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The function of contrasting pelage markings in artiodactyls

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Comparative studies of pelage coloration in mammals suggest that certain prominent markings on an otherwise uniform pelage background serve in communication. We matched the position and coloration of contrasting markings on the bodies of all even-toed ungulates to ecological and social variables in order to ask whether marks are used in communication generally, as a signal to predators, or as a signal to conspecifics. Controlling for phylogeny, we found that many marks are located in prominent visible positions on the body; that flank marks seem to amplify stotting and leaping, which are pursuit deterrent signals; and that front leg marks may amplify foot stamping, an antipredator signal. We found that upper leg markings, particularly markings on the podials, are associated with group living hinting at an intraspecific communicatory function. Surprisingly, we found that contrasting marks do not reliably indicate position of scent glands across this taxon and that many white marks may have a cryptic function. These results extend and contradict those of previous analyses and force us to conclude that contrasting pelage marks have a number of functions in this taxon including pursuit deterrence, intraspecific signaling, and possibly even crypsis. *Key words:* color patches, intraspecific communication, pursuit deterrence, signals, ungulates. *[Behav Ecol 21:78–84 (2010)]*

In contrast to recent studies of insects (Stevens et al. 2008) and birds (Senar 2006), most attempts to understand the evolutionary significance of coloration in mammals have focused on the whole body. Generally, uniform body coloration in mammals is believed to be driven by the need to avoid detection by predators (crypsis) with the whole pelage matching the background in which animals live (Sumner 1921; Dice 1947; Stoner, Bininda-Emonds, et al. 2003; Stoner, Caro, et al. 2003), although it is recognized that there are additional physiological consequences to overall pelage hue (e.g., Hetem et al. 2009). Similarly, overall patterned coats are thought to match the background of light playing through a veil of leaves or tall grass (Stoner, Caro, et al. 2003). In predators, these coloration patterns may additionally serve to hinder prey-detecting approaching predators (Mottram 1915; Cott 1940; Ortolani and Caro 1996; Stankowich and Coss 2007). A great many mammals, however, are not uniform in color and instead have contrasting color patches on their body (Caro 2009), markings that are presumed to serve a function different than background matching (Stevens and Merilaita 2009). Ungulates are a case in point: Many species have patches of black or white on a uniform brown, gray, or reddish-brown background. Because black pelage, at least, is melanin based and melanin is costly to produce (Margalida et al. 2008), attempts have been made to explain these prominent patches of colored pelage on their legs, flank, neck, and face.

Specifically, Stoner, Caro, et al. (2003) found that 1) artiodactyls with prominent markings on their flanks are diurnal and live in open environments. Broken down by family, bovids with side bands on their flanks were found in desert habitats, whereas cervids with these markings were found in tundra habitats, although, none of these findings were significant after controlling for phylogeny. Because a contrasting patch of pelage with a well-defined border could serve to break up the outline of the body (Cott 1940), these patches could be disruptive. Side bands were also found in group-living species. 2) Dark leg markings were associated with living in deserts and living in large social groups, white leg markings with diurnality. Conspicuous leg markings (dark and white combined) were found in species inhabiting deserts and grassland/bushland habitats where they might be easily seen and so could be used in communication. 3) Dark and white face markings were found in diurnal species and in group-living species, which they thought might indicate intraspecific communication, but the association between white faces and diurnality also suggests thermoregulation. 4) White rumps were seen in diurnal species, in those living in open habitats, and in cervids living in intermediate-sized groups suggesting either communication or thermoregulation.

In short, the findings of Stoner, Caro, et al. (2003), the only systematic coloration study of this taxon, hint that localized body markings are often involved in communication, but the findings were preliminary, not straight forward, and open to alternative interpretations. We sought to ask more specific questions about the type of coloration and position of markings in even-toed ungulates as they relate to communication. We used the same simple categorical variables as in previous comparative studies of coloration in mammals (Caro 2005a). We had 3 simple hypotheses concerning communication. 1) Markings in artiodactyls are signals. Here, we surmised that if color patches are signals, we would expect marks to be found more often in species living in environments where those marks are easily visible. 2) Markings signal to predators. Here, we expected marks to be found more often in species that send overt behavioral signals to predators and, further, that they would be located on and attract attention to the body area associated with predatory defense. 3) Markings signal to conspecifics. Here, we expected either 1) that species that live

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in groups with conspecifics are more likely to have markings because they might allow conspecifics to monitor each others' presence while foraging or to reassemble after fleeing from a predator, whereas solitary species have to attract each other only for mating (see Beauchamp and Heeb 2001) or 2) that markings would be found in locations on the body where scent glands are found if coloration were to serve as a reminder of an individual's ability to mark a territory. Pelage marks and scent glands are certainly associated in other mammalian taxa (Macdonald 2009).

