SIMILARITY IN HABITAT ADAPTATIONS OF ARCTIC AND AFRICAN UNGULATES: EVOLUTIONARY CONVERGENCE OR ECOLOGICAL DIVERGENCE?

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ABSTRACT: Caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) partition habitat use in the Arctic differently in relation to their morphological, physiological, and behavioral attributes. Adaptations to Arctic habitats by caribou result in an energy-costly lifestyle in contrast to the energy-conservative adaptations of muskoxen. In southern Africa, impala (*Aepyceros melampus melampus*) and blesbok (*Damaliscus dorcas phillipsi*) show parallel adaptations, with impala more closely mirroring caribou, and those adaptations of blesbok resembling muskoxen. Comparative abilities of these ungulates to adapt to habitat parameters derive from their morphological, physiological, and behavioral capacities. Habitat constraints determine energy-nutritive requirements, forage digestibility, forage selection and intake rates, locomotive efficiency, thermal regulation, water requirements, avoidance of predation, and insect harassment and parasitism. Although overlap occurs, or has occurred, in distribution of these geographically paired ungulate species in both the Arctic and southern Africa, partitioning of habitat use has been dependent on species-specific selection of microhabitat components.

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Caribou *(Rangifer tarandus)* and muskoxen *(Ovibos moschatus)* in the Arctic show adaptations to their environment similar to those of impala *(Aepyceros melampus melampus)* and blesbok *(Damaliscus dorcus phillipsi)* in southern Africa (Fig. 1). Although widely separated geographically and by latitude, the habitats of caribou and muskoxen in the Arctic and the impala and blesbok in southern Africa, share pronounced seasonality. From summer to winter in the Arctic and from wet to dry season in southern Africa, the range of forage abundance, quality, and availability is large, as is the range in cost of water acquisition. Vulnerability to predation, insect parasitism and harassment also vary with seasonal changes in landscapes (Helle and Aspi 1984, Downes et al. 1986).

I compare the parallel adaptations of 2 arctic-dwelling ungulates, muskox and caribou, to their high-latitude environments, with the adaptations of blesbok and impala to their southern African environments. Species-specific morphology of these ungulates has constrained and shaped their adaptations to extreme seasonal variability in forage quality and quantity, water availability, temperature extremes, and strategies to avoid predation, insect parasitism and harassment. A major constraint on strategies adopted by these species that enable them to occupy their respective habitats is the associated energy cost of their adaptations. Where similarities exist in adaptations of evolutionarily distinct species of ungulates, with wide geographical and latitudinal separation in response to common environmental parameters, I ask: is this the consequence of evolutionary convergence or eco-

