

EVOLUTION OF A RUMP PATCH IN ALASKAN MOOSE: AN HYPOTHESIS

R. Terry Bowyer¹, Janet L. Rachlow^{1,2}, Victor Van Ballenberghe³ and R. Dale Guthrie¹

¹Institute of Arctic Biology, and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska 99775; ²Present address: Department of Range, Wildlife, and Forestry, University of Nevada-Reno, Reno, NV 89512; ³U.S.D.A. Pacific Northwest Research Station, Institute of Northern Forestry, 201 East 9th Avenue, Suite 206, Anchorage, Alaska 99501

ABSTRACT: Dark rump markings in Alaskan moose (*Alces alces gigas*) are hypothesized to function as a rump patch. These pelage characteristics are likely an example of rapid evolution because dates for the oldest *A. alces* in Alaska (ca. 9,000 years BP) suggest a post-glacial subspeciation of moose in North America. Moreover, mitochondrial DNA shows no subspecific variability, suggesting that moose were not isolated for long periods of time by the Wisconsin ice sheet. The occurrence of a rump patch in Alaskan moose is consistent with increasing gradients of rump-patch size exhibited by mule deer (*Odocoileus hemionus*), and red deer and wapiti (*Cervus elaphus*) that inhabit increasingly more open habitats. Likewise, Alaskan moose live in more open habitat, are larger in body size, more social, and have larger, more complex antlers than conspecifics in North America that lack striking rump markings. These attributes also are correlated with larger and more conspicuous rump patches in other cervids. We believe the group cohesion hypothesis offers the most likely explanation for dark rump markings in Alaskan moose.

ALCES VOL. 27 (1991) pp.12-23

Both geographic and ontogenetic variation in pelage color of moose (*Alces alces*) has been noted previously (Murie, 1934; Flerov, 1952; Peterson, 1955; Bubenik, 1987; Geist, 1987a, 1987b; Sokolov and Chernova, 1987). Alaskan moose (*A. a. gigas*), however, possess a striking pattern of coloration that has not been fully described or interpreted. The purpose of this paper is to provide a detailed account of pelage markings in Alaskan moose and to discuss the evolutionary history and potential function of this unique characteristic.

DESCRIPTION OF PELAGE COLORATION

Moose inhabiting the contiguous United States and Canada (*A. a. shirasi*, *A. a. andersoni*, *A. a. americana*) have been described as a homogeneous dark brown (Franzmann, 1981) to dark brown with a grayish breast and abdomen (Peterson, 1955). Likewise, Sokolov and Chernova (1987) noted that most moose in the Soviet Union pos-

sessed gray-brown sides and abdomens with black-brown or black on the lower sides. Nevertheless, they also described substantial regional variation in pelage color of moose in the Soviet Union. Geist (1987a) contrasted the morphology of European moose (*A. a. alces*) with the American-type moose. His drawing (p. 13) reflects similar patterns in pelage markings in American moose, but Alaskan moose are by far the most strikingly marked of the subspecies.

Alaskan moose exhibit coloration ranging from light, grizzled blond to dark brown. Amid this variation, one pelage characteristic is constant - a band of black hair extending across the rump and tapering downward along the flanks to the shoulder (Fig. 1). The shorter, darker hair on the rump lies more smoothly against the body than does the surrounding pelage, giving this dark band a shiny, reflective appearance. The dark band is made more conspicuous by lighter pelage across the back and white hair extending down the posterior of the hind legs, and occasionally forward onto the lower abdomen. A completely white

