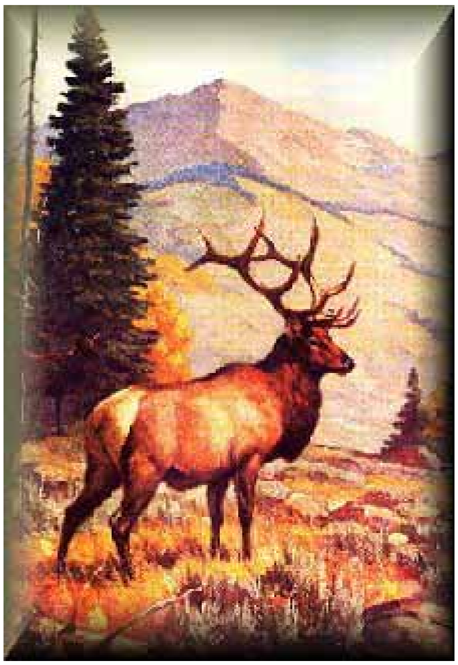
Elk

(Cervus Canadensis)



| Subspecies Typical to North America |

Ranges where they are found |

The "Grey Ghost" may very well be one of the greatest challenges for today's Bowhunters. Volumes have been written by Outdoorsmen and Wildlife Managers about these Magnificent Beasts, yet mystery seems to surround them. They truly hold a special place in the Bowhunter's Heart.

Elk have long been classified by biologists into at least six subspecies. Biologist Olaus Murie, who studied them extensively over a lifetime, catalogues them as follows:

EASTERN (Cervus canadensis canadensis)--The same species discovered by the first white men in North America. For simplification here, it is defined as all elk east of the Rocky Mountains, although a few "eastern" elk undoubtedly took refuge in the Rockies when driven from the Great Plains and Black Hills.

ROCKY MOUNTAIN (Cervus canadensis nelsoni)--The elk of the Rockies and West, other than Pacific Coast. Most of the top trophies listed in record books (such as Boone and Crockett Club's world annals) belong to this longer-tined species. (Note: This species is sometimes classified Cervus elaphus.)

ROOSEVELT (Cervus canadensis roosevelti)--The dark species inhabiting rainforests of Washington, Oregon, British Columbia, Canada, and, to an extent, northern California. These elk are often larger (but not necessarily heavier) than the Rocky Mountain variety.

MANITOBAN (Cervus canadensis manitobensis)--Elk of Manitoba and Saskatchewan. Some historically crossed the border into Great Lakes states.

MERRIAM (Cervus canadensis merriami)--Now extinct species which lived in the Southwest, mainly Arizona and New Mexico.

TULE (Cervus nannodes)--The nearly extinct "dwarf" wapiti of central California marshes and tule swamps.

Tule Elk

If this rundown seems complicated let's hereafter refer to all elk as merely Cervus canadensis. Most encyclopedias and reference texts do the same. After all, the elk don't care what we call them in English or Latin. But we should know as much as possible about the various species, and differentiate between location and hunting techniques. We will also see how elk were hunted in the past. It may help us locate and outwit them today.

It could be debated how the wapiti arrived in North America. But most ungulate scientists attribute it to migration after the last Great Ice Age from Asia (where elk still thrive) over a "land bridge" into western Alaska. From there they pushed down through Canada into the present-day United States. One of the first to record observations of the "great deer" was Giovanni da Verrazzano in 1542.

Others who followed described elk as "fairly widespread" along the Eastern Seaboard. They were frequently sighted from New England almost into the Deep South. Georgia, Florida, and thereabouts was, in fact, about the only region in the U.S. where elk did not seem to dwell in numbers.

Ancient elk bones were also discovered on Alaska's Afognak Island. But the herds that are there now are of the reintroduced Roosevelt species.

Roosevelt Elk

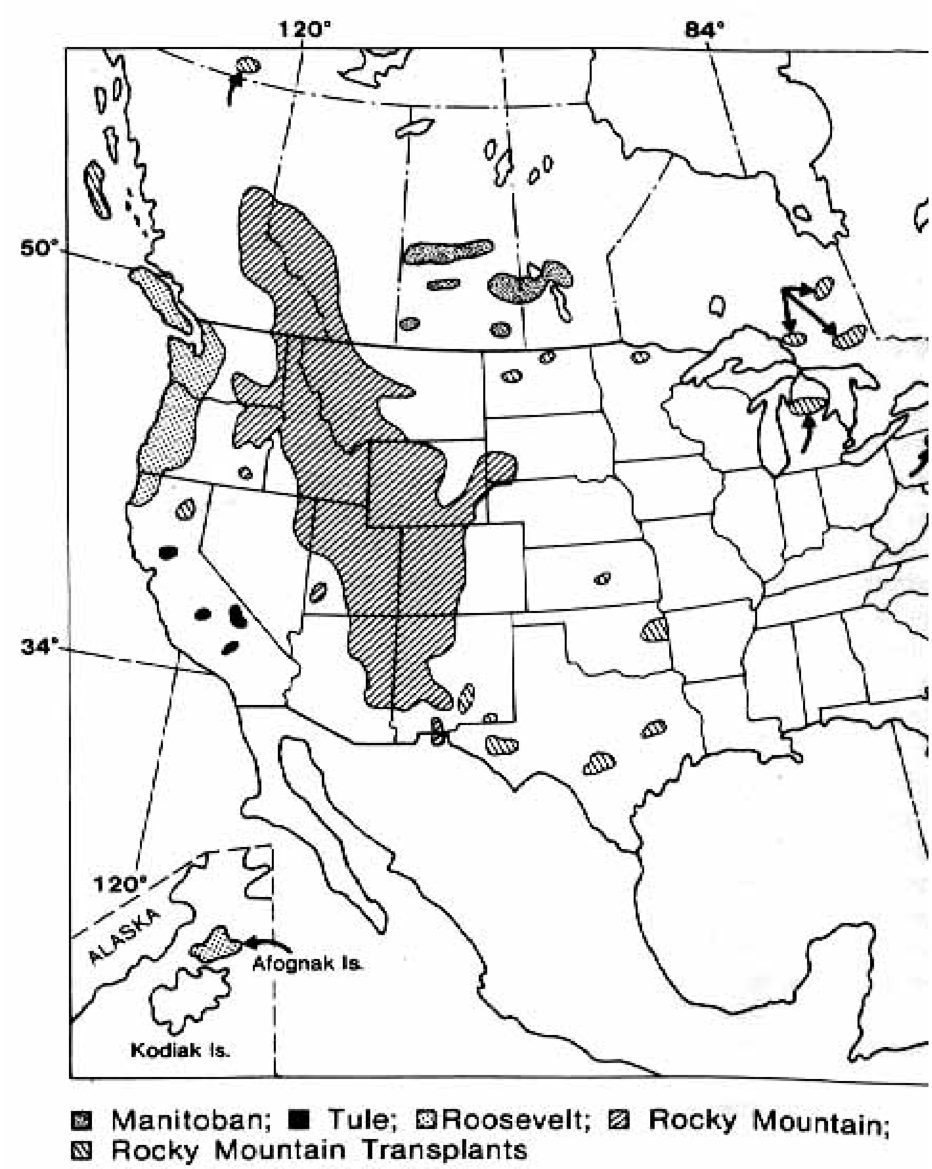
It is well documented that the Europeans named this new member of the deer family "alke" after their Old World moose. Of course, this became confusing later when American moose were also discovered. But by then the name stuck, albeit altered slightly. Only the Shawnee and a few neighboring Indian tribes labeled it something else: wapiti, or "light deer."

Scientists later would adopt the Shawnee name to avoid the technical misnomer, elk. Of course, the Piute Indians of the Great Basin used neither appellation, for they were among the few early Americans who had never observed the creature.

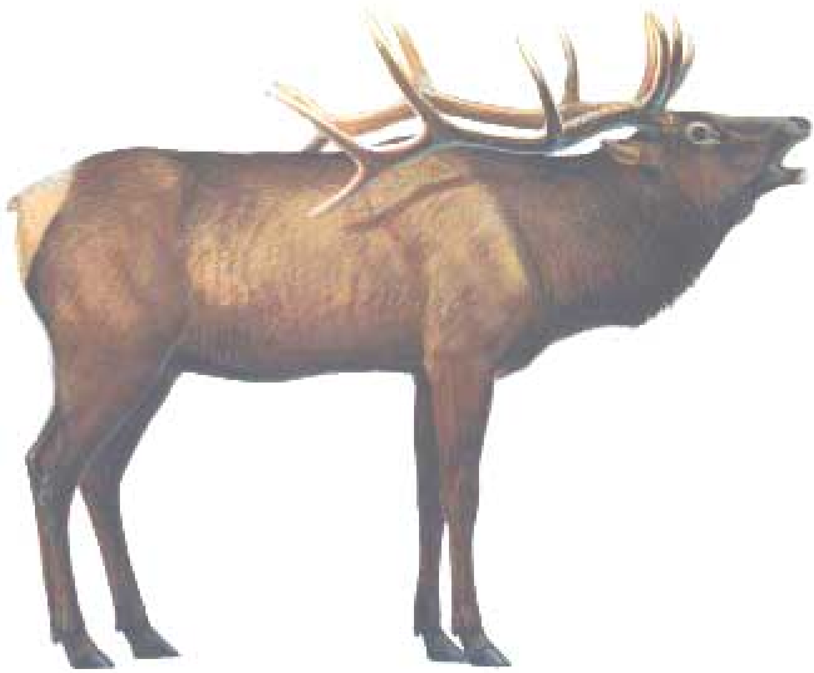
Elk flourished from Maine (few early journals mention them, but elk bones were later located there) across the Adirondacks, Alleghenies, and Appalachians, through Kentucky-Tennessee all the way to Louisiana. From there they thrived westward to the Pacific Ocean, save only the desert Great Basin. Michigan, Minnesota, and Wisconsin harbored large elk populations. So did Illinois, Indiana, and Pennsylvania, although wapiti disappeared there more quickly due to a rapid civilization influx. Naturalist Ernest Thompson Seton estimated some 10 million elk lived in North America before arrival of the Europeans. But numbers plummeted to about 100,000 by 1907. Populations stabilized for the next two decades, but many of the elk were non-huntable inhabitants of the Yellowstone Park and Grand Teton ecosystems.

Over the next 75 years, Abolition of Market Hunting, development of Modern Wildlife Management Practices, and diligent work of dedicated Sportsman brought Wapiti back from the brink of extinction. They currently number between 500 & 750 thousand strong.

The six subspecies Ranges are display graphically below:



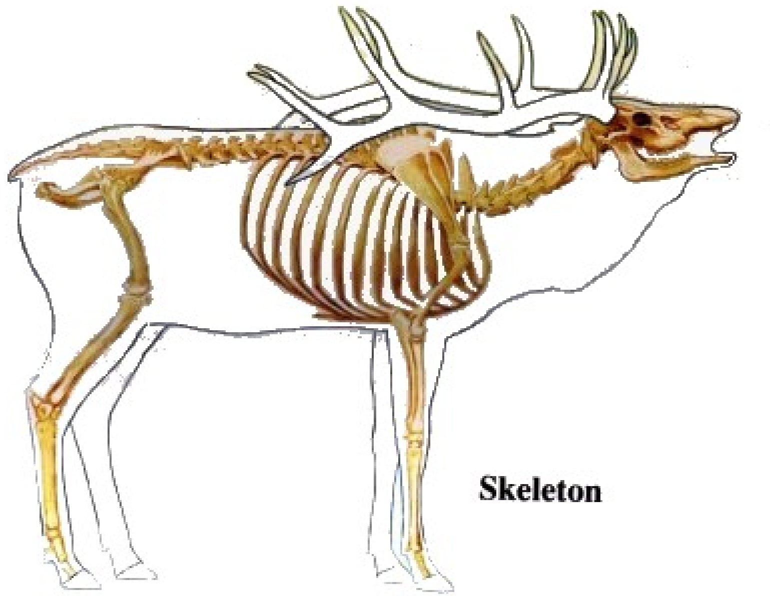
| Outward Appearance | Skeletal System | Musculature System |
| Nervous System | Circulatory System | Digestive System |



Outward Appearance: The coloration pattern of elk is dependent on maturational processes--mainly sexual maturation. How the development of the sexual glands affects hair quality and coloration in males and females is not well understood.

Both ends of the elk's body are accentuated heavily by contrasting colors. The head is dark brown, but generally there is a lighter ring surrounding the eyes. The chin is light brown with a black spot near the angle of the mouth. Ears have whitish hairs inside the shell and a black spot on the lower anterior edge. The neck and throat have long, dark (sometimes nearly black) hairs, known as the mane. Some animals have lighter hairs on the throat, similar to the throat patch in red deer or mule deer.

Guard hairs of the body have different colors, ranging from light brown to pale or sandy yellow. The rump patch accentuates the rear end. It is contrasted on both sides by black lines. The legs and belly also are nearly black. The coloration pattern of the hide changes with the stages of maturation. In extremely old bulls, the flanks may be very pale and the head nearly black. Elk color changes may be the result of genetic isolation. Harper et al. (1967:11) pointed out that: "Coat color was the best method for distinguishing the elk of the Prairie Creek 'herd' from animals not normally resident to the area. The Prairie Creek elk had a dull, light-colored coat while the coats of the 'outsiders' approach the darker color described by Skinner (1936)."



Skeletal System:

The skeleton gives an Elk protection, support, and movement. It's also a site for calcium storage and the production of red blood cells. An Elk's skeleton is made of bone.
Development and Growth of Skeleton.....the skeleton of the elk is not substantially different from that of the other species of the superspecies Cervus elaphus. All belong to the plesiometacarpal (having rudiments of the lateral metacarpals only at their upper ends) group, characteristic only of deer that originated in the Old World (see also Frankenberger 1959, Slaby 1962, Szaniawski 1966).

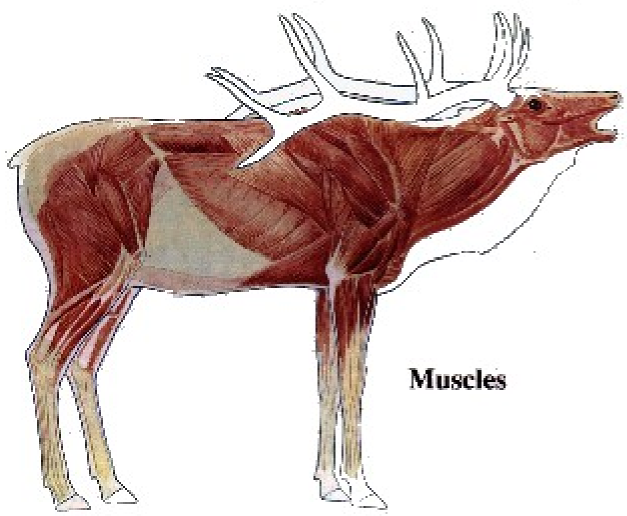
Little is known about skeletal growth in elk. Using red deer data, which show that fresh weight of the skeleton is 6.4-7.2 percent of the dressed weight (Bubenik 1959b), the skeletal weight of fully grown elk (Blood and Lovaas 1966, Dean et al. 1976) can be estimated to be about 46 kilograms (101 pounds) for bulls and 41 kilograms (90 pounds) for cows. Eighty percent of this weight could be gained within the first 18-24 months, and the animal is fully grown between the sixth and seventh year of life (Bubenik 1959b, Flook 1970b).

Mature animals whose pubic region of the pelvic bone has fused exhibit diameters averaging less than 15.5 centimeters (6.1 inches), and probably are bulls, while those exhibiting larger diameters undoubtedly are cows (Denney 1957).

According to Knight (1966), who studied the bone characteristics associated with aging in elk, and Szaniawski (1966), who examined skeletal variations in red deer, there are great phenotypical variations--features resulting from the simultaneous influence of hereditary and environmental factors. How flexible are elk showing these variations? Studies of red deer (Vogt 1947, Pfandl 1977, A. B. Bubenik unpublished) show that they can respond quickly and positively to improved feeding or social conditions by changing their phenotypical characteristics. Populations of phenotypically small animals may be either malnourished, socially distressed, or both.

Limb skeleton. The growth and increase in size of one part related to the growth of the organism as a whole, such as of the leg bones in elk, exhibit data on the lengths of the ulna, humerus, and femur that are being debated. But, as McMahon (1975) pointed out, bone diameter should be considered as well as length in evaluating the limb bone growth. Shorter bones are thicker; longer ones are thinner. It is interesting that the ranges for leg bones in females are smaller than for males.

