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Article

Do bovids evolve hindquarter markings for anti-predation?

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Abstract

Conspicuous coloration in animals serves many functions such as anti-predation. Anti-predation strategies include motion dazzle and flash behavior. Motion dazzle markings can reduce the probability of being preyed on because the predators misjudge their movement. In flash behavior, prey demonstrate conspicuous cue while fleeing; the predators follow them; however, the prey hide their markings and the predators assume that the prey has vanished. To investigate whether bovids use conspicuous hindquarter markings as an anti-predatory behavior, we undertook phylogenetically controlled analyses to explore under what physiological characteristics and environmental factors bovids might have this color pattern. The results suggested that rump patches and tail markings were more prevalent in bovids living in larger-sized groups, which supports the hypothesis of intraspecific communication. Moreover, we observed the occurrence of conspicuous white hindquarter markings in bovids having smaller body size and living in larger groups, suggesting a motion dazzle function. However, the feature of facultative exposing color patterns (flash markings) was not associated with body size, which was inconsistent with predictions and implied that bovids may not adopt this as an anti-predator strategy. It was concluded that species in bovids with conspicuous white hindquarter markings adopt motion dazzle as an anti-predation strategy while fleeing and escaping from being prey on.

Key words: anti-predation, bovid, flash behavior, hindquarter markings, interspecies communication, motion dazzle.

Color patterns in animals are driven by 3 main functional evolutionary forces: crypsis, signaling (communication), and various physiological considerations (Caro 2005). Conspicuous color patches can be used as intraspecific and interspecific signals. In intraspecific signals, which are between family members, color patches help individuals communicate with each other (Hirth and McCullough 1977). For example, conspicuous white spots behind felids' ears enable intraspecific communication in closed habitats, which is under conditions of poor visibility (Galván 2020). Communication can also be between different species ranging from anti-predation, food acquisition, anti-parasite, and host acquisition (Caro and Allen 2017). For example, conspicuous small markings can be used to attract a predator's attention away from other characteristics that are more advantageous for the detection of the prey (Thayer and Thayer 1909). Contrasting color patterns of some terrestrial carnivores (mammals: carnivores) indicate that they possess toxic anal gland secretions (Stankowich et al. 2011).

Animals usually use blocks of color for communication rather than overall coloration, and markings are usually located on outward-facing parts of the body, such as the ears, face, tail, and rump, related to their ecological and behavioral characteristics (Caro 2005). During the escape, bovids usually face the predator with their hindquarter parts. Therefore, the conspicuous markings on this part may have an anti-predation function. Otherwise, there should be no markings on the hindquarter at all to avoid being detected by predators. The principles of this anti-predatory mechanism include conspicuous body parts to intimidate the predator to stop attacking (Eifler and Eifler 2010), confuse the predator (Palleroni et al. 2005), demonstrating to the predator that it may be futile to continue hunting them (Barbour and Clark 2012), flash behavior (tricking the predator to look for false clues related to their appearance) (Malcolm 1974), or make it difficult for predators to estimate their speed and trajectory (Thayer and Thayer 1909).

Tail marking is common in ungulates specifically in those living in larger groups, open habitats, and are diurnal (Stoner et al. 2003). Tail marking is used as intraspecific signals (Stevens 2005). For example, goitered gazelles *Gazella subgutturosa* (Blank 2018) and white-tailed deer *Odocoileus virginianus* (Lagory 1987) use tail waving and exposing of white rump patches to signal alarm and cohesion to group members, which are displayed mostly by adult females to communicate with their young fawns.

Similarly, rump patch is considered to have a function as physiological regulator (Spinage 1986). The white rump of the bighorn sheep *Ovis canadensis* acts to deflect heat in the desert (Estes 2012). It may be also a sign of support for subordination behavior and has appeasement qualities (Guthrie 1971), coming from the expansion of color in the genital area near the anus to stimulate erotic sentiments in their partner. When used as a warning to members of other species, the rump patch will exhibit different visual patterns along with different ways of swinging the tails to indicate the level of alertness (Alvarez et al. 1976). As an anti-predation strategy, it is also a signal of social cohesion between individuals and the group when fleeing (Hirth and McCullough 1977).

