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Paper No. 56

# Management Implications of Behaviour in the Large Herbivorous Mammals

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## INTRODUCTION

Since man first pursued animals he has been a student of animal behaviour. In all hunting cultures the reputation that arose from success in the hunt and the survival value this brought to the individual, his family or his social unit has been of social and selective importance. The more intimate relationship between man and animals associated with captive rearing and animal husbandry required even more detailed knowledge of animal behaviour.

Thus a substantial part of the knowledge of feral and rural man has concerned itself with such aspects of animal biology as the nature of the foods sought by different species, the daily and seasonal movements of important animals, their response to the presence of man, the ways that their peculiar characteristics could be turned to man's advantage as a hunter. Interest in the roots of wildness and the ways in which the animals' capacity for adaptive behaviour and learning could be used to train animals to man's use required much more detailed understanding of health and disease, of nutrition and nurture, of response to impoundment and many other features of the behaviour of the relatively small group of animals that were domesticated.

Understanding of these attributes of animals, empirically gained by early man, was adequate to the needs of human density at that time. The application of the methodology of science, however, has greatly expanded the sophistication of our understanding and has distributed it over a much wider spectrum of animals. This increased understanding has been accompanied by a growing concern for the plight of many species whose survival is threatened by burgeoning human population.

Despite rapid extension of our knowledge of animal behaviour over the last thirty years, our understanding is still fragmentary and still involves only a small fraction of the larger mammals.

Central themes are now discernible, but the extension of our inquiry to a wider group of species is revealing an increasingly complex series of variations upon these themes.

The purpose of this review is to focus attention on the many behavioural features of ungulate mammals, reported to this Symposium, that have direct or indirect potential for improving our management of large wild herbivores.

I will review these under the following headings:

1. Strategies of range occupancy
   (a) Variations on the themes of territoriality, home range and nomadism
   (b) Special requirements and their influence on distribution
   (c) Social constraints upon density
2. Behaviour of neonates in relation to dam and physical environment
3. Feed selection and interspecies compatibility
4. Response to physical alteration of the environment by man
5. Tameability and controlability
6. Social constraints upon harvest and management
   (a) The role of the aged in the maintenance of tradition
   (b) The role of the separate senses in establishing critical distance

(c) Structure and dependence relationships within groups
(d) Sex ratios and reproductive efficiency

7. Behaviour and techniques of research

8. Behavioural constraints upon non-consumptive use.

While it is obvious that understanding of the finest details of the behaviour of animals we seek to manage may be the key to success in our efforts, one must nevertheless recognize the limitations of this knowledge. The order of priority for large mammal conservation must recognize as fundamental a place to live that provides the specific needs in food, water, shelter and special facilities, and, as well, protection from overkill.

As long as agriculture removes living space, war destroys habitat and decimates wild stock, as well described by Mendelssohn (Vol. 2 of these Proceedings, Paper 40, p. 722 ff.) referring to gazelles in Israel, or the developers have free run of natural areas, behavioural data have little to contribute to conservation.

If, however, societal affairs are orderly, if peace prevails; if we recognize the important place of these creatures in the human environment and have as our goals to optimize production, to restore species locally extinct, to ensure that viable populations exist even if only on small refuges, then behavioural information is most useful.

## 1. STRATEGIES OF RANGE OCCUPANCY

### (a) Variations on the themes of territoriality, home range and nomadism

The least formalized strategy of range use would be random movement throughout the year by both sexes and all ages. However, few ranges are sufficiently homogeneous or few species sufficiently adaptable to make this type of strategy a useful one in their adaptive repertoire. Some populations of African elephants, as described by Laws (Vol. 2, Paper 26, p. 9), come close to this pattern but only where water is widely distributed and feed is evenly dispersed. Here the nomadic unit is of two types: the lone male or small group; and the matriarchal family unit of five or more individuals probably related to the senior female.