MATERIALS AND METHODS

Because most characteristics of interest were categorical in nature (i.e., presence vs. absence) or distinctly bimodal in their distribution, we ran phylogenetically corrected comparative tests using Pagel's (1994) method. We first characterized the presence or absence of black and white markings on 198 species of artiodactlys. We considered black and white markings separately because they are rarely found side by side in this taxon (Caro 2009). We distinguished between dappled and striped body markings that cover the entire flank and are likely used in crypsis from localized black and white color markings in specific body regions; the latter are the focus of this study. Using descriptions and photographs in Nowak (1999), Wilson (2005), and online image searches, we coded the presence or absence of dark/black and light/white pelage separately in different regions of the body as viewed laterally with the flank facing the observer. Positions of marks on the legs were broken down by corresponding skeletal position (Figure 1): "phalanges," "metapodials" (metacarpals, metatarsals, canon bones), "podials" (carpal and tarsal joint), "ulna/tibia," and "elbow/knee." The "flank" included the humerus, shoulder girdle, and trunk, whereas the "rear" included the femur, pelvic girdle, and glutteal area. Note, the rear does not include the "rump patch" that lies beneath the tail and is sometimes continuous with the ventrum, and that is visible from a posterior vantage; the functional significance of this region has been studied in some depth elsewhere, (e.g., Hirth and McCullough 1977; Stankowich 2008) and is large enough in some species to be implicated in thermoregulation (Stoner, Caro, et al. 2003). The "neck" included the anterior surfaces of the cervical region and upper torso, and the "face" included the pelage covering the entire cranium and mandible. For certain tests, body regions were then grouped into the following categories: "lower legs" (markings on the phalanges or metapodials), "upper legs" (markings on the podials, ulna/tibia, or elbow/knee), "front legs" (markings on the anterior phalanges, metacarpals, carpals, ulna, or elbow), and "upper body" (markings on the flank, rear, neck, or face).

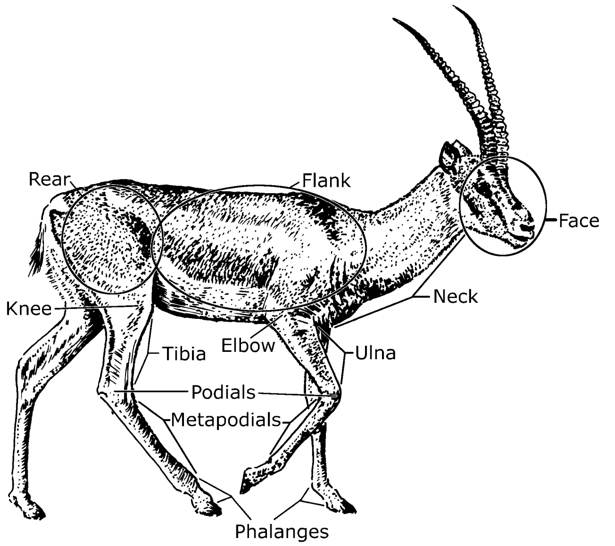

Figure 1
Schematic demonstrating how the different body locations were defined for the categorization of color markings. Metapodials included both metacarpals and metatarsals and podials included both carpals and tarsals. Body parts were also combined into regions: lower legs (phalanges and metapodials), upper legs (podials, ulna, tibia, elbow and, patella), and upper body (face, neck, flank, and rear). Line drawing of male Grant's gazelle (*Nanger granti*) kindly provided by Professor Richard G. Coss.

Hypothesis 1: markings are signals

We first tested if the presence of markings was associated with living in habitats where those marks would be most visible. We used previously scored habitat categories from Caro et al. (2004) and Stankowich and Caro (2009). In some cases, these previously reported scores were updated and edited for accuracy. For each species, the presence or absence was scored for living in "dense forest," "light woodland," "grassland," and "desert" (Table 1) because these represented the darkest and brightest habitats available. We tested if markings of any kind on any part of the body were more likely to be found in brightly lit habitats (light woodland, grassland, and desert); if dark markings on any part of the body were more likely to be found in light habitats; and if light markings on any part of the body were more likely to be found in dark habitats (dense forest).

