to 4 pm and did not include dawn and dusk. We observed the serows through binoculars (×10) or spotting scopes (×25–50), and the range of observation distances was approximately 15–80 m. Distances between the serows and the observer were recorded by eye and a digital distance meter. When we encountered serows, we stopped and began our observations. The serows were already alert to the presence of an observer in almost all encounters. When the serows did not perceive the observer, we continued observations until they did, and we also recorded the animal’s behavior and other data items after the observer was perceived. We recorded the habitat structure (open or closed), terrain type (flat area, mid-slope area, or steep-slope area), observation distance, group size, group type, individual IDs, and flight response. The observation distances were classified as: 0–15 m (“near distance”), 16–40 m (“mid-distance”), and > 40 m (“far distance”). A group was defined as when individuals were within 20 m of each other. Group types were classified as: solitary adult male, solitary adult female, solitary juvenile (0–2 years old), mother–kid pair, adult male–female pair, and male–female–kid trio. We classified the flight response as: (1) no flight (no individual in the group fled) or (2) flight (all individuals in the group fled). Flight was defined as running away and leaving the area entirely, whereas foraging, resting, or walking was regarded as no

flight. Instances of flight usually occurred immediately, within 10 s of being spotted (Takada et al., 2018).

Additionally, some of the serow sightings analyzed in this study were published in Takada et al. (2018), and we reevaluated these data. We tested whether the flight response of the serows was affected by any of the following five factors:

1 Terrain type (flat area, mid-slope area, or steep-slope area)
2 Habitat structure (open or closed)
3 Season (growing season or non-growing season)
4 Observation distance (near distance, mid-distance, or far distance)
5 Group type (solitary adult male, solitary adult female, solitary juvenile, mother–kid pair, adult male–female pair, or male–female–kid trio).

2.4. Statistical analyses

We completed the following analyses in R version 3.4.1 (R Core Team, 2017). To test the effects of terrain type, habitat structure, season, observation distance, and group type on the ungulate's flight response, we used the probability of flight as our dependent variable (1 = flight, 0 = no flight) 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 terrain type, habitat structure, season, observation distance, and group type. IDs were used as a random effect to minimize the influence of variation among individuals. A likelihood ratio test (LRT) was used to test differences in the probability of flight among the terrain types (flat or mid-slope areas versus steep-slope area), habitat structures (open versus closed), seasons (growing versus non-growing), observation distance (near distance or mid-distance versus far distance), and group types (solitary adult male, solitary adult female, solitary juvenile, mother–kid pair, or adult male–female pair, versus male–female–kid trio). All significance tests referred to the type-II analysis with the package 'car' (Fox and Weisberg, 2011). We performed Wald tests to assess whether the effect of every factor included in the LRT was statistically significant.

We also tested the effects of individual differences in the ungulate's flight response in the situation where the most individuals could be observed (the combination of terrain type, habitat structure, and season). We used the probability of flight as our dependent variable (1 = flight, 0 = no flight) and fit a generalized linear model (GLM) with a logit-link function, binomial error distribution, and individual IDs as the fixed term. We also used an LRT to test differences in the probability of flight among the IDs.

To test whether habitat use was different among the group types, we fit the conditional logistic regression model in the analysis using the package 'nnet' (Venables and Ripley, 2002). The habitat types (flat–open, flat–closed, mid–open, mid–closed, steep–open, and steep–closed) where serows were sighted were used as the dependent variable, and the group types (solitary adult male, solitary adult female, solitary juvenile, mother–kid pair, adult male–female pair, versus male–female–kid trio) were used as the fixed effect. We performed a LRT to assess whether habitat use differed among the group types. When habitat use significantly differed among group types, we calculated habitat selection indices (Manly et al., 2002) for each group type. When habitat use did not significantly differ among the group types, we calculated habitat selection indices regardless of the group type using pooled data for all group types. Habitat selection indices were calculated by measuring the relationship between habitat use and estimates of habitat availability (Manly et al., 2002). Confidence intervals of the selection index were estimated, as described below, to statistically test whether the serows used the habitat randomly. Manly's selection indices (*wi*) were calculated as:

$$wi = ri / ni$$

where *ri* is the ratio of the number of sightings of serows in habitat *i* to the number of sightings of all serows (sightings in habitat *i* / all sightings), and *ni* is the ratio of the length walked in habitat *i* to the total walking length (walking length in habitat *i* / total walking length). The Bonferroni confidence interval of *wi* is given by:

$$wi \pm Z_{(\alpha/2)} \times SE(wi).$$

Confidence intervals overlapping 1 indicated that serows used that habitat randomly; confidence intervals with a minimum limit of > 1 indicated significant habitat selection; confidence intervals with a maximum limit of < 1 indicated significant habitat avoidance (Manly et al., 2002). The value of $Z_{(\alpha/2)}$ was set at 2.58.

