

OVER-WINTER SURVIVAL STRATEGIES OF NORTH AMERICAN CERVIDAE

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ABSTRACT: Adaptations relating to over-winter survival in North American *Cervidae* (*Alces alces*, *Cervus elaphus*, *Odocoileus hemionus*, *O. virginianus*, *Rangifer tarandus*) are reviewed. All species adapt by varying physiological and behavioral mechanisms consistent with energy conservation. Adaptations of major importance are decreases in metabolism and activity that become pronounced as environmental conditions restrict access to quality forage. Shifts and adjustments to lower quality forage are accompanied by decline in forage intake and use of habitat which ameliorate weather conditions. Secondary adaptations include social behavior and resource partitioning based on sex and social rank.

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North American *Cervidae* adapt to variation in environments in numerous ways. Behavioral, physiological, and morphological attributes are implicated in this process, and specific strategies vary among species and populations, by sex, age, and social group. We review adaptations relating specifically to pattern and process in survival over-winter.

PHYSIOLOGICAL STRATEGIES

All North American *Cervidae* occupying northern environments characterized by long, severe, or variable winters show strong seasonal rhythms in physiology. Adaptations most commonly cited in association with over-winter survival include: (1) accretion and mobilization of body fat; (2) gastrointestinal changes to use of forage with high dry matter/low nutrient content; (3) reduced forage intake; and (4) reduced metabolic rate.

Marked fat accretion during later summer through autumn and mobilization during winter is perhaps the most basic and important adaptation for survival in northern environments (Anderson et al. 1972, Bandy et al. 1970, Dauphine 1976, Flook 1970, Mautz 1978, Schwartz et al. 1987). Lower body fat content and reduced seasonal variation is typical of *Odocoileus* spp. in the southeastern

United States characterized by milder, less variable climate (Johns et al. 1984). Fluctuations in fat accretion and depletion are greatest with males (Mitchell et al. 1976). Males may lose as much as 30% of their maximum fall weight, as reported for caribou (Dauphine 1976) and white-tailed deer (Dusek et al. 1989), while females lose less than 20%.

Rate of forage intake generally declines as forage supplies deteriorate during fall and winter (White et al. 1987). Animals also may become less selective in foraging during winter (Renecker and Hudson 1986). Exceptions occur when high energy forage is available in the form of acorns (Harlow et al. 1975) or crops (Dusek et al. 1989, Moen 1968). Dry matter intake generally is related to both forage type and availability (Wickstrom et al. 1984). Caloric intake may be reduced as much as 35-40% in winter from summer, as reported for caribou (McEwen and Whitehead 1970). Similar declines in forage intake have been reported for penned deer (French et al. 1955, Bandy et al. 1970, Ozoga and Verme 1970), moose (Schwartz et al. 1984, Renecker and Hudson 1985), and elk (Westra and Hudson 1981).

Resource partitioning in winter also may occur. Watson and Staines (1978) reported that red deer females may require higher

quality forage than males during winter. However, such observations also could reflect availability of different quality forages within areas used by the two sexes (Harper 1962), or avoidance of heavily grazed areas by adult males (Clutton-Brock *et al.* 1987). Miquelle (1990) observed male and female moose to choose different forages in winter in central Alaska.

Reductions in activity generally coincide with reductions in forage intake. This reduces energy expenditures, probably as an adaptation to cold temperatures and poor forage (Gates and Hudson 1979). Mule deer reduce activity and bed in areas that provide shelter from prevailing cold winds in winter (Miller 1970, Wood *et al.* 1989). Craighead *et al.* (1973) observed reductions in activity in winter among elk.

Silver *et al.* (1969) reported declines in fasting metabolic rate of white-tailed deer from summer to winter with differences between individuals. Thermal neutral metabolic rates were lower for black-tailed deer (*O. h. sitkensis*) in mid-winter than at other times of the year (Parker 1988). Metabolic heat production of this diminutive subspecies is greater than for the larger inland subspecies (Parker *et al.* 1984). Declines in metabolic rate have also been reported for moose (Regelin *et al.* 1985) and caribou (Ryg 1983).

BEHAVIORAL PATTERNS

Selection of habitats and microsites that ameliorate severe weather by reducing wind chill and snow depth or by increasing access to forage may be a primary mechanism for adaptation among northern cervids. Migration to suitable winter ranges commonly occurs among all species. Associated 'yarding' behavior in white-tailed deer in the north central and northeastern United States and Canada (Gill 1957, Telfer 1967) is similarly an adaptation to deep snow that impairs mobility.

Where available, both deer species select

dense coniferous cover (Hanley 1984, Verme 1965). In prairie and broken open terrain in the northern Great Plains, rough topography receives disproportionately high use during winter (Severson and Carter 1978, Swenson *et al.* 1983, Wood *et al.* 1989). Even there, however, local densities of mule deer may be comparatively higher in local areas or patches of conifer cover (Swenson *et al.* 1983).