Hoof and body measurements. The only data found on the elk hoof and front leg, concerning "hoof load" and "chest height," were estimates by Telfer and Kelsall (1971). They indicated hoof loads of bulls ranged from 560-910 grams per square centimeter with an average of 750 (0.19-0.31 pound per square inch, with an average of 0.26). Hoof loads of cows ranged from 480-860 grams per square centimeter, with an average of 620 (0.16-0.29 pound per square inch, with an average of 0.21). The only critical measurement is the front hoof width, because the front legs carry more load than do the hind legs. Length can vary considerably, depending on the animal's activity (Bubenik et al. 1978, Alexander et al. 1980). Chest height was found to vary. Bulls ranged from 78-95 centimeters in chest height, with an average of 88 (30.7-37.4 inches, with an average of 34.65). Cows ranged from 77-94 centimeters, with an average of 83 (30.3-37 inches, with an average of 32.7). Shoulder height for bulls was about 150 centimeters (59 inches) with a known maximum of 162 centimeters (64 inches); for cows, shoulder height was about 135 centimeters (53 inches).



Musculature System:

Muscle and Meat Content: The water content of fresh red deer meat was found to be

77.8 percent, and protein content varied from 21-24.3 percent. The glycogen level was found to be relatively high--0.491 percent. Also, muscle fibers are finer than those of any livestock (Popovic 1964).

Fat Deposits: Fat levels in elk and red deer depend on nutritional and social conditions, and sex, age, and season (figures 39 and 40). Rump fat thickness can reach 70.1 millimeters (2.76 inches) in August (Flook 1970b).

In red deer, fat is stored first in the bone marrow, then deposited around the kidneys intestines, and stomach cavity, in that order (Riney 1955). Mobilization of fat reserves should follow in reverse order.

Fat that infiltrates bone marrow changes the color and texture of the marrow, making it possible visually to estimate the grade of fat present. Femur marrow generally is used for fat analyses.

Sometimes a combination occurs, which may be misleading. As long as there is relatively firm texture with no dark red color, the fat content is 60-95 percent. This may be too rough an estimate. A midwinter fat content of 40-50 percent could indicate a potentially dangerous situation, while a 70-80 percent fat content before winter is not high enough to insure survival. Some animals die of exhaustion with 20 percent fat in the bone marrow. The only totally reliable method of fat estimation is chemical analysis of fresh or deep-frozen marrow (Horwitz 1965), which is expensive. .Greer (1968a) proposed a simple method, adequate for field use, based on the rigidity of the bone marrow--a property that changes with fat content. A piece of marrow is put in a calibrated plexiglass container and left standing upright to self-compress. No compression equates to 95 percent fat. Ten percent compression means a fat content of 55-65 percent; compression of 20 percent indicates fat content of 15-35 percent.

According to the study of Stockle et al. (1978), measurement of bone marrow fat can be improved using the "Hobart Percentage Fat Indicator." Marrow fat itself was not found to be a reliable indicator of physical condition in deer.

Nervous System: Neurophysiology is the study of how nerves control functions and processes of living matter. An understanding of neurophysiology is essential to understanding and managing elk behavior. As Manning (1972:1) stated: "Any study of behavior which is not mindful of physiology is very unrealistic."

Modern wildlife management should be based on physiological features that reflect the status of the individual, sex or age class, and population. Such features develop as neuroendocrine (inner secretory activity controlled by nerves) responses to the inner condition and the outer environment or umwelt. Internal or external stimuli reach the brain in the form of neural (conducted by nerves) or humoral (brought by the body fluids--mainly blood) information.

The nervous system of Elk is divided into two basic parts:

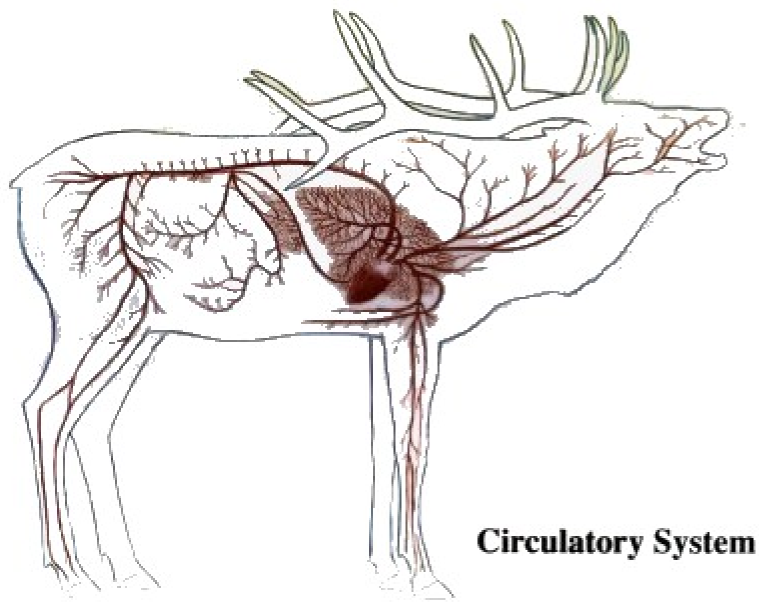
1. the central nervous system (brain and spinal cord) and
2. the peripheral nervous system (nerves and ganglia).

Important and relatively large structures of the brain include the cerebral hemispheres, optic lobes, and cerebellum.

The cerebral hemispheres (cerebrum) are the dominant coordinating centers of the brain. The cerebrum controls most of the body's activities as well as instinctive and conditioned behavior.

The cerebellum controls the Elk's posture and balance.

The spinal cord extends the length of the vertebral column with bundles of both motor and sensory nerves.



Circulatory System: With respect to management concerns, there are three important organs of the elk's circulatory system that deserve particular attention--the heart, lungs, and spleen.

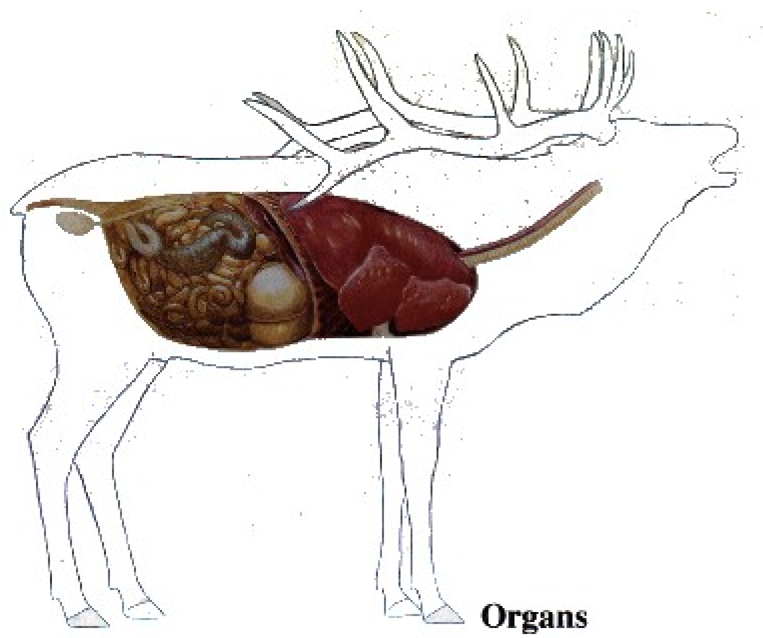
Heart. According to Boyd (1970), the heart weight/dressed weight index for Rocky Mountain elk two years and older varies from 0.93-1.47 percent. Data on red deer show lower variation--from 0.78-1.12 percent (A. B. Bubenik unpublished). Using a mean value of 1.2 percent, the heart weight of an elk with a dressed weight of 136.5 kilograms (301 pounds) should be 1,638 grams (3.61 pounds). A large bull of 363 kilograms (800 pounds) dressed weight (Madson 1966) should have a heart of 4,358 grams (9.62 pounds).

The most comprehensive data on heart rate were collected by Lieb and Marcum (1979:25). The heart beat was found to vary from 36-65 beats per minute, having a seasonal and circadian rhythm, with the minimum in winter and maximum in summer. Mean monthly maximum resting heart rate varied from 1.13-1.28 times the mean monthly minimum resting heart rate. Lieb and Marcum suggested that ". . . this variation aids in maintenance of a homeothermic body temperature under conditions of a 24-hour ambient temperature cycle. Maximum resting heart rates occurred on the average 2.7 hrs after maximum ambient temperatures. For minimum ambient temperatures, minimum heart rates lagged 1.9 hrs on the average." Injury and parturition elevate the heart rate considerably. The Lieb and Marcum (1979) data differ slightly from those of Ward et al. (1976), whose telemetry data show the heart rate to be much lower in cow elk. A mature cow exhibited a heart rate of 46.8 + 8.2 beats per minute when resting, and 60.3 + 9.2 when feeding. A yearling bull's heart rate was 68.3 + 7.8 beats per minute in a resting period, and 84.3 + 9.9 when feeding. The yearly averages were 54.3 beats per minute for the cow, and 75.7 for the bull.

Lungs. There are no published data concerning the lungs of elk. Using the general physiological formula (Schmidt-Nielsen 1975) that lung volume (in liters) = 0.063 x body weight' 02, elk should have a lung volume of 20-23 liters (5.3-6.1 gallons).

Spleen. The spleen is an important producer of blood cells--primarily Lymphocytes. Erythrocytes can be stored in large amounts. The spleen of red deer and, therefore, of elk as well, belongs to the blood-storing type, which is characteristic of endurance runners (Hart-wig and Hartwig 1974). Therefore, spleens of animals that die minutes after being wounded

will be of much lower weight than spleens of animals that die instantly.



Digestive System:

Digestive Tract The mouth, tongue, and sublingual and parotid glands form the opening of the digestive tract. The tongue works by grasping food bites and moving food regurgitated from the rumen. Food is tasted by means of thousands of small skin protuberances, or papillae, on the upper surface of the tongue. Food then is swallowed into the esophagus. Between the bottom of the esophagus and the stomach or abomasum are three large tubular sacs (diverticula)--the rumen, reticulum, and omasum.

Rumen, reticulum, omasum, and abomasum. The rumen, reticulum, and omasum comprise the forestomachs, each with a different size and function. The inner wall contains mucous glands and many papillae enclosing the vascular tissue. Beneath that is the middle layer of thick smooth muscles, which induce rhythmic contractions.

The rumen in Cervus has three blind sacs (Bubenik 1959b). In red deer, their volume, together with the reticulum, grows until the second year of life. There is great individual variation that is not exactly dependent on body weight. At this age the rumen-reticulum volume is approximately 39 percent of live weight or 29 percent of dressed weight during August.

As body weight gains further, these percentages decline to 23 and 18, respectively. The volume is season-dependent, being largest at the end of the summer and smallest in winter (A. B. Bubenik unpublished). Food is stored in the rumen for several hours. It is regurgitated in several intervals and exposed to bacterial fermentation, which decomposes the food's cell walls and enables an effective digestion in the stomach and gut.

The atrium--a chamber-like entrance between the esophagus and rumen on one side and the reticulum on the other--is relatively large. From here, a small opening leads into the reticulum. The reticulum has a mucous membrane in the form of ridges that divide the inner surface into many-sided, honeycomblike ridges (polyhedrals) that occasionally have smooth papillae.

The omasum is characterized by many leaves or folds, with granular, partly keratinized (changed into hornlike tissue) papillae. Inside the leaves are relatively strong muscular and vascular tissues. By muscle contractions, a great amount of water can be pressed out and resorbed from the predigested food.

The abomasum is the ruminant's true stomach, along with the bottom (fundic) portion and the outlet between the stomach and the duodenum (pyloric region, or portion of the small intestine).

The whole area of the forestomach is supplied with nerves by the nervus vagus (either of the tenth pair of cranial nerves providing sensory, motor, or secretory impulses) which monitors contractions of the forestomach walls. It enables the mixing of food in the rumen and helps in separating small food particles from those too large for digestion in the reticulum, sending them back into the rumen with water resorption in the omasum.

In newborn cervids, forestomachs are small in comparison to the large abomasum. They begin to develop with the first solid food eaten (including soil, feces of older conspecifics and, from the second week on, fresh plants). By about four months of age, mature proportions of the volumes of all the stomachs are achieved.

Elk belong to the extraordinarily adaptable ruminants of the intermediary or mixed-feeder type (Hofmann 1973, Hofmann and Steward 1972, Hofmann et al. 1976, Church and

Hines 1978). They can switch from one food to another, which makes them biologically very successful even in marginal umwelts. They can consume mixed grass, forbs, and browse, although they show a clear preference for grass-forb strata (Harper et al. 1967). Elk are well-adapted to seasonal changes in food conditions, calling for decreased or highly activated fermentation processes in the forestomachs. Within three weeks, red deer can rebuild the structure of mucous membranes and papillae to adapt to these changes (Hofmann et al. 1976). The seasonal volume changes of rumen-reticulum follow those of the omasum-abomasum.

The liver plays an important role in the metabolic processes (Kappas and Alvares 1975), and from a management view three points deserve attention. Liver produces glycogen (the high energy carbohydrate) and stores Vitamin A. In males, a large amount of lipids (fats and sterols insoluble in water but able to be metabolized) is transferred from adipose tissues to the liver prior to and during the rut. At the peak of this temporary fat accumulation (steatosis), fat content can be raised to 49.8 percent (Flook 1970b). The fat droplets change the liver color from deep red to yellow or pink.

During the rut the liver in red deer can reach 170 percent of its normal value (A. B. Bubenik unpublished) or, in elk, about 1.2 percent of body weight (3.5 kilograms: 7.7 pounds) (Boyd 1970). In this way bulls have a large, easily metabolized energy source, and thus can survive partial or total starvation during the period of active rut.

Kidneys remove surplus urea--one of the substances of urine of mammals toxic to the blood--by excretion in urine. In ruminants, some urea is recycled. This occurs in the liver, which uses nitrogen in the urea for building new proteins (Thelemann and Hennig 1973). The mean weight of the kidneys in mature elk is 290 grams (0.64 pound) (Boyd 1970). The elk, as with other ruminants, can recycle a portion of its own urea and use it as a nitrogen source for building proteins. According to Westra (1977) the amount of urea recycled was not influenced significantly by exposure to outdoor ambient temperature. Expressed in terms of grams of urea per unit of metabolic mass (Wkg075), a general decline in urea recycling occurred from October through to June with a transient rise in April.

In addition it must be mentioned that the elk used in this study were growing and were supplied with a diet containing 4.25 kilocalories per gram (0.14 kilocalorie per ounce) and 17.2 percent crude protein, which are values far above the natural supply in winter. The copper concentration of the elk liver changes with area and age, but not sex. Mean copper values ranged from 356 milligrams per kilogram (161.5 milligrams per pound) of fresh matter in fetus/neonates to 10.5 milligrarns per kilograrn (4.76 milligrams per pound) in mature animals (Reid et al. I980).

Digestion: Because cellulose membrane resists stomach enzymes, plant food cannot be utilized efficiently by the digestive processes in the abomasum, which is specialized for digestion of the cell's contents. Herbivores, therefore,
have adapted their digestive tracts to allow parts to be invaded and inhabited by a high density of microorganisms, introducing enzymes capable of destroying the cellulose membrane.

There are ciliate protozoans and both aerobic and anaerobic bacteria present in the rumen. The ciliates are important because their bodies are a significant source of highly nutritious proteins and can increase substantially the protein available to the ruminant. Direct microscopical counts of protozoa in elk are in the normal range for domestic ruminants, but are about twice those of cattle on a highly nutritious diet. Anaerobic and aerobic culture counts in elk are about the same as expected from cattle on diets consisting mainly of hay, that is, low aerobic and normal anaerobic counts (McBee et al. 1969).
It is not known if rumen bacteria in elk are resistant to starvation, as has been found in mule deer (DeCalesta et al. 1974).

Rumen pH and Water Content: The pH of the rumen is slightly acidic--between 6.2 and 6.4 (McBee et al. 1969). The water content is about 82-94 percent (Bruggemann et al. 1965). Bubenik (1959b) and Hobson (1974) found that, in red deer, water content of the rumen fluid plays an important role in microbiological activity of the rumen. When water supply is restricted, the appetite begins to fail.

Excrelion Processes: Undigested nutrients, or products of catabolic processes, are eliminated mostly by the gut. The defecation rate in elk is dependent on the speed at which food is propelled through the digestive tract. Lochman and Barth (1967) showed that, in red deer, passage of food through the digestive tract is dependent on diet composition and the sex of the animal.
According to observations of elk defecation rates, calves defecate about 20 percent more frequently than do older animals. A calculated, average defecation rate of 12.52 pellet groups per elk per day (Neff et al. 1965) was based on Rocky Mountain elk in Arizona feeding on a mixed herbaceous-browse diet.
This average could vary in cases in which the percentage of calves and yearlings in the population fluctuates substantially. These experiences with elk pellet counts should be checked for validity in other locations. Pellet consistency is dependent on the amount of

water ingested. Hard, well-shaped pellets are common through autumn and winter. Size depends on the age of the animal, and shape is sex-specific in both red deer and elk (Taylor-Page 1957, Murie 1954).