The difference between herd nomadism and migration are important in several respects. Both are probably strategies designed to make use of regions where the adequacy of resources varies seasonally or from year to year, in ways which make possible the survival of a larger population by a moving pattern of use rather than a sedentary one under which maximum population would be determined by capacity at the time when the limiting resource is minimal.

Many northern ungulates are seasonally migratory—most wild sheep populations, wapiti (*Cervus elaphus*), moose (*Alces*) and odocoileine deer in mountainous terrain, as well as pronghorn (*Antilocapra*) and saiga (*Saiga*). In most of these, population units have well-defined seasonal ranges and move between them in a predictable way. In all of them the winter range is the scarce resource and all that have access to mountains evince acrophilia, which leads them to remain at the highest possible altitude on the winter range slopes. This behaviour is most strongly evinced by the males and in them is one feature leading to a higher mortality rate.

The caribou and reindeer (*Rangifer*) populations of the tundra and subtundra areas also are migratory, but the degree of attachment to the same winter ranges appears to be less precise. It might be said that some Arctic *Rangifer* populations are nomadic within vast but discrete ranges, each serving one or more panmictic herds but with little interchange between herds on adjacent ranges (Bergerud, Vol. 2, Paper 29, p. 552; Kelsall, 1968). This pattern of herd definition and range use can lead to great differences in age structure, turnover rate and population trend on adjacent areas of approximately identical carrying capacity. There is nothing in the behaviour of the caribou to suggest that it has ever departed from this pattern.
The arid lands of Africa also have nomadic components, as for instance the oryx (*oryx spp.*), wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*), the plains zebra (*Equus burchelli*) and the Thomson's gazelle (*Gazella thomsoni*). On the plains



of East Africa where these species abound, rains while seasonably predictable are local (Bell, 1971). This feature has led the migratory plains game to follow the rains, moving with the seasons from grassy plains to open savannah and forest edge by traditional routes modified to make use of precise localities where rain has fallen in amounts sufficient to stimulate new plant growth. There are features in the behaviour of both wildebeest and Thomson's gazelle that suggest that these species descended from more sedentary ancestors. I refer, in particular, to the transitory male territories set up quickly whenever the herd pauses. In all of the species mentioned there are sedentary populations where conditions permit.

Comparable seasonal influences in Ceylon have produced a similar pattern of movement in the Asian elephant (*Elephas maximus*), as shown by McKay and Eisenberg (Vol. 2, Paper 39, p. 708).

The oryx and eland are probably more truly nomadic than the other species mentioned, as they are less dependent upon free water. The latter indeed is probably the most highly evolved socially of the African antelopes, in that it is alone in substituting male rank hierarchy for territoriality in any of its forms (Estes, Vol. 1, Paper 8, p. 183). This gives the eland unique advantages in game ranching, as it more nearly corresponds to cattle in behaviour and thus presents opportunity for somewhat similar management.

Obviously, species with migratory-cum-nomadic habits require ranges of very large size. In addition, the area must include the seasonal components and opportunities without which the herds cannot survive. Management of such species therefore imposes unique demands that require new patterns of range allocation such as the preservation of migration corridors connecting areas of seasonal importance.

The American bison (*Bison bison*) is an example of a species that has been totally displaced from its former range by man. It survives only as protected 'specimen' herds.

The zebras (*Equus burchelli* and *E. zebra*) are probably unique in being nomadic but harem forming.

A number of species are described as evincing male territoriality closely similar to that characteristic of many species of passeriform birds. The territory is breeding ground and feeding ground for the incumbent male either through the breeding season, if there is such, or throughout the year.