3. Results

3.1. Flight response

A total of 335 sightings were recorded. The serows were mostly solitary (81.8%). In the remaining 18.2% of sightings, 17.3% consisted of groups of two animals, which were typically one mother with one offspring or an adult male–female pair; and 0.9% of the sightings were of three animals that consisted of one adult male–female pair with one offspring.

Overall, 62.7% of the serows fled and 37.3% did not flee. The LRT indicated that the flight response was significantly associated with each of the four variables: terrain type (GLMMs, LRT, $\chi^2 = 16.1$, df = 2, $P < 0.001$), habitat structure (GLMMs, LRT, $\chi^2 = 14.7$, df = 1, $P < 0.001$), season (GLMMs, LRT, $\chi^2 = 27.3$, df = 1, $P < 0.001$), and group type (GLMMs, LRT, $\chi^2 = 14.9$, df = 5, $P < 0.05$). The relationships between these variables and the percentage of serows that took flight or did not flee is shown in Table 1. Serows fled significantly more often in flat and mid-slope areas than in steep-slope area (GLMMs, Wald test, SE = 0.4, z = −3.3, $P < 0.001$). Serows fled significantly more often in open than in closed shrub communities (GLMMs, Wald test, SE = 0.3, z = 3.8, $P < 0.001$) and in the non-growing season than in the growing season (GLMMs, Wald test, SE = 0.3, z = −5.2, $P < 0.001$). Mother–kid pairs fled significantly more often than other group types (GLMMs, Wald test, SE = 0.1.2, z = 3.0, $P < 0.01$).

Table 1
The flight or no flight response (expressed as percentages) of Japanese serow (*Capricornis crispus*) in each terrain type, habitat structure, season, and among group types. Flight = all individuals in the groups fled; No flight = no individuals in the groups fled. Flat area = obliquity < 10°; Mid-slope area = 10–20°; Steep-slope area = > 20°; Open = areas of clearcut logging and dwarf bamboos; Closed = areas of shrub thickets. The growing season (May–September) and non-growing season (October–April), respectively, correspond to the serow's nursery season (periods of parturition and lactation) and non-nursery season (periods of rut and pregnancy).

	Number of sightings	Flight	No flight
Terrain type			
Flat area	48	83.8	16.2
Mid-slope area	95	70.5	29.5
Steep-slope area	192	53.6	46.4
Habitat structure			
Open	103	72.8	27.2
Closed	232	58.2	41.8
Season			
Growing (nursery)	147	49.0	51.0
Non-growing (non-nursery)	188	73.4	26.6
Group type			
Solitary adult male	129	50.4	49.6
Solitary adult female	102	63.7	36.3
Solitary juvenile	43	62.8	37.2
Adult male–female pair	34	79.4	20.6
Mother–kid pair	24	95.8	4.2
Adult male–female–kid trio	3	100	0

Table 2
The flight or no-flight response (expressed as percentages) of each individual Japanese serow (*Capricornis crispus*) in the combined situation of steep-slope area (obliquity > 20°), closed habitat (shrub thickets), and during the growing season (May–September). Flight = all individuals in the groups fled; No flight = no individuals in the groups fled.

Group composition	ID	N	Flight	No flight
Solitary male	M1	6	33.3	66.6
	M2	7	0	100
	M3	8	25	75
	M4	2	50	50
Solitary female	F1	5	40	60
	F2	5	40	60
	F3	6	0	100
	F4	2	50	50
Solitary juvenile	K1	2	50	50
	K2	2	0	100
	K3	2	100	0
	K4	1	0	100
	K5	2	50	50
	K6	1	0	100
Adult male–female pair	M1-F1	1	100	0
	M2-F2	1	0	100
Mother–kid pair	F1-K1	1	100	0
	F2-K2	2	100	0
	F1-K3	2	100	0
	F3-K4	3	66.6	33.3

Conversely, the LRT indicated that the observation distance did not influence the flight response (GLMMs, LRT, $\chi^2 = 4.3$, df = 2, $P = 0.1$).