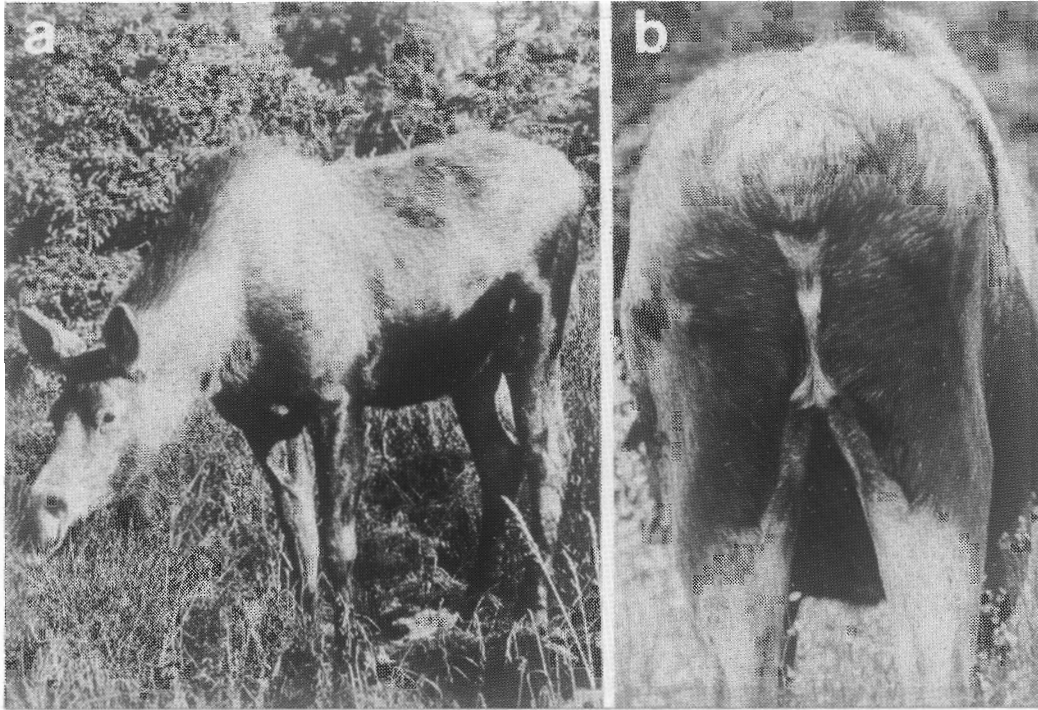


Fig. 1. Cow moose in Denali National Park and Preserve, Alaska showing typical rump markings in (a) lateral and (b) rear views. Note how the dark, glossy hairs on the rump stand out from surrounding pelage (photography by V. Van Ballenberge).

color morph of moose, which is not an albino, occurs in Alaska (Franzmann, 1981); those animals lack dark rump markings.

Dark rump markings in *A. a. gigas* are not well developed in calves. Animals 1 1/2 years of age clearly show the presence of such markings, but the dark rump-band is not fully developed and not as shiny as in older moose. The striking pelage characteristics of Alaskan moose are expressed completely in animals ≥ 2 years of age. This vivid color pattern does not result from hair along the back and sides fading; the dark band is evident year-round, even during the spring molt. We hypothesize that dark rump markings evolved as an adaptation to more open habitats in Alaska and may function in a manner analogous to rump patches in other ungulates.

Rump-Patch Evolution

Rump patches have evolved independently in the Artiodactyla, Lagomorpha, and Rodentia (Guthrie, 1971). The social impor-

tance of signals involving markings on both the head and rump of ungulates has been recognized for many years (Darwin, 1872; Portmann, 1960; Bubenik, 1982; and many others). Most modern researchers agree that displays of the rump patch function primarily as alarm signals in most species (Harvey and Greenwood, 1978), but an intuitive understanding and consensus regarding the mechanisms underlying their evolution has not been reached.

Among ungulates, rump patches often include a conspicuous pattern of contrasting-colored pelage on the rear or underside of the tail; sexual dimorphism in rump patches is rare (Guthrie, 1971). There is a strong positive relationship between the size of horn-like organs and of rump patches (Guthrie, 1971). Rump-patch displays may be augmented by piloerection of hairs (Kitchen, 1974), specialized gaits (Caro 1986; Pitcher, 1977), alarm vocalizations (McCullough, 1969; Bowyer



and Kitchen, 1987), or release of alarm pheromones (Muller-Schwarze, 1974), which ostensibly reinforce behaviors elicited by these displays. Ungulates without rump patches include less gregarious, forest-dwelling species that attempt to escape predation primarily via crypsis (Hirth and McCullough, 1977). Some woodland species, especially white-tailed deer (*Odocoileus virginianus*), possess rump patches that may be displayed conspicuously (flagging) if cryptic behavior fails (Hirth and McCullough, 1977). Ungulates with exceptionally large body size that are less susceptible to predation, such as Rhinocerotidae and Elephantidae, and ungulates that possess formidable weapons and an effective group defense, such as Tayassuidae and the muskox (*Ovibos moschatus*), also lack rump patches (Hirth and McCullough, 1977), as do most Bovini (Guthrie, 1971).

Open Habitats, Body Size, and Patterns of Coloration in Cervids

A clear pattern exists among the Cervidae for body size, antler size, and rump-patch size to increase with openness of the environment. Indeed, this pattern has been particularly well documented for subspecies of mule deer (*Odocoileus hemionus*) by Cowan (1936) and for red deer and wapiti (*Cervus elaphus*) by Geist (1987b). An increasing gradient in the size of rump patches is especially evident in black-tailed and mule deer, ranging from the small-sized patch in *O. hemionus sitkensis*, which inhabits densely forested areas in Alaska, to the larger patch of *O. h. hemionus*, which occupies open lands in the western United States (Cowan, 1936). Geist (1987b) discusses additional environmental factors that may lead to the evolution of such characters; however, a complete enumeration of these ideas is beyond the scope of this paper. The important point is that cervids inhabiting more open habitats would be expected to be larger, have more conspicuous coloration, and be more gregarious than conspecifics living in more densely forested (closed) habitats (Hirth,

1977).