There are no published measurements of elk pellets. This is regrettable, because such knowledge could be used during pellet counts to differentiate pellet groups according to the sex and age of the animals that deposited them.

Source Material: "Elk of North America; Ecology and Management" Thomas & Toweill (Stackpole Books)

Wapiti Behavior

Studies of animal behavior in the last several decades have enabled the actions of animals to be viewed from a new perspective that has been termed "social ethology," "ecological ethology," or, more recently, "sociobiology. In essence, animal behavior has been cast into a systems perspective wherein individual elements are examined not only by themselves but also as a part of the entire framework that relates behavior, morphology, physiology, and ecology. Theoretical work continues to develop rapidly in this area. The systems perspective has led to penetrating in-sights and explanations useful in explaining the behavioral biology of large mammals, including that of elk.

The adaptive behavioral strategies adopted by a species are the product of its genetic and social inheritance and its learning abilities as influenced by the constraints and opportunities of the environment in which it lives. Thus, the many similarities of Elk to other northern deer and bovines can be traced to similarities of adaptive strategies in similar ecological conditions. For example, elk bulls fatten during the period prior to the rut, and use stored energy to subsidize expensive rutting activities. They also maximize the time available for rutting by minimizing the time spent feeding. Many small and medium-sized northern deer and bovines use this identical strategy. Many differences between elk and other northern ungulates, however, stem from the fact that the elk is an Old World deer.

First, regardless of where elk are found, only minor adaptive changes are to be expected in their physiology and morphology relative to local conditions. Conversely, environmentally induced adaptations in the elk, such as are recognizable in the closely related red deer, will not be found, despite the fact both forms occupy similar habitats. For instance, even though elk live in forests in North America, the bulls have a high-pitched bugle--a vocalization adapted to open landscapes. The ancestral, forest-dwelling Izubr stag from Manchuria, as would be expected, has a deep roar--a sound better adapted to carry long distances through the forest.

Second, the elk has been subject to more selection under conditions of geographic dispersal and colonization than any other Old World deer. Colonization selects for efficient combat, and consequently, elk should differ from closely related red deer or the ancestral Siberian populations of the Izubr stag by exhibiting such characteristics as larger body size and more sophisticated antlers and combat behavior.

Behavioral differences between populations of the same species in unlike habitats are shown in two ways. The first source of difference is self-evident: unlike habitat conditions can cause similar individuals to act quite differently. The second and more important source is far from self-evident: differences in resource availability cause significant differences in environmentally induced (phenotypic) development in individuals from different populations. These phenotypic differences are reflected in both body form (morphology) and behavior. The greater the availability of resources, the better developed are body tissues of low growth priority, leading to larger bodies and antlers, longer skulls, greater fat depots, fewer malformations, and a better immunity system and therefore less parasitism and pathology. Behaviorally, greater availability of resources leads to greater overall vigor in activity--more play, more dominance displays by males, longer and more frequent suckling periods of calves, a relative reduction in overt aggression, and greater roaming. Under such conditions individuals have a high rate of reproduction and can be expected to disperse readily. They are best labeled a "dispersal" phenotype, as opposed to a "maintenance" phenotype, which represents the other end of the spectrum. A trained observer, therefore, can evaluate quickly the state of a population by behavioral and morphological criteria, and relate findings to expectations he may have because of the quality of habitat available to the animals.

Finally, it is essential to realize that today, natural populations of elk are dealt with only rarely, and even those populations are atypical. Typical natural elk populations are a phenomenon of the past. When reviewing accounts of early travelers who witnessed the Plains darkened by elk, the reader can only imagine what such elk populations looked like. Furthermore, elk are no longer subject to intense predation by wolves and bears, except in a few cases in national parks. Yet it is the freedom to exploit a landscape and come in contact with a diversity of predators that has shaped the biology of elk throughout all but its very recent past.

FORAGING STRATEGIES

General Principles

Compared with its ancestral form, the red deer, the elk apparently has shifted in its habitat preference toward open landscape, and in its feeding habits toward grasslike vegetation. Both species lived in cold, temperate climates-the elk more so than the red deer. The race ancestral to North American elk, as well as to the Altai elk, is the primitive elk or Izubr stag of Siberia. Both elk and red deer are ecotone (areas wherein different vegetational types meet) forms, adapted to both forest and open plains.

In its grazing adaptations the elk compared with grazing bovids differ with absence in elk of a highly specialized dentition. However it does have a large rumen, approximating in relative size that of bovine grazers. Its rumen structure is complex, and the rumen papillae also are reminiscent of those in true grazers. However, available evidence still places the elk into Hofmann's category of an "intermediate" feeder--one not fully adapted to a diet of coarse fibrous forage. As an ecotone species, the elk is expected to combine features adaptive to woodlands as well as plains, and thus be diverse in its anti-predator strategies, food habits, habitat preferences, and social behavior. It also is expected to be sexually dimorphic (the sexes should differ in appearance and/or behavior), but significantly less so than the red deer. This is due to the elk's leanings toward life in open landscapes. In essence, when male and female elk mingle in large herds on the open plains, females not only must compete against males, but also discourage males from courting and harassing them. The solution repeatedly encountered that females mimic males.

Females of plains-dwelling ungulate species tend to grow large in body, have secondary sexual characteristics similar or identical those of males, and act like males. Therefore, in herding species from the open plains, females often tend to look like males, as illustrated by many African antelope, the American bison, and the caribou. The female caribou mimics the two-to three-year old males with whom the female normally competes in winter. From body weights compiled weights of red deer stags exceed those of hinds by a factor of about 1.55. The sexual dimorphism of stags expressed in body weight varied from 1.54-2.10; the stags being relatively larger in the cold, eastern parts of Europe. Sexual dimorphism of the same order l.60-l.74 is found in sika deer. However, according data compiled, bull elk exceed cow elk in weight only by an average of 1.28 (1.19-1.38 range from 12 studies). Cow elk are thus relatively larger than red deer hinds comparison with males of their respective species. Cow elk also have a throat mane, as do bulls, while red deer hinds do not.

While the coat color of woodland forms may be either cryptic or dark (the latter as an in thermo-regulation), the coat color of an open plains form need not be cryptic and may even be light. Coat color as a factor in thermo-regulation. Where the view is not obstructed conspecifics, and where they are conspicuous anyway, external coloration and coat pattern may reflect social selection more than selection by way of avoiding predators. Therefore, brighter and more contrasting and showy coat styles and coat patterns, organized to catch and hold the attention of the viewer, are expected in plains forms as compared with woodland forms. Comparison of red deer and elk bears this out.

Ecotone species, particularly those in cold-temperate regions, can be expected to be highly opportunistic, that is, readily adaptable and able to take advantage of favorable situations. The elk may be more this way than the red deer (which already is a very plastic species), judging from the former geographic range (which in area exceeds that of the red deer) and the diversity of biomes (plant and animal communities) that elk occupy.

Elk may have reason to be opportunistic. They are larger in body size, and consequently experience a gestation period about 16 days longer than that of red deer, and therefore have a shorter time between spring and the onset of the rut to get into breeding shape. Yet due to larger body size their rate of fattening is less than that of red deer. In summer they must ingest an amount of food far greater than predicted for their larger body size. To do this they must search for areas with a concentrated food supply, minimize (in summer) the fiber content of their forage, exploit a greater range of the fiber content of forages eaten annually, and improve mechanisms of passive intra-specific competition (indirect competitive interaction within a species) for the most abundant and nutritious forage. They also must select habitats in which the pulse of biological productivity (cycle of annual production) between spring and the rut is large enough to meet the requirements of pre-rut fattening in bulls and lactation in cows, plus adequate fattening to permit cows to come into estrus.

The greatest concentration of food is found where an animal has access to the entire food-producing (photosynthetic) layer of vegetation. For elk, this is in grasslands. Grasses have a relatively high fiber content compared with browse, but this is not a great hindrance to elk due to their large body size. The initial increase in body size, and of necessity, rumen size, is a consequence of dispersal and colonization through mechanisms described under the concept of "dispersal theory". In essence, during dispersal into favorable but uncolonized landscapes, individual elk encounter an abundance of resources and grow large phenotypically. However, under these conditions the larger individuals out-compete the smaller ones, for various reasons, leading to a genetic increase in the body size of the colonizers. This process preadapted elk for the expansion of their ecological niche (role) into grazing.

As one travels from arctic to tropical habitats, and from early seral stages to climax plant communities, the pulse of annual productivity declines. Body size is related directly to the amplitude of the annual productivity pulse. This is one reason why black-tailed deer from high-altitude ranges are bigger in body size than are such deer from the climatically milder, low-altitude ranges). Similarly, small-bodied deer, with a low productivity pulse, are found in maritime climates as opposed to dry, cold, continental climates, as is known for red deer. Therefore, a large-bodied animal that depends on a high rate of food intake between the onset of vegetation growth and the rut must occupy progressively more disturbed ecosystems (which are characterized by a high pulse of productivity) as it colonizes from north to south or it must become smaller in body size. Thus, in their southern lowland distributions elk are expected to become more dependent on valleys with flooding rivers and shrinking water bodies during summer and to decrease in body size. The Tule elk at least partly fulfills these expectations.

Traveling from north to south one also notes that plants become more fibrous and carry more defenses against being eaten by herbivores; the forage of the north, or the alpine, is more digestible. This suggests not only that there may be selection for more complex and larger grinding teeth as a northern form colonizes southern latitudes, as indeed is shown by the Tule elk of California, but also suggests the following phenomenon. A northern form can rely on a strategy of depositing massive stores of fat in summer to subsidize a diet of desperately meager winter forage. The rather defenseless, highly digestible northern or high-altitude vegetation permits a massive food intake coupled with rapid digestion. The temperate zone red deer maintains a summer intake only some three times that of winter. Alaskan moose, however, reached a summer intake six times that of winter. Moose are able to attain in four months a fat store adequate to supplement some eight months of fasting. Elk, compared with the ancestral red deer, are a northern and continental form adapted to live through longer winters. Compared with red deer, elk are expected to have a relatively higher food intake in summer and rely more on fat depots for over-wintering than do red deer. Regardless of whether elk grow fatter than do red deer, by virtue of being larger and having a relatively lower metabolism, an elk can survive longer on the same relative fat store than can a red deer. For instance, a 260-kilogram (573-pound) cow elk carrying some 20 percent of her body weight as fat is theoretically expected to survive some 72 days on her fat alone (assuming a maintenance requirement of 100 kilo-calories per kilogram of body weight 0.75). An equally fat central European red deer hind, weighing only about 100 kilograms (221 pounds), is expected to survive only 56 days. Conversely, without growing appreciably fatter than a red deer, an elk could survive a winter almost one4hird longer than could a red deer, by virtue of being two to three times heavier in body weight. Or, the elk could rely on much coarser forage than could the red deer, in winters of equal length and severity, since the elk would require a smaller fraction of its maintenance requirement to be satisfied from food ingested daily. These, I emphasize, are theoretical expectations as yet unverified.

To herbivores in regions of relatively low productivity, food is not a defensible resource. Thus, it is suspected that individuals compete passively by eating the preferred food faster, locating preferred food earlier than other con-specifics, using the behavior of competitors as a clue to the whereabouts of superior food and quickly capitalizing on it, and having better learning ability about the clues and circumstances signaling superior food. The more intense the passive competition, the more individuals must be independent agents. Therefore, individuals must be influenced very little by social bonds even though they may live gregariously. Thus one does not expect a close bonding of females and their grown offspring once the latter begin to reproduce. The data on this point are inconclusive. If migratory populations of red deer are compared with elk, elk appear to show less cohesion between individuals than do red deer. However, other studies of a non-migratory population of Roosevelt elk along California's coastal beaches, found individuals closely bonded in distinct groups. Absence from the cow groups amounted only to some 35 percent and some 66 percent from bull groups; 78 to 91 percent of the elk had a filial bond. These elk lived mainly on large patches of permanent grasslands along beaches and valley bottoms. Other studies on non-migratory Roosevelt elk and found them socially quite labile. Study animals, however, exploited logged-off areas that were reverting to forest. These elk presumably were less often in sight of each other. Elk in the Rocky Mountains are migratory and follow melt lines of snow; they have opportunity to be opportunistic. Not so in these elk, which exploited the same environment characterized by an absence of snow, by long growing seasons, and by large stable patches of preferred habitat. Their choice of where to go appeared to be limited. A study of non-migratory elk population in Michigan, it was found that these elk also were socially very labile. Here too the presence of extensive cover, only small clearings, and snow create conditions favoring movements by individuals in an opportunistic search for forage.

In populations with a low reproductive rate, a very close association is expected between females and offspring older than one year. Like red deer, elk have opted for a reproductive strategy maximizing investment per offspring, and thus may extend maternal care of yearlings in the absence of a calf.

The Role of Opportunism

Opportunism should express itself as migration between seasonal home ranges, following sprouting vegetation from the lowlands to alpine habitats, and from southern exposures to northern ones, from the open to the closed canopy, or along retreating waterlines of annually flooded or marshy areas. It also should result in elk taking advantage of locally abundant food sources brought about by ecological and climatic factors. That the ancestral red deer is most opportunistic has been established. For elk, some of these expectations have been verified in part; others are not yet studied. Seasonal migrations have long been recognized. So too has opportunism, such as wintering on small thermal areas kept free of snow and supporting various aquatic and marsh plants in highly productive condition, as found in Yellowstone National Park, or by consistently selecting the spots with the highest density of favored forage.

The extent to which elk follow shifting lines of plant growth has not been studied, but numerous suggestions to this effect are found in the literature. Moreover, observations of the food habits of red deer and elk suggest strongly that the animals move to sprouting vegetation wherever possible. This is shown in McCullough's (1969) study of Tule elk in California. Elk will exploit mast wherever it is available, as do red deer.

I also expect them to feed on natural ensilage formed after the first killing frosts in areas with lush, tall, herbaceous vegetation. Observations suggest this for red deer, as does the observation that red deer change food habits after severe frost and snowfall. Elk are expected to exploit local spots of high productivity-predation, disturbance, and access permitting. Elk also should utilize mineral licks at the time of great hair, antler, and body growth, much as do sheep and mountain goats. Red deer and Elk are known to frequent mineral licks in early summer.

One can look at opportunism from another perspective: a large-bodied ungulate that does not have subhypsodont (tall-crowned, long teeth that close their roots sometime during the animal's adult life) or hypsodont (teeth whose roots remain open and ever-growing) grazing dentition, even though it may take a very high percentage of its food as grasses and sedges, must shift to diverse food sources of low fiber content once grasses mature and have abundant tough fiber. This implies seasonal migration and frequent local movements, which in turn implies an ability to compensate for various local deficiencies.

If the aforementioned indications are true, the elk cannot be an r-selected species (a species who focus on high productivity rather than efficiency in utilization of its habitat and low rates of reproduction as survival mechanisms). It must be a K-strategist, exploiting the habitat in its home ranges by a great diversity of means. It shifts with circumstances created by soil (edaphic) and climatic factors, and thus, once having colonized an area, remains close to the carrying capacity of its home ranges. The more opportunistic an ungulate such as elk, the more migratory it tends to be, the larger are individual home ranges, the broader are its food habits, the less likely it will be to evolve a reproductive strategy of maximizing birth number of litter size, and the more likely that birth will be of single young. This reveals a certain similarity between elk and caribou in which twin births are rare (as in elk or red deer), in contrast to moose or mule, black-tailed and white-tailed deer.

Foraging Strategies of Cows and Calves

Within a population, different sex and age classes can be expected to have different food habits. The calf's strategy is to rely on milk as long as possible and select the most digestible parts of the forage in order to maximize growth and thus the chances of winter survival and escape from predators. The calf must select for the most digestible parts of the forage in winter for two reasons. First, due to its smaller size, and thus relatively larger surface to mass ratio, it has a higher metabolic rate, requires relatively more food, and can satisfy this need only by selecting for more digestible forage than do cows or bulls. Second, it does not have large fat deposits to subsidize its body maintenance in winter. Therefore, calves should ingest forage of low fiber content and be far more selective in forage selection, move about more, and feed in a less sustained manner. Although the calf requires relatively more food, its absolute food requirements are much less than those of adult elk. It therefore has more time to search for food items of superior quality. Moreover, if adults take over the function of looking out for predators, calves can be less watchful and devote more time to feeding, thus maximizing the quality of forage ingested.