The conspicuousness of tail markings and rump patches in bovids may indicate an anti-predatory function. It has been shown that conspicuous color patches can intimidate, confuse, or distract predators. Alternatively, they may also be used to reduce the probability of predation when animals escape through flash behavior and motion dazzle. Disruptive markings may draw the predators' attention toward them and away from the prey's outline, thus conceal their contour from being detection. However, disruptive markings and motion dazzle markings are sometimes both referred to as dazzle markings. Distracting markings can hide the animal's outline from predator detection, but due to the fact that disruptive markings are thought to work best when they contain high contrast patterns, they may also have another function of motion dazzle, making it more difficult for predators to catch moving prey (Stevens et al. 2008).

Flash behavior is how a predator may be confused or distracted by an abrupt demonstration of a conspicuous color marking or producing noise during movement; the predator follows the color marking or noise and suddenly the prey hide the color patches or become silent; the predator is deceived by the sudden disappearance of the prey as the predator assume the prey has disappeared; however, the prey rest in normal cryptic position after hiding the color patches (Malcolm 1974).

Flash behavior has evolved in many taxa including different species of Orthoptera, Phasmatidae, Mantidae, and Saturniidae with larger body size to own hidden contrasting color signals, though not in Sphingidae (Loeffler-Henry et al. 2019). In leaf-footed bugs, species with hidden white markings were significantly larger whereas those that reveal red/orange coloration were the same size on average as species without a hidden color display (Emberts et al. 2020). In experiments on humans, humans as predators were asked to click on artificial computer-generated prey on screens, the results showed that participants were more likely to fail to find prey with flash behavior, compared with continuously cryptic fleeing ones, where the survival rate of flashing prey was 20% higher (Loeffler-Henry et al. 2018). Prey with dynamic color change was captured less often and less accurately than a static white or background matching prey (Gopal 2018). Another experiment on human subjects has also demonstrated that flash behavior is more effective in anti-predation in larger artificial prey (Bae et al. 2019). These studies suggested that anti-predation color markings that can be concealed are more likely to be present in large-bodied species because they are more likely to be detected and pursued, or because color markings in large-bodied preys are more effective at deterring predator than that in small-bodied ones. These arguments that large body size is associated with hidden conspicuous color markings should apply universally to other taxa using these signals, like bovids.

Experiments in other taxa and on computers suggest that we need to reevaluate the function of hindquarter markings of species in bovid other than interspecific signals, cohesion to group members, and physiological regulator. In lagomorphs taxa, cape hares *Lepus capensis* (Kamler 2008) and black-tailed jackrabbits *Lepus californicus* (Kamler and Ballard 2006) facultatively show conspicuous white block behind their black ears, and in ungulate taxa, black-tailed deer *Odocoileus hemionus columbianus* (Stankowich 2008) and white-tailed deer *O. virginianus* (Caro et al. 1995) erect the tails when fleeing. They also suggest that they may have functions of flash behavior.

High contrast patterns may also function as motion dazzle, which makes estimates of speed and trajectory difficult by the predators (Thayer and Thayer 1909), prevalent in amphibians (Hamalainen et al. 2015), reptiles (Murali and Kodandaramaiah 2018), and some mammals (How and Zanker 2014). It has been verified in humans: in a computer game where a human "predator" was asked to click on the computer-generated prey that moves in the background on the screen, researchers found that some high-contrast conspicuous patterns, such as stripes and zigzags, are equally difficult to capture compared with uniform camouflaged targets (Stevens et al. 2008), and those with a dazzling pattern were considered to move more slowly than unpatterned ones (Scott-Samuel et al. 2011). Motion dazzle patterns may also work by affecting the perceived direction of movement (Hughes et al. 2017). When the prey is stationary, dazzle markings may also work by producing a crowding effect, whereby a predator's perception of prey is influenced by other distractors, and the higher the contrast between the distractors and the prey, the stronger the effect is (Chung et al. 2001). Studies of motion dazzle markings have mostly focused on stripes or zigzag patterns, but other patterns such as circles (Hamalainen et al. 2015) and block markings (Santer 2013) also have the role of motion dazzle. These markings were more likely to occur as the group size gets larger (Negro et al. 2020). The reason may be that such markings increase the "confusion effect," where the success of a predator's attack decreases as the size or density of the group increases, benefiting the individuals in the group. This is thought to be due to the increased difficulty for predators to track 1 prey among many (Hogan et al. 2016).