If our idea that dark rump markings in Alaskan moose function as a rump patch is correct, then a consistent trend of increasing antler and body size, as well as gregariousness, should be evident for moose inhabiting more open environments. *A. a. gigas* has long been recognized as the heaviest of the subspecies (Flerov, 1952; Peterson 1955), and possesses the largest and most complex antlers (Van Ballenberghe, 1982; Gasaway *et al.*, 1987; Geist, 1987a). Within cervid species, or even populations, a tendency exists for males with larger body mass to have larger antlers and be the most dominant individuals (McCullough, 1982; Bowyer, 1986); this pattern also holds for moose (Prieditis, 1979). Moreover, in comparison to body mass, openland cervids—especially *A. a. gigas*—have larger antlers than those living in closed, forested habitats (Geist, 1987b). Further, moose in Alaska occur in larger groups than populations elsewhere in North America (Peek *et al.*, 1974), and large bulls are able to establish dominance over smaller males and acquire access to these large groups of females during rut (Peek *et al.*, 1986; Miquelle, 1990). Indeed, we have observed a harem mating system for moose in interior Alaska with groups of >30 individuals. Thus, Alaskan moose possess other physical and behavioral characteristics that are consistent with the presence of a rump patch.

Another prediction of our hypothesis is that variation in pelage color should occur in more open areas outside Alaska. K. N. Childs (Minst. Environ., British Columbia, pers. commun.) reports that moose living mostly above tree line are lighter in color than those inhabiting forested areas of British Columbia. Sokolov and Chernova (1987:367) noted that East-Siberian moose are differentiated from those inhabiting West-Siberia by “a dark coloured band stretching from the neck and withers down to the back,” but no information was provided on habitats occupied by those

moose. Bowyer has observed large, dark-colored moose near the Kolyma Reservoir in the Soviet Far East that lacked obvious rump markings, but those animals inhabited areas mostly below tree line. Guthrie, on the other hand, collected three moose from tundra areas in northeastern Siberia that possessed dark rump markings; however, these animals were not as vividly marked as Alaskan moose. Moreover, Chernyavsky and Domnich (1989:15) provide a photograph of a large moose (*A. a. buturlini*) with obvious rump markings from the Soviet Union.

Colonization and Subspeciation by Moose in North America

Insights into the pelage markings of moose can be obtained from a more complete understanding of their evolutionary history. An ancestral Alcini, *Cervalces gallicus*, first appeared in Eurasia during the early Pleistocene (Azzaroli, 1985). By 30,000-40,000 years BP, *Cervalces* certainly had reached the New World, with *C. scotti* spreading across the mid-continent of North America (Guthrie, 1990a). Dates as early as 100,000-200,000 years BP, however, are possible for the first *Cervalces* in North America (Geist, 1987a), although Churcher and Pinsof (1987) believe such earlier dates are unlikely. Likewise, *C. latifrons* (= *A. latifrons*) was evolving rapidly toward modern moose (*A. alces*) in Eurasia (Guthrie, 1990a). Obviously, some taxonomic confusion exists with respect to these early moose-like animals; for simplicity and clarity we have adopted the nomenclature of Churcher and Pinsof (1987). Although some believe that *C. scotti* gave rise to modern moose, it is more likely that *Cervalces* became extinct in North America during the Wisconsin glaciation, and the New World was colonized a second time by moose (*A. alces*) from Eurasia (Geist, 1987b; Guthrie, 1990a; Sher, 1987).

Traditional views of moose subspeciation hold that North America was colonized by

Alces in the late Wisconsin or early Holocene (Kurtén and Anderson, 1980). Earlier records of *Alces* from North America (Peterson, 1955) probably result from misidentifying fossil remains of *Cervalces* as *Alces*. Peterson (1955) hypothesized that subspeciation in North America was the result of glacial ice separating moose in Beringia from those isolated to the south of the ice sheet during the Sangamon and Wisconsin periods (Fig. 2a). Thus, the present-day differences among moose subspecies in North America was thought to be produced largely by glaciation (Peterson, 1955; Kelsall and Telfer, 1974).

Recent radiometric dating of antler collagen from *A. alces* in Alaska places the oldest specimen at 8,740±70 years BP (Guthrie, 1990a). A corridor probably existed between Beringia and areas south of the ice sheet as early as 14,000 BP (Burns, 1990; Catto and Mandryk, 1990), and some retraction of the ice sheet probably occurred by ca. 10,000 years BP (Kelsall and Telfer, 1974), raising questions about the viability of ideas concerning subspeciation in moose resulting from isolation caused by the glaciers. Indeed, Geist (1987a) postulated that *A. alces* spread postglacially in North America. If moose older than ca. 14,000 BP cannot be found in Alaska, then Geist's description of moose colonization is supported. More importantly, this means that subspeciation of moose is likely based on adaptations to different habitats, and that these adaptations are an example of extremely rapid evolution.

