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Gait Patterns in Snow—a Possible Criterion to Differentiate Sika Deer and Japanese Serow Tracks

Authors: Enari, Hiroto, Akamatsu, Moeri, Yamashita, Junpei, Kanayama, Nozomu, Iida, Motoki, et al.

Gait patterns in snow—a possible criterion to differentiate sika deer and Japanese serow tracks

Hiroto Enari*, Moeri Akamatsu, Junpei Yamashita, Nozomu Kanayama, Motoki Iida and Haruka S. Enari

Yamagata University, 1-23 Wakabamachi, Tsuruoka, Yamagata 997-8555, Japan

Abstract.   There is a compelling need to develop user-friendly and sensitive techniques to monitor sika deer (*Cervus nippon*) populations in snowy regions, where initial stages of deer invasion have been observed. In snow, we can easily detect footsteps of terrestrial mammals, which often serve as a useful index of population size. Here, we examined the possibility of identifying tracks with similar hoof prints left by two sympatric ungulates, sika deer and Japanese serow (*Capricornis crispus*), using gait patterns. We then recorded tracks of free-ranging deer and serows on the snow by following ~200-km survey routes in the Tohoku region. We successfully recorded the gait patterns of 27 deer and 34 serows. Our key findings were as follows: 1) the step width of deer tracks (mean and *SE*, 20.3 ± 0.7 cm) was substantially narrower than that of serow tracks (26.9 ± 0.8 cm); 2) step width was less sensitive to body size and ground conditions for both species; and 3) the step width of 22.5 cm became an optimal threshold to maintain a reasonable classification accuracy ($> 80\%$) for both species. Thus, the gait patterns serve as a possible criterion for identifying the tracks of these two ungulates.

Key words: *Capricornis crispus*, *Cervus nippon*, hoof print, population monitoring, tracking.

For most ungulate species, the energy cost of locomotion in snow increases exponentially as the sinking depth approaches chest height (Fancy and White 1985). In the case of sika deer (*Cervus nippon*) distributed in the Far East, > 50-cm-deep snow cover largely regulates their locomotion, and consequently, they rarely occupy regions with > 100-cm-deep snow cover because of their morphological foot features (Takatsuki 1992). Contrary to this widely believed theory, however, the distribution of sika deer in Japan has now expanded to include cool-temperate forests with snow exceeding 2 m in depth (Ministry of the Environment 2021). Moreover, deer population densities observed in some snowy regions of northern Japan have already grown to the point where irreversible vegetation loss has occurred through heavy herbivory (Enari and Enari 2020). For effective prevention of the rapid increase in sika deer populations, especially in snowy regions, user-friendly techniques for population monitoring during the initial stage of deer invasion (i.e., the lag phase in population dynamics) are now required (Enari et al. 2017, 2019).

In snowy regions, we can easily detect footsteps of various ground-dwelling mammals on the snow; these are useful indices to assess their abundance and habitat use (Becker et al. 1998; Enari and Sakamaki 2011, 2012; Kojola et al. 2014; Honda et al. 2022). In the three main islands of Japan (i.e., Honshu, Shikoku, and Kyushu), three ungulate species sympatrically occur under natural conditions: sika deer, Japanese serow (*Capricornis crispus*), and wild boar (*Sus scrofa*) (Ohdachi et al. 2015). Among these, tracks on the snow left by boars are frequently identifiable. This is because they leave species-specific hoof prints formed by the set of hoof and dew claws and often create U-shaped gutters while moving by dragging their stomach on the deep snow because of their short chest height (Seki et al. 2015; Fig. 1a). During early winter with heavy snowfall, most deer tracks are also distinguishable because they tread down fresh snow and develop narrow trails by repeatedly using the same tracks (Minamino et al. 2007; Fig. 1b), but serows (i.e., ungulates with hoof prints similar to those of deer) rarely do (Hayashi 1997). However, such distinct deer

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Fig. 1. Typical gait patterns in the snow by different ungulates, photographed in northern Japan: (a) wild boar, (b) sika deer (repeated use), (c) sika deer (single use), and (d) Japanese serow.