The presence of dazzle markings is also related to body size (Kodandaramaiah et al. 2020). In lizards, the dazzling effect produced by stripes is more beneficial in small lizards than in large lizards, with the marking redirecting a lethal attack to the lizard's tail or leading it to fail, where the probability of success of this effect is greater in smaller lizards (Murali and Kodandaramaiah 2018). This relationship has also been verified in crustaceans snapping shrimps (genus: *Alpheus*) (Elias et al. 2019). In bovid, however, studies of field observations or simulation experiments have remained scarce so far. The strongest indication of motion dazzle can be found in the Tibetan gazelle *Procapra picticaudata*, their white heart-shaped patch occupy most part of the rump, and makes it difficult for predators to judge the trajectory and speed of movement of individuals from behind and misidentify individuals when they flee in groups. Although some research has been conducted on other taxa and through computer-based gaming for human to perceive themselves as "predators" yet research on bovids is still scanty.

Using phylogenetic comparative analyses, we tested whether the function of hindquarter markings (including those on the rump, tail, and tail tip) in bovids is a signal for intraspecific communication, or is used to avoid being preyed on/confuse predators from following them to prey on them. If these markings are used for intraspecific communication, then we assume that an increase in hindquarter markings will be related to group size and habitat openness. For the second hypothesis, first, we tested whether conspicuous hindquarter markings occur in bovids with larger groups and smaller body size, which are conditions that support the hypothesis of motion dazzle. Second, to test whether conspicuous markings of bovids are used for flash behavior, we divided the conspicuous hindquarter markings into those that can be hidden and those that are always present and checked if conspicuous hidden markings are found in larger species.

Materials and Methods

We constructed a list of the 126 bovids excluding extinct and domesticated species to score whether conspicuous rumps, tail markings, and tail tip markings exist in the species of bovids. Contrasting markings on the tail tip were scored separately from the rest part of the tail as some bovids may have both a contrasting tail and a contrasting tail tip (Supplementary Figure S1).

We used information on coloration patterns obtained from illustrations in Bovids of the World (Castelló et al. 2016) and from the Google Image to score whether species of bovids had rump markings, tail markings, and tail tip markings (dependent variables defined in Supplementary Table S1). We also scored whether species have a conspicuous rump or ventral portion of the tail that can be exposed only by lifting the tail as some bovids do not reveal hidden conspicuous markings until their tails are raised. Then the data on whether the behavior of tail-flagging exists was taken from appendices in Caro et al. (2004). Species were categorized into those that can hide and expose conspicuous hindquarter markings, those that cannot hide them, and those that do not have conspicuous hindquarter markings at all. We examined Bovids of the World (Castelló et al. 2016) to identify whether markings on the rump, tail, and tail tip exist on species of bovids, and then checked against IUCN Redlist (https://www.iucnredlist.org). The marking scores by the 2 authors (L.C. and C.Y.) matched closely. For all variables, a value of 1 was assigned to species demonstrating a given trait and 0 to species that did not display the trait.