The white rhinoceros (*Ceratotherium simum*) (Owen-Smith, Vol. 1, Paper 15, p. 341), Defassa waterbuck (*Kobus defassa*) (Spinage, Vol. 2, Paper 33, p. 635), Grévy's (*Equus grevyi*), dik-dik (*Madoqua kirki*), are all in this category. In each of these only the adult males are territorial while the rest of the population roams over the territories of a number of males within a herd home range. In most of these species the subadult males leave the female herd and form groups of their own. Where such occurs the bachelor herds are usually excluded from the male territories and if these represent the choicest environment two consequences arise. First, the bachelor herds are forced into less suitable areas and are likely to experience increased mortality from a number of sources. Secondly, the nursery herds of female and young gain less competitive access to the choicer range areas defended by the territorial males.

Vicuna (*Vicugna vicugna*) and several of the harnessed antelopes form harem groups that occupy territories throughout the year. In all these the young males, and in the vicuna the young of both sexes, are ejected from the territory to become nomadic. The young females either remain with the harem or join another.

The forest-inhabiting duikers (*Cephalophus*) of Africa (Ralls, Vol. 1, Paper 4, p. 114), the small Asian cervids *Muntiacus* and *Tragulus*, and probably the neotropical cervid *Mazama*, have the extreme of territoriality, in which one male and one female occupy and defend an area, or each sex occupies and defends a territory against others of its own sex (Eisenberg and McKay, Vol. 2, Paper 30, p. 158). From this the young of both sexes are ejected shortly after weaning.

Estes (Vol. 1, Paper 8, p. 183) states that 29 species (i.e. 42% of the African bovids) are solitary and apparently monogamous. If the territories are larger than the food

resource would permit, species in this category may not be as productive under game ranching circumstances as are herding, polygamous species.

The final variation is the 'lek' form of territoriality discovered and elucidated by the Buechner (Vol. 2, Paper 49, p. 853) in the Uganda kob (*Adenota kob*). In this species only a small proportion of the males are at any one time holders of the small leks that are densely clustered upon traditional breeding grounds. Large herds of mixed age and sex inhabit rangelands centred upon the lek areas. Each of these herds appear to constitute a deme, probably the offspring of the males of that breeding ground. The leks are breeding grounds only, as they are in such lek-holding birds as sharp-tailed grouse (*Perioecetes phasianellus*) and sage grouse (*Centrocercus urophasianus*). All breeding takes place on the leks.

This strategy gives rise to a very select fraction of the males holding leks and from these the females tend to favour only a few as mates. Thus this pattern may provide for highly selected male genetic input.

It has been suggested that the confinement of males within relatively small and sharply-defined territories serves to protect the proestrus females from too much disturbance by over-zealous courting males, (e.g. in *Antilocapra*. see Bromley and Kitchen, Vol. 1, p. 356). This is certainly one of the consequences of territoriality but there is no demonstration of its importance to the species. The ewes in the non-territorial bighorn sheep (*Ovis canadensis*) are herded and harrassed constantly during the day or so prior to estrus, frequently by groups of males. During estrus they are served repeatedly, usually by more than one male, up to as many as 50 times in a 24-hour period (Geist, 1971a), but there is no indication that these are forced services, nor that there is a relationship between amount of disturbance experienced by the female and her subsequent well-being or fecundity.

A number of management constraints arise from each of these strategies of range use. The requirement for male territories or for harem territories appear to be reasonably precise; the boundaries tend to persist over many years in those species that have been studied in this way. Thus if management is directed toward encouraging a maximum density it can probably only succeed when the requirements of a territory are understood and can be manipulated. An important item of information concerns the features that govern minimum area of a territory and this in the long run will govern the predictable attainment.

In general the male territories, because their special requirements are more precise than those of the herd range, are likely to be limiting in the management sense. This will be particularly true of lek-breeders. Thus the male territories will require special protection against take-over for other uses by man, also against frequent disturbance as by hunting, highways or low flying air traffic, or even by tourists. Furthermore it is usually territorial males that fall victim to hunting and poaching.