Fig. 2. Method used to measure gait patterns of ungulates in the snow.

trails are rarely left during late winter when the snow surface becomes hard due to repeated melting and refreezing. As a result, single-use tracks of sika deer and serow cannot be distinguished on the basis of their hoof prints (Seki et al. 2015; Fig. 1c and 1d).

Here, we examined the possibility of identifying the species of ungulate using gait patterns. Indigenous knowledge among traditional hunters in northern Japan holds that sika deer leave narrow tracks because of their specific gait pattern, with the hoof prints closer together than serows. We tested this hypothesis by comparing the gait patterns of the two ungulates in various fields in northern Japan and discussed the efficacy of deer population monitoring using tracks in the snow.

Materials and methods

Data sampling

We recorded the gait patterns of free-ranging deer and serows by following survey routes (total length ~200 km) on skis during the late winter (late February–March) of
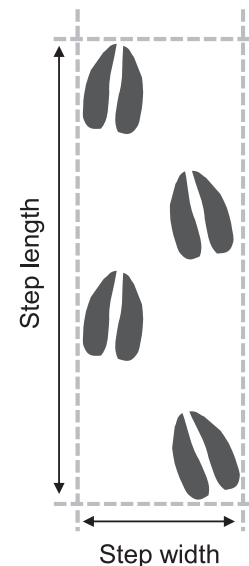
2022. We set these routes in the Shirakami mountains (41°N, 140°E; length ~30 km), Hakkoda mountains (40°N, 141°E; ~20 km), Chokai mountains (39°N, 140°E; ~10 km), and Aizu mountains (37°N, 139°E; ~130 km). We measured snow depth every ~1 km on each route using a graduated snow probe; the snow depth ranged from 1.0–2.5 m. Whereas serows commonly occupy every mountain range, wide distribution of sika deer has only been observed in the Aizu mountains (Ministry of the Environment 2021).

We recorded hoof prints left in the snow only under the following conditions: (1) fresh tracks with sharp hoof prints, (2) single-use tracks, (3) tracks left on flat terrain, (4) tracks made while walking (i.e., not gallops made while running), and (5) tracks left by individuals of all sexes and ages, except for yearlings. The body size of both ungulate species commonly shows a sharp growth curve until two years of age, regardless of sex differences (Takatsuki 2006; Ochiai 2016), and therefore, we did not identify sex and age of each track. We judged small hoof prints emerging concurrently with normal-sized ones (estimated as parents') as those of yearlings. When detecting appropriate tracks, we traced them and confirmed species identification with any of the following evidences: (1) visual sighting of animals; (2) feces—we judged > 200 sticky fecal pellets per fecal pile as serow's and < 100 non-sticky fecal pellets per pile as deer's according to Yamashiro et al. (2013); (3) hair—the winter pelage of deer is easily broken because its cortex gets

thin during winters, but that of serow is not (Kondo 2013); and (4) bite marks on tree bark—sika deer feed extensively on bark (Yokoyama et al. 1996) but serows rarely do (Ochiai 1999). Where at least one piece of evidence was available, gait patterns were recorded by measuring step width and length (i.e., the length of three steps as an approximate index of body size) (Fig. 2). We measured the gait patterns only once from an independent stretch of tracks, which were located more than 300 m from each other, to avoid pseudo-replication from the same individual.

Analysis

To determine the factors influencing step width for each species, we initially evaluated correlations among step width, step length, and snow depth at the tracks measured. In addition, we checked for regional differences in step width. Aside from the Aizu mountains, there have been only limited number of heavy snow regions where the population density of deer was sufficiently high to evaluate their gait patterns thus far. Therefore, we evaluated the regional differences only for serows by using one-way analysis of variance (ANOVA).