Independent variables that describe the behavior and ecological conditions of the species were taken primarily from Bovids of the World (Castelló et al. 2016) and supplemented with data from Stoner et al. (2003) (independent variables defined in Supplementary Table S2). We recorded the averages of the shoulder height (centimeters) for each species instead of body mass because shoulder height likely has a greater influence on the probability of a species being seen than the body mass does. If only a maximum or a minimum was available, it was used as the final average. Shoulder heights were $\log_{10}$ transformed to fit normality distributional assumptions. Since species living in more open habitats may be easier to be found by predators, following Caro (Stankowich and Caro 2009), we created an openness score for each species to include the primary habitat types (1 or 2 types of habitats per species). We created openness scores for each habitat type (dense forest = swamp = 0.001, light forest = 0.1, scrubland = 0.2, grassland = 0.75, rocky = 0.9, and tundra = desert = 1), which were drawn up according to the habitats' relative coverage each habitat provided that decide the extent to which animals can be hidden. Animals are more visible and easier to be seen in those habitat types with higher openness scores. For activity pattern, diurnal activity is assigned a value 1, crepuscular/nocturnal = 0, if the species is both diurnal and nocturnal, it is assigned of 0.5 for this trait. As for group size, we categorized group size for each species into a 1–4 scale: 1 = "solitary only," 2 = "solitary and intermediate-sized groups," 3 = "intermediate-sized groups only," and 4 = "intermediate-sized and large groups."

We extracted the tree from the published species-level phylogeny tree set downloaded from the 10k Trees Website (Arnold et al. 2010) and trimmed it to exclude extinct and domesticated species. As all dependent variables were binary (0/1), we ran linear regressions for binary data using the phylogenetic generalized linear mixed model with the binary PGLMM function in the "ape" package (Paradis et al. 2004) in the R 4.0.2. The independent variables in the models at the beginning included $\log_{10}$ shoulder height, openness scores, group size, and activity pattern. To test the influence of these 4 variables in different hypotheses affecting the evolution of hindquarter markings in bovids and to determine which of these predictor variables best explained the dependent variables, we used the stepwise model selection method, and this method allows different predictor variables to compete with each other to determine which are included in the final model: all 4 variables were simultaneously tested against each other, 1 variable was entered at a time, and the variables were re-evaluated at each step. Variables that did not contribute to the model were removed and predictor variables may be added and removed several times until the optimal model was obtained. The relative fit of the models was assessed using Akaike's Information Criterion (AIC), the smaller values of which indicate that the model fits the data better with fewer parameters used (Burnham and Anderson 2004). The best model selected using AIC was shown in Supplementary Table S3.

The segmentation point for factors entering into the model was set at $P = 0.05$ and only those factors with probabilities less than this value were in the model. The phylogenetic signal is reported as σ^2, which is the scalar magnitude of the phylogenetic variance–covariance matrix. A value of $\sigma^2 = 0$ implies no phylogenetic signal and larger values indicate a stronger signal (σ^2 has no upper bound). We presented P values for the hypothesis of no phylogenetic signal in the residuals testing whether σ^2 is statistically significantly greater than 0. We reported for each test the number of species included (N), phylogenetic signal σ^2, Z-statistic, and P-value.

Results

First, we included shoulder height, openness scores, group size, and activity patterns as an independent variable in 3 separate models for each color markings. For rump markings, only group size was included in the final model and had a significant effect on rump marking presence ($N = 126$, $\sigma^2 = 2.170$, $P = 0.001$; group size $Z = 2.015$, $P = 0.031$), where species living in larger group size were more likely to have rump markings (Figure 1). Group size and shoulder height were included in the model of the presence of the tail markings, the presence of which had a significant positive correlation with the former variables, but did not reach significant level with the shoulder height ($N = 126$, $\sigma^2 = 2.322$, $P < 0.001$; group size $Z = 2.051$, $P = 0.040$; $\log_{10}$ height $Z = -1.647$, $P = 0.100$; Figure 2). However, the intercept-only model (i.e., null model) fitted best if the presence of the tail tip markings, meaning none of the 4 factors are included in the model.