The situation where the most individuals were observed was in the combination of steep-slope area, closed habitat, and during the growing season (Table 2). The LRT indicated that the flight response was significantly associated with IDs (GLM, LRT, $\chi^2 = 34.8$, df = 19, $P < 0.05$), which meant that individuals differed in their flight response. For all females, the flight frequency was higher when kids were present than when kids were absent (Table 2).

3.2. Habitat use

The total distance walked during the study period was 789.5 km; Table 3 shows the walking distance in each terrain type and habitat structure. All group types of serows were most often sighted in steep–closed habitat (> 31%; Fig. 1). There was no significant difference among group types of the number of sightings in each habitat (LRT, $\chi^2 = 18.8$, df = 25, $P = 0.8$). Selection indices were calculated regardless of group types, using data pooled for all group types (Table 4). Selection indices indicated that serows selected the steep–closed (terrain–habitat) combination significantly more often (Table 4); furthermore, the indices revealed a significant tendency for serows to avoid the flat–open and mid–open habitats, but to use the flat–closed, mid–closed, and open–steep habitats randomly (Table 4).

Table 3
Observer walking distances (km) in each terrain type and habitat structure on the south-facing slope of Mount Asama, central Japan, during 163 days of study effort. Flat = obliquity to < 10°; Mid-slope = 10–20°; Steep slope = > 20°; Open = areas of clearcut logging and dwarf bamboos; Closed = areas of shrub thickets.

Terrain type	Flat area	Mid-slope area	Steep-slope area	Total
Habitat structure				
Open	104.1	99.8	130.4	334.3
Closed	99.9	167.6	187.7	455.2
Total	204	267.4	318.1	789.5

4. Discussion

In this study, the Japanese serows were mainly solitary, a tendency similarly found in several previous studies (e.g. Akasaka and Maruyama, 1977; Sakurai, 1981; Ochiai, 1993; Kishimoto and Kawamichi, 1996). More than half of the observed serows fled on contact with a human observer; comparable proportions were observed by Recarte et al. (1998) for fallow deer, by Mrlik (1990) for roe deer, and by Lagory (1987) for white-tailed deer. Our findings indicate that the physical environment, namely terrain type, habitat structure and season, influences the flight response of Japanese serow. Moreover, the data indicate that the social environment (i.e. group type) also influences the flight response of serow.

One frequently considered aspect of the context of flight behavior is the security provided by an animal's immediate physical environment (Stankowich, 2008). Closed settings provide security (Rowe-Rowe, 1974; de Boer et al., 2004) by offering the possibility to escape detection by predators (Takada et al., 2018). In addition, forest-dwelling ungulates like the serow are thought to use crypsis as an anti-predator strategy (Brashares et al., 2000; Stoner et al., 2003; Caro et al., 2004; Takada et al., 2018); accordingly, closed settings are thought to importantly reduce the predation risk for forest-dwelling ungulates (Estes, 1974; Jarman, 1974). Likewise, we observed that serows fled less often in closed habitat and during the growing season. Steep-sloped terrain may also provide security against predators (Bleich, 1999), particularly for mountain-dwelling ungulates (Schaller, 1977; Festa-Bianchet and Côté, 2007). Predator encounters and attacks are less of a risk in these areas where mountain ungulates can move more easily than the predator (Bleich et al., 1997; Frid, 1997; Bleich, 1999; Corti and Shackleton, 2002); thus, fleeing to steeper terrain is an important anti-predator strategy in many mountain ungulates, including Japanese serow (Akasaka, 1974; Mishra and Johnsingh, 1996; Grignolio et al., 2007; Hamel and Côté, 2007). We similarly observed that serows in a steep-slope area fled less often. Together, these findings support our first prediction (i) and suggest that steep slopes and low-visibility conditions provide the Japanese serow with greater security against predators. In addition, we observed that serows selectively used the steep–closed terrain–habitat combination which provides relatively good security, and avoided the flat–open and mid–open habitats which provide less security for serows. This result suggests that serows select more secure habitat to decrease their predation risk.