In the horned ungulates, males approaching senility will possess horns of maximum size. From the standpoint of trophy hunting therefore, the old males, no longer capable of maintaining a territory, will be available and select. Their removal will be of no consequence to the maintenance of the population. It many species, e.g. waterbuck, giant sable, kudu, etc., they are likely to be solitary. Sinclair's finding (Vol. 2, Paper 36, p. 676) that male African buffalo may have a long post-reproductive life, during which they are frequently solitary, indicates that here is a surplus class in the population that can be removed without reducing the productive capacity of the herd. Their removal by hunting will therefore present added recreational challenge and may be done with minimum disturbance to the herd. Removal of a surplus of females will require a different strategy.

Within the ungulate species it is possible to recognize two categories upon the basis of the pattern of dispersal of young. Some species, usually solitary or territorial species, disperse their young. In these the young are vulnerable to many forms of mortality arising from this displacement into habitat that is unsuited to the species or exposed to unusual hazards, such as hunting, poaching, predation or seasonal shortage of feed or water. Even so, the 'dispersers' are constantly providing young to colonize new habitat or to re-enter former range now restored to usefulness. In other words, these species are equipped to respond quickly to new opportunities.



On the other hand, the social species which conserve their young present a more difficult management situation. Re-created range will be slow to re-colonize and the task of re-introduction will bear behavioural limitations peculiar to these species (Geist, 1971a).

### (b) Special requirements and their influence on distribution

Not too much has been reported upon the special requirements of some ungulate species that will to some extent influence distribution and perhaps abundance. Each species has its food preferences, water requirements, its response to the presence or absence of cover. Some species, as the Cape buffalo, are relatively non-specific in their demands for facilities. They are therefore adaptable to many kinds of environments and broadly distributed. The African elephant also has a wide range of tolerance.

Of the rather special requirements only water is amenable to management within the limits of economic strictures. Small springs can be successfully developed to produce large amounts of water through many months or year round. Thus, where a water source is limiting range occupancy, it may be possible to provide it.

At the other extreme, some species such as the red and black lechwes (*Kobus leche*) and reedbuck (*Redunca arundinum*) are closely tied to the reed beds associated with permanent wet land, as are the klipspringer (*Oreotragus*), the mountain goat (*Oreamnos americanus*) and others to rocky terrain. The extent of these special habitat types will serve to set limits on distribution and abundance of such species.

Many migratory herds of barren ground caribou return annually to about the same areas to give birth (Kelsall, 1968). These have been described as having distinctive attributes that apparently attract the parous females. We do not know how essential these areas are to the maintenance of the herd; whether indeed they could as readily give birth somewhere else and are merely following a tradition which has lost its importance. Bergerud (Vol. 1, Paper 20, p. 395) makes no mention of special birth facilities required by caribou in Newfoundland. But you do have them for mountain caribou.

Estes (pers. comm.) refers to the important role of termite hills in the feeding regime of the giant sable antelope in Angola. Here the critical element is apparently grass of unusual nutritive content growing in these highly fertilized areas. If this is so, such circumstances could be artificially provided in an area of intensive management, or in an area such as a park or reserve especially dedicated to maintaining the species.

### (c) Social Constraints upon Density

I have already commented upon some of the obvious implications of social organization upon the density achieved by ungulates of different social types.

It is axiomatic that highly territorial species in which males and females acquire and defend fairly large territories will be able to achieve relatively lower densities than species tolerant of crowding. This will not be true if the species has evolved so as to defend a territory only large enough to provide a safe amount of feed for the territory-holder and his family group during years of scarce food. It will be particularly restrictive if the basis of the territory is a scarce resource, such as water, which would provide more than is needed by the territory owner. However, water is usually a common property resource, even among ungulates, and is seldom included in a territory restricted to the exclusive use of the resident male.

Apart from distribution patterns that limit overall density, there are other social influences that are well known in some species of mammals.