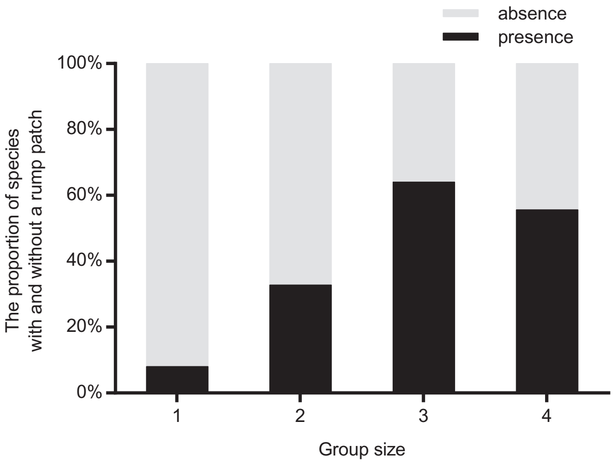

Figure 1. The proportion of bovid species with (black bars) and without (gray bars) a rump patch in relation to group size.

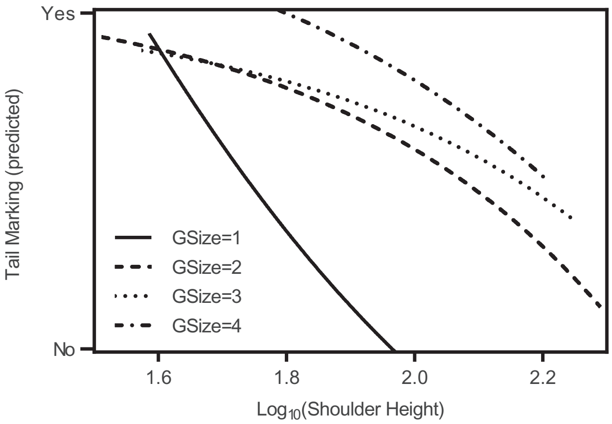

Figure 2. Predicted values of bovids having conspicuous tail markings (0 = no/1 = yes). Each are plotted against $\log_{10}$ shoulder height in centimeters for solitary (GSize = 1), solitary and intermediate (2–50) sized groups (GSize = 2), intermediate-sized groups only (GSize = 3), and intermediate and large (>50) groups (GSize = 4).

In the second step, we examined the presence of conspicuous hindquarter markings, which means evolving a conspicuous rump, tail markings, or tail tip markings. Group size had the greatest effect on the presence of the conspicuous markings whereas shoulder height did not pose any effect ($N = 126$, $\sigma^2 = 2.565$, $P = 0.003$; group size $Z = 2.533$, $P = 0.011$; $\log_{10}$ height $Z = -0.784$, $P = 0.433$; Figure 3A). Separately, group size had a greatest effect on the presence of conspicuous white markings, followed by shoulder height ($N = 126$, $\sigma^2 = 1.819$, $P = 0.002$; group size $Z = 2.816$, $P = 0.005$; $\log_{10}$ height $Z = -1.939$, $P = 0.053$; Figure 3B). The openness scores had a significant impact on the presence of conspicuous dark hindquarter markings ($N = 126$, $\sigma^2 = 1.49$, $P < 0.001$; openness scores $Z = 2.257$, $P = 0.024$; Figure 3C).

To test whether the hindquarter markings serve for flash behavior, we divided bovids into 2 groups according to the definition of flash behavior: those that can expose their markings while fleeing and hide them while stationary, versus those that have conspicuous markings but always show them or those that do not possess them. The former is considered to be a possible candidate for flash behavior. Shoulder height was included in the model, but did not have a significant effect ($N = 126$, $\sigma^2 = 4.744$, $P < 0.001$; $\log_{10}$ height $Z = 0.339$, $P = 0.735$). Following Caro et al. (2020), we divided bovids into those without conspicuous hindquarter markings or those whose markings can be hidden versus those whose markings cannot be concealed. We found a positive correlation between group size and this trait whereas shoulder height was not included in the model ($N = 126$, $\sigma^2 = 2.491$, $P < 0.001$; group size $Z = 2.236$, $P = 0.024$; Figure 4). Species were also classified in another way: bovids are without conspicuous hindquarter markings versus those that can expose them or always show them. However, no factors were included in the model.