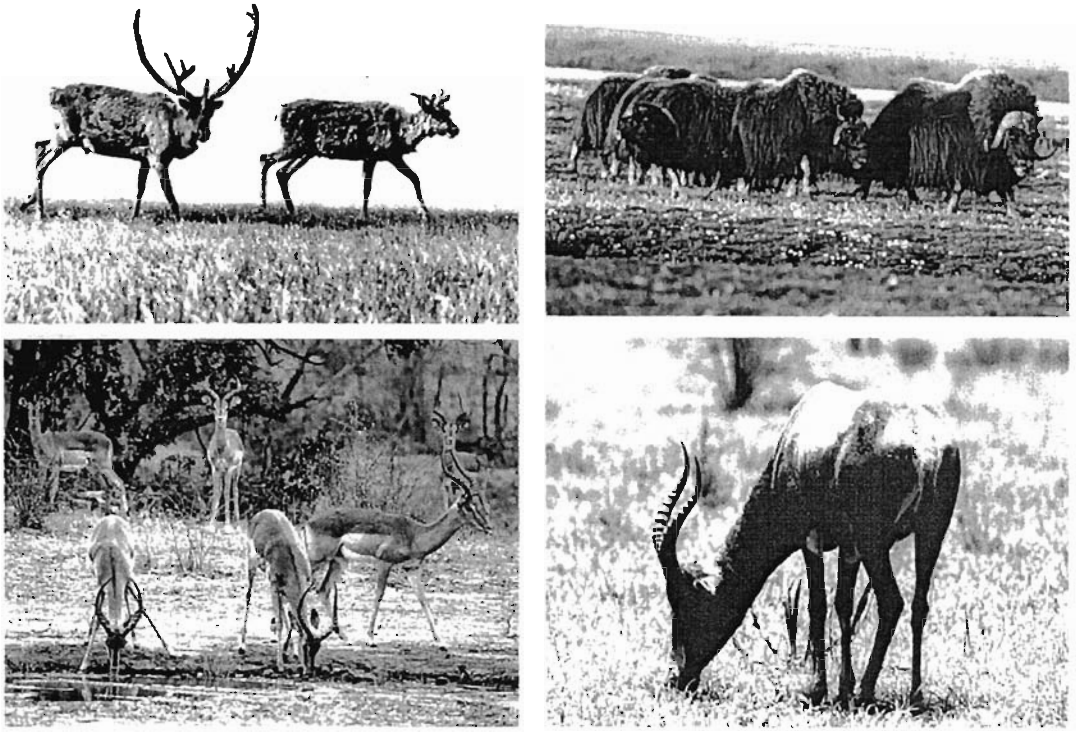

Fig. 1. Body morphology of the caribou (upper left) and muskox (upper right), the only two ungulates adapted to the open landscape of the Arctic, in comparison to the impala (lower left) and blesbok (lower right) that show adaptations to their habitats in southern Africa comparable to the caribou and muskox.

logical divergence? More explicitly, I ask whether similarities of adaptation to environmental parameters observed in ungulate species that are widely separated geographically are primarily the consequence of their evolutionary derived morphological and physiological characteristics? Alternatively, are these similarities in their adaptations to widely divergent habitats merely the consequence of the dominant influence of similar parameters in the disjunct environments?

Morphology

Muskoxen and blesbok are larger bodied, have greater rumen-reticulum capacity, and greater relative size of the cecum-colon than their habitat counterparts, caribou and impala. On average, muskoxen are about twice as heavy as caribou (Klein 1992, Staaland and Olesen 1992), and blesbok are, on average, about one-half again as heavy as impala (Klein and Fairall 1986). The ratio of rumen-reticulum weight for muskoxen versus caribou, where both species are present in Greenland, was about 2 to 1 in summer and 3 to 1 in winter (Staaland and Olesen 1992). For blesbok versus impala in South Africa, rumen-reticulum volume was 2 to 1 at the beginning of the rainy season (Klein and Fairall 1986). Staaland et al. (1979) reported that hind-gut length was relatively larger in Svalbard reindeer than mainland reindeer, and suggested that this was an adaptation to the low-quality, graminoid-dominated forage that characterized their diet in winter. Similar differences in hind-gut length in blesbok and impala (5.28 versus 3.50 m; Klein and Fairall 1986) also likely account for differences in diet quality noted among these species.

Foraging Dynamics

Caribou, like impala, have been classified as mixed feeders and muskoxen as bulk feeders by Hofmann (1983) on the basis of their gut and mouth morphology. The blesbok (although not included in Hofmann's classification), has greater gut capacity and a broader mouth than the impala, and would be classified among bulk feeders (Owen-Smith 1982, Klein and Fairall 1986). Winter diets of most mainland caribou are dominated by lichens, which have high digestible energy and low nitrogen content, whereas in summer caribou select green forage in early phenology, which has high nitrogen, phosphorus, and digestible energy (Klein 1990). Graminoids are a major component in the diet of muskoxen, especially in winter (Klein 1992). During summer, however, muskoxen, like caribou, attempt to feed selectively for high-quality plant parts in early phenology. Muskoxen are constrained in this regard by their broad muzzle, large volume of forage required for gut fill, and generally large group size, all of which may limit their ability to forage selectively in the patchy vegetation characteristic of the habitats they occupy (Klein and Bay 1994). Impala are selective mixed feeders, grazing heavily on nutritious and highly digestible new growth of graminoids during the rainy season in southern Africa, whereas during the dry season, browse dominates their diet (Klein and Fairall 1986).

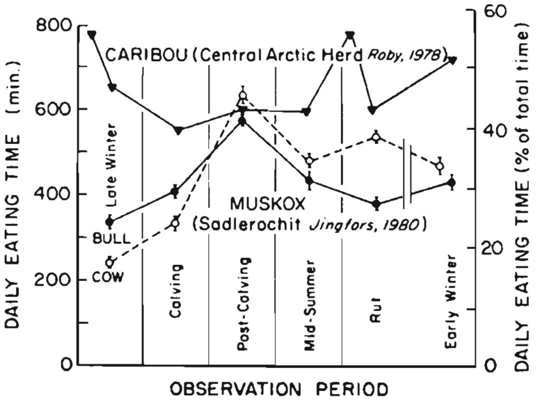

Fig. 2. Comparable seasonal variation in daily time spent eating by caribou and muskoxen where both species were present in northern Alaska (from Klein 1986, sources Roby 1978, Jingfors 1980).

Differences in time spent feeding in summer by muskoxen and caribou (Fig. 2) reflect the bulk-feeding strategy, and associated short daily feeding time of muskoxen (Jingfors 1980) in comparison with the more selective foraging of caribou, requiring a longer daily feeding time (Roby 1978). Differences in their morphology, physiology, and response to insects, however, also influence feeding efficiency and the time involved in feeding (Klein 1992). A similar pattern of bulk feeding by blesbok versus selective feeding by impala also has been described (Du Plessis 1968, Dunham 1982). Klein and Fairall (1986) reported a similar relation between daily feeding times and bulk versus selective feeding in blesbok and impala, respectively, in southern Africa (Fig. 3).