A recent study of mitochondrial DNA (mtDNA) from subspecies of moose in North America revealed no intraspecific variation (Cronin, 1989, 1991). This outcome lends additional support to the idea that subspeciation of moose in the New World is a comparatively recent event. Rate of mtDNA evolution (Brown *et al.*, 1979) for large mammals is thought to be about 2% per million years (Shields and Kocher, 1991); hence, recent subspecific divergence in moose might go

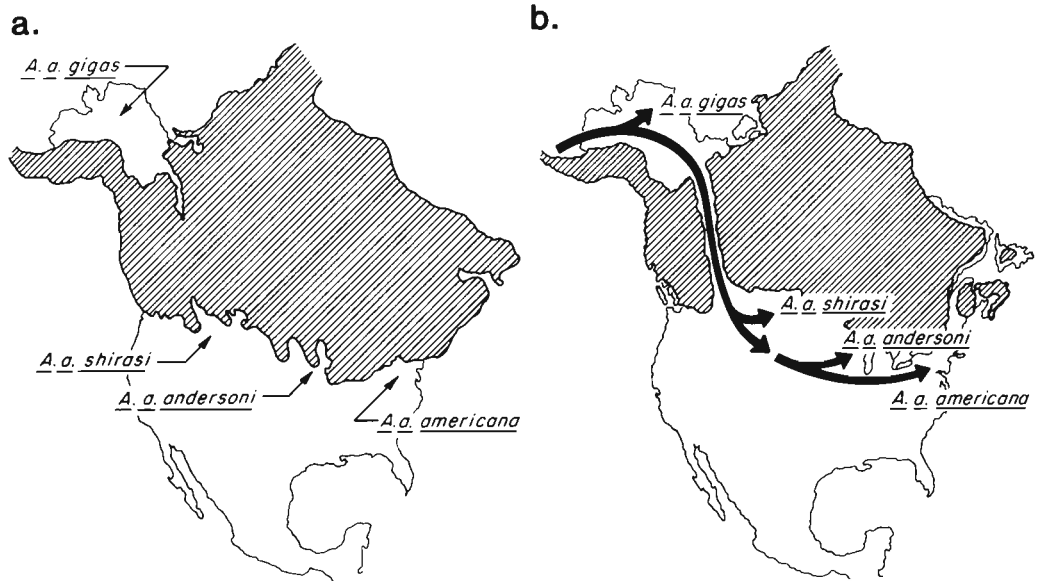


Fig. 2. a) Traditional view (Peterson 1955) of moose subspeciation in North American caused by the ice-sheet (shaded area) isolating moose in Beringia from those to the south. b) The ice-free corridor hypothesis for subspeciation in North American moose (ca. 14,000 years BP), allowing a recent colonization of the New World.

undetected using some mtDNA procedures. Further, these data suggest that moose in North America share a common maternal lineage, offering additional support for post-glacial subspeciation without long periods of isolation caused by the ice sheet.

A lack of mtDNA variability does not mean that subspecies of moose are without morphological and genetic differences. For instance, moose in Scandinavia show substantial genetic variability at a diallelic locus coding for phosphomannose isomerase over short geographic distances (Chesser *et al.*, 1982). Moreover, North American subspecies of moose show strong divergence in a number of morphological characteristics (Peterson 1955; Gasaway *et al.*, 1987).

The most likely pattern of postglacial dispersion, then, is that depicted in Figure 2b; this pattern is consistent with recent dates of *Alces* in Alaska (Guthrie, 1990a), and with mtDNA analysis (Cronin, 1989, 1991). We do not imply, however, that *Alces* initially colonizing Alaska during the late Pleistocene were identical to present-day moose. Indeed,

those ancestors of modern moose were significantly larger (Guthrie, 1984). Early colonizers likely encountered open environments with sparse, low shrubs and grasses (i.e., the remnants of mammoth-steppe vegetation; Guthrie, 1990b). Thus, the small body size, dark coat color, small group size, and absence of striking pelage markings of moose that inhabit the lower United States and Canada most likely represent adaptations to living in a dense boreal forest.

Extensive grasslands over the Great Plains (Kelsall and Telfer, 1974) and perhaps *Parelaphostrongylus tenuis*, a parasite of white-tailed deer that causes "moose sickness," may have helped limit the southward expansion by moose (Geist, 1987a). Nudds (1990), however, questioned the importance of this meningeal worm in limiting the range of modern-day moose, and Clark and Bowyer (1986) reported that moose in Maine were successfully expanding their distribution into areas inhabited by white-tailed deer infected with this nematode. Another important constraint upon the southward expansion of moose

may have been their poor thermoregulatory capabilities at high ambient temperatures (Renecker and Hudson, 1990). Whatever the limiting factors of their environment, moose today inhabit closed boreal forests in the lower United States and in Canada (Peterson, 1955), and more open habitats throughout much of Alaska (Van Ballenberghe, in press). Moose in southeastern Alaska, however, are smaller and darker than those in other areas of the state, and are likely *A. a. andersoni* that colonized that area from British Columbia (Klein, 1965). Antler morphology indicates that a zone of intergradation may occur between *A. a. gigas* and *A. a. andersoni* in the southern Yukon Territory (Gasaway et al., 1987).

HYPOTHESES EXPLAINING A RUMP PATCH IN MOOSE

Our observations strongly suggest the presence of a dark rump patch in Alaskan moose. For this idea to be tenable, however, it should fit with modern hypotheses concerning the evolution of rump patches in ungulates, and offer some explanation for unusual color and shape of this pelage characteristic.