Discussion

We found that bovids living in larger groups were more likely to have conspicuous hindquarter markings (Figures 1 and 2). This result validated earlier studies that found an association between the existence of white rump patches and group size (Stoner et al. 2003), tail markings, and group size (Stoner et al. 2003). It can therefore be concluded that these 2 markings in bovids may have a signaling function directed at group members. In the models explaining the existence of hindquarter markings in bovids, group size and shoulder height were the main influencers. In contrast, the openness score

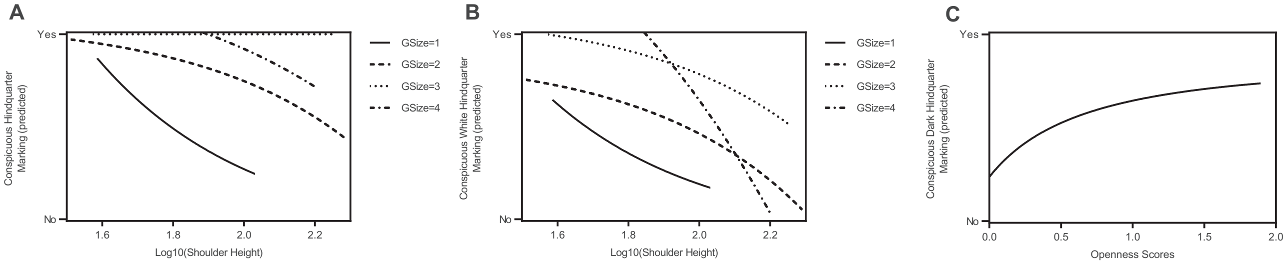

Figure 3. Predicted values of bovids having: A) conspicuous hindquarter markings (0 no/1 yes), B) conspicuous white hindquarter markings (0 no/1 yes), and C) conspicuous dark hindquarter markings (0 = no/1 = yes). Each are plotted against $\log_{10}$ shoulder height in centimeters for solitary (GSize = 1), solitary and intermediate (2–50) sized groups (GSize = 2), intermediate-sized groups only (GSize = 3), and intermediate and large (>50) groups (GSize = 4).

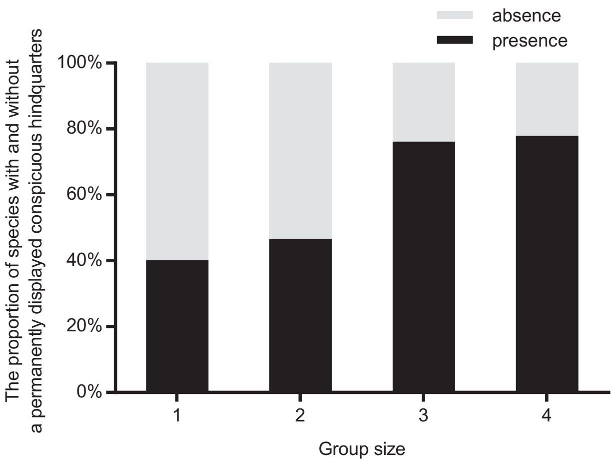

Figure 4. The proportion of bovid species having permanently displayed conspicuous hindquarters (black bars) versus inconspicuous or hidden hindquarters (gray bars) in relation to group size.

could only explain whether bovids had conspicuous dark hindquarter markings and was less effective in explaining the other dependent variables, suggesting that the relationship between it and hindquarter markings in bovids may be due to its significant correlation with other predictors in the previous studies.