Mutual avoidance reaction may be operative in non-territorial ungulates as it is in certain carnivores such as *Felis concolor* (Hornocker, 1969). It may well be involved at the group level in undisturbed African elephants. Feeding behaviour that leads to the avoidance of ground contaminated by urine and excrement reduces the carrying capacity of an area. The extent to which this is operative between species rather than within species has not been reported. If it is usually an intra-species repugnance, we

have here another sound reason for mixed species populations, rather than the encouragement of single species, if high density with maximum utilization of range resources is an objective (Kiley, Vol. 2, Paper 31, p. 606).

A number of unrelated concomitants of population density have emerged. Thus Estes (Vol. 1, Paper 8, p. 183) comments upon the amount of time spent by social species on the 'alert' rather than feeding. In such species, lone animals or those in small groups spend a significantly greater proportion of their time watching and listening for danger than do those in large groups. This could have importance in the nutrition of the animals in low density, dispersed populations.

Markgren (Vol. 2, Paper 42, p. 756) finds that in moose, where the sex ratio is normally closer to 1 : 1 than in deer of the general *Cervus* or *Odocoileus* or *Rangifer* types, only where densities are high can very low proportions of males to females be tolerated without reduced birth rate. In this species the amount of time spent in courtship and pair bonding, along with the highly synchronized estrus, makes wide searching for a mate by either sex impossible. There is, however, suggestive evidence that the North American moose may be more effective in mate search than the moose of Scandinavia. In North America both sexes use advertising calls to extend their contact orbit—a behaviour not found in Scandinavia.

Several behavioural features may act in antagonistic fashion. Thus increased density in social species finds increase in the time spent relaxed rather than alert. On the other hand, there may be an increase in antagonistic behaviour. Beyond an unspecified critical density, numbers may interfere with effective mother-offspring bonding and give rise to ineffective mothering. At the same time the individual young in a large group may be less conspicuous and less subject to predation loss than if alone with its mother or in a small group.

Populations of low density may also suffer the loss of important genetic material and of traditions essential to the effective use of the habitat.

## 2. BEHAVIOUR OF NEONATES IN RELATION TO DAM AND PHYSICAL ENVIRONMENT

In general the newborn young of the large herbivores can be divided roughly into those species which follow the mother very soon after they are born (followers, or *nachfolgen* type) and those that secrete themselves and are visited periodically by their mother (hiders, or *abliegen* type: Walther, 1961, see also Lent, Vol. 1, Paper 1, p. 31). Among the North American species *Odocoileus virginianus* and *hemionus*, *Cervus canadensis*, *Alces*, and *Antilocapra* are among the *abliegen*, while *Bison*, *Ovibos*, *Rangifer*, *Ovis* and *Oreamnos* are follower species.

Lent (Vol. 1, Paper 1, p. 19), in his extensive review of the behaviour associated with birth and the subsequent period of mother-young bonding, has indicated a number of aspects that can have significance to those who seek to manage ungulates in the wild, on game ranches or in captivity.

The need for privacy at time of birth varies, and its significance even to those social species that usually seek it is not well known. In general it can be expected that privacy at birth is probably most important among solitary or semi-solitary species and least in such highly-mobile dense-herding kinds as American bison, wildebeest or barren ground caribou. The critical issue is the amount of time needed to establish a firm bond between the mother and her newborn. The establishment of mutual recognition, the initiation of appropriate following or joining behaviour, nursing and other forms of mutual response, involves the full catalogue of sensory input and steady reinforcement through a critical period. If this opportunity is denied through overcrowding with loss of privacy, through harrassment by predators, tourists, air or ground traffic, there is likely to be an increased incidence of desertion, of inadequate recognition by either mother or newborn of the other, inappropriate nursing behaviour, inhibited milk flow or other forms of maladjustment, the end product of which will be increased loss of the young. The bond is more rapidly formed by the mother than her offspring, and more effectively by the experienced female than by the primiparous one. However, it is the time required by the slower partner of the learner pair that must govern the conditions provided.