The cow's feeding strategy, apart from being affected by an anti-predator strategy somewhat different from that of the bull, probably is affected also by her ability to store fat and probably vitamins and minerals (and maybe some protein) from nourishment obtained from abundant summer and autumn vegetation. The greater these stores the more fibrous her winter forage can be, or the less forage is required in winter. As discussed earlier, a large-bodied cow has a lower rate of metabolism than does a small-bodied cow, and therefore can last longer on the same fraction of body weight stored as fat. Clearly one adaptation to longer winters is an increase in body size. The upper limits on how much fat an ungulate may store probably is set by predators, which may find obese individuals relatively easy prey. Thus, large body size (which offers protection from many predators) plus the body stores also permit the cow elk to emphasize formation of groups in open grassy landscapes in winter as an anti-predator strategy. That strategy selects for large-bodied calves, reinforcing the reproductive strategy of single births in elk and maximizing maternal investment in the calf

The concept of body stores that "supplement income" in seasons of scarcity, though not unknown, has not received much attention in ungulates. Reference is made to it in Russian work on reindeer, in which the skeleton serves as a store of metabolic salts in winter and which, therefore, becomes increasingly lighter and more fragile during winter and into spring. Vitamins are stored in the liver and fat, and are depleted during winter.

Foraging Strategies of Bulls

The elk bull's feeding strategy must differ from that of cow elk. Being larger than the cow, the bull can feed on more fibrous forage. The red deer studies bear this out. if the bull is to maximize his reproductive fitness, he must not compete for forage with the mothers, or even prospective mothers, of his offspring. He either must avoid their presence or evolve different food habits. Although food habits of cows and bulls differ somewhat in elk and red deer, the differences are not great. However, if large body size in bulls is adaptive in combat, then bulls ought to seek out areas with abundant high quality forage during summer when their body growth is maximal. Since the cow's objective in maximizing reproductive fitness is to maximize security for the calf from predation (while the bull's is to maximize body growth), the bull can compromise security in favor of foraging while the cow compromises on forage quality and abundance in favor of security. These differences in interest could account for the spatial segregation of sexes. This hypothesis predicts that, in summer, bulls on the average feed on better forage than do cows, and that they fall prey to predators relatively more frequently.

In addition, bulls have a different survival strategy from cows. Due to the shortness of the rut, bulls----like many northern ungulates----use body fat to subsidize their activities during the rutting season, and thus gain maximum time for engaging in rutting activities by minimizing time spent feeding. However, this depletes their fat depots and therefore their ability to subsidize their food intake in winter. Therefore, the bull's strategy must be to hoard not only enough fat to pay for rutting expenses but more than that. The greater the surplus left after the rut, the greater the bull's likelihood of living and rutting another year. This also suggests that bulls must give priority to living in locations where a maximum of highly digestible food can be obtained in summer.

How important summer nutrition can be to cold-climate ungulates is illustrated by the chamois. Male chamois establish and defend rutting areas over the sites of the best summer forage. In essence, they defend fattening territories. The ungulate literature is quite consistent with the hypothesis that males suffering caloric bankruptcy also suffer far greater mortality.

Considering the foregoing, it is understandable why bulls, compared with cow elk, suffer far greater wear on their teeth. The cow transforms food molecules in excess of maintenance to milk in summer and to fat only later in the season; the bull degrades food molecules to meet the demands of body and antler growth as well as fattening. The amount of fat accumulated by elk is not known. For red deer, however, data show that stags accumulate more fat than do hinds, even barren hinds. Thus, stags process more food per unit of lean body mass than do hinds. Moreover, the bull elk are larger than the cows, but the size of their dentition has not kept up with their body size, or with their increased rate of fattening. The upper tooth row in elk is only about three percent longer in bulls than in cows, while the lower tooth row in bulls is less than three percent longer. This means that bulls have somewhere between 9 percent more tooth mass than do cows. However, bulls have a body mass some 28 percent greater than cows have. Since metabolism decreases with body size, the actual body masses of bulls and cows. cannot be compared directly. It is necessary, therefore, to compare their "metabolic sizes", which is their weight in kilograms raised to the 0.75 power. Even then, bulls are approximately 21 percent larger than cows. These figures indicate that bulls have a tooth wear some 15 percent or more greater per year than do cows. In red deer, however, differential tooth wear in the sexes was not found.

Formation of body fat (lipogenesis) is calorically very expensive, since roughly one calorie of heat is liberated for every calorie stored as fat. Therefore, the bull must get rid of large amounts of heat and choose his habitat and behavior accordingly. In mountainous habitat, the bull can be expected to go into cooler areas, higher elevations, and shadier slopes and thickets than would cows. In lowlands he is expected to enter shade. Red deer in lowland areas practice evaporative cooling by wallowing in watery, muddy wallows, particularly during fattening in late summer. This not only cools but also gives some protection from biting flies. Hinds wallow less than stags, as might be expected from their lesser fat depots and the loss of ingested food molecules through their milk.

After the rut, only elk bulls that have retained their fat depots can afford to feed on coarse forage and thus be free to associate with cows. The more fat that bulls lose, and the more antler punctures they suffer during intraspecific fighting that result in infection, the more they must search for pockets of nutritious forage to maximize energy available for maintenance and repair. They also must not associate with cows following the rut, lest, exhausted from rutting and readily identified by their large antlers, they become the preferred target of culling predators. To avoid culling predators such as wolves, bull elk either must congregate in large herds away from cow herds or become relatively invisible, by avoiding areas where predators occur or by becoming difficult to locate. These latter requirements are maximally met if the bulls leave areas of continuous wintering habitat in favor of areas that contain widely dispersed small patches of habitat (such as may be available at the periphery of wintering areas), if bulls favor snow depths and conditions in which predators have difficulty traveling, or if they hide among tall shrubs of forests. The older a bull becomes and the more fat he loses during the rut, the less he ought to associate with cows, the more solitary he ought to become, and the more likely he is to winter in very restricted localities. It may be that it is the exhausted bull's inability to shift to qualitatively better forage that ultimately kills him.

The foregoing hypothesis accounts reason-ably well for winter dispersion of elk, and for red deer. Elk bulls winter at higher elevations in the mountains than do cows, and adult elk segregate by sex, except for a sprinkling of young bulls among the cows. The hypothesis suggests that it is the bulls that must avoid and leave the cows, not vice versa, as will be discussed later.

Since elk are associated with forest ecotones, they periodically exploit the superior quality and quantity of forage that follows in the wake of a forest fire. For cows, small bums ought to be of lesser attraction, being incompatible with the cow's prime antipredator strategy of joining with many others into a herd in open habitats. To the bulls, however, small burned areas provide opportunities for amassing large stores of fat and growing heavy sets of antlers during summer, thereby maximizing rutting competence. These areas also enhance winter survival of bulls by providing them with qualitatively superior forage. Since wildfires cannot be predicted, and small burns are not easily found in a carpet of climax forest, elk must find these burned areas by random exploration. The first bull to find a bum of quality is likely to benefit greatly. Consequently, greater wandering in bulls than in cows is expected-and was found. Bulls should pioneer during dispersal, which they do. Also, wandering is at a maximum in one- to two-year-old bulls, as expected. Bulls also should be more socially labile. This too was found.

If, as hypothesized, cow elk must compromise forage quality and quantity in favor of security, but bulls must compromise security in favor of better forage, then young bulls ought to leave female home ranges, particularly during the period of maximum body growth, in summer. Cows ought to disperse their sons from the maternal home ranges, but not their daughters. Therefore, cows ought to be more aggressive toward yearling sons than toward yearling daughters.

A yearling is dispersed twice-once prior to its dam's giving birth to another calf, and on a second occasion during the rut. Dispersal carries an increased risk of mortality, identified in yearling bulls. An increased yearling mortality because of dispersal ought to lead to lower male-female ratios in wild elk herds than in confined herds, because dispersal by yearling bulls is impeded in confined herds and its associated mortality eliminated. And in fact this is the case. For example, in the fenced areas of Elk Island National Park, Alberta, compared with Banif or Jasper National Parks, also in Alberta, there were 85 and 37 bulls per 100 cows. Murphy (1963) also noted a high adult male-female ratio of 55:100 in an enclosed population.

Compared with red deer, elk have been exposed to more colonization and, therefore, selection under conditions of expanding populations. Some of the consequences are selection for more frequent and intense social interactions (and therefore greater expenditure of energy by bulls during the rut) and sophistication of the bull's means of active competition. This includes the growth of larger, sophisticated antlers. One consequence of the elk's dispersal history is that the Siberian elk (from the Altai) may be more similar to the Rocky Mountain elk than the latter is to the Tule elk. Both Altai and Rocky Mountain elk are exceedingly similar to each other and apparently quite similar to the elk that vacated Beringia following the Wisconsin glaciation. Thus suggesting that the subspecies Cervus canadensis canadensis should apply to both the Altai and Rocky Mountain elk while not including the Tule and Roosevelt elk may have merit.

A second consequence of this dispersal is a meeting of advanced elk of the Altai race with the ancestral Izubr stag in eastern Siberia. The larger antlers in Altai elk are due to different genetic potential, as was shown in Siberia on elk ranches. Attempts to ranch the Izubr stag for its antlers were abandoned because, under the best conditions, Izubr stags produced much smaller antlers than did elk of the Altai race.

A third predicted consequence is that male elk will have a higher mortality rate than do red deer stags. Thus, the ratio of males to females ought to be lower for elk than for red deer. In red deer populations the sex ratio on four reserves ranged between 63 stags: 100 hinds, while for two reserves containing elk it was 27-33 bulls: 100 cows. The latter comes close to the sex ratios in natural populations of American elk. This is compatible with the predictions of the dispersal theory-that elk bulls wear themselves out more easily during the rut than do red deer stags, and subsequently suffer increased mortality from diverse causes.

The Law of Least Effort

The strategies of foraging previously discussed indicate how to maximize intake. The converse----the law of least effort-deals with means of reducing energy expenditures for maintenance. An individual maximizes the resources available for reproduction by developing both types of strategies. The law of least effort predicts that with increased forage density, roaming ought to decline (and likewise that with a decline in forage density, roaming ought to increase). This should result in a smaller home range in summer than in spring, or even in winter (provided snow is no major hindrance). These findings appear surprising because of an unfortunate confusion: the habitat available for exploitation does expand in summer, but it is the population, not the individual, that disperses across summer ranges.

The law of least effort is apparent in all activities performed by elk. The loyalty of elk to their home range is one such expression. In their daily time budget, feeding and resting occupy about 95 percent of the time. The remainder of the day is spent in walking and standing, except during the rutting season. Energy expenditure clearly is reduced to a minimum. In winter, elk tend to feed where snow is shallow or locally absent, to move to where it is softest, to walk in single file where it is deep, and to change their food habits to minimize the need to paw snow from forage or to plow through it. Elk should be expected where possible to abandon migration in favor of exploiting a limited area with year-round availability of food. Conversely, major waves of dispersal ought to be associated with food shortages.

The tendency of elk to search out the dense conifer thickets has been interpreted as an adaptation whereby elk reduce heat loss. A cover of dense conifers indeed would act as thermal cover and reduce heat loss, particularly during very cold winter nights with clear skies. An elk would be expected to lose more than two-thirds of its heat via longwave radiation during cold weather----radiant heat loss being proportional to the difference between the surface fur temperature of the elk and the surface temperature of the surrounding cover. Since on a clear night the sky may attain a "surface" temperature of -62 degrees Celsius (-80 degrees Fahrenheit), but the surface temperature of the conifer branches over an elk are likely to be at ambient temperature, clearly the elk would reduce its radiant heat loss by moving under conifer branches at night. Moreover, convective heat loss also is reduced in a conifer stand, since the trees act as a barrier to air currents.

However, the good thermal qualities of dense cover may be quite incidental to the fact that the cover satisfies the elk's security needs. The thermal qualities of conifer cover may be inconsequential to an elk; it may not necessarily need thermal cover. The elk is a large-bodied mammal with a very low surface to mass ratio. It needs an external insulation much lower than that of a mountain sheep to attain a critical temperature that only rarely is exceeded in the open in winter. (The critical temperature is that at which an animal can maintain its normal body core temperature while metabolizing at the normal resting rate.)

Conversely, during sunny winter days an elk is expected to gain a small thermal advantage by exposing itself to the sun's rays. if the elk were as black as a moose it might gain substantially, since black animals absorb a greater heat load when exposed to the sun than do lighter-colored animals.

A moose is expected to gain relatively more heat and reduce its cost of maintenance. Webster (1971) indicated that a black cow exposed to sunlight might save one third of a megacalorie of fat from oxidation for every megacalorie of sunlight failing on its body. Considering that the amount of energy in sunlight increases from 1.07 calories per-square-centimeter-per-minute at sea level to 1.38 and 1.45 calories per-square-centimeter-per minute at 2,000 meters (6,562 feet) and 3,000 meters (9,842 feet) respectively, there is ample reason to suspect that ungulates living in mountains would take advantage of this. However, elk are not black, nor do they act like moose in the Canadian mountains and search out solar-bowls above timberline in winter.

This is explained by further consideration of Hamilton's (1973) color theory in relation to the elk's adaptive exploitation of coverless terrain. If, in exploiting open areas, elk are exposed to cold ambient temperatures at night, they would be expected to evolve a thicker, more insulating fur coat than moose have. This expectation remains to be investigated. Heavier fur also reduces heat gain from the sun during the day, but it becomes a liability if the animal must move rapidly and metabolize accordingly. In fact, the problem faced by the elk, according to Hamilton's (1973) reasoning, is how to get rid of body heat from a large, well-insulated body in the event of exertion. A dark fur would increase the heat load during a sunny day and make demands on the elk's thermoregulatory mechanisms. Like any placental mammal the elk is expected to metabolize at least briefly during exertion at a rate of up to 40 times basal. This generates a tremendous heat load and courts thermal damage to tissues. if an elk already shedding heat maximally under a hot sun were surprised by a predator, it would most likely collapse from heat stroke shortly after galloping off. This would be more likely to happen if the elk were as black as a moose. To keep its core temperature low, without exercising its heat shedding mechanisms, the elk would have to be as heat-sensitive as a moose and move into shady cover. This would not be possible in coverless terrain. In coverless terrain, therefore, ungulates--which may have to run hard and very suddenly----are expected to have a light glossy coat color that reflects the sun's rays. In short, the elk--in its evolution toward exploitation of open grasslands--~s expected to become lighter in coat color than its ancestor, the forest-adapted red deer. A dark-colored animal can take advantage of the sun's radiation to lower its maintenance cost in winter, but only by having thermal cover to which to retreat when the sunlight is too intense, and by having a relatively thin hair coat. But having a thin coat also forces the animal to take cover when the ambient temperature is low, and binds it to forested landscapes. In elk it is expected that light coat color, a coat of relatively great insulative value, a great insensitivity to heat or cold, and excellent mechanisms of shedding heat all go together. This remains to be investigated. However, it is difficult to conceive how otherwise elk would be able to live in the icy cold of the Yukon Territory or the northern Canadian prairies on the one hand, and in hot and dry valleys in southern California on the other. Moreover, the Tule elk of California, exposed to the highest ambient temperatures and solar incidence compared with other sub-species, is also the lightest in color, as expected from Hamilton's (1973) color theory-while the forest-dwelling Roosevelt elk is the darkest of the subspecies.

ANTIPREDATOR STRATEGIES OF COWS AND CALVES

Advantages of Grouping

An ungulate feeding on open plains does so under a severe handicap. When feeding, it cannot readily sense the approach of a predator. It can do so mainly only when its head is raised, but to do this interrupts feeding. Yet to ungulates that must feed selectively, feeding is a very time-consuming chore; it takes from one-third to one-half an elk's 24-hour time budget, for example. This predominance of feeding in the time budget is valid for all ungulates whose daily activity has been investigated, even if the 24-hour time budget has not.

When an individual feeds in the company of others, the first advantage it gains is a saving in the amount of time spent watching for signs of a predatory threat, and a corresponding in-crease in time available for selective feeding. Given the breakdown of activity during feeding reported, one can calculate that when not resting-excluding the months of August and September----cow elk spend about 14 percent of their time either standing or walking, and 86 percent of their time feeding. Unless feeding is done synchronously (there is no evidence of this), a group of seven cow elk would be required so that on the average one or another head would be raised throughout the activity period. Clearly, if feeding must occupy a greater proportion of time, the minimum group size required for security must be greater. By clustering with other individuals on open plains an individual reduces a predator's chances while maximizing its own time for selective feeding. Grouping in the open, thus, is as much an antipredator strategy as a feeding strategy.