These mechanisms of adaptation by deer seem to apply as well to elk, though specialization in habitat use may be less pronounced. Habitat selection by elk may be primarily related to relative abundance of forage sources (Irwin and Peek 1985). Shifts to predominantly conifer cover during harsh winter weather are apparent when such cover is available, but use of topography, and reduction of activity also serve to reduce energy expenditure (McCorquodale *et al.* 1986). Elk are larger, more mobile, and more gregarious than deer: they also are more generalist in foraging habits. When elk occupy grass communities, they are able to meet minimum energy requirements as snow depths increase better than deer, particularly when forage biomass is relatively high (Wickstrom *et al.* 1984). Parker *et al.* (1984) suggested that over-winter behavioral, as well as physiological responses to ambient temperatures may be a function of differences in body size between the species.

Habitat selection for caribou appears related to variations in snow depth and hardness between habitats (Pruitt 1959, Fancy and White 1985). Caribou feeding on arboreal lichens in winter require a sufficiently dense snowpack for support and access to lichens (Edmonds 1988, Edwards and Ritcey 1959, Servheen and Lyon 1989). Caribou feeding on terrestrial lichens and associated low growing forage seek areas where snow is shallow and light enough to allow them to dig craters.

Habitat selection in moose in boreal forest appears related to behavior, palatability, and availability of forage, snow, and weather

conditions (Peek *et al.* 1976). As winter severity increases, moose preferences appear to change from high forage producing areas to areas of higher cover and lower forage abundance (Telfer 1984). Shiras moose occupying mountainous terrain may winter in riparian willow communities, with or without adjacent conifer cover, as deep snows force them into the lowest elevations (Dorn 1970, Houston 1968, Peek 1974). Snow depths in areas where willow communities are important winter range are characteristically less than in areas where moose winter in mature conifer stands (Peek *et al.* 1986).

In addition to habitat selection, there is evidence that all species exhibit spatial or niche separation between sexes, and perhaps also by social rank. Adult males of all species may winter apart from other sex and age groups (Hirth 1977, Main and Coblenz 1990). This resource partitioning may serve to optimize individual access to forage while minimizing competition between sexes.

Adult bull elk generally segregate into small groups away from other groups in winter (Franklin *et al.* 1975, Peek and Lovaas 1968). A rank order similar to that reported for red deer stags by Clutton-Brock *et al.* (1982) may also prevail. Increased sparring by bulls just prior to antler shedding could serve to reaffirm the rank order (Franklin *et al.* 1975). This rank order may serve to provide access to forage to individuals depending upon their rank. Since the rut occurs in late September and early October, male elk may be able to partially recover losses of energy incurred during breeding before the onset of winter (Flook 1971). Expressions of dominance have also been noted for white-tailed deer at feeding areas in winter (Ozoga 1972).

In barren-ground caribou, adult males usually remain in small bands segregated from the large winter concentrations of cows and calves and juvenile groups, which concentrate on the most favorable winter ranges (Parker 1972). Also, females carrying their

antlers through winter while adult males are antlerless may confer dominance to females over males during that period (Parker 1972). Barrette and Vandal (1986) reported that woodland caribou, which dig craters in the snow to feed on lichens, exhibit a dominance hierarchy which allows individuals of higher rank to displace individuals of lower rank at feeding craters. Rank was based in part on antler size and in groups of mixed sexes and ages, and females with larger antlers were able to displace males with smaller antlers.

Moose tend to be most aggregated in fall and winter, with variation between populations related to habitat, population density, and sex ratio (Peek *et al.* 1974). Adult bulls tend to segregate from other groups of moose after they shed their antlers in early winter (Miquelle 1990). Adult bulls appear to disperse as winter progresses and over-winter alone or in small groups, without much social interaction. Sweanor and Sandegren (1986), however, reported significant social interaction and extensive association among both sexes in winter in Sweden. Observed variations in social interaction in winter may be related to population density and availability of forage.

CONCLUSIONS

Despite considerable variation in adaptations between and within populations, a general strategy for over-winter survival is apparent for the five cervid species in North America. All adapt to severe winters by varying physiological and behavioral mechanisms consistent with an energy conservation strategy. Of major importance are decreases in activity and metabolism. These are related to a diminished quality and quantity of forage, and are most pronounced when and where environmental conditions restrict access to resources. Shifts to lower quality diet are typically accompanied by a decline in forage intake, relaxation of forage choice to acceptance of what is available, and shifts to habitats

which ameliorate severe weather. Alternatively, in the absence of vegetative cover, animals take advantage of topographical variation to accomplish this same purpose. Specialization among some species, such as elk, may be less pronounced because of their large body size and generalist foraging behavior. Nevertheless, local weather, forage, topography, and vegetation also may contribute to observed variation within and among species.

Secondary adaptations apparently center around social behavior and resource partitioning based on sex and social ranking. Adult males of all species tend to segregate themselves, at least to some extent, from other segments of the population in winter. In total, over-winter survival is a mix of reducing energy cost by minimizing social interaction, reducing predation risk, and selecting habitats which facilitate energy conservation. Access to high quality forage or milder winter conditions will affect the degree to which these energy conservation strategies are practiced.

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