There is a possibility also that a female which has failed to establish a satisfactory bond with her newborn on 2 or 3 successive births may be permanently impaired and thus removed from the production pool of the population (Kiley, Vol. 2, Paper 31, p. 603). All these considerations point to the importance of constraints when one plans for situations in which ungulates are exposed to man-made disturbance. If the births are usually concentrated in special time and places, as they are in caribou, protection can be focused appropriately. Where there is a diffuse season of birth, though the danger of major interference with the reproductive input of an entire herd as a consequence of local and time concentrated disturbance is less, the problem of how to provide adequate privacy will extend over a longer time and may require some restriction of access on the part of tourists, to provide for a planned sequence or 'ribbon of sanctuary areas' available throughout the entire period of birth.

The essential period of private contact between mother and young (the 'critical period') may be as short as 5 minutes (goat) or 45 minutes (Grant's gazelle), one hour in caribou (Lent, Vol. 1, Paper 1, p. 38), or as long as six hours in *Antilocapra* (Prenzlow, 1964); thus detailed information on the species specific characteristics of the neonate period can be important to intensive management. Musk ox seem particularly vulnerable to disturbance at this time of birth, as a consequence of their prolonged critical period.

The amount of disturbance tolerable after the critical period but during the hiding period, of species with this habit, has not been studied but could be important. This may be of special concern in species with a very long period before the young begin following their mothers. This may extend over three or four months in some of the antelopes (Lent, Vol. 1, Paper 1, p. 25).

## 3. FEED SELECTION AND INTERSPECIES COMPATIBILITY

Few of the presentations to this symposium deal with the feed selection of different species co-inhabiting the same ranges. Selection of feed plants and parts of plants has been the subject of several other studies. Cowan (1943) has referred to the degree of feed separation evinced by bighorn, Rocky Mountain goat, caribou, moose and black-tailed deer in the Rocky Mountains of Alberta and British Columbia. He revealed essential compatibility on joint use of large areas. At the same time the elk or wapiti is known to have extensive overlap in feed selection and habitat occupancy with all these species.

The ungulates of Africa, by virtue of their very long period of evolution in multi-species associations, are more specialists in their feed selection (Casebeer and Ross, 1970), and consequently lend themselves to a greater variety of compatible co-occupancy of given areas of rangeland. At the same time, designing for efficient range use in the African region requires more detailed information and more refined planning, in terms of the species mix and the relative number of each component, than in more youthful biomes.

As an example of the successful application of the species mix technique in the operation of a game ranch, Johnstone (Vol. 2, paper 52, p. 890) lists 17 species of big game managed for meat and trophy production on a 57,000-acre ranch in Rhodesia. It is anticipated that 10% cropping per annum will be the sustaining rate. That should yield about 21 lbs of meat per acre, a yield well in excess of the production when the same area was managed for cattle.

Deane and Feely (Vol. 2, Paper 51, p. 882) describe a similar strategy of multi-species stock on a 2,700-acre ranch. Here 14 big-game species are used to provide a dramatic example of the potential compatibility of many species on even small areas. It is doubtful whether the selection of species was done on the basis of information upon plant food selection by the wild species to be used. However, the mix is stated to be more productive than the usual monoculture of domestic livestock. The total yield of game meat after 5 years of management is 12-14 lbs per acre. This is the product of a biomass of just over 100,000 lbs per square mile, where 60,000 lbs is sought as a long-term average.

## 4. RESPONSE TO PHYSICAL ALTERATION OF THE ENVIRONMENT BY MAN

Bergerud (Vol. 2, Paper 29, p. 559) with specific reference to free-ranging caribou, suggests that the behavioural repertoire contains elements that are relatively fixed responses to such stimuli as the arrival of a hunting man or of a traditional predator (wolves). Such responses he regards as of ontogenetic origin and relatively automatic. Other elements of behaviour are generalized responses to environmental stimuli that are changeable and demand an adaptable response mechanism. The latter involves learning and provides for behavioural adaptation to new situations. Examined against this hypothesis most species appear to possess components of their environmentally induced responses falling into both of these categories.