The second advantage of grouping is that if a predator strikes it is more likely to strike a peripheral member than a core member of the group. if it is a culling predator, by definition it is more likely to catch an injured or weak member of the group. This greatly increases the safety of the healthy, non-discrepant, centrally located members of the group. Thus the best way for an elk to feed in the open plains is in close proximity to others, provided the group is not so large as to force individuals to move widely to feed as a result of reduction of forage through competition with other group members. Both red deer and elk group in the open; and the more open the area the larger the groups.

A necessary consequence of the aforementioned anti-predator strategy is rapid flight in full view of the predator, and this requires speed and stamina on the part of the individual, and a terrain suitable for rapid flight. Understandably, elk tend to avoid areas covered in logging slash or deep snow. Nor do they prefer soft, boggy ground.

Elk not only must run long distances, but do so in security. Here leadership is of advantage, which in elk, invariably, involves an older cow. Leadership role to falls to cows with many social bonds; studying red deer, found it to fall to an older calf-leading hind. An older cow also may serve as rear guard during flight-staying behind and watching the danger. These individuals were cows with few social bonds. How this phenomenon arises is not at all clear.

For an open-country ungulate as compared with a forest species, long flights from predators are necessary to prevent rapid rediscovery by the predators. Calves face a period of great susceptibility to predation shortly after birth, and ungulates have adopted a variety of strategies to deal with this susceptibility. If large in body an ungulate may protect its young by singly or collectively attacking predators. However, although a cow elk is large, it apparently is not large enough to confront and chase away wolves from its young. Nor do bull elk defend calves against wolves, as bison or musk-ox bulls do. Only exceptionally will elk turn and face wolves, as indicated by one observation of I. McT. Cowan. Nor do elk gang up on wolves, although they will gang up and mob single coyotes.

Also, ungulates may synchronize calving, saturating a tiny calving ground and thus swamping predators with young. By producing milk for a single calf only, a cow enables the calf to grow rapidly beyond the body size of greatest susceptibility. The swamping strategy is an option of ungulates highly adapted to life on open plains. Among the deer, it is practiced only by caribou, and then only by those living in large migratory herds. It is not found in elk.

A third strategy is to disperse young animals (neonates), which hide and stay in seclusion until they have outgrown the vulnerable period. Despite their large size, elk have retained the probably ancient "hider" strategy common to medium-sized ungulates, including the ancestral red deer.

The "Hider" Strategy

In the hider strategy, young that are colored to blend with the surroundings have little scent that would attract predators, and not only are very silent but also select their own hiding places and crouch in immobility in the face of danger.

This strategy is embellished by wide dispersal of females prior to parturition, selection of birth sites rarely visited by conspecifics and presumably predators, and removal of all evidence of birth by the female, by such methods as devouring the placenta and various birth membranes and ingesting earth and vegetation soaked by birth fluids. Other aspects of this strategy are removal of evidence of the young by ingesting its urine and feces; separation of mother and young during all but a very short portion of the day when the young is suckled and stimulated to void; a greater vigilance by the female; readiness of the cow to attack minor predators near her calf and noisily decoy larger-bodied ones from the vicinity; and leading the calf to safer localities if the original birth site should be visited by predators.

A consequence of these adaptations is that calves bleat if in danger. This protects them against at least small-bodied predators such as coyotes. That cow elk are effective against coyotes and that their absence increases coyote predation on young calves are suggested by indirect evidence in McCullough's (1969) work. Calves also must respond to signals from the cow, coming out of hiding to suckle, or dropping from sight at the cow's warning signal. The former signal has been described as a nasal whine or high-pitched neigh, and may be emitted several times before the calf comes or responds by returning the call. The warning of a cow elk consists in part of an alarm bark, which triggers its calf to dive into cover and crouch (prone response). Barking may cause older calves to run to their mothers and stand attentively, or to flee with her; it need not lead to crouching. The prone response to barking begins to wane in red deer within three or four days. During the crouch, elk and red deer calves minimize motion by becoming rigid. Even during the period of seclusion prior to cow and calf joining the herd, the calf may bolt from its hiding place if the predator is close, and over a short distance it may be able to outrun a pursuer. This may be sufficient to bring it close to its mother and ensure her protection, or it may permit the calf to hide again suddenly, provided it can put a visual barrier between itself and the predator. Muscular rigidity thus may serve in the retention of muscle tone or muscle fitness as a prerequisite to bolting.

Calves may join other calves and their dams quite early, often within the first week. For red deer calves, the initial hiding phase lasts three to four days. Elk calves may be secluded more or less together while the cows remain nearby. Thus, the hider strategy slowly gives way to the normal anti-predator strategy of the cow elk, which is to gather with others in the open, flee from disturbance, outrun the pursuer, and relocate away from predators. The change to the normal strategy may be accomplished alter three weeks; prior to that time the calf hides while the cow flees.

The hider strategy entails minimizing contact between mother and young. Consequently, the calf is suckled only four to six times during the 2~hour period while it is in seclusion. However, the suckling durations are quite long. In the Tule elk these lasted an average of 40.3 seconds (range 15-120 seconds, n = 20). It is suspected that the duration and frequency of suckles will vary with the quality of the elk population, as they do in mountain sheep. The cow elk usually initiates and terminates suckling. During suckling the cow licks her calf-a behavior that becomes gradually less frequent as the calf grows larger.

The hiding strategy of the cow can amount to nothing if her offspring of the preceding year follows her, alerts predators to their presence, causes the calf to misimprint (select the wrong animal for its "mother image"), and suckles the cow-thus depriving the calf of nourishment. The solution is to break the mother-young bond before parturition, and this takes place only about two weeks before the next birth.

After red deer and elk yearlings segregate from their dams, the female yearlings tend to remain close to their mothers once the latter return with calves. Male yearlings tend to wander off, frequently alone, to join male groups or to visit other female groups. Cow elk tend to be hostile to male yearlings, but less so to female yearlings; they also are rather hostile to other cows about the time of parturition.

The essence of the hider strategy is to minimize encounters of young elk and predators. Predators are thought to form search images when, after catching a particular kind of prey, they set out in search of another of the same kind of prey. Therefore it is to the adult elk cow's reproductive advantage to bear her calf either earlier or later than the majority of other cows in a population. In southern latitudes with extended seasons of vegetative growth, natural selection is likely to favor cows that do not calve synchronously. The expected effect is an extended birth and rutting season for elk from southern latitudes.

Calves in Herd Life

After the calf has entered herd life, it must not detract from the group's efficiency at anti-predator adaptation. Consequently, the cow does not protect her calf against herd members, even though calves may suffer some abuse or occasionally be killed by antler blows from bulls. The calf must learn to avoid harm on its own. if a cow were to take sides, this could lead other cows to leave her presence, thus reducing the group's gregariousness and ability to spot predators. It also could lead to the aggressive cow being avoided, and therefore frequently finding herself at the group's periphery, where vulnerability to predation is greatest.

Moreover, aggression in the herd would raise the cost of maintenance to each member due to the excitations caused, and a reduction in time for foraging. It would not permit maximizing indirect competition and would result in less milk being available to the calf of a protective cow. Not only do cow elk fail to protect their calves from other cows-and very rarely fight with each other except when alarmed by the herding activities of bulls, but they also lick and groom each other, usually when resting after a feeding period.

A cow must maximize the growth of her own calf, permitting it alone to suckle. This rule has rare exceptions, such as a yearling being allowed to suckle a calf-leading cow elk. This also is true for red deer. Cow elk and red deer hinds usually repulse strange calves.

The only individuals the elk calf is not regularly repulsed by when it initiates social con-tact are other calves. This leads to the formation of calf groups within nursery groups (groups composed of most of the calves in a group with a few adult cows-an anti-predator mechanism). A calf group seems to focus attention on one adult female for a protracted period of time, much as is found in mountain sheep, giving rise to the so-called "babysitting" phenomenon. I consider this a misinterpretation and suggest that it is the calves that affix their attention on the cow and not vice versa. A tendency to focus attention on one adult at a time would minimize confusion in times of imminent danger. The calves would bolt after one adult-the one they were associated with as a group. Once the danger is past and the band has halted, calves may search out their mothers. Excitation suckling (suckling as a direct result of stimulation, as following fright) after disturbance, as reported in some other ungulates, may be present in elk but has not been reported. It would promote the calf's searching for its mother as soon alter excitation as possible.

The calf, however, does derive some benefit from its mother's dominant position, such as being able to move into shelter while yearlings are excluded. Adults will displace calves from good feeding spots, but it may be that this is done less to calves close to a very dominant female. This remains to be established and the normal "heeling response" of calves ensure this. Observations suggest that, when separation occurs, the cow returns to where she last saw her calf. A distress call by the calf may bring other elk on the scene, and it is expected that a cow searching for its young would be particularly sensitive to such calls. In the first two weeks of life and maybe even thereafter, calf elk have difficulty recognizing their mothers; the cows appear to recognize their calves by scent, as is the case for the female-young relationship of other ruminants.

It can be assumed that a cow elk improves her ability to rear calves to maturity as experience is gained. This is indicated by the differences between cows giving birth for the first time and those that have reared several calves. Cows having reared a calf may "imprint" on this process, as observations of moose have indicated.

Response to Predators

When something unusual has been detected by a herd member and subsequently the herd becomes alarmed, it is not necessarily in the herd's best interest to bolt. Spontaneous bolting could unduly subject to predation the calves that could not run as fast as adults. In-stead, the source of disturbance is sought for identification so that the response may be matched to the danger, in accordance with the law of least effort. This is "curiosity" behavior. It is linked with "alarm" behavior in which the individual assumes an "alert posture" disturbance, and struts in a stiff, unusual gait to inspect the disturbance closely. An alarm bark may be uttered repeatedly during this procedure, and it ceases once flight is taken. Alarm behavior is relatively rare and unusual, and contrasts sharply with normal activities. It is this discrepancy which, according to current understanding of animal communication, makes alarm behavior effective as a signal-generating arousal.

Responses to predators may range from mobbing, as with coyotes, to ignoring the predator, to flight---and desertion of the area of disturbance for an undetermined length of time. The latter is a response of elk to mountain lion kills. Elk may put a great distance between themselves and the source of their disturbance; they flee as a group. They, like red deer may learn to avoid areas where they have been disturbed repeatedly, in so doing abandoning migrations and ranges, altering their habitat preference, and changing from daytime to nighttime activity. In short, they may change their behavioral patterns drastically. Here they are responding not so much to opportunities of habitat as to interference's or barriers imposed by human beings. Batcheler's (1968) hunting experiments on red deer are most instructive. A necessary consequence of their learning ability, however, is that when not disturbed, elk readily adjust to humans, as shown in national parks, and that they can be domesticated, as shown on deer farms in the Soviet Union, China, and more recently New Zealand if the progressive shift from foraging on grasses to foraging on forbs in spring and early summer suggests that forbs are a more nutritious forage than grasses, one would expect that elk not only vacate open landscapes progressively, but also become less gregarious. Indeed, Knight was able to show the former; the latter was shown only for bulls. This suggests that the post-calving gregarious-ness of cows is an anti-predator strategy to protect the calves, inasmuch as cows unencumbered by calves otherwise would be free to exploit tall shrubs and forest just as bulls do. It also suggests that, as calves become more capable, the gregariousness of calf-leading cow elk should decline, and cows should move progressively farther into cover as their group size declines. The predictions of this hypothesis are that lone cows are more likely to exploit a diversity of habitats, have a habitat preference closer to that of bulls, and, next to bulls, are most likely to disperse and colonize.

ANTIPREDATOR STRATEGIES OF BULLS

Independence versus Grouping

In the annual life cycle, bull elk face quite different problems than those of cow elk. During summer they appear to require more food than do cows, and to maximize body size, fat deposition, and antler growth. In forested areas, free from the constraints of parental in-vestment, they may explore small areas of highly productive forage. This demands a secluded life-style to minimize contact with predators. It also selects for mobility and relatively large home ranges for bulls in summer, and less loyalty to established home ranges than expected from females. The former expectation has been verified for red deer and elk; for the latter expectation there is only indirect evidence. The greater tendency of males to roam and be independent of others is directly observable and is reflected in the tendency of the yearling male to make contact only rarely with its mother once she has given birth to a subsequent calf. It also is reflected in their higher mortality and the fact that bull elk colonize before cows do. A tendency by bulls to assume a hider strategy would be reflected in their being more silent than cows, and this is quite noticeable. Nursery bands in particular are very noisy due to frequent calling by cows and calves. Bulls also would be seen less frequently in open areas than would cows.

In open country, however, bulls must gather into groups to reduce predation for reasons outlined earlier. They must not join cows though, in order to minimize competition with the prospective or actual mothers of their offspring and, at times, with the offspring as well. This would not apply to bulls that rut with cows different from those with whom they choose to live. Under these circumstances they would not reduce their own reproductive fitness but, instead, that of other bulls.

There is, however, a more important reason for bulls to minimize contact with cow elk and stay away from them for all but the short rutting period. Since bulls are less abundant than cows, they are very conspicuous in a female herd, particularly if they are large-bodied, long-antlered, older bulls. Because they are different in appearance (discrepant) from females, they ought to attract the attention of predators. As long as the bulls are in excellent physical shape, this probably matters little, since they likely can outdistance a culling predator. However, after the rut, when the bulls----particularly the older ones----have lost condition, it would be fatal to them. They would not only readily full victim to a culling predator, but each fallen bull would encourage predators to hunt bulls selectively. If bulls are to maximize their chance of survival, they must either change in appearance and assume the external appearance of cows, or segregate from cows. This hypothesis was developed by Bromley (1976) as a result of his studies of pronghorn to explain the shedding of horns in bucks immediately after the rut, and extended by Geist and Bromley (1978) to the Cervidae.

Note that the foregoing predicts that in the case of sexual segregation it is the bull that avoids cows. It is expected that the sex in lower abundance will avoid the sex of greater abundance. An area is colonized first by males, and large herds of males may be found on it. Later the same areas at the same seasons will be devoid of males while females utilize the areas. In this instance, clearly it is the bulls that have with-drawn from an area they found acceptable and used in large numbers a few years before. Altmann's (1952) observation that bull and cow groups may flee in different directions when disturbed is consistent with this hypothesis.

Once segregated from cows following the rut, large bulls may hide in cover to recuperate from the effects of the rut, as is commonly found in red deer, or they may form large bands in the open. Such grouping is expected where elk are dependent on open landscapes with grassy vegetation, and Knight's (1970) data suggest that this is the case. Where few elk are present, bulls probably will hide after the rut, as was indicated by the observations of Roosevelt elk.

Antlers and Dominance

If antlered, dominant elk gain from their hierarchical position (rank) during winter at times of limited accessibility to forage, it is disadvantageous for bulls to cast (shed) antlers. As an anti-predator strategy, gregariousness is not compatible with weapons that maximize pain to the victim and invite retaliation. Use of antlers permits wrestling (which do not inflict pain) during sparring, and signals the rank of the bull; flailing with forelegs to enforce dominance would inflict pain and reduce gregariousness. Red deer stags with antlers removed experimentally or cast naturally are subjected at once to harassment by antlered subordinates, and lose rank or retain it only by increased aggressiveness. They regain rank only when other stags are antlerless, and even then it is a rank held insecurely. Under conditions of forage shortage, antlerless stags are disadvantaged compared with antlered ones. Stags therefore are expected to disperse after antler casting, as would be reflected in reduced gregarious-ness. This was shown for elk by Knight's (1970) data. The frequency of lone bulls increased immediately after antler casting. Bull elk are most gregarious during the period of antler retention in winter---a period that coincides with maximal use of open country. After shedding their antlers bulls are found more frequently in cover, and feeding more on forbs and browse. A reduction in gregariousness immediately after antler-shedding also is known among red deer stags.

Retention of antlers and the continuation of sparring matches maintain a stable dominance hierarchy among bull elk. It is a hierarchy that should express itself in a maximum amount of time available for maintenance during winter and a minimum of energy expended on aggression. Therefore, one would expect red deer and elk to retain antlers as long as they congregated in open areas during winter and until reduction in snow cover reduced forage competition and permitted the animals to disperse. If the foregoing hypothesis is valid, the retention of antlers in red deer and elk would be predicated on the length of winter under which these forms evolved. The elk-a more cold-adapted form originating in Siberia (thought to retain its antlers longer than does the red deer.

A scrutiny of the rutting and antler-casting dates of various Eurasian races of red deer and elk, showed the following. Red deer had the highest rutting activity between September 20 and October 5, and lost antlers in the second half of February. Elk races, including the Izubr stag, had rutting peaks between September 1 and 24, and shed antlers in the second half of March. Thus, the red deer stags retained their antlers about 150 days and the elk retained theirs for approximately l90 days.