We then built a binomial logistic regression model to test the current hypothesis by evaluating whether step width served as a valid criterion for species identification. For this purpose, we assigned mammal species (1, deer; 0, serow) as an objective variable and step width as an explanatory variable. We conducted this analysis using the *glm* function in *R* v.4.0.2 (R Development Core Team 2021). To assess the predictive ability of the model, we used the area under the curve (AUC) of the receiver operating characteristic (ROC) approach using the *roc* function of the package, *pROC*; values range from ≤ 0.5 (no predictive ability) to 1.0 (perfect prediction) and > 0.8 indicates robust model prediction (Araújo et al. 2005). Based on this ROC analysis, we calculated an optimal cutoff value to identify a reasonable threshold of step width to differentiate sika deer from serows. For this calculation, we assigned the ROC point closest to the top-left part of the plot (i.e., perfect sensitivity or specificity) and calculated the positive prediction value (PPV, or the proportion of correctly classified instances among deer tracks predicted by the model) and negative prediction value (NPV, or the proportion of correctly classified instances among serow tracks predicted by the model) at the cutoff value. The package, *ggpot2*, in *R* was used to represent the graphical results of all these analyses.

Results

We succeeded in recording the gait patterns of 27 deer and 34 serows with valid evidence. The distribution of step width of deer and serow indicated differences (Fig. 3). All indices (mean, median, and frequency, shown by kernel density peak) of deer were lower than those of serows.

The correlation matrix showed no significant relationships among step width, step length, and snow depth: specifically, correlation coefficients (r) were 0.00 ($P =$ 0.98) at "step width × step length" and 0.38 ($P = 0.05$) at "step width × snow depth" for deer, and –0.11 ($P =$ 0.55) at "step width × step length" and –0.26 ($P = 0.14$)
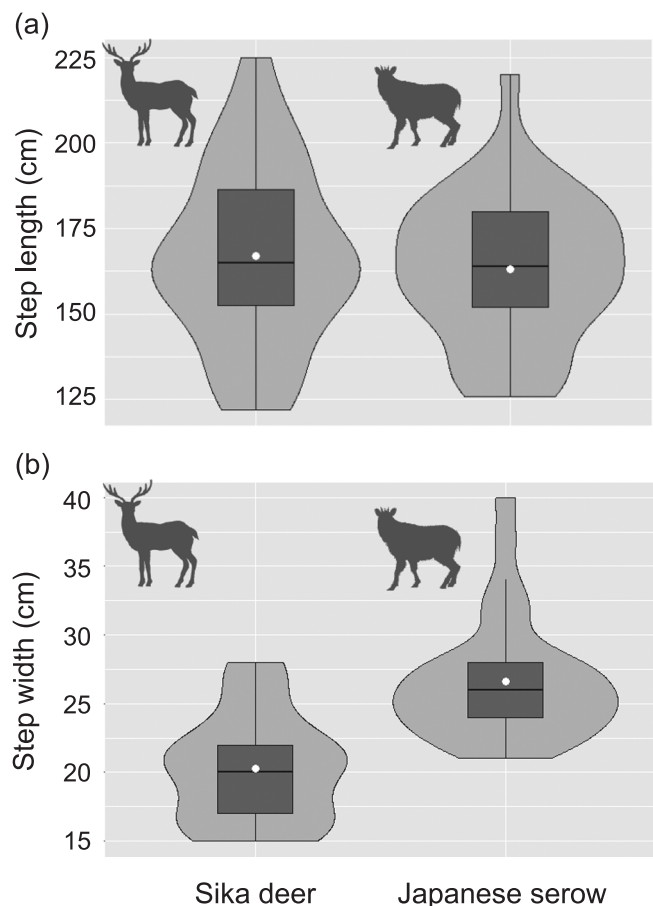

Fig. 3. Violin plots representing frequency distributions of (a) step length and (b) step width in sika deer ($n = 27$, with 25 individuals from the Aizu mountains and two from the Shirakami mountains) and Japanese serow ($n = 34$, with 15 individuals from the Aizu mountains, nine from the Shirakami mountains, eight from the Hakkoda mountains, and two from the Chokai mountains) using Gaussian-based kernel density. Box plots and white spots inside the plots show those variations (median, range, and 25th–75th percentiles) and mean values, respectively.
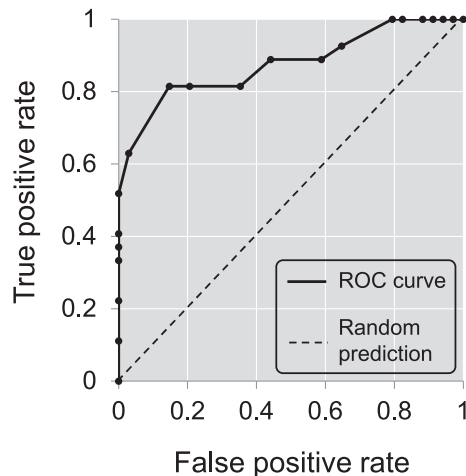
Fig. 4. Receiver operating characteristic (ROC) plot of the binomial logistic regression model for species discrimination based on the gait patterns of sika deer and Japanese serow.