Bergerud further suggests that appreciation of the category of the response can provide a basis for predicting the probable reaction of a species to the presence of man and such artifacts as roads, railroads, aircraft and automobiles. As stated by him: 'The seriousness of human disturbance should be considered in the light of the perceptive and escape adaptations caribou have evolved in association with wolves. For example, a road or a building are not factors that have been prior phylogenic contingencies'. He points out that caribou have no aversion to roads, respond by temporary alert to the noise of a car, but flee from the motion of a car. Similarly low-flying aircraft and helicopters provide alarming motion but the noise of high-flying aircraft does not. Klein (1971) also comments on the response of caribou to unusual stimuli. In addition to motion he found caribou to evince alarm in the presence of overhead electric power lines and to avoid crossing bridges. In the latter instance it may be that the hollow sound may be similar to that of thin ice and thus elicits the avoidance response appropriate.

Tourists in the African National Parks will have noted the lack of response to automobiles by most large wildlife. I suggest that this results from the similarity between size and shape of the automobile and their evolutionary companion, the rhinoceros. Where cars are used by hunters to approach game, a learned response is developed.

Johnstone and Deane and Feely (Vol. 2, Papers 52 and 51) have commented upon the problem of shooting game for butchering on game ranches and suggest that night shooting with powerful lights prevents the development of a learned flight response to the presence of automobiles.

There are few species that do not learn to flee at long distance from man where shooting of large mammals is prevalent. Bergerud (Vol. 2, Paper 29, p. 579) suggests that caribou are vulnerable to hunting because of their innate curiosity and of a failure to detect and to flee from a stationary man any more than from a stationary wolf. They do learn quickly to respond to human odour.

Few, if any, wild ungulates learn to respond appropriately to altered natural features that have acquired dangerous characteristics in the alteration. Thus deer and other species attempt to swim irrigation ditches as they would rivers and drown when unable to climb out; moose populations confronted with a newly-flooded reservoir across their migration route will attempt to swim it and drown, due to the debris that litters the shoreline. Where such modified natural features are entered into an environment, care should be exercised to include also recognizable signals of the hazard: drift fences to direct moving animals away from the danger area, or escape facilities incorporating clues designed to lead the animals into the appropriate recognition and response.

The expanding search for fossil fuels and the resulting demand for the construction of pipelines through the wilderness range of barren ground caribou in Alaska and Canada, are already demonstrating the need for meticulous studies of the behaviour of this species. Child (Vol. 2, Paper 46; p. 805) reports preliminary observations of caribou and reindeer in contact with various types of simulated pipelines. It is not unexpected that these animals avoid the strange artifacts and often refuse to go either over or under them despite the provision of apparently suitable opportunity.

More recently, I have seen individual caribou and small groups that have become accustomed to these pipelines and use underpasses freely. They seem to cross over only if they can see over. It is tempting to suggest that ways can be devised to train, or lead caribou herds to pass both over and under pipelines without delay, but the techniques have not yet been devised. Perhaps the restoration of main caribou trails across the disturbed area, the scattering of dung or urine or the scent from the leg glands might serve to allay fears. Identification of the criteria that identify caribou travelways to the animals and the introduction of these into the disturbed area, all offer potential solutions.



I have seen no references to the role of such major artifacts as pipelines in the reduction of populations of large mammals of the desert areas of the Middle East.

In considering the impact of major artifacts (highways, pipelines, electric power lines) into the range of the large wild ungulates of open landscapes, one is concerned not only with the outright obstruction of normal movement of the population, deflection away from important resources or denial of access to part of the normal range. Of equal concern is delay, induced even where the animals sooner or later negotiate the obstruction. Delay and disturbance can have an important effect upon the energy budget of animals (Geist, 1971a).