Tule elk bulls retain antlers for about 185 days after the rut, if one measures the interval from the midpoint of the rut to the midpoint of antler shedding. For Roosevelt a retention period of antlers after the rut of about 185 days for Roosevelt elk.

Retention of antlers in bull elk throughout the winter is seen as an indirect consequence of its antipredation strategy, namely, grouping together with other bulls while exploiting grasses, sedges, forbs, and browse on open landscape.

Antlers are a "luxury" tissue of low-growth priority, as evidenced by how changes in antler size and shape follow environmental factors or illness of the animal. Managers of deer estates and reindeer managers in Siberia are aware that antlers in red deer are an expression of the animals' health and that antler growth in stags and calf production are correlated. That antlers are a luxury tissue also is revealed by the close correlation between number of antler points and body weight of red deer stags. However, there was no correlation between antler length and fighting success, though the number of antler points was correlated weakly with fighting success. This may be because heavier stags have a better chance of winning contests. Also a parallel increase in body and antler weight in red deer from eastern Germany after these animals were past eight years of age.

COMMUNICATION

Contact Sounds and Alarm

The rule that an individual must maintain homeostasis and obey the law of least effort dictates that an individual must live in a predictable social environment. Predictability in the social environment has to do with gaining access to resources essential to maintaining reproduction, for example, the selection of partners for mating. To facilitate this at the least cost is the purpose of communication.

Communication is predicated on an animal's ability to monitor its environment, detect the usual from the unusual, and respond instinctively by withdrawal or approach. Communication operates through all sensory channels along which signals can be transmitted-sight, sound, taste, smell, touch. Communication is subject to some selection according to habitat, but is generally conservative and resistant to selection so that different species of the same family or tribe show surprising similarity in their means of communication.

In a forest-dwelling ungulate, stealth and silence are utilized in order to reduce contact with predators. In ungulates of the open plains, no such selection is expected, and noisy behavior and showy coloration are characteristic. In the elk-an ecotone species with strong leanings toward open country-both these abilities should be evident, depending on where the animal is found. In addition, a solution to another problem is demonstrated. When a group moves into shrubbery or other tall vegetation, how can individuals differentiate noises of conspecifics from those of predators? In the open, the production of constant noise by the group through vocalization obstructs noises generated by predators. Yet this is inconsequential because predators can be sighted readily in such a setting, and the moment conspecifics cease feeding and vocalizing, the ensuing silence alerts the less wary members of the group to the presence of danger. Silence, contrasted to noisy background, is a signal of danger. When feeding in dense shrubbery, loud vocalizations may attract predators and permit them to approach unseen, hide from sight behind cover, and use the herd noise to mask their own sounds.

It is adaptive, therefore, for an animal not to vocalize when in a herd that is feeding in habitat that obstructs visibility. Yet, feeding individuals will make some noise. How can it be distinguished from that made by an approaching predator? The solution in red deer and elk, just as in the marsh-dwelling Pere David's deer and the caribou, which exploits taiga forests in large bands, appears to be "knuckle cracking." Every time an individual walks, its legs emit an unmistakable click that remains distinct regardless of what substrate the animal walks on. A grazing companion emits a diagnostic noise in rhythm with its steps that no predator can equal. Thus, friend can be distinguished from foe.

Knuckle cracking in red deer appears to be produced only by the front legs. In limping animals injured in the back legs, it sounds in exact rhythm with the movements of the front legs. It is a dull sound compared with the hi8h-pitched, short click of the caribou, in which both front and hind legs produce sound. McCullough (1969) described knuckle-cracking in elk. My observations suggest that it is not nearly as audible as the clicks produced by caribou.

The cessation of knuckle-cracking and feeding noise is a signal to be on the alert. if nothing follows, a calf then might reduce alertness (the cow may be lying down rather than in an alert posture). if cessation of activity was produced because of an elk noting a suspicious sound, then the cow would protect her calf by remaining alert. In dense cover she would have no option but to vocalize. This is the probable reason for the alarm bark of elk-a sound produced mainly by cows, and common to Old World deer as a whole.

The subsequent alarm behavior of elk has been well-described by McCullough (1969). As indicated earlier, it alerts by deviating from common behavior in the rigid stance, erect posture, deliberate tension, halting gait -termed "warning gait"-unusual side to-side movements of the head, hackney trot when changing vantage points, and barking. All are actions strongly deviating from the normal feeding-walking-standing activities of elk. Therefore, such discrepant actions arouse, as inferred from numerous studies on arousal. Once in flight, elk tend to be silent.

Weapons

Most signals elk use in communication do not function in the strategy of predator avoidance, but rather in the relationship among individual elk. At the lowest level, they ensure priority of access to scarce resources by displacement of one individual by another. This, in conformity with the law of least effort, usually is not achieved by displacing the competitor physically but by parasitizing his tendencies to withdraw from stimuli conveying threat.

The weapon most commonly used by elk to gain access to resources for maintenance are the front hooves. Elk also retain, as a phylogenetic relict, a very weak tendency to bite. Bulls may also use their antlers to gain access to resources. They resort to front legs as weapons during antler growth and frequently alter-wards. The threat of front legs as weapons is so effective that antlered bulls subjected to front-leg attack respond in kind and only exceptionally use antlers against an opponent who threatens with front-leg flailing. This also explains why adult cows may dominate antlered three-year-old bulls as well as yearlings.

The front legs can be used to the fullest effect only when the animal rises on the hind legs; it is from this posture that opponents flail at each other. It also can be seen that elk will deliver a blow simply by raising a front leg and smacking an opponent or giving him a push. The push, however, is also a threat, as is the act of rapidly raising a front leg while in contact with the opponent and touching it with the anterior surface of the lower leg, or snapping the leg hard on the ground producing an audible sound.

Threats

A threat, as opposed to a display, is an iconic signal, that is, one in which the form of the signal coincides with the implication, thus allowing an accurate prediction by the receiver. In a threat, the animal shows clearly which weapons are about to be used, by performing motions that bring the weapon or weapons into readiness for use. The elk can slap, and since this requires raising the head and forebody, it is the raising of the head and forebody while orienting toward the opponent, plus degressing of ears, that serves as the basic threat. It is a universal threat of deer, and has been described and illustrated in part or whole by many investigators; it is referred to herein as the head-high threat. Stamping, touching, or pushing aside a conspecific using a front leg also serves the same function, but is used only against clearly inferior opponents.

Elk cows in particular also will bite each other and threaten accordingly. In approaching an opponent in high-head threat, a cow or bull will retract the upper lip as if exposing rudimentary canines, grind the teeth and utter a soft hissing sound. In full intensity, the nose points almost upward, the eyes roll forward as if to maintain the slit of the pupil horizontally, and the tongue may protrude from the side of the mouth. Yet, instead of biting, this phylogenetically ancient behavior (shared by red deer and other Old World deer) is followed by the deer suddenly leaping upward to flail with the legs----the animal's teeth no longer an adequate weapon.

Bull elk with velvetless antlers threaten by snapping the antlers forward at an opponent, who usually evades them. Invariably, bluffs threaten greatly inferior adults in this manner, but not nearly as often as they threaten other bulls of equal rank. On some occasions the antlered aggressor may leap after the departing opponent and jab its side. It also may terminate the charge with a hard slapping of the ground with its front leg and a series of sharp grunts. My observations of captive elk, red deer, and sika stags revealed that threatening bulls will spring into a rush and either attempt to gore the opponent or terminate the rush with ground slapping the moment the opponent makes any movement to terminate contact, particularly if the latter averts its eyes.

Although cow elk and red deer hinds do not have antlers, they may use a "horn threat" occasionally, and even butt an opponent. Other times, hinds may act as if they possess antlers, as in play-like behavior around wallows. On such occasions I have seen red deer hinds execute the very same weaving actions that in red deer stags ensure antler contact during sparring.

There are other classes of threat besides those with weapons, but significantly, they either are absent or do not function often in a social context. Elk have no distinct defensive threat as moose do, nor do they often use a rush threat (a threatened charge, signaled by a short rush with head elevated), although bulls may use it against greatly inferior males during the rut. Cows use rush threats against coyotes, and on the basis of observations of red deer, they probably also grind teeth and expose their canine teeth during such confrontations.

The inclination of individual elk to live in a predictable social environment, the effect of weapons, and an ability to learn combine to produce the dominance hierarchy. The dominance hierarchy is an incidental result of animals learning to avoid or become subordinate to those they cannot force to withdraw. Once a hierarchy is established, elk settle down to maximizing food intake and reducing energy expenditures as best they can. Among red deer stags a hierarchical dominance based on flailing with front legs is weak, and relative rank positions change. However, hierarchical dominance is quite rigid if based on antlers as weapons, shields, and rank symbols.

if elk tend to greater gregariousness than red deer because of greater use of open landscapes and grasses, then it may be expected that elk would be more peaceful than red deer. There are no data to test this hypothesis. In zoos, at least, sika deer-a more primitive, forest-adapted species than the red deer---bite extensively. This provides a hint that the hypothesis may be valid.

Overt aggression certainly is not very common in elk. It flares up over access to such concentrated defensible resources as salt licks, resting places, wallows, or preferred forage sites. Larger animals displace smaller ones with threats or strikes or by pushing them out of the way; young elk and cows widely separated in dominance have the highest rates of aggression. It also flares when the animals are excited and crowded and thus denied freedom of action, as in response to being herded by a rutting bull. Overt aggression is marked when the cow beats and chases off her yearling prior to birth. Observations suggest that even during normal grazing, dominant individuals are alert to others finding preferred food; the dominants then displace them.

However, most resources on which an elk depends cannot be defended profitably; a greater than equal share can be attained only by indirect competition.

Submission

Since fighting is costly, it pays for dominant animals to do little of it and for subordinate animals to terminate it quickly. Particularly for species in which gregariousness functions as an anti-predator strategy, it does not pay for the dominant animal to evict a companion from a group or be avoided by others. Thus, a signal has developed whereby a subordinate acknowledges the dominance of a greatly superior elk and precludes overt aggression on the part of the dominant. Such a signal is termed "sub-missive behavior".

In elk, as in almost all Old World deer, sub-missive behavior takes the form of depressing the head and neck, extending the muzzle, dropping the ears, and making rapid chewing motions with the jaws. As Barrette's (1975) studies on muntjac indicated, the latter behavior is derived from feeding. Feeding in response to aggression is distributed widely in ruminants, but is ritualized in elk and other members of the genus. Resting subordinates may crouch and lie flat in response to dominants, almost as if assuming an infantile hiding crouch. Grazing subordinates may turn away from the dominant and leave while grazing or at a walk. But if they trot away, the submissive behavior is likely to be shown. In captivity, when pursued by a large rough male, red deer hinds and elk calves occasionally utter a squeaking or tremulous call. There is no indication that this submissive behavior is shown by adult bulls. It is basically a behavior of females and immature animals, as would be predictable from their greater gregariousness.

Sparring

From studies of conditioned responses, it is predictable that it pays the dominant to rein-force its position periodically, and for the subordinate to test the competence of its dominants. It pays for the dominant to ignore the subordinate as much as possible, despite the subordinate's threats. However, it must assert itself frequently in order to keep the subordinate conditioned to withdraw. As yet little can be said about behavior conforming to these expectations in cow elk. It is manifested in bulls as sparring matches that begin shortly after they shed their antler velvet, and which are again common in spring shortly before the bulls shed their antlers.

Sparring matches are a ritual, and appear to function in the aforementioned context since they take place primarily among equals. Bulls aggregating after the rut may establish their respective dominance ranks by fighting with antlers, as observations on red deer stags have indicated.

Sparring matches then would maintain dominance. Therefore, the sparring matches of red deer and elk are fundamentally different from those of mule and white-tailed deer, in which sparring occurs among non-equals except in yearlings, and has nothing to do with testing dominance. In sparring, as in many other aspects of their biology, New World deer differ greatly from Old World deer. Under no circumstances can sparring matches be equated with fights; they are distinctly different phenomena.

In elk, a sparring match among equals is signaled by a careful approach with lowered head, the antlers performing slow side-to-side movements. The initiator thus solicits a sparring match; he does not advance in a dominance display, but signals with intention movements. Soliciting also may include nodding, which bobs the antlers forward. Nodding probably occurs only among well-acquainted bulls. Significantly, the soliciting animal does not spread its legs noticeably or crouch as if anticipating a forceful lunge. The antlers may be engaged slowly, with weaving motions of the head; such motions may be conspicuous when the partners are several feet apart. McCullough (1969) observed these motions in elk sparring at a bush between them. Once engaged, the opponents push and twist heads. Disengagement is honored, during which one or both bulls avert their eyes, acting as if looking into the distance. Eye aversion as a temporary cut-off in sparring appears to be wide-spread among ruminants. One of the bulls may remain standing with lowered head until the other again squares off.

During sparring, bulls and particularly younger bulls may emit a squealing sound. It may be emitted even by subordinate red deer stags chased by a larger stag, or by stags courting a hind. Disengagement is as gradual as engagement. However, it may have a playful ending, particularly in young bulls which jump backward with bobbing and weaving motions of the head or run side by side bobbing antlers at each other.

Sparring may escalate into a short fight in which an opponent flees, as in red deer. This obscures the difference between sparring and fighting. Greatly unequal elk bulls merely spar, as expected if sparring was dominance related. Larger bulls spar more violently than smaller ones.

In red deer during the rut, what still may be termed sparring matches among large rutting stags. These matches retained not only elements of sparring but also of dominance displays and, thus, were intermediate in their form between sparing and combat. Apparently they also were intermediate in the frequency between the common sparring matches on one hand and the very rare combat of bulls on the other. Such sparring matches among large bulls also apparently occur with elk, since herd-bulls make antler contact with other bulls during the rut. These engagements normally do not develop into true dominance fights, as indicated by the scarcity of diagnostic dominance-related displays and the short duration of these clashes.

Sexual Competition

The Rut and Male Advertisement

The behavior of bull elk and red deer stags coincides closely with the advertisement hypothesis. Advertisements of the bull are its diverse dominance displays, bugling, wallowing, and self-impregnation with urine-and its antlers. In the case of bugling, the larger-bodied an animal, the deeper and louder a sound it can produce. The pitch of a call can be a clue to body size and, furthermore, combative potential or dominance rank. Thus, the older and larger the male, the deeper its call ought to be. This is found in both red deer and elk. The call also ought to be longer and louder in old bulls, as it probably is, but this has not been investigated yet. In elk, final portions of the bugle call terminate in a deep, guttural, resonating roar.

If the bull is to maximize advertising, its call must reach as far as possible. However, the audibility of a sound at a distance depends on its pitch. High-frequency sounds travel farther than low-frequency sounds in unobstructed landscapes. In landscapes covered by tall vegetation, however, high-frequency sounds lose their energy to leaves and stalks of vegetation and are absorbed quickly. Low-frequency sounds impart less energy to the vegetation they traverse and, therefore, travel farther in dense vegetation than do high-frequency sounds. The forest-adapted red deer thus ought to use a lower-frequency sound spectrum than the bull elk, which are adapted more to open landscapes. This expectation is fulfilled. Moreover, the elk does not form a resonating chamber with his jaws and lips as the red deer does when roaring. The elk keeps an open mouth with somewhat retracted lips during the bugle, and does not withdraw the tongue deep into the throat. These differences explain the differences in facial features between elk and red deer, such as the fleshier and broader nature of the muzzle of the latter.

The deep resonating part of the elk bull's bugle is low in volume and does not travel far, and there is a good reason for this. It should function only for the benefit of his immediate harem, since the low frequency of the call would not carry far anyway. The elk bugle is of considerably greater duration than the roar of the red deer stag. if the bugle or roar is an advertisement:

1. It ought to be uttered mainly when females are most active, and therefore either more likely to come to the advertisement of a bull or leave him in favor of an advertising competitor. Thus, bugling should follow the daily activity rhythms of females closely.