In gregarious ungulates, sexual differences in vulnerability and reproductive strategy are thought to cause differences in flight response according to sex (Ciuti et al., 2008). Gregarious ungulates mainly have a polygamy or promiscuity mating system (Estes, 1974) and display sexual body-size dimorphism (Weckerly, 1998; Loison et al., 1999; Pérez-Barbería et al., 2002). Smaller-sized females seem to be more vulnerable to predators than larger males (Ruckstuhl and Neuhaus, 2002). To maximize their reproductive success, males must maximize their body condition and mate with multiple females, whereas females should survive longer periods and maximize the survival of their offspring (Main et al., 1996; Ruckstuhl and Neuhaus, 2002; Mooring et al., 2003). Accordingly, more vulnerable and sensitive females showed a stronger flight response compared with males (Ciuti et al., 2008). Based on such background information, females were thought to select secure settings more often than males (Berger, 1991; Mysterud, 2000; Mooring et al., 2003; Grignolio et al., 2007). In contrast, our results reveal no sexual differences in flight response and habitat use by a solitary ungulate, the Japanese serow. The serow has little sexual dimorphism in body size (males ≥3 years old: mean body weight ± SD, 35.9 ± 4.5 kg; females ≥3 years old: 38.4 ± 5.0 kg; females/males body-weight ratio = 1.06 [Miura, 1986]) and morphology (Ochiai et al., 2015), thus there is thought to be no difference in vulnerability based on the sexes. Additionally, the serow exhibits intra-sexual territoriality and a monogamous mating system (Kishimoto and Kawamichi, 1996; Ochiai and Susaki, 2002). To maximize their reproductive

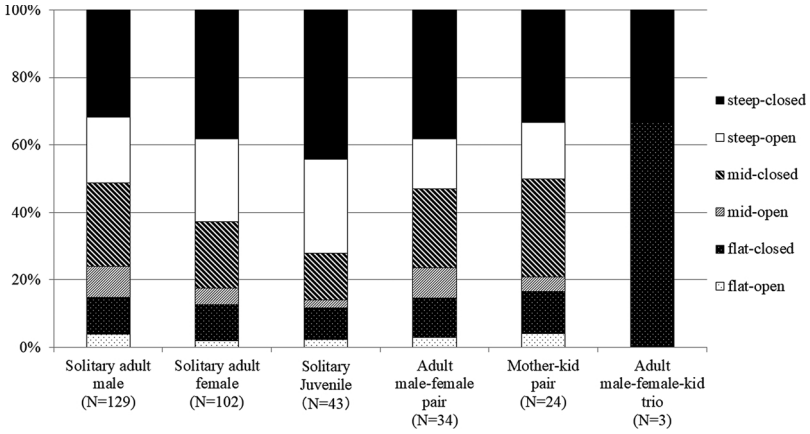

Fig. 1. Observation frequency (%) of each group type of Japanese serows (*Capricornis crispus*) in each habitat type (terrain–habitat combination), as sighted on the south-facing slope of Mount Asama, central Japan, between October 2011 and May 2015. Flat = obliquity to < 10°; Mid-slope = 10–20°; Steep slope = > 20°; Open = areas of clearcut logging and dwarf bamboos; Closed = areas of shrub thickets.

Table 4
Manly's selection index (*wi*) and statistical results of the Japanese serow's presence in each habitat on the south-facing slope of Mount Asama, Japan, based on sightings over the approximately 4-year study period. Flat = obliquity to < 10°; Mid-slope = 10–20°; Steep slope = > 20°; Open = areas of clearcut logging and dwarf bamboos; Closed = areas of shrub thickets.