Caro et al. (2020) observed that for the hindquarter markings of artiodactyls, small solitary species were not conspicuous but large group-living species were usually conspicuous (Caro et al. 2020). In our study, we improved the methods, for instance instead of directly taking group size and body size as predictive variables, we filtered 4 main factors including body size, group size, habitat openness, and activity pattern and included them in the models. Because of the scale of the study (we focused on bovids instead of artiodactyls), our results differed from those of Caro et al. (2020). If viewed separately, the conspicuous white hindquarter markings were associated with group size and shoulder height such as more likely markings were present in larger group size and smaller body size (Figure 3B). We assumed that it may indicate that white markings serve as an anti-predation strategy, motion dazzle, which may explain why the hindquarter markings of bovids were always conspicuous instead of being concealable. Contrasting body patterns promoting dazzle camouflage are widespread in group-living mammals (Negro et al. 2020), observations in lizards and experiment on computers have shown that dazzle markings tend to appear in smaller prey (Kodandaramaiah et al. 2020), it is therefore reasonable to assume that in large mammals of the bovid family, the evolution of dazzle markings is similarly related to the drive by the group size and body size. For example, the Tibetan gazelle *P. picticaudata* is endemic to the Tibetan Plateau, with a shoulder height of about 60 cm, often in groups of 2–10 individuals (Li 2016). When escaping, their heart-shaped white rump patch is directed toward the predator, which makes it difficult for an observer to determine the trajectory and speed of a single individual in the group; in addition, their high-contrast hindquarter patterns of individuals can blur the entire group, potentially causing predators to lose reference points within the group and misidentify individuals (Yu 2019, personal observation).

In the test for whether bovids have flash behavior, we linked the presence of hindquarter markings to the presence of tail-flagging behavior, establishing 3 categories as potential ways of flash behavior. However, we did not find that this behavior was positively correlated with body size but only found that the presence of permanently displayed conspicuous hindquarters increases with group size (Figure 4). Most bovids have not evolved hindquarter markings that are hidden and evolved them as always exposed. It is maybe because even small bovids have a large enough body size compared with insects, and a larger group is easily detectable, which makes it difficult for them to remain cryptic after fleeing and hence they use permanent conspicuous hindquarter markings to confuse their predators.

Our results also showed that conspicuous high-contrast hindquarter markings were more likely produced in bovids with larger group sizes, which validate the hypothesis of the intraspecific communication function. However, since white markings are also associated with body size and the current findings strongly suggested that it would be unwise to assume that color patterns associated with group size must serve a communication function. In an analysis of body color patterns in butterflyfishes (Family: Chaetodontidae), no effect of group size was found on the evolution of vertical or horizontal stripes (Kelley et al. 2013). Besides, many bovids possess a white rump patch, which may play a role in communication with their group members, even predators, but they may also have a thermoregulatory function when reflects sunlight (Bicca-Marques and Calegaro-Marques 1998). Previous studies and our results have shown that color patterns may have additional functions in animal groups that are not used for communication. There may be several possible explanations for the correlation between conspicuous hindquarter markings and group size. Bovids are likely to combine such patterns with camouflage, thermoregulation, intra- and interspecies communication, for example, the dilution and confusion effect in group-living bovids (Hogan et al. 2016).

In summary, our results suggested that there are 2 possible functions for conspicuous hindquarter markings in bovids. 1) In social bovids for intra-species communication, for example, as a warning signal to notify individuals within the group when faced with predation risk and 2) with the function of motion dazzle to reduce the chance of being preyed upon when fleeing. However, the possibility that motion dazzle in bovid is a way of escaping from predation needs to be explored. So far, studies of dazzle markings have focused on the color patterns of individuals, but these studies do not address how individuals in a group interact with each other through their color patterns and the effectiveness of this interaction to escape from predators. Behavioral observations in several bovid species (e.g., in the Tibetan gazelle) are needed to determine how their conspicuous hindquarter markings interact in groups and to what extent they affect predators. There is a need to investigate that whether motion dazzle is employed by bovid as an anti-predation strategy and to clarify its effects on an individual within a group and its effects on predators.

Author Contributions

Z.L. and C.Y. designed the study. C.Y., S.N., and L.C. collected the data. C.Y. analyzed the data and wrote the manuscript. S.U. and Z.L. revised the first draft of the manuscript.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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