Several hypotheses have been forwarded to explain the function and thereby the evolutionary history of rump-patch displays. These displays may have evolved as: (1) an intraspecific warning mechanism (Estes and Goddard, 1967); (2) an intraspecific appeasement gesture that functions secondarily as an alarm signal (Guthrie, 1971); (3) a pursuit-invitation signal to predators (Smythe, 1970; 1977); (4) a pursuit-deterrent signal to predators (Woodland *et al.*, 1980); and (5) a group-cohesion signal (Hirth and McCullough, 1977).

Estes and Goddard (1967) noted that individuals often engaged in rump-patch displays when confronted with or fleeing from a predator, and hypothesized that this display served to warn other members of the group about potential danger. This signalling, how-

ever, may make the individual more obvious to the predator, and thereby increases the risk to the signaller (Maynard Smith, 1965). Consequently, evolution of rump-patch displays would be difficult to explain as an intraspecific warning mechanism unless kin selection, group selection or reciprocity were invoked. Because ungulates often assemble into temporary, unrelated groups (Hirth and McCullough, 1977) where rump-patch displays may be common, and because the special conditions for group selection to operate would seldom, if ever, occur (Williams, 1966), this hypothesis offers an unlikely explanation for the development of either the striking pelage coloration or the behaviors associated with rump patches for most ungulates (Hirth and McCullough, 1977). Likewise, the transient nature of moose aggregations (Peek *et al.*, 1974) make it difficult for this hypothesis to account for rump markings in Alaskan moose.

Guthrie (1971) argued that rump-patch displays evolved initially as an intraspecific submissive gesture to appease dominant animals. Thus, presentation of the rump patch by subordinates served to redirect the aggressive behavior of dominant individuals. Ultimately, rump patches acquired the additional function of a warning mechanism by prey animals presenting the submissive display to predators. Geist (1971) described the mimicking of a copulatory posture to appease dominant animals in mountain sheep (*Ovis* spp.), but whether this hypothesis will account for rump patches in other ungulates is less certain. For instance, neither white-tailed deer nor pronghorn (*Antilocapra americana*) display their rump patches during copulation (Hirth and McCullough, 1977). Dominance mounting and obvious displays of the dark rump markings during copulation are rare or absent in Alaskan moose (pers. obs.), making this hypothesis unlikely.

Two related hypotheses, "pursuit invitation" (Smythe, 1970, 1977) and "pursuit deterrence" (Woodland *et al.*, 1980), also have

been proposed to explain the adaptive significance of rump patches. The first of these ideas holds that a prey animal that has detected a predator could display its rump patch and thereby elicit the premature pursuit of the predator while it was still a safe distance away. Likewise, the pursuit-deterrence hypothesis assumes that the rump patch and associated behaviors advertise the ability of the prey to elude capture, and in consequence, discourages the predator. Although these hypotheses may be applicable to species such as white-tailed deer, which have the ability to turn the rump-patch display "on and off" by raising and lowering their tail, both fail to explain the occurrence of large, permanent rump patches that cannot be "turned off."

The fundamental flaw in both "pursuit" hypotheses is that it would be maladaptive for ungulates with large rump patches that cannot be concealed to continually elicit pursuit or to advertise their ability to escape predators. The pursuit-invitation hypothesis assumes that prey can dupe predators into chasing them when the likelihood of success is low, and that there is little difference between the energetic costs of fleeing from predators than from simply moving to keep predators at some "safe" distance; both of these assumptions are probably incorrect (Coblentz, 1980). Moreover, it is unclear why some prey (those with nonconcealable rump patches) should continually elicit the pursuit of predators irrespective of the distance between prey and predator, and under circumstances where the prey was unaware of the predator (Hirth and McCullough, 1977). A pursuit-deterrence signal (i.e., the prey is healthy) presents a similar problem. Unless display of the rump patch has a cost so that weak, sick or otherwise infirm individuals cannot engage in this behavior, then "cheating" by disadvantaged prey would be expected (Caro, 1986). Consequently, predators would have to pursue prey continually to "test" their physical condition. Because rump markings in moose cannot be

"turned off," these "pursuit" hypotheses are untenable.

The final hypothesis considered is that of group cohesion (Hirth and McCullough, 1977). Conspicuous rump patches are thought to assist group members in maintaining contact while fleeing predators or to induce new animals to join the group to become part of the "selfish herd" (*sensu* Hamilton, 1971). There are at least two potential problems with this hypothesis: 1) a group-cohesion signal is poorly located on the rear of the animal, both for signalling to conspecifics or in having the predator follow a group member back to the signaller as the group aggregates (Bildsten, 1983; Smythe, 1977); and 2) some openland, gregarious ungulates, which evidently do not have weaponry against predators or an effective group defense, lack rump patches -- especially the Bovini (Guthrie, 1971).