Water Requirements

Water requirements are based on rate of water turnover, which is a function of ambient temperature, activity, metabolic rate, diet, morphology, habitat, and behavior. The tritiated water technique of Holleman et al. (1982) indicated rates of water turnover of 2.95 l/day/100 kg for blesbok and 7.18 l/day/100 kg for impala when measured in southern Africa in summer, whereas comparable rates in winter were 3.17 and 6.44 l/day/100 kg, respectively (Fairall and Klein 1984). During the dry season in southern Africa, impala were observed to visit water sources daily, whereas blesbok

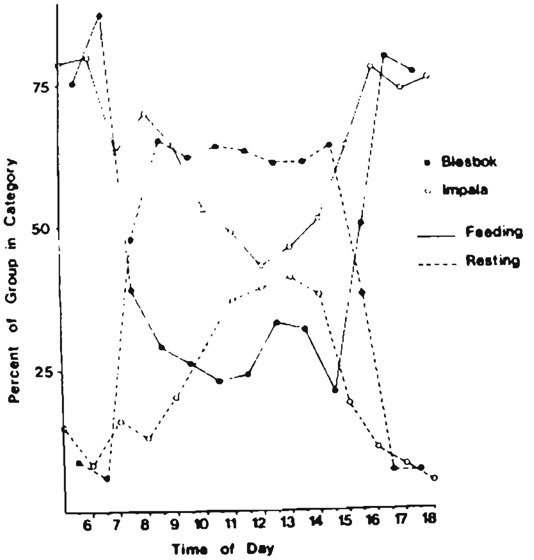

Fig. 3. Comparative daily feeding and resting times of blesbok and impala recorded in southern Africa near the end of the annual dry season (from Klein and Fairall 1986).

used water sources only every second or third day (Klein and Fairall 1986).

Rates of water turnover for muskoxen and caribou show more pronounced seasonal variation than was observed for blesbok and impala. Muskoxen (White et al. 1984) and caribou (Cameron et al. 1982) had comparable water requirements, but daily requirements for water were reduced by factors ≥5 from summer to winter in Alaska. Although water can be obtained in winter in the Arctic from snow, the high energetic cost to bring about a phase change in water and to raise it to body temperature (6-14% of daily energetic expenditure; Soppela et al. 1992), presumably has selected for extreme water conservation in both muskoxen and caribou. The low water requirement of caribou in winter, in contrast to their energetically costly life style, may be explained partially by the low-nitrogen content in lichens that dominate their diet, thus minimizing the need for water for excretion of osmotically active products in their urine (White 1975, Soppela et al. 1992).

Energy Conservation and Thermoregulation

Muskoxen are less active throughout the year than caribou, as indicated by daily activity budgets. Daily time spent lying for muskoxen in Alaska and the Canadian high Arctic recorded by Jingfors (1980) varied from 44-60% throughout the year, whereas mean time spent lying for caribou recorded by Roby (1978) in northern Alaska was 35%. In southern Africa during August through October, Klein and Fairall (1986) observed that blesbok spent 34% of their daily activity lying, and impala 4% of their time in that behavior. The low amount of time spent lying by impala was partly a consequence of their standing rather than lying when ambient temperatures were high (> 31°C; Klein and Fairall 1986). A pronounced reduction in daily activity during winter, when forage quality is low and availability restricted, is characteristic of both muskoxen (Jingfors 1980) and blesbok (Du Plessis 1968).

Klein and Fairall (1986) reported a wider tolerance for extremes in ambient temperature among blesbok than impala. They also observed that when night temperatures often were < 0°C in winter, blesbok basked in the morning sun before initiating activity, presumably to increase body temperature. Conversely, in contrast to impala, blesbok often did not seek available shade when ambient temperatures exceeded 31°C, which presumably resulted in heat loading, as has been observed in camels (*Camelus dromedarius*) (Schmidt-Nielsen et al. 1957). This strategy may minimize the cost of thermoregulation in environments with large gradients in day-night temperatures. Impala, like blesbok, reduced activity under high ambient temperature; however, unlike blesbok they sought shade and remained standing, presumably to increase exposed surface for evaporative cooling (Klein and Fairall 1986).

Muskoxen, in contrast to caribou (Klein 1996), have a low surface to body mass ratio, have dense under-wool, and lack capacity for cooling through piloerection of pelage. On warm days of summer, even in the high Arctic where there are few harassing insects, muskoxen generally rest on residual snow banks when available, or may enter water to cool themselves (personal observations). Caribou, by rapid shedding of winter pelage at the onset of summer, and with piloerective capability, have a greater thermoregulatory flexibility than muskoxen, which in turn is adaptive to their active life style.