2. Bulls ought to silence advertising competitors. Thus, bugling by a non-herd bull close to a harem-guarding bull should attract the latter, and this is what happens. A bull calling close to a harem is likely to be answered, searched out, and attacked by the herd bull. This is common for both elk and red deer.
3. A cow-guarding bull must out-advertise an advertising competitor. Therefore, bull elk ought to answer the calls of other bulls, which they tend to do. Bulls guarding harems should bugle more frequently than those who are not, as a means of countering rivals' advertisements and as a reinforcement of socially positive experiences of the female. This should result in older bulls bugling more than younger bulls, who may be inhibited further from bugling by bugles of large bulls close by. Data are entirely in line with this expectation. The only exception should be when a large bull has treated cows more "considerately" and differently from the treatment they experience from unsuccessful rivals. He then may permit himself the luxury of reducing advertising because the cows will show less inclination to leave his harem. To maintain the loyalty of harem cows, a bull must ensure that his behavior is experienced by the cows as different from that of rivals. First, he can offer protection from the incessant harassment by younger bulls so that the cow finds rest in his presence. Second, a large bull can be quite gentle in courting, whereas a young bull must dart in if the opportunity becomes available and court as quickly as possible before the herd bull is alerted and reacts. Thus, there is a definite distinction between the hasty courtship of a young bull and that of an old bull. The cow probably experiences a real difference. When she signals submission and moves from the bull after he has closed in courtship approach and licked her vulva and tail region, the large bull actually stops. He bugles right after the courtship, associating for the female the socially positive experience of being licked and relief from pursuit with the bugle or roar. Thus, females ought to be conditioned positively to the bugle; it is an integral part of the courtship sequence.
4. Females ought to be attracted to the bugle. No experimental evidence is available to show whether or not they are, but there are observations that indicate they may be. For example, in the Hellabrun Zoo of Munich, Germany, where red deer stags of different subspecies came into rut at different times, hinds whose stag had not yet begun to roar clustered at the fence closest to a roaring stag, paced the fence hastily, and watched the rutting stag through the fence. As expected, they terminated this activity once their own stag began to roar. Deer farmers have noted that apparently the hind usually chooses the stag, rather than vice versa.

Therefore, red deer hinds apparently were attracted to stags in large part on the basis of the stags' antlers. Stags deprived of a significant part of their antlers were unable to keep hinds. This suggests that antlers serve partly as rank symbols and partly to keep hinds close to a stag once he has attracted them. The size of antlers is, after all, a sensitive indicator of the stag's health, vigor, size, and ability to procure forage in the face of competition. Although antler size did not correlate with fighting success, the number of antler points did correlate with a red deer's harem-holding capability. Moreover, in fallow deer the courtship behavior of the male is totally illogical unless the assumption is made that the palms of the antlers attract females.

It was predicted that individuals would maximize their reproductive fitness not only by successful competition for mates and resources, but also by directly reducing the reproductive fitness of others. In this respect, bull elk interfere with mating by others, and cows deny milk to calves that have lost their mothers.

Urine Spraying, Wallowing, and Horning

To maximize his advertising efficiency the bull ought to advertise in more than one way. Closely linked to bugling are urine marking and the opening of the preorbital gland, which should release a scent during bugling. At the last phase of the bugle, the bull elk palpitates his belly in rhythm with terminal yelps, and sprays urine towards his belly or the ground. The palpitation can be clearly seen, even in dim light, since the light-colored portion of the belly behind the penis bobs up and down. The belly hair ahead of the penis orifice is soaked with urine and tinted a very dark brown. It can be assumed that the more a bull bugles, the more it sprays urine, and the more the urine smells. Thus, the sheer intensity of the scent a bull emits should signal its rank.

Urine spraying, however, is quite a variable process in elk and red deer. It may be the dribbling of a few drops or large rhythmic discharges of urine from an erected penis, varying from a stream aimed at the neck mane to a fine mist sprayed in a cone against the belly. It always is accompanied by palpitation. The urine is released almost at right angles to the erected penis. When voluminous discharge occurs, it usually takes place at a wallow the bull digs with its front legs and which he horns-interrupted by bugling-with his antlers. The bull tends to lower his head to the ground during urine spraying, and thus his neck mane gets doused as urine sprays forward between his legs. Once the wallow is dug, the bull lowers himself onto it, rolls on his side, and proceeds to rub his neck mane on the edge of the wallow. He cakes the side of his face and his chest, belly, legs, and sides with mud. The penis may remain erect during wallowing, and the bull may continue to spray urine during wallowing. I have observed this in captive red deer as well.

After wallowing, the bull may move to a tree and vigorously rub his mud-soaked neck against the trunk, a behavior universal to large-bodied Old World deer. Bulls tend to return repeatedly to the same wallow, and may be observed resting in their wallow for long periods. Wallowing is done mainly by large bulls - as expected from the advertisement hypothesis----but wallows also attract yearlings and even cows. Struhsaker (1967) noted gamboling (playful bounding) and stotting (excitation jumping) by yearling bulls in the vicinity of the wallow-signs of considerable excitation.

Observations confirmed this for red deer, and also have observed red deer hinds "horn" wallows, paw and roll in them, gambol around them, and from them attack other approaching hinds. Large, captive red deer stags gamboling during wallowing early in the rut, as well as rising on hind legs and thrashing branches high in trees with their antlers-a behavior common to primitive Old World deer. The latter behavior was described as "preaching".

McCullough (1969) found wallowing to be infrequent in Tule elk. He related this to the scarcity of moist soft ground, because bulls wallowed whenever they had opportunity. Thrashing of vegetation, accompanied by urine spraying, appeared to be the substitute.

Horning of vegetation is, like wallowing, an alternative behavior associated with urine spraying. It begins early in the rut and increases in frequency, and probably in intensity, during the rut. Like wallowing, it is an activity largely of older bulls and may occur without visible cause or in response to the advertisements of other bulls. It is a dominance display in which weapons are exercised----at times for the apparent benefit of opponents just prior to a fight. It is a noisy activity, augmenting the advertisement and often leaving a conspicuously peeled pole. When not contacting the tree trunk with his antlers, a bull may scrape the tree with his teeth (McCullough 1969), sniff, and rub his head against it. Thrashing can be quite variable, apparently depending on the kind of vegetation available. Wallowing, urine spraying, and vegetation horning are part and parcel of the attention-getting activities of rutting bull elk; they are not manifestations of classical territoriality.

Urine spraying has been confused by observers with ejaculation. The advertisement hypothesis predicts, furthermore, that the earlier a bull advertises, and the earlier he positively conditions cows, the more likely they are to remain with and be bred by him. This prediction hinges on the assumption that bulls advertise individualistically, so that a cow is conditioned to a particular bull and, consequently, advertisements by other bulls are ineffective in luring her away. Observations that red deer stags have distinctly different patterns of vocalization and retain these patterns in different ruts vindicate the above assumption. As expected, vocalizations, urine spraying, horning, and wallowing begin two or three weeks before the onset of the first estrus period in hinds. Old stags begin to associate with hinds earlier and advertise earlier than do young stags. It can be inferred from indirect evidence that stags in good physical condition begin advertising earlier than those in poor condition.

Coming into rut early permits stags with velvet-free antlers to dominate at once those whose antlers still are covered by velvet. The sensitive velvet stage probably dampens the latter stags' tendency to challenge the dominant later. Experiments with altering antlers indirectly support this expectation; red deer stags with inadequate antlers were repeatedly defeated, and avoided not only overt aggression but in some cases even the presence of other stags.

Herding and Courting by the Bull

After a bull has attracted females, it may not be enough to condition them positively in order to hold them, he may have to resort to blocking their escape. This results in herding-an action that affects a bull's courtship behavior and gives rise to the harem phenomenon. Without herding, cows would remain close to the, bull strictly of their own volition, and could come and go as they pleased. Herding keeps the harem together, but only with the cows' acceptance, since they can bolt from the bull despite all herding efforts. It is, after all, in the cow's interest to investigate as many potential mates as possible.

The herding posture of bull elk is derived from the head-high threat posture, which is seen clearly in sika stags too. In red deer stags there are some distinction between the head-high threat and herding, but the greatest differences are in elk. During herding a bull elk assumes a low-stretched posture with his head normally below the level of the withers. Leaving the main body of his harem he circles toward a cow at a trot or rapid walk, and thus comes toward her at a tangent. His head is averted from the cow, his eyes wide open, and the preorbital glands may be open. He may palpitate (flutter abdominal muscles) during the approach, and utter a series of yelps. McCullough (1969) heard tooth-grinding by herding bulls. Cows that are the object of this herding display usually depart rapidly, going back to the group in submissive posture. However, bulls that caught up with females were observed to bob their antlers at them1 or rush and even gore them. A bull's rush at a cow may terminate with two to four sharp, cough-like barks----just as any aggressive rush at a subordinate rival terminates. The herding display is, thus, a serious threat.

Right after herding, a bull elk often stops and bugles while oriented away from the cow and harem. Concession of the aroused cow to herding is reinforced by bugling, just as the bugle reinforces a cow's experience of "being in control" when courted by the dominant harem-holding bull. After all, the cow "makes" the bull bugle by stopping his courtship with her submissive behavior.

A variation of herding is for a bull to block an escaping cow's way, first by a broadside stance m which the bull arches his back while in herding posture, and then by whirling to-ward the cow and snapping his antlers at her. I have seen young bulls herd cows in a head-high threat posture outside the rut. Based on observations there are no significant or evident differences in herding behavior between bull elk and red deer stags, except for a slight difference in posture.

A bull that often approaches cows in a herding posture creates a problem, since cows tend to withdraw in response to a bull in that posture. How does the bull signal a difference in intention when counting? The solution adopted by elk is to make courtship the antithesis of herding.

This is noticeably more pronounced in elk than in red deer. In courtship, the bull uses a posture, orientation, sounds, and tactile stimuli diametrically opposed to those used in herding. He approaches frontally, not tangentially, and his head is raised high and the antlers are tilted sharply upwards, not backward. He may exaggerate his posture by crouching slightly at the rear, rising sharply in the shoulder region on an extended front leg, and assuming a rapid, trippling approach. He often palpitates when approaching, and keeps his ears forward. He plops softly with his tongue and flicks it as an intention movement corresponding to licking, and no yelps or sharp coughs are uttered. He licks the female on the croup and about the tail and does not inflict pain with his antlers. If the cow stands, the bull licks not only her vulva area and croup, but also her back, withers, and head. A cow may look back and touch muzzles with the bull. Most often, however, she responds with a rapid withdrawal in submissive posture, at which the bull stops and bugles. After courtship, and presumably after tasting some of the cow's urine, the bull may lip-curl. This type of courtship is typical for older bulls. A cow being chased by a bull intensifies the submissive display by snakelike motions of her head. She also will work her jaws occasionally while looking back at the bull licking her. This too is a response of resting cows to the approach and licking of a bull. Jawing directed at a bull is a signal of preparation to flee. It is logical only in the context of a breeding system based on male advertisement and harem herding. In a system in which the male pursues a female wherever she goes until she is in a receptive state, jawing would be a useless signal.

Breeding

A cow approaching heat is detectable by her reduced feeding and, indeed, overall activity. For much of the time she merely stands about, occasionally licking her side, hindquarters, and vulva. She does not withdraw from the bull as often, and the bull is permitted to lick her more often. In turn, the cow may lick the vulva, at which time her vaginal orifice may dilate and close. At this stage red deer stags may respond with jawing if the female should jaw. That is, the male uses a submissive behavior that, in this context, is appeasement. Elk bulls detect a cow's receptivity about half a day or less before it occurs.

When close to receptivity, the cow not only stands when the bull initiates a courtship approach, but also assumes a slightly spread-legged stance, lifting her tail and spreading the hair in her anal and vulval region. She may quiver in the haunches and twitch her legs. The bull then may slide his chin, neck, and chest onto the cow, while his erect penis appears to make small searching motions and slides back and forth in the horizontal plane. At this stage, the bull does not clasp the cow with his front legs. Instead, his front legs hang downward along the cow, while most of his weight is balanced on his back legs. This is a precopulatory mount, of which there usually are several, interrupted by his continued licking of the cow. Morrison (1960a) observed an average of 4 (range of 1-16) precopulatory mounts in captive elk, and others have observed an average of 5-8 precopulatory mounts (range of l-33) in free-ranging Tule elk.

In actual mating, the elk bull suddenly coils backward, in extreme cases throwing head and neck up and back until his chin points upward. Simultaneously he clasps the cow about the midsection and bounds upwards in the rear, leaving the ground completely. A cow occasionally is knocked down by such a thrust, but usually she is propelled forward, at which time she jumps from under the bull. With back arched, head lowered, and tail raised, she remains standing. Some blood may flow from her vagina; frequently she voids urine and mucous. Other cows, yearlings, and calves may approach her, sniffing at her rear and at the urine on the ground. She may continue to lick her sides occasionally for several minutes after copulation, before she resumes grazing or wanders off to lie down. The arched-back (lordosis) posture may be held for up to one-half hour, although Morrison found it to last an average of nine minutes. According to his observation, semen transfer also may take place without the spectacular copulatory jump of the bull.

A cow's arched back posture may entice a bull to mount. There are reported cases in which red deer stags mounted other stags wounded by a shot and standing with arched back. McCullough (1969) noted that the slightly arched-back and spread-legged posture of nursing elk cows tended to excite bulls.

Immediately after successful copulation, a bull may bugle and exhibit a high level of aggressive behavior toward rivals in his vicinity. I have observed the same aggressive behavior (with the exception of the bugle, of course) in mule deer. Also, consistent with the hypothesis that red deer and elk must hold females after attracting them, there is some evidence for postcopulatory attention and care by the male. Red deer stag have been observed to return repeatedly to a hind in heat and lick her head, neck and body.

Female Courtship

Courtship of the male by the female is not common in ungulates. It has been described incompletely in the literature on deer, and only once for wild elk. Others gave an excellent account of it in captive elk. It was observed and partially described in red deer. It has been observed it in red deer and several other species of Old World deer.

In view of these cumulative observations, a number of expectations can be identified.

Female courtship is the most powerful expression of female choice. In all observed instances, it was directed at a large bull. In fact, observed cows in heat drive off yearling bulls. Female courtship contains tactile components to rouse the ball, such as licking and nibbling at his face, neck, and body. Other components include diving under the bull's neck and rubbing her back and side along his chest, or rubbing her body full length along his from shoulder to rump. A cow may rub her head and neck on the ball's, and twist her neck so as to rub against the ball with the back of her neck. She also may gently "horn" his body.

She may also use behavior associated with sex, such as partially or completely mounting the bull or presenting herself in lordosis. Also used by the cow are aggressive patterns such as head-bobbing at the bull and butting him with her forehead. In addition, a cow uses "coquette jumps" and "coquette runs," in which she makes an exaggerated jump away from the bull, then kicks and runs off. This triggers the bull into running after her. During the run, the cow gambols and circles back.

Estrus cows to prance in front of a bull, move a few steps away, look back, then back up to the ball, quiver in the hindquarters, twitch hocks, and quiver when mounted. The actions of the cow appear to be arousal-generating, which hastens copulation by a tired bull.

Harem Defense and Dominance Fights

In a breeding system based on male advertisement, the bull necessarily maximizes competition for himself. He therefore must defend the results of his investment against other bulls. As indicated earlier, one way is to "personalize" his advertisement while bonding cows, so that they are less attracted to rivals. Invariably, however, the harem bull is surrounded by rivals and must not permit them to get close to his harem, lest the harassment cause the cows to leave. Young bulls or grossly unequal ones are chased off by a harem-herding ball, who rushes at them in a nose-up weapon threat accompanied by teeth grinding and hissing----quite similar to his behavior while herding. In red deer, most dominance fights are among 7-lO year-old stags, and take place at the height of the rutting season, when most copulations occur.

Since the costs of defense are high in time and energy, the male must use every conceivable ploy to protect his investment at least cost. He not only must educate rivals to his superiority before the rut, but use displays of dominance and various psychological tricks rather than fighting. For instance, by wallowing and darkening the body the male ought to look unusual to his opponent, and, according to arousal theory, generate fear. In various species of Old World deer (including red deer), males may be careful to keep vegetation and soil debris--acquired by horning--on their antlers, thereby enlarging their apparent antler size. When noting a rival, males not only may call much louder, but also may spray urine and exercise weapons by horning shrubs and soil with a show of vigor, and by generating loud noises. These displays should help to avoid a full-scale fight. Evidence of their intimidation value is needed.

If contact is made with the opponent, it pays to fight as little as possible. Consequently, in red deer and elk, short clash fights or sparring matches develop (around the harem) in which neither male risks a full-scale fight, particularly early in the rut. Even a full-scale dominance fight is confined to equals. It is preceded by a lengthy series of displays, and the individuals do not take ad-vantage of every opportunity to escalate the confrontation. Thus, not every defeated rival is gored, despite repeated opportunities. Moreover, contests among harem bulls and challengers may take the form of several short dominance fights interrupted by pauses in which the harem ball chases off smaller males while the challenger abstains from interference.

The full-blown dominance fight among elk or red deer is seen rarely. It has been described in detail for the red deer and, in less detail, for elk.