at "step width × snow depth" for serows. This means that step width was rarely influenced by body size and ground conditions in both species. We then checked the regional differences in step width of serows among the different mountains (excluding the Chokai mountains with small samples; Fig. 3) and found no significant differences among them ($F_{(2, 29)} = 2.21$, $P = 0.13$, effect size $\eta^2 = 0.13$).

We successfully built a highly predictive regression model to indicate the discriminant criterion of the gait pattern; the mean and 95% confidence interval of the AUC was 0.87 and 0.78–0.97, respectively (Fig. 4). The coefficients (mean ± *SE*) of intercept and step width were 10.57 ± 2.86 ($P < 0.001$) and –0.46 ± 0.12 ($P < 0.001$), respectively. This means that the probability of tracks being identified as serow increases as the step width increases. The ROC curve provided the optimal cutoff value to identify a threshold step width of 22.5 cm. According to this cutoff value, the PPV (i.e., accuracy rate for deer tracks) and NPV (i.e., accuracy rate for serow tracks) were 81.5% and 84.8%, respectively.

Discussion

Our findings support the indigenous knowledge (i.e., the current hypothesis) that distinct differences in gait pattern exists in sika deer and serows when the snow depth exceeds 1 m (Fig. 3). Given that the step width was less influenced by body size for both species when excluding tracks of yearlings, the step width (threshold at 22.5 cm) likely serves as a possible criterion for spe-

cies identification to maintain a reasonable classification accuracy of > 80%. Of course, we might further improve the accuracy by using more discriminant criteria. However, considering that simple techniques are preferable for population monitoring to maintain continuity and enhance intra- and inter-observer reliability (Morrison 2009), our ready-to-use criterion would be useful, especially for on-site practitioners.

Our study cannot provide any direct evidence of why deer adopt these specific gait patterns in deep snow. For animals in bipedal locomotion, step width is generally sensitive to movement speed and decreases with increasing speed (Bishop et al. 2017). Unfortunately, to the best of our knowledge, there have been no behavioral or morphological rationales regarding the differences in step width of quadrupedal animals thus far. However, a reasonable interpretation might be available from an abductive inference derived from well-known interspecies difference relating to antipredator strategies: namely, serows adopt more stable gait patterns by widening step width since they often use steep slopes or cliffs as refuges from predators (Takada et al. 2019), whereas deer prefer enhancing the speed of movement to escape from predators by narrowing step width because they rarely use such terrain (Nowicki and Koganezawa 2001; Seki and Hayama 2021). This possible hypothesis should be a worthwhile challenge for the future.

It should be noted here that the accuracy of this discriminatory criterion is not guaranteed in the absence of hard-packed snow exceeding 1 m in depth. In addition, the present study could not verify the regional differences in morphology of sika deer distributed in heavy snow regions, which might possibly influence the step width. We analyzed the gait patterns of deer mostly recorded in the Aizu mountains, where the deer populations have originated from the Kanto region (Toma et al. 2021). When the deer populations with different origins from that region expand into heavy snow regions in the future, there will be a need to reconfirm the validity of the current discriminatory criterion. Besides, due to the methodological constraint, we could not examine the influence of sex and age differences on step width. Although the discriminatory criterion was less affected by body size, this unexamined issue should be addressed in the future in terms of behavioral or morphological differences according to sex or age.

Finally, users would be encouraged to make a careful judgement by tracing tracks to explore additional evidence for species identification (as shown in "Data

sampling") when the step size observed is very close to the discriminatory criterion.

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