Some of the real but subtle consequences of disturbance are to be seen in the observations of Baskin (Vol. 2, Paper 27, p. 530), Kiley (Vol. 2, Paper 603) and Gauthier-Pilters (Vol. 2, Paper 28, p. 542) that unguarded herds of reindeer, sheep and camels respectively are in better 'condition' than herds under the direct control of men. Herding apparently causes disruption of feeding, resting and ruminating. It may increase the intake of poisonous plants and reduce grazing selectivity (Kiley, Vol. 2, Paper 31, p. 607. Furthermore, this author observes that even mild harassment in domestic herds increases fighting, hypersexual mounting and wounding, and depresses milk production. She emphasizes that an occasional loud noise is more disturbing than frequent predictable loud noises.

Vincent (Vol. 2, Paper 54, p. 907) reports from South Africa that stress imposed on wild adult females during late pregnancy led to serious losses of adult and newborn animals. The stress was associated with live capturing.

All these studies point to the general principle that optimum utilization of a habitat, and optimum production from a population, can only be realized in a known and predictable social and physical environment. The introduction of a wide variety of surprises induces avoidance reactions and excitability. These lead to greater energy demands and inefficient use of habitat (Geist, 1970b).

From this viewpoint certain management objectives for National Parks become obvious. For instance, it is important to habituate the animals to people, to normal transportation vehicles and other potentially disturbing things. To encourage wilderness is to arrange for inefficient range use.

It is equally important not to introduce new sources of disturbance. This is of particular concern during periods of the year when food is scarce and energy demands high as they may be during northern winters. One thinks of snowmobiles or other O.R.V's in National Park or game refuges, as a case in point, even if used only by wardens.

## 5. TAMEABILITY AND CONTROLABILITY

Even though wildness is known in some species to be a heritable characteristic (Leopold, 1944), many if not all species of big game can learn to accept man as a harmless associate. Indeed, Parker and Graham (1971) make the point that wild ungulates can live in proximity to man, if man permits. The problem then is one of human behaviour. There is no comment upon this feature by any of those contributing to the present symposium, but Geist (1971b) dwells on the point at length.

Hand-reared young of most species, if not all, learn to 'imprint' upon man and to evince no fear of him; they may indeed become highly aggressive toward him, or court him. This capacity to learn to accept the near presence of man without alarm is different from the capacity to adapt to the close contact situations of domestication, including herding, haltering, harnessing, saddling, packing or milking. There must be a wealth of experience with this feature of African ungulates that is unrecorded. It

is well-known that the Indian elephant quickly adapts to domestication, while the African elephant is reputed to be less amenable. Eland are reported to domesticate fully, permitting haltering and milking. Plains zebra have been trained to harness. I have no success in persuading Odocoileine deer to accept the halter and to be led by it; on the other hand, *Rangifer* responds quickly and *Alces* (Heptner and Nasimovic, 1968) may do so but only in experienced hands.

Gilbert (Vol. 1, Paper 11, p. 247), in his account of the influence of foster rearing of young fallow deer (*Dama*) upon the behaviour of these individuals as adults, remarks that young foster-reared or completely domestic goats were still wild toward man. My experiments with the rearing of newborn wild-taken, black-tail and white-tail deer support this finding. Young raised by hand-reared and completely docile females remained almost as wild as wild deer, whereas fresh caught young, hand-reared, became docile, though with marked individual and racial differences. Clearly there is, in some species, a major element of inherited wildness which is modified by experience.

Another aspect of this topic is the extent to which the young of different species will submit quietly to physical restraint—such as being carried. From experience with a limited variety of species, I am tempted to suggest that the 'hider' species will permit restraint during the hiding phase but not after that, even when imprinted on man. I would expect the 'follower' species to resist handling from birth.

Early in human history, man discovered that certain species could be easily impounded or directed toward traps or slaughter areas. Mendelssohn (Vol. 2, Paper 40, p. 725) reports this as part of the Bedouin attack on the gazelles (*Gazella dorcas*, *G. subgutterosa* and *G. gazella*). Similar techniques were used in parts of arctic North America with the barren ground caribou and doubtless by other