We next tested if the presence of markings on the upper and lower legs were more likely to be found in taller species where markings might be seen more easily either by conspecifics or predators. Despite the fact that larger artiodactyl species are able to see farther than smaller species (Kiltie 2000), the issue is that smaller artiodactyls will be more easily obscured by a given height of vegetation and they skulk to avoid predation, both of which make them more difficult to see. We used

Table 1
Descriptions of ecological and behavioral variables

Variable	Definition
Habitat variables	
Dense forest	Alpine, boreal, deciduous, mixed, timberland, tropical forests, and jungle
Light forest	Woods, woody areas, or woodlands, open, sparse, or light forests
Grassland	Meadows, prairie, savannah, and steppe grasses
Desert	Deserts and semideserts
Stott/leap/bound	Any vertical leaping into the air during flight that 1) slows down flight speed and 2) is not necessary to clear objects on the ground (e.g., fence) or move to a new precarious position (e.g., rocky outcropping)
Snort	An audible expellation of air through the nose, often sounding like barking
Foot stamp	Raising 1 foot off the ground and striking the ground below (often repeatedly) with the hoof while standing in 1 place
Social species	Any species that is found in groups of 3 or more at least some of the time
Solitary species	Any species that spends all of its time alone, with a mate, or with its own offspring, and does not associate with other conspecifics in groups of 3 or more

previously scored height categories from Stankowich and Caro (2009) based on shoulder heights, where the cutoff between tall and short species (75 cm) was realistically based on selecting a point in the bimodal distribution at a threshold where shorter species were becoming very rare and taller species began to appear (i.e., short $<$75 cm, tall $\geq$75 cm). We tested if markings on all individual parts of the body, and on the body in general, were more likely to be found on tall species compared with short species.

Hypothesis 2: markings are signals to predators

We tested to see if the performance of certain antipredator behaviors is associated with markings on the area of the body where those behaviors originate or are focused. To test if pursuit deterrent signaling behavior during flight is associated with markings on any part of the body, we scored as many species as possible for the presence of stotting or leaping behavior. We relaxed Lingle's (1992) technical definition of stotting, "vertical leaping with all 4 legs leaving the ground simultaneously with the legs held stiff and straight while the animal is airborne" (p. 181), and included other similar gait patterns (e.g., pronking, bounding, leaping, and "rocking-horse gaits") present during flight that are "*not*" associated with or necessary to clear obstacles on the ground (e.g., fences, rocks, or vegetation) or move from one inaccessible place to another (e.g., rocky outcroppings or ledges). The intention of this definition was to identify species that leap during flight when they are not required to because the performances of these behaviors are more likely to be directed at the predator as a signal of physical agility and speed. To score this variable, we used descriptions from a variety of published sources (Shortridge 1934; Allen 1940; Roberts 1954; Heptner et al. 1961; Schaller 1967, 1977, 1998; Harrison 1968; Banfield 1974; Sokolov 1974; Leuthold 1977; Kingdon 1979, 1982; Feldhamer 1980; Sterndale 1982; Lumpkin and Kranz 1984; Dalrymple 1985; Shackleton 1985; Spinage 1986; Mares et al. 1989; Skinner and Smithers 1990; Estes 1991; Kingswood and Kumamoto 1996, 1997; Sokolov and Lushchekina 1997; Nowak 1999; King 2005; Wilson 2005) and personally communicated accounts from expert naturalists with first hand observational experience with certain species in the wild (see Acknowledgments). We used this information and our combined experience to judge the flight behavior of each species and tested this "stotting/leaping" variable against color markings on all parts of the body.

Next, we used previously scored variables on "snorting" and "foot-stamping" behavior in artiodactyls (Table 1; Caro et al. 2004) to test for associations between snorting and face markings and between foot stamping and markings on the front legs. Snorting has been labeled a pursuit deterrent signal (Caro 1994, 2005b), whereas foot stamping has, on the basis of circumstantial evidence, only been linked to intraspecific communication informing conspecifics of an approaching predator. Here, we assumed foot stamping was an antipredator signal.

Hypothesis 3: markings are signals to conspecifics

To test whether markings high on the body where they are more visible are directed at conspecifics, we categorized species as "always solitary" versus "sometimes grouped" based on published data (Table 1; Caro et al. 2004). We tested this "sociality" variable against marking locations on the upper body and upper legs.