Coblentz (1980) noted that many ungulates have a field of vision that may approach 360°; hence, the location of conspicuous coloration on the rump may not be so problematical. Further, among some ungulate species, the contrasting pelage extends around onto the sides of the animal (e.g., topi, *Damaliscus korrigum*) or the animal possesses contrasting markings along the sides that may be involved in alarm signalling (e.g., springbok, *Antidorcas marsupialis*). Moreover, benefits that accrue to animals that become part of a group over those obtained by remaining solitary are thought to include a reduction in the probability of a predator selecting an individual as prey, more eyes, ears and noses with which to detect the predator (or alarm signals of conspecifics that have done so), and the potential for the group to confuse the predator (Bertram, 1978). These benefits mitigate potential detriments resulting from the costs of signalling. Indeed, predators of ungulates are more efficient at capturing prey separated from the group (Kruuk, 1972; Miller, 1975; Schaller, 1968) and behave more predaceously toward smaller groups of prey (Bowler, 1987).

Clearly, the confusion of predators is an important corollary to the group cohesion hypothesis. Rump patches, in conjunction with the erratic movement and repositioning of animals in a fleeing group, may help to confuse predators (Kitchen, 1974). The success rate of predators is known to decline when they select new prey to chase during the course of a pursuit (Kruuk, 1972).

The apparent lack of rump patches among some openland bovids presents an additional problem for the group cohesion hypothesis. One possibility might be that some animals occur in such large groups that a conspicuous signal to promote further cohesion is unnecessary, but this notion is difficult to test. The absence of this characteristic also may be simply a phylogenetic constraint, but this is not a compelling argument; rump patches have evolved independently in several orders of mammals (Guthrie, 1971). Moreover, where Bovini inhabit open terrain and are subject to predation by large, effective predators, pronounced rump patches have evolved - the best example is the striking rump patch of the banteng (*Bos javanicus*), which is preyed upon by tigers (*Panthera tigris*) on Java (Hoogerwerf, 1970).

We hypothesize that any coloration that contrasts markedly with an animal's environment and can be made more visible by associated alarm behaviors might function as a rump patch. Several other conditions, however, should be present to satisfy this idea of contrasting coloration. First, such ungulates should be gregarious, and their pelage should differ markedly from more cryptically colored young. It would be inappropriate to invoke this idea to explain the striking markings on lesser kudu (*Tragelaphus imberbis*); these animals are camouflaged for living in a forest. We believe, however, this hypothesis may explain the coloration of American bison (*Bison bison*). American bison are extremely gregarious bovids that inhabit the Great Plains; calves have light-reddish pelage that blends

well with dry grasses on the plains for much of the year. Adults, however, are a dark, chocolate brown that contrasts markedly with their environment (Guthrie, 1990b). Conversely, wisent (*Bison bonasus*) occur in smaller groups and inhabit more forested parklands of Europe; both young and adults are a similar, cryptic color (Guthrie, 1990b:159). Bizarre markings among some perissodactyls and girrafids may also fit this hypothesis, but more investigation is needed. In any event, proposed problems with the group cohesion hypothesis are fewer than with other notions of rump patch evolution and are consistent with rump markings in Alaskan moose (Table 1).

Why do moose possess a dark rump-patch rather than a light one? For a rump patch to be visible, it must be either darker or lighter than the surrounding pelage. Visibility in relation to the environment also may influence the evolution of such a feature, as we postulated for American bison. In a northern climate where snow is present on the ground for up to 9 months, a dark rump-patch may be more visible than a lighter one. Further, some African ungulates such as topi and waterbuck (*Kobus defassa*) bear similar dark markings across the rump; investigations into the function of these markings may shed further light on the evolution of a dark rump-patch in Alaskan moose.

ACKNOWLEDGMENTS

The personnel of Denali National Park and Preserve provided support during periods when we were making observations of Alaskan moose. We thank D. R. Klein and V. C. Bleich for their helpful comments. D. Borchert provided Figure 2.

Table 1. Comparison of some hypotheses forwarded to explain the evolution of rump-patches in ungulates, and their relevance to Alaskan moose.

	HYPOTHESIS	PREDICTIONS
1.	Intraspecific warning signal (Estes and Goddard 1967).	Requires kin-selection or reciprocal altruism. Hirth and McCullough (1977) rejected the kin-selection model, and unstable grouping behavior of moose precludes reciprocal altruism.
2.	Intraspecific submissive gesture (Guthrie 1971).	Requires dominance mounting for evolution, and such behavior is rare in North American moose.
3.	Pursuit-invitation signal to predators (Smythe 1970).	Does not sufficiently explain presence of a rump patch in openland species like Alaskan moose that cannot "turn off" the signal.
4.	Pursuit-deterrent signal to predators (Woodland <i>et al.</i> 1980).	Predators would be selected against responding because prey might "cheat," making evolution improbable.
5.	Intraspecific signal promoting group cohesion (Hirth and McCullough 1977).	Group sizes and openness of habitat consistent with predictions.