A dominance fight between a harem bull and a challenger is preceded by loud calling until the opponents sight one another. Horning, together with palpitation, then takes place on the part of both. They approach frontally, but turn sharply and circle each other approximately 15-20 paces apart, or move off in a parallel walk about 3-10 paces apart. They avoid looking at one another-a typical component of mammalian dominance displays. Antlers are tilted forward from a slightly raised head. In two instances bulls tilted their antlers slightly at their opponents; in both instances this was done by the eventual loser. As expected, the dominant bull acts, in the display, as if the rival were not present. The parallel march may develop into a trot, and the bulls may not retain an exactly parallel position; one may trot well ahead of the other. Both bulls may bugle during the march. This parallel march may continue for some 200 or more paces. The bulls may pursue a straight path or a winding one. They suddenly turn 180 degrees and continue the march in the direction from which they came. One or both may sweep the antlers over the ground during the turn, as if ready to catch the opponent's attack should it come. The turn also may contain some horning and bugling or, in the red deer, roaring, before both march off again. Witnessed a herd bull on a steep slope immediately move uphill of his rival and retain this favorable position during the march; reported this in red deer. A head-on clash develops suddenly, or alter a short pause m which the opponents have squared off with lowered antlers and a crouched posture. They may rake the ground with their antlers prior to the clash.

The signal for the parallel march to turn into a clash, according to observations of red deer, is the tipping downward of the antlers by one of the rivals. The fight may develop into a forceful pushing contest, in which a stag or bull gains an uphill position and quickly pushes his opponent downhill for several hundred meters. On the level, pushing may go back and forth or, in the red deer, change into circling. In circling, red deer stags spin around one another with locked antlers; this has not been observed among fighting elk. Elk bulls, however, may twist their necks forcefully from side to side, a behavior not reported for red deer. If it occurs in red deer, it probably is less frequent than in elk, judging from the relatively and absolutely smaller occiput and occipital condyles in the red deer.

The bulls soon breathe very heavily. They are crouched closely to the ground with legs spread widely. Their fight with locked antlers is essentially a wrestling match. It develops necessarily out of one function of their antlers, namely, as a shield to catch the opponent's attack.

Should a rival stumble, it may be gored. Quick attacks by one bull on the unprotected flank of the other do occur. The combatants may pause by with-drawing and standing parallel to one another. One may flee from this position when the other renews the attack. Flight also may occur if one frees his antlers and whirls away from his opponent. With lowered antlers, the victorious bull may leap alter the fleeing one and possibly gore him.

Invariably, the victor will utter a series of sharp, rough barks, then stop and bugle in the direction of the departing loser. The latter may bugle back. Pursuit by the victor is no more than about a half-dozen long jumps. Bulls show signs of exhaustion alter a fight, and after some horning and urine spraying the victor moves back to his harem and may lie down. Butler (1974) emphasized that engagements in red deer stags are highly variable.

The costs of fighting may be more than merely the loss of some body reserves and a period of exhaustion and breeding opportunity. Fighting leads to wounding far more frequently than observed, since bulls remove blood by licking, and most punctures soon close over. Yet limping and an occasional open wound can be seen, as well as, on rare occasions, a broken antler. Bulls may carry visible scars on their bodies following the rut. Fighting can result in broken necks, mortal antler punctures, and festering wounds that make wounded males susceptible to predation or increase their cost of maintenance so much that they become some of the first victims of winter mortality. The tanned hides of old bull elk, compared with those of cows and yearling bulls, are covered by healed scars. For combat dam-age in red deer. Fighting mortality is by no means insignificant. In Germany's tightly managed elite hunting estate of Rominten, about five percent of red deer stags were expected to die of fighting per year. Males with large complex antlers were considered especially susceptible to death. One study in Russia made of red deer stags found dead in the wild-13 percent of these animals died of direct combat damage. Clearly, combat must be the last means of gaining access to a scarce resource.

Antlers of the elk bull serve as (1) weapons, (2) defenses to parry the attacks of opponents, (3) organs to lock together with opponents in fighting to permit lull-strength wrestling, and (4) rank symbols. In the latter case they act as a symbol of size class, as well as a symbol of personal dominance, since bulls appear to recognize each other on the basis of antler structure. These functions have been verified in red deer.

RUTTING STRATEGY AND ENVIRONMENT

The differences between the behaviors of red deer and elk are in part logical consequences of increased open-country preference by elk. The elk bull's visual signals are more conspicuous than those of red deer stags, as illustrated on the one hand by its more-contrasting coat markings (such as a larger, brighter, black-rimmed rump patch and contrasting leg, neck mane, and body colors), and on the other hand by its behavior. Such behavior includes the sharply antithetical herding and courtship postures, the accentuated posture during the parallel display march, and the escalation of movements to a rapid pace during the broadside display walk or run. There are no documented reports of a slow, stiff approach and display march in elk after bulls have lost their antler velvet. Only Altmann (1952) described a stiff, slow circling with lowered head, but these were bulls in velvet on the summer range. It may be that bulls have a distinctly different dominance display when in velvet than after shedding, as is found in some primitive Old World deer. More exacting summer observations are required.

The bull elk bugle also reflects an open-country preference; it has a long-distance component (high frequency) and a short-distance component (low frequency). The latter, like the roar of the red deer stag, does not carry far.

Due to its large body size, the elk ruts earlier than the red deer stag. Due to the longer winters under which it evolved, it also casts antlers later, leaving barely enough time to grow antlers prior to rutting. The distinct fattening period of red deer stags-between the shedding of velvet and the beginning of the rut-is absent in elk. As soon as elk bulls shed velvet, they begin to associate with cows. On northern ranges there is a short break between velvet shedding and the outset of courting and harem formation.

On the southern edge of the elks' distribution-assuming the Tule elk studied are representative-rutting activities commence before the bulls have shed their velvet. This is due to the spread of the calving period over a greater time in southern areas. Here, bulls have no more time to complete the antler-growth cycle, but must compete for estrus cows and guard harems before their antlers mature and the velvet is shed. This is a remarkable phenomenon.

All this appears to be a consequence of the elk--a Siberian or Beringian form--dispersing southward in North America into latitudes with short winters and long growing seasons. Elk and bighorn sheep are rare examples of northern mammals colonizing southern latitudes. It appears that both southern elk and bighorns are beset by problems that are expected for cold-adapted forms adapting to warm climates, extended seasons, and hardy forages resistant to grazing. Elk and bighorn sheep very likely are associated with warm climates only since the melting of the Wisconsin glaciers. This implies that as yet both species are poorly adapted to southern latitudes, and, more importantly, that their existence there is due only to the absence of the American megafauna which became extinct. These extinctions removed a diversity of specialized grazers and large carnivores in whose presence the elk was a very rare animal indeed. Thus, elk, bighorns, and probably other recent American large mammals are abundant due only to the absence of the original competitors, the American Pleistocene megafauna.

The dispersal history of elk-arriving as a giant deer in America----has made it part of another phenomenon. It Is one of the American giants. Where comparison is possible between Eurasia and America, it is in America that the largest form of a species is found; these giants invariably are at the end-point of their dispersal. Thus, the largest of all elk subspecies are found in America, comparing skull measurements from American and Asiatic elk. Here also are found the biggest moose, caribou, bison, rupicaprid, pachycerine sheep, elephant, wolf, brown bear, true lion, sabre tooth tiger, giant rupicaprid-and such endemic American giants as the huge short faced bear, dire wolves, and elephantine edentates.

The lessened competence of elk to deal with mild, temperate climates is illustrated by its dispersal history in New Zealand when compared with that of the red deer. The elk dispersed less. Deer farmers in New Zealand also have noted that elk are more susceptible to diseases than are red deer. This is not surprising since northern forms are not nearly as much subjected to diseases and parasites as are forms from lower latitudes. The elk also were found to be rather "lazy"; this is a rather necessary prerequisite to fattening which occurs anyway at a lower rate than in red deer, and which is vital to the elk for reasons discussed earlier.

Another consequence of extended calving-and therefore mating seasons-is the sequential holding of harems by bull elk. This was first described by McCullough (1969) for Tule elk, and later reported for Roosevelt elk in northern California by Franklin and Lieb (1979). These researchers recognized primary bulls-the first, largest, and oldest bulls to hold harems. These held the largest harems and held them longest, but lost condition and were replaced by secondary bulls, which in turn were defeated by tertiary bulls after they be-came exhausted. Opportunistic bulls entered cow groups when large bulls were temporarily absent. In the moist temperate climate of Scot-land and the northern Hebrides, with its long vegetative season, rutting seasons of introduced deer also are stretched, and one finds that the very largest stags abandon harems before the end of the rutting season.

Since the bull elk ruts earlier in the year than does the red deer stag, it appears that he also could recuperate better from rutting activities and enter the winter in better condition for survival. This should lead to a choice of either rutting intensely for a few rutting seasons or rutting less intensely, recovering from rutting more quickly (and thus being in better condition to survive a severe winter), and maximizing the number of rutting seasons.

However, this choice is not possible for elk, although it is the choice of red deer in the more maritime climates of Europe. Here, after summer, a new flush of grass growth commences in autumn. Thus red deer stags can avail themselves of a rich forage sup-ply after the rutting season, which permits them to recover from the exhaustion of the mating season. The winter that follows is relatively mild and short compared with winters of continental Siberia and northern North America. Red deer stags appear not only to grow older than do bull elk, but they may even begin a spurt of body and antler growth when their vigor in rutting declines after seven years of age.

In Siberia and continental, cold temperate North America, winter sets in soon after the elk rutting season. There is no flush of new vegetation in autumn. To the contrary, killing frosts subdue the vegetation. For elk there is no opportunity comparable to that enjoyed by red deer stags to feed on abundant, rich, green vegetation after the rut. This indicates that bull elk cannot recover as readily as red deer stags from the strains of the mating season. Moreover, now the bull elk's large body size is against him. Because, relative to body size, a bull elk has a lower metabolism and food in-take than does a red deer stag, the elk's rate of fattening also is lower. Granted equally good forage after the rut, the bull elk will still recover more slowly than the smaller, more primitive red deer. Therefore, bull elk have little option except to maximize breeding effort per rutting season, rather than maximize the number of rutting seasons. Since bull elk are not expected to recover their body stores after the rut, they also are expected to experience a higher rate of winter mortality than do red deer stags, resulting in a shorter life expectancy. Moreover, since cow elk deplete little of their fat stores during the rut, they are expected to have a low winter mortality. Therefore, there ought to be a differential mortality between male and female elk, but not necessarily such a mortality differential in red deer. Stags can recover some of the fat depots lost during the rut. Indeed, red deer stags appear to live relatively longer than bull elk, although one must review the data comparison with caution. Bull elk have a considerably shorter life expectancy and higher mortality than cows, but the same apparently is not true for red deer in Scotland.

Among red deer from central Europe, it was found that the closer the sex-ratio came to unity, the less body weight stags would lose during the rutting season. This indicates that large stags can control both harems and competitors better under such conditions, discouraging smaller stags from competition, much as has been found among mountain sheep. Stags in populations with relatively many males and low losses of body weight during the rut are likely to live a long time.

Neumann's (1968) report of a red deer stag population in eastern Germany, in which stags that survived past seven years of age showed a marked growth spurt and increased in both body weight and antler size, was a startling discovery. This phenomenon, not reported from red deer living at high density in open landscapes, may be explained as follows. Red deer stags have a maximum of social activity between the ages of five and seven, as is found in bighorn sheep. Stags (or rams) surviving beyond that stage are less active during the rut, save energy, probably have a better life expectancy, and potentially can resume body growth. Whether they will resume growth probably depends on (1) their ability to escape frequent challenge by other stags and thus exhaustion, and (2) superb forage regime following the rut. In productive forests, with a low density of deer and exceptional forage in which older stags can hide with a small harem and not be challenged repeatedly, the conditions appear to be ideal for the Neumann phenomenon to occur.

The strategy of first coming into condition for rutting and then maintaining good condition for a maximum time-although quite noticeable in red deer -is best shown in the Tule elk. Due to constant selection for extended rutting seasons in areas with long vegetative growth seasons, large Tule bulls begin to rut long before smaller ones, and are replaced by formerly inferior competitors after the midpoint of the rut. This size-dependent succession of rutting males is seen nowhere more clearly.

Some observers have suggested that rutting bull elk and red deer stags are territorial. However, bull elk do not maintain a defended unit of landscape as a territory, even though they may spend most of the rut on a restricted area and return annually to the same place. It is false to speak of a "moving territory" defended by the stag, for such a characterization is a contradiction in terms. Others contend red deer stags are not territorial during the rut, and carry this conclusion to bull elk. Both act quite differently from bovids with an obligatory breeding territory, and are not comparable to them.

MANAGEMENT IMPLICATIONS

How to make use of one's knowledge of behavior in the management of elk depends on the management problems and objectives with which one is involved. To Europeans, the detrimental impact of red deer on forest plantations is important; in North America and with respect to elk, this is a minor concern. To Europeans, harassment of large wild mammals is not important. This is quite understandable, because having few places to go the animals learn the futility of trying to escape from humans-which closely follows the predictions arising from the study of learned helplessness. In North America, where there are large areas of marginal productivity that provide space for animals to escape from humans, harassment is of concern, since productive habitats are readily deserted when disturbance is excessive.

Despite great interest in trophies and trophy hunting, managing big game populations for trophy production is rudimentary in North America, compared with what Europeans know and do. The latest insights into how to manage ranches in Texas to produce large white-tailed deer bucks seem to result from a rediscovery of old knowledge. Similarly, there has been, as yet, only small interest in North America on how to hold elk for commercial production of their velvet antlers, a practice of long standing in northern China and Siberia, and more recently in New Zealand. One such operation is located north of Gardner, Montana, along the Yellowstone River. Game ranching for meat in the United States also is possible now only on such areas as Indian reservations and private game farms. On such farms in Texas, raising mammals to be hunted for their trophies is a going concern.

A knowledge of the signals used by elk and their meaning is valuable for anyone in close daily contact with elk, in order to avoid "unpredictable" attacks by bulls. In particular the weak forms of dominance display should be known, for they signal the approach of real danger. However, since the elk acts as if ignoring the human, such signals usually are misread.

Of more concern to the manager of free-ranging wild elk should be an understanding of the relationship between the quality of the environment and the phenotypic development of ungulates. There is evidence that ungulates from different environments develop not only morphologically into different phenotypes, but also behaviorally. In general, luxurious body development is linked with good feed, a luxurious (diverse, frequent, intense) social behavior, and a high reproductive rate. Therefore, there is a distinct possibility of reading from the body condition, behavior, and reproductive rate of the animals the kind of environmental conditions they are experiencing. Elk in an expanding, dispersing population look and possibly act quite differently from those in a stable, overcrowded population. A knowledge of condition and behavior would help not only to round out the picture, but even more importantly to permit quantitative monitoring without the need to remove individual animals from the population to obtain data. This is one practical reason why the relation of behavior to phenotype in elk requires study. That phenotype shows a great variation among elk populations was shown to be the case by Hutton (1972), who questioned the present subspecific taxonomy. He showed that the variation in elk skulls among populations was largely of the type with which animal scientists are familiar and which can be produced experimentally by changing nutrition.

The concept that males and females search out somewhat different habitats throws doubt on the notion that a reduction of males in a population will lead to expansion of the female segment. This idea is predicated on the assumption that male and female elk have identical habitat and food preferences. On the basis of present evidence, it is more likely that males withdraw to previously unexploited areas should the female segment of the population increase.

There is reason to be concerned with what elk learn from encounters with humans, a subject covered in part by the broad concept of harassment. Large northern mammals show an amazing capacity both to associate with humans where not hunted or otherwise pursued, and to avoid humans where pursued. Differences in the behavior of elk inside and outside national parks are the result of striking adaptive responses, although this is studied infrequently. There is reason now to consider seriously the question of relocating elk or other wild ungulates from areas traditionally used by the animals. Key areas converted to other activities through water impoundment, mineral extractions, human transportation corridors, and other human developments have to be replaced through habitats designed by resource managers on a space and pattern acceptable to elk. This may include conditioning elk not to enter sanctuaries in response to hunting pressure, to avoid transportation corridors, to leave haystacks alone on ranch lands and to ignore hikers in the back country. It also may include means and ways of increasing the area of use of small elk populations in the hope of expanding those populations.

Improved understanding of the adaptive strategies of elk permits the manager to "read" the population in question, interpret its habitat, and predict the actions of individual elk. Ultimately it makes the manager more knowledgeable, and inevitably leads to better husbandry of elk.

Source Material: "Elk of North America; Ecology and Management" Thomas & Toweill (Stackpole Books)