Finally, using previously published data (Gosling 1985), we tested whether color markings amplify the ability of species to scent mark, that is, provide a signal that improves the receiver's ability to attain more information about scent marking through attracting visual attention to a gland (see Hasson 1997; Gualla et al. 2008). We scored species for the presence or absence of skin "scent glands" on the "head" (vestibular nasal, interramal, frontal, antorbital, suborbital, subauricular, postcornual, or occipital glands), "rear" (inguinal), "podials" (carpal and tarsal glands), "metatarsals," and "phalanges" (interdigital or unguicular glands). Each of these gland locations was tested against the marking category for the same part of the body (e.g., head glands vs. face markings), and the combined score of glands on the legs (carpal, tarsal, metatarsal, and phalanges) was tested against markings on an expanded lower leg marking variable (i.e., phalanges, metapodials, or podials).

Analyses

We used a published Cetartiodactyla supertree (Price et al. 2005) as a base tree and resolved as many polytomies as possible primarily using Marcot (2007). Other taxon-specific polytomies were resolved using Pitra et al. (2004: Genus *Cervus*), Mona et al. (2007: *Sus*), Kuznetsova and Kholodova (2003: Antilopinae), Pidancier et al. (2006: *Capra*), and Huffman (2009). The composite tree can be found in the Appendix. We related all variables in the combinations described in the hypotheses above using phylogenetically uncorrected χ^2 tests using SPSS 17.0; when expected cell values were less than 5, Fisher's Exact tests were used instead. As nonsignificant χ^2 tests were unlikely to achieve significance in phylogenetically corrected tests and in order to limit the overall number of statistical tests, we only subjected those tests with $P <$ 0.10 to subsequent phylogenetically corrected Pagel's (1994) tests for correlated changes to account for shared ancestry using Mesquite 2.5 (Maddison and Maddison 2008) with $\alpha = 0.10$. All P values and log likelihood differences (LDs) between 8 and 4 parameter models from Pagel's tests were calculated from 10 000 simulations using 10 extra iterations per simulation.

RESULTS

Hypothesis 1: If color patches are signals, we would expect them to be found more often in species living in environments where they can be seen.

We compared whether species that had color patches on any place on the body irrespective of marking color lived in habitats where the color patches might be easily seen. We found that all color patches were more likely to be found in species that lived in light woodlands compared with species that did not live in this habitat ($\chi^2 = 3.396$, df = 1, $P = 0.065$; log likelihood difference$_{(8\text{par}-4\text{par})}$ (LD) = 4.349, $P = 0.0433$). This was not true of grassland or desert-living species ($\chi^2 = 0.066$, df = 1, $P = 0.797$; $\chi^2 = 0.694$, df = 1, $P = 0.405$, respectively) examined by themselves, however. More specifically, we found that dark patches on the body, irrespective of their position, were more likely to be found in species living in light woodlands, and in grasslands (light woodlands: $\chi^2 = 8.668$, df = 1, $P = 0.003$, LD = 2.61, $P = 0.2228$; grasslands: $\chi^2 = 4.789$, df = 1, $P = 0.029$, LD = 1.65, $P = 0.4101$) although not in deserts ($\chi^2 = 1.207$, df = 1, $P = 0.272$). None of these results held after controlling for phylogeny, however. Interestingly, white patches, irrespective of position, were not associated with living in dense forests where they might be visually apparent ($\chi^2 = 0.106$, df = 1, $P = 0.745$).

If marks are signals to conspecifics or to predators they should be located on parts of the body where they would be visible from moderate to long distances, above occluding vegetation. Therefore, large species should be able to afford to have marks lower down on their body (i.e., on their legs) than small species, whose lower bodies are more likely to be occluded by vegetation. We found that lower leg marks were found significantly more often on medium-height and tall species than on short species ($\chi^2 = 3.575$, df = 1, $P = 0.059$, LD = 4.08, $P = 0.1152$), specifically on the phalanges ($\chi^2 = 5.015$, df = 1, $P = 0.025$, LD = 3.35, $P = 0.1662$) and to some extent on the podials ($\chi^2 = 3.515$, df = 1, $P = 0.061$, LD = 2.52, $P = 0.2456$), although significance was lost after controlling for phylogeny. We also found that upper leg marks were found significantly more often in tall and medium-height species than in short species ($\chi^2 = 12.999$, df = 1, $P = 0.000$, LD = 3.57, $P = 0.1477$), specifically on the ulna/tibia and elbow/knee ($\chi^2 = 8.703$, df = 1, $P = 0.003$, LD = 3.74, $P = 0.1084$; $\chi^2 = 8.115$, df = 1, $P = 0.004$, LD = 16.84, $P = 0.0003$, respectively); elbow/knee results were highly significant after controlling for shared ancestry. But, as predicted, marks high on the body where they could be easily seen (e.g., flank, rear, face, or neck combined) were equally likely to be found in species of all heights ($\chi^2 = 0.856$, df = 1, $P = 0.355$).

Hypothesis 2: If color patches signal to predators, we would expect them in species that send overt behavioral signals to predators and, further, that they would attract attention to the pertinent body area.

We surmised that if marks signaled to a predator they might be found particularly in species that are known to use behavior to signal to predators—in species that stott or leap, foot stamp, or snort (Caro et al. 2004). We found that species with flank markings were found significantly more often in species that are known to stott/leap ($\chi^2 = 5.178$, df = 1, $P = 0.023$, LD = 8.88, $P = 0.0002$; Table 2). However, associations between stotting/leaping and marks on other parts of the body (i.e., phalanges, metapodials, podials, ulna/tibia, and elbow/knee) were not significant (χ^2 all $P > 0.1$).

Species that foot stamp were more likely to have color patches on their front legs than species that do not foot-stamp ($\chi^2 = 4.854$, df = 1, $P = 0.028$, LD = 2.54, $P = 0.2243$), although this did not hold after controlling for phylogeny.

In contrast, there was no relationship between the presence snorting and facial markings ($\chi^2 = 1.672$, df = 1, $P = 0.196$).

Hypothesis 3a: If color patches signal to conspecifics, we would expect species that live in groups to have markings.

If color patches serve in intraspecific communication, as a passive recruitment signal in socially foraging herbivores, we would expect them to be found in group-living species. We found that marks on the upper legs were significantly more likely to be found in group-living species (Fisher Exact probability test, $P = 0.017$, LD = 9.27, $P = 0.0015$), specifically markings on the podials (Fisher Exact test, $P = 0.017$, LD = 10.05, $P = 0.0004$). There was a slight tendency for facial markings to be associated with group living (Fisher Exact probability test, $P = 0.087$, LD = 2.23, $P = 0.3549$).

Table 2

Relationship between the presence of flank markings and stotting/leaping behavior

		Flank markings		
Stotting		Absent	Present	Total
Absent	Count	84	5	89
	Expected	*79.9*	*9.1*	
Present	Count	48	10	58
	Expected	*52.1*	*5.9*	
	Total	132	15	147

$\chi^2 = 5.178$, df = 1, and $P = 0.023$.

Hypothesis 3b: If color patches signal to conspecifics, we would expect species that use scent glands in social communication to have markings covering the scent gland.

We also tested whether marks amplified scent-marking behavior in artiodactyls. We pitted species with skin glands used for social communication (Gosling 1985) against marks in the same region of the body but found no relationship between the presence of glands on the head, rear, or legs and the presence of color markings on the same region of the body (χ^2 tests: all $P > 0.05$).

DISCUSSION

We uncovered a number of associations between contrasting pelage color patches and ecological and social variables. Generally, there was an association between having a color patch and living in fairly open habitats where visibility might be high, and dark patches were seen more often in species living in fairly open habitats, although not after controlling for shared ancestry. Our prediction that taller species would have marks lower on the body than smaller species was satisfied, although only marks on the elbows and knees remained significant after phylogenetic correction. Nevertheless, this finding supports the hypothesis that markings are used as signals because the lower parts of the bodies of shorter species are more likely to be occluded by vegetation, than the lower parts of the bodies of taller species. Taller species have more "canvas" to display markings because a greater proportion of their body is visible above a given amount of vegetation, than the bodies of shorter species.

Some of our predictions that patches are used to signal to predators were borne out. We found that flank markings were associated with stotting or leaping after controlling for phylogeny (Table 2). This strongly suggests that flank marks serve to amplify the vertical leaps made during these antipredator behaviors. Stotting in Thomson's gazelle *Eudorcas thomsoni* (FitzGibbon and Fanshawe 1988) and leaping in impala *Aepyceros melanopus* (Caro 2007) are well-established pursuit deterrent signals. Our results contradict previous speculative notions that flank marks serve as disruptive coloration or are used in intraspecific communication. Our definition of flank markings was slightly broader than that of Stoner, Caro, et al. (2003), and our definition of stotting was more catholic than theirs, but that is unlikely to account for the difference in interpretation. Instead, given that the earlier study made functional conclusions on the basis of habitat associations that could be interpreted in other ways but that this study found a direct association between flank marks and stotting or leaping, we are inclined to put far more stead in flank stripes being an antipredator amplifier. This is the first time that this function of flank markings has been directly implicated in artiodactyls. We cannot tell, however, whether this mark draws the predator's attention to the gait (i.e., amplifies the meaning of the signal), makes it difficult for a predator to follow an individual fleeing in a group, or makes it difficult to target accurately its final leap, bite, or blow at a solitary victim (similar to Kingdon 1982 supposition regarding the metapodial markings on the impala).

There was some evidence that front leg markings draw attention to foot stamping, but these results held only in cross-species analyses. Caro et al. (2004) found foot stamping associated with white leg markings and suggested that it was a visual rather than an auditory signal and was directed

Appendix A. Phylogenetic tree of Artiodactyla used in this study.

at conspecifics. Whatever the target recipients of this behavior, leg marks may amplify it, and the association needs further attention.

We found a strong association between living in groups and upper leg markings, particularly markings on the podials. This suggests that these markings could possibly be involved in group cohesion, although this is speculative. For example, if animals move and graze simultaneously with their head down, clear markings on the legs might be easier to track visually and indicate the direction of group movement above the background "noise" of many thin legs moving back and forth in all directions. Nonetheless, the body outline alone should be sufficient to see a conspecific. Emphatically, we found no association between color patches and presence of scent glands in the same area. This is a surprising result because some authors have suggested that facial markings, for example, the black spot on oribi *Ourebia ourebi,* draw the attention of conspecifics to a territorial animal scent marking (Kingdon 1982), and there are individual species with scent glands that have highly contrasting colored hair covering them.

We were particularly struck by the fact that white markings were not more likely to be seen in species living in dense forests. In carnivores, white patches on the proximal surface of pinnae are found in species living in dense forests suggesting that they allow offspring to follow their mothers easily (Ortolani and Caro 1996), and in mammals, white blazes are associated with aposematism (Caro 2009), but the lack of association in artiodactyls suggests that either white patches are used in both crypsis and communication (although not necessarily simultaneously) or they are not used in communication at all.

We did not find clear associations for all of the color patches that we examined. This suggests that 1) some body markings have no signaling function, 2) some body markings have a signaling function that has fallen outside the scope of systematic comparative studies completed to date, or 3) the same body markings on different species may have different signaling functions based on species ecology. We feel the first hypothesis is weak because the marks that we considered are probably not large enough to be involved in temperature regulation (we excluded rumps for this reason), but dark marks on the face and around the nose might help heat air entering nasal passages (Margalida et al. 2008). The second idea has some merit—predictions about sexual signaling and badges of status were not tested in this study. Absence of sexual dichromatism in artiodactlyl patches (see Caro 2009) argues against sexual signaling, however, but badges of status, for instance on the neck cannot be dismissed at present and deserve detailed study. The third idea also has value as we know that the same morphological traits can have different functions in different species. For example, Stankowich and Caro (2009) found that horns in female bovids evolved multiple times either in exposed species for use in defense against predators or in species where females defend territories for use during conspecific agonism. Indeed, one of the main problems with functional analyses, and systematic comparative analyses in particular, is that characters with multiple functions (e.g., signaling to conspecifics, accentuating antipredator behavior, and accentuating territorial behavior) may have opposing predictions resulting in none of the predictions for any one function being satisfied (Stankowich 2008).

In conclusion, our analyses indicate that several contrasting markings in even-toed ungulates are likely involved in communication. Clearly, certain prominent marks are involved in reifying pursuit deterrent signals, and others may be involved in signaling to conspecifics although the nature of the signal is unclear. We are therefore forced to conclude that there are no unitary explanations for prominent marks in even-toed ungulates and that the functional significance of the color and position of marks in this and probably other mammalian taxa must be examined on a case-by-case basis.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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APPENDIX A

Phylogenetic tree of Artiodactyla used in this study.

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