REFERENCES

- AZZAROLI, A. 1985. Taxonomy of Quaternary Alcini (Cervidae, Mammalia). *Acta Zool. Fennica* 170:179-180.
- BERTRAM, B. C. R. 1978. Living in groups: predators and prey. Pages 64-96 *in* J. R. Krebs and N. B. Davies, eds., *Behavioural ecology: an evolutionary approach*, Sinauer, Sunderland, 494 pp.
- BILDSTEIN, K. L. 1983. Why white-tailed deer flag their tails. *Amer. Nat.* 121:709-715.
- BOWYER, R. T. 1986. Antler characteristics as related to social status of male southern mule deer. *Southwest. Nat.* 31:289-298.
- _____. 1987. Coyote group size relative to predation on mule deer. *Mammalia* 51:515-526.
- _____, and D. W. KITCHEN. 1987. Sex and age-class differences in vocalizations of Roosevelt elk during rut. *Amer. Midl. Nat.* 118:225-235.
- BROWN, W. M., M. GEORGE, Jr., and A. C. WILSON. 1979. Rapid evolution and animal mitochondrial DNA. *Proc. Natl. Acad. Sci. USA* 76:1967-1971.
- BUBENIK, A. B. 1982. The behavioral aspects of antlerogenesis. Pages 389-499 *in* R. D. BROWN, ed., *Antler development in Cervidae*. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX, 480 pp.
- _____. 1987. Behaviour of moose (*Alces alces* spp.) of North America. *Viltrevy Suppl.* 1:333-365.
- BURNS, J. A. 1990. Paleontological perspectives on the ice-free corridor. Pages 61-66 *in* L. D. Agenbroad, J. I. Mead, and L. W. Nelson, eds., *Megafauna and man: Discovery of America's heartland*. Univ. Northern Arizona, Flagstaff, 143 pp.
- CARO, T. M. 1986. The functions of stotting: a review of the hypotheses. *Anim. Behav.* 34:649-662.
- CATTO, N., and C. MANDRYK. 1990. Geology of the postulated ice-free corridor. Pages 80-85 *in* L. D. Agenbroad, J. I. Mead, and L. W. Nelson, eds., *Megafauna and man: Discovery of America's heartland*. Univ. Northern Arizona, Flagstaff, 143 pp.
- CHERNYAVSKY, F. B., and V. I.

- DOMNICH. 1989. Elk in the North-East of Siberia. Nauka, Moscow, 126 pp.
- CHESSER, R. K., R. REUTERWALL, and N. RYMAN. 1982. Genetic differentiation of Scandinavian moose *Alces alces* populations over short geographical distances. *Oikos* 39:125-130.
- CHURCHER, S. C., and J. D. PINSOF. 1987. Variation in the antlers of North American *Cervalces* (Mammalia; Cervidae): Review of new and previously recorded specimens. *J. Vert. Paleo.* 7:373-397.
- CLARK, R. A., and R. T. BOWYER. 1986. Occurrence of protostrongylid nematodes in sympatric populations of moose and white-tailed deer in Maine. *Alces* 22:313-321.
- COBLENTZ, B. E. 1980. On the probability of pursuit invitation signals in mammals. *Amer. Nat.* 115:438-442.
- COWAN, I. McT. 1936. Distribution and variation in deer (genus *Odocoileus*) of the Pacific coastal region of North America. *Calif. Fish Game* 22:155-246.
- CRONIN, M. A. 1989. Molecular evolutionary genetics and phylogeny of cervids. Ph.D. Thesis, Yale Univ., New Haven.
- _____. 1991. Mitochondrial-DNA phylogeny of deer (Cervidae). *J. Mammal.* 72:553-566.
- DARWIN, C. 1872. The expression of the emotions in man and animals. Reprint 1965, Univ. Chicago Press, 372 pp.
- ESTES, R. D., and J. GODDARD. 1967. Prey selection and hunting behavior of the African wild dog. *J. Wildl. Manage.* 31:52-70.
- FLEROV, K. K. 1952. Musk deer and deer. *Fauna of U.S.S.R. Mammals* 1(2):1-257.
- FRANZMANN, A. W. 1981. *Alces alces*. *Mammal. Species* 154:1-7.
- GASAWAY, W. C., D. J. PRESTON, D. J. REED, and D. D. ROBY. 1987. Comparative antler morphology and size of North American moose. *Viltrevy Suppl.* 1:311-325.
- GEIST, V. 1971. Mountain sheep: A study in behavior and evolution. Univ. Chicago Press, 383 pp.
- _____. 1987a. On the evolution and adaptations of *Alces*. *Viltrevy Suppl.* 1:11-23.
- _____. 1987b. On speciation in Ice Age mammals, with special reference to cervids and caprids. *Can. J. Zool.* 65:1067-1084.
- GUTHRIE, R. D. 1971. A new theory of mammalian rump patch evolution. *Behaviour* 38:132-145.
- _____. 1984. Alaskan megabucks, megabulls, and megarams: the issue of Pleistocene gigantism. *Spec. Publ. Carnegie Mus. Nat. Hist.* 8:482-509.
- _____. 1990a. New dates on Alaskan Quaternary moose, *Cervalces-Alces*—archaeological, evolutionary, and ecological implications. *Current Res. Pleistocene* 7:111-112.
- _____. 1990b. Frozen fauna of the mammoth steppe: The story of blue babe. Univ. Chicago Press, 323 pp.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theoret. Biol.* 31:295-311.
- HARVEY, P. H., and P. J. GREENWOOD. 1978. Anti-predator defense strategies: some evolutionary problems. Pages 129-151 in J. R. Krebs and N.B. Davies, eds., *Behavioural ecology: An evolutionary approach*. Sinauer, Sunderland, MA, 494 pp.
- HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildl. Monogr.* 53:1-55.
- _____, and D. R. McCULLOUGH. 1977. Evolution of alarm signals in ungulates with special reference to white-tailed deer. *Amer. Nat.* 111:31-42.
- HOOGERWERF, A. 1970. *Udjung Kulon: The land of the last Javan rhinoceros*. E. J. Brill, Leiden, 512 pp.
- KELSALL, J. P., and E. S. TELFER. 1974. Biogeography of moose with particular