Energy Cost of Predation Avoidance

Caribou reduce vulnerability to predation through group vigilance, alertness, and by fleeing from their major predator, the wolf (*Canis lupus*) (Lent 1974, Klein 1999). The energetic cost of this strategy can be high for individual caribou when predator density is high and caribou group size is small. Muskoxen, when approached by wolves, usually run short distances to high ground, where in a compact group adults face attackers (Gray 1974). In favorable terrain this strategy of defense involves a low expenditure of energy.

In southern Africa, lions *(Panthera leo)* have been a major predator of impala, and presumably blesbok, prior to the extirpation of blesbok as free-living populations in natural habitats. In open grasslands, the natural habitat of blesbok, cheetahs *(Acinonyx jubatus)* also were likely one of their major predators (Pettifer 1981). Blesbok, like caribou and many other ungulates occupying open habitats, have evolved to rely on group vigilance to alert the group to approaching predators, and they employ large-group cohesion to confuse predators when fleeing attack (Pettifer 1981). Major predators of impala include the cheetah and lion, as well as the leopard *(Panthera pardus),* a species that favors the savanna and riparian habitats of impala (Smithers 1983). Predation avoidance behavior of impala, although dependent on group vigilance and synchronization of individuals within the group in response to attack by predators, varies considerably from that of blesbok. Riparian and savanna habitats favored by impala limit visibility, and allow predators to stalk close to them before attacking. Impala, as an adaptation to this habitat-related predation, employ group confusion of predators when under attack through "spronking" (erratic high leaping) that frustrates the attempt of predators to target an individual animal (Walther 1969, Jarman and Jarman 1973). This alarm behavior also enables dispersal of the group into the surrounding cover. This predation-avoidance strategy, while effective, has a high associated energy cost in contrast to behavior of blesbok. Indeed, Pettifer (1981), reported impala to be taken by cheetahs less frequently than blesbok in relation to their density.

Role of Parasitic Flies

Both blesbok and caribou are parasitized by host-specific nasal botflies, blesbok by *Gedoelstia hassleri* (R. Miller and M. W. Mansell, personal communication) and caribou and reindeer by *Cephenomyia trompe* (Murie 1935). Caribou are also host to the skin warble fly (*Hypoderma tarandi*). Host specificity of insect parasites likely is related to behavior of the host species and the habitats they occupy. The flies, during their free-living stage when reproduction requires re-infection of their hosts, are possibly favored in relocation of their host species by large group size. Helle (1981) suggested that the tendency of reindeer to decrease group size when parasitic flies become abundant was a behavioral adaptation to minimize parasitism by the flies. In open habitats where large predators are present, however, reduction in the group size of the prey would reduce their efficacy of predation avoidance (Jarman and Jarman 1973).

The open, semiarid habitats of the blesbok, where density of passerine birds is low, may result in low predation on pupae of the nasal bot present on the ground as well as predation on adult flies. In contrast, absence of nasal-bot parasitism of the impala may be a consequence of the savanna and riparian habitats favored by impala. During their pupal and adult phases, parasitic flies presumably would be more vulnerable to predation by birds, which are more abundant in savanna and riparian habitats than in open grassland. There is a physiological cost associated with hosting infestations of larvae of skin warble and bot flies by caribou and reindeer (Oksanen et al. 1992); however, the additional energetic costs of harassment by the adult flies throughout much of the distribution of caribou, and the associated avoidance behavior they employ, are substantial (Reimers 1980).

Evolutionary Convergence or Ecological Divergence?

Does evolutionary convergence or ecological divergence account for similarities observed in adaptations of Arctic and African ungulates to their habitats? What conclusions can be drawn from this comparative analysis of geographically paired, but distinctly different, ungulate species existing at opposite ends of the earth? Morphological and physiological characteristics, as well as the basic behavioral patterns of the muskox, caribou, blesbok, and impala, are a product of their evolutionary pathways that have determined, as well as limited, the potential of these species to adapt to their distinctive habitats. These characteristics include body size, mouth and gut morphology, digestive physiology, pelage, leg length, presence or absence of weapons for predator deterrence, water and temperature regulatory mechanisms, as well as genetically fixed and learned patterns of behavior.

Ecological divergence that characterizes the muskox and caribou in the Arctic and the blesbok and impala in southern Africa, and that has resulted in parallel habitat adaptations of muskoxen and blesbok on one hand and caribou and impala on the other, however, has been driven by environmental factors. Dominant among these have been seasonality, range and abundance of forage types and their digestibility, ambient variation in temperature, and types of predators and parasites. Both evolutionary convergence and ecological divergence, therefore, have been the drivers that account for the similarities in adaptation of muskoxen and blesbok and of caribou and impala, respectively, to their Arctic and African habitats.

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