Terrain type	Flat		Mid-slope		Steep slope	
Habitat structure	Open	Closed	Open	Closed	Open	Closed
wi	0.23	0.90	0.52	1.03	1.28	1.52
SE(*wi*)	0.07	0.14	0.11	0.11	0.14	0.11
Bonferroni (high)	0.41	1.25	0.80	1.30	1.63	1.80
Bonferroni (low)	0.04	0.54	0.24	0.75	0.93	1.23

success, males must survive, maintain territory for long periods, and successfully mate exclusively with a single female as it is difficult for them to mate with multiple females (Kishimoto, 2003). A female must also survive, maintain territory for long periods, and maximize survival of her offspring. Thus, we found no significant differences between the sexes in their flight response and habitat use since serows possess little sexual difference in vulnerability and reproductive strategy. These findings support our second prediction (ii) and suggest that a monogamous mating system and undeveloped sexual dimorphism is associated with no differences in the flight response and habitat use between the sexes.

We predicted that females with a kid will flee more often than other group types, since a kid might be more vulnerable than adults (Main et al., 1996), consequently increasing this group type's perception of predation risk. Indeed, our results show that females with a kid fled more often than other group types. These results partially support our prediction (iii) and show that the presence of a kid plays a key role in affecting the flight response in the serow. This result confirms the assumption of the reproductive strategy–predation-risk hypothesis (Mooring et al., 2003), according to which the reproductive success of females is determined by the survival of their offspring, and selective pressure favors those behaviors that reduce predation risk (e.g. quick flight in response to any source of risk for the offspring) (Mooring et al., 2003). Ensuring the survival of their offspring is a high priority for females; accordingly, females with a kid are more likely to react to a potential predator (Schoener, 1971; Ciuti et al., 2008). Even so, we also predicted that females with a kid would utilize secure habitats more often than the other group types. However, there were no differences in habitat use among the group types, thus these results do not entirely support prediction (iii). All group types of serows selected the safest habitat type (steep–closed habitat) and avoided the habitats that provided little security (flat–open and mid–open habitats). This finding is dissimilar to the reports of many previous studies of gregarious ungulates, which showed that females with young offspring used more safety habitat than did males (Bon et al., 1995; Bleich et al., 1997; Corti and Shackleton, 2002; Mooring et al., 2003; Ciuti et al., 2004). Our data indicate that the presence of a kid in a social group does not affect habitat choice in the serow; we speculate that the absence of a difference may be associated with the intra-sexual territoriality of this species. Kishimoto (2003) showed that serows that held territory continuously used more than 80% of their home-range area in a 72-h period. This suggests that it is necessary for an individual to continuously use the entire home range to maintain a territory. Maintaining the territory is essential for reproductive success in both males and females (Kishimoto, 2003). Thus, all territory-holders, including females with a kid, might periodically use a habitat that provides less or little security so as to maintain their entire territory; consequently, this may amount to no differences in habitat use among group types.

In conclusion, the physical environment (particularly terrain and visibility conditions) influences the flight response in Japanese serow, and utilizing steep terrain and low visibility conditions are thought to be an important anti-predator strategy in this species. The effect of the social environment (namely sex and group type) on flight response in the serow differs from that in some gregarious ungulates, and only the presence of a kid affected the serow's flight response. Such differences between species of ungulates are likely associated with differences in sexual dimorphism and social organization, specifically the mating system and territoriality.

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References

Aastrup, P., 2000. Responses of West Greenland caribou to the approach of humans on foot. Polar Res. 19, 83–90.
Akasaka, T., 1974. Japanese serow in the wild. Wildlife 16, 452–458.
Akasaka, T., Maruyama, N., 1977. Social organization and habitat use of Japanese serow in Kasabori. J. Mammal. Soc. Jpn. 7, 87–102.
Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.
Berger, J., 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Anim. Behav. 41, 61–77.
Bleich, V.C., 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. J. Mammal. 80, 283–289.

Bleich, V.C., Bowyer, R.T., Wehausen, J.D., 1997. Sexual segregation in mountain sheep: resources or predation? Wildl. Monogr. 134, 3–50.
Brashares, J.S., Garland, T., Arcese, P., 2000. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behav. Ecol. 11, 452–463.
Bon, R., Joachim, J., Maublanc, M., 1995. Do lambs affect feeding habitat use by lactating female mouflons in spring in areas free of predators? J. Zool. 235, 43–51.
Bullock, D., Kerridge, F., Hanlon, A., Arnold, R., 1993. Short-term responses of deer to recreational disturbances in two deer parks. J. Zool. 230, 327–332.
Caro, T., Graham, C., Stoner, C., Vargas, J., 2004. Adaptive significance of antipredator behaviour in artiodactyls. Anim. Behav. 67, 205–228.
Ciuti, S., Davini, S., Luccarini, S., Apollonio, M., 2004. Could the predation risk hypothesis explain large-scale spatial sexual segregation in fallow deer (*Dama dama*)? Behav. Ecol. Sociobiol. (Print) 56, 552–564.
Ciuti, S., Pipia, A., Ghiandai, F., Grignolio, S., Apollonio, M., 2008. The key role of lamb presence in affecting flight response in Sardinian mouflon (*Ovis orientalis musimon*). Behav. Process. 77, 408–412.
Corti, P., Shackleton, D.M., 2002. Relationship between predation-risk factors and sexual segregation in Dall's sheep (*Ovis dalli dalli*). Can. J. Zool. 80, 2108–2117.
De Boer, H.Y., Van Breukelen, L., Hootsmans, M.J., Van Wieren, S.E., 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildl. Biol. 10, 35–41.
Estes, R.D., 1974. Social organization of the African Bovidae. In: Geist, V., Walther, F. (Eds.), IUCN Publication mew series No. 24: The Behaviour of Ungulates and Its Relation to Management. IUCN, Morges, pp. 166–205.
Festa-Bianchet, M., Côté, S.D., 2007. Mountain Goats: Ecology, Behavior, and Conservation of an Alpine Ungulate. Island Press, Washington.
Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression. URL. second edn. Sage, Thousand Oaks, CA. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion.
Frid, A., 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. Anim. Behav. 53, 799–808.
Gentry, A.W., 1992. The subfamilies and tribes of the family Bovidae. Mammal. Rev. 22, 1–32.
Grignolio, S., Rossi, I., Bassano, B., Apollonio, M., 2007. Predation risk as a factor affecting sexual segregation in Alpine ibex. J. Mammal. 88, 1488–1497.
Hamel, S., Côté, S., 2007. Habitat use patterns in relation to escape terrain: are alpine ungulate females trading off better foraging sites for safety? Can. J. Zool. 85, 933–943.
Holmern, T., Setsaas, T.H., Melis, C., Tufto, J., Røskaft, E., 2016. Effects of experimental human approaches on escape behavior in Thomson's gazelle (*Eudorcas thomsonii*). Behav. Ecol. 27, 1432–1440.
Horejsi, B.L., 1981. Behavioral response of barren ground caribou to a moving vehicle. Arctic 34, 180–185.
Jarman, P., 1974. The social organisation of antelope in relation to their ecology. Behaviour 48, 215–267.
Kishimoto, R., 1988. Age and sex determination of the Japanese serow *Capricornis crispus* in the field study. J. Mammal. Soc. Jpn. 13, 51–58.
Kishimoto, R., 2003. Monogamy: mating strategies and partnerships in birds, humans and other mammals. Social Monogamy and Social Polygyny in a Solitary Ungulate, the Japanese Serow (*Capricornis Crispus*). Cambridge University Press, Cambridge, UK, pp. 147–158.
Kishimoto, R., Kawamichi, T., 1996. Territoriality and monogamous pairs in a solitary ungulate, the Japanese serow, Capricornis crispus. Anim. Behav. 52, 673–682.
LaGory, K.E., 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. Anim. Behav. 35, 20–25.
Langbein, J., Putman, R., 1992. Behavioural responses of park red and fallow deer to disturbance and effects on population performance. Anim. Welfare 1, 19–38.
Loison, A., Gaillard, J., Pélabon, C., Yoccoz, N.G., 1999. What factors shape sexual size dimorphism in ungulates? Evol. Ecol. Res. 1, 611–633.
MacArthur, R.A., Geist, V., Johnston, R.H., 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. J. Wildl. Manage. 46, 351–358.
Main, M.B., Weckerly, F.W., Bleich, V.C., 1996. Sexual segregation in ungulates: new directions for research. J. Mammal. 77, 449–461.
Manly, B., McDonald, L., Thomas, D., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Springer Science & Business Media.
McLaren, M.A., Green, J.E., 1985. The reactions of muskoxen to snowmobile harassment. Arctic 38, 188–193.
Mishra, C., Johnsingh, A., 1996. On habitat selection by the goral *Nemorhaedus goral bedfordi* (Bovidae, Artiodactyla). J. Zool. 240, 573–580.
Miura, S., 1986. Body and horn growth patterns in the Japanese serow, Capricornis crispus. J. Mammal. Soc. Jpn. 11, 1–13.
Mooring, M.S., Fitzpatrick, T.A., Benjamin, J.E., Fraser, I.C., Nishihira, T.T., Reisig, D.D., Rominger, E.M., 2003. Sexual segregation in desert bighorn sheep (*Ovis canadensis mexicana*). Behaviour 140, 183–207.
Mrlik, V., 1990. Disturbance of the roe deer (*Capreolus capreolus*) in agrocoenoses of Southern Moravia. Folia Zool. Brno 39, 25–35.
Mysterud, A., 2000. The relationship between ecological segregation and sexual body size dimorphism in large herbivores. Oecologia 124, 40–54.
Ochiai, K., 1993. Dynamics of Population Density and Social Interrelation in the Japanese Serow, Capricornis crispus. Ph.D. thesis. Kyusyu University, Fukuoka.
Ochiai, K., et al., 2015. *Capricornis crispus* (Temminck, 1836). In: Ohdachi, S.D. (Ed.), The Wild Mammals of Japan, second edition. Shoukadoh Book Sellers and the Mammalogical Society of Japan, Kyoto, pp. 314–317.
Ochiai, K., Susaki, K., 2002. Effects of territoriality on population density in the Japanese serow (*Capricornis crispus*). J. Mammal. 83, 964–972.
Pérez-Barbería, F.J., Gordon, I., Pagel, M., 2002. The origins of sexual dimorphism in body size in ungulates. Evolution 56, 1276–1285.
Core Team, R., 2017. R: a Language and Environment for Statistical Computing. URL, Vienna. R foundation for statistical computing, Austria. https://www.R-project.org/.
Recarte, J., Vincent, J., Hewison, A., 1998. Flight responses of park fallow deer to the human observer. Behav. Process. 44, 65–72.
Rowe-Rowe, D., 1974. Flight behaviour and flight distances of blesbok. Ethology 34, 208–211.
Ruckstuhl, K.E., Neuhaus, P., 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. Biol. Rev. 77, 77–96.
Sakurai, M., 1981. Socio-ecological study of the Japanese serow, *Capricornis crispus* (Temminck) (Mammalia: bovidae) with reference to the flexibility of its social structure. Ecol. Physiol. Jpn. 18, 163–212.
Schaller, G.B., 1977. Mountain Monarchs. Wild Sheep and Goats of the Himalaya. University of Chicago Press, Chicago, Illinois.
Schoener, T.W., 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2, 369–404.
Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173.
Stankowich, T., Reimers, E., 2015. Mammals. In: Cooper JrE.W., Blumstein, T.D. (Eds.), Escaping from Predators: An Integrative View of escape Decisions. Cambridge University Press, Cambridge, UK, pp. 63–87.
Stoner, C., Caro, T., Graham, C., 2003. Ecological and behavioral correlates of coloration in artiodactyls: systematic analyses of conventional hypotheses. Behav. Ecol. 14, 823–840.
Takada, H., Nakamura, K., Takatsuki, S., Minami, M., 2018. Freezing behavior of the Japanese serow (*Capricornis crispus*) in relation to habitat and group size. Mamm. Res. 63, 107–112.
Taraborelli, P., Gregorio, P., Moreno, P., Novaro, A., Carmanchahi, P., 2012. Cooperative vigilance: the guanaco's (*Lama guanicoe*) key antipredator mechanism. Behav. Process. 91, 82–89.
Thompson, V.D., 1989. Behavioral response of 12 ungulate species in captivity to the presence of humans. Zoo Biol. 8, 275–297.
Tyler, N., 1991. Short-term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. Biol. Conserv. 56, 179–194.
Vandenheede, M., Bouissou, M., 1993. Sex differences in fear reactions in sheep. Appl. Anim. Behav. Sci. 37, 39–55.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics With S, fourth edition. Springer, New York.
Weckerly, F.W., 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. J. Mammal. 79, 33–52.