- reference to western North America. *Naturaliste Can.* 101:117-130.
- KITCHEN, D. W. 1974. Social behavior and ecology of the pronghorn. *Wildl. Monogr.* 38:1-96.
- KLEIN, D. R. 1965. Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. *Arctic* 18:7-20.
- KRUUK, H. 1972. The spotted hyaena: A study of predation and social behavior. Univ. Chicago Press, 335 pp.
- KURTÉN, B., and E. E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia Univ. Press, NY, 392 pp.
- MAYNARD SMITH, J. 1965. The evolution of alarm calls. *Amer. Nat.* 99:59-63.
- McCULLOUGH, D. R. 1969. The tule elk: Its history, behavior, and ecology. Univ. Calif. Publ. Zool. 88:1-209.
- _____. 1982. Antler characteristics of George Reserve white-tailed deer. *J. Wildl. Manage.* 46:821-826.
- MILLER, D. R. 1975. Observations of wolf predation on barren-ground caribou in winter. *Internatl. Reindeer and Caribou Symp.* 1:209-220.
- MIQUELLE, D. G. 1990. Behavioral ecology of moose in Denali National Park and Preserve, Alaska. Ph.D. Dissert., Univ. Idaho, Moscow, 141 pp.
- MULLER-SCHWARZE, D. 1974. Social function of various scent glands in certain ungulates and the problems encountered in experimental studies of scent communication. Pages 107-113 in V. Geist and F. Walther, eds., *The behaviour of ungulates and its relation to management* IUCN Publ. (n.s.) 24, 940 pp.
- MURIE, A. 1934. The moose of Isle Royale. *Misc. Pub. Mus. Univ. Michigan* 25:1-44.
- NUDDS, T. D. 1990. Reproductive logic in retrospect: The ecological effects of the meningeal worms. *J. Wildl. Manage.* 54:396-402.
- PEEK, J. M., R. E. LERESCHE, and D. R. STEVENS. 1974. Dynamics of moose aggregations in Alaska, Minnesota, and Montana. *J. Mammal.* 55:126-137.
- _____, V. VAN BALLEMBERGHE, and D. G. MIQUELLE. 1986. Intensity of interactions between rutting bull moose in central Alaska. *J. Mammal.* 67:422-426.
- PETERSON, R. L. 1955. North American moose. Univ. Toronto Press, 280 pp.
- PITCHER, T. 1979. He who hesitates, lives. Is stotting antiambush behavior? *Amer. Nat.* 113:453-456.
- PORTMANN, A. 1960. *Die Tiergestalt.* Fr. Reinhardt Verlag, Basel., 274 pp.
- PRIEDITIS, A. A. 1979. Interrelation between body weight and horn size in European elks (*Alces alces*) of different age. *Zool. Zhurnal* 58:105-110.
- RENECKER, L. A., and R. J. HUDSON. 1990. Behavioral and thermoregulatory responses of moose to high ambient temperatures and insect harassment in aspen-dominated forests. *Alces* 26:66-72.
- SCHALLER, G. B. 1968. Hunting behavior of the cheetah in Serengeti National Park. *E. Afr. Wildl. J.* 6:95-100.
- SHER, A. V. 1987. History and evolution of moose in USSR. *Viltrevy Suppl.* 1:71-97.
- SHIELDS, G. F., and T. D. KOCHER. 1991. Phylogenetic relationships of North American ursids based on analysis of mitochondrial DNA. *Evolution* 45:218-221.
- SMYTHE, N. 1970. On the existence of "pursuit invitation" signals in mammals. *Amer. Nat.* 104:491-494.
- _____. 1977. The function of mammalian alarm advertising: social signals or pursuit invitation? *Amer. Nat.* 111:191-194.
- SOKOLOV, V. E., and O. F. CHERNOVA. 1987. Morphology of the skin of moose (*Alces alces* L.). *Viltrevy Suppl.* 1:367-375.
- VAN BALLEMBERGHE, V. 1982. Growth

and development of moose antlers in Alaska. Pages 37-48 *in* R. D. Brown, ed., Antler development in Cervidae. Caesar Kleberg Wildl. Res. Inst., Kingsville, 480 pp.

_____. In press. Behavioral adaptations of moose to treeline habitats in subarctic Alaska. 3rd Internatl. Moose Symp.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton Univ. Press, 307 pp.

WOODLAND, D. J., Z. JAAFAR, and M. KNIGHT. 1980. The "pursuit deterrent" function of alarm signals. *Amer. Nat.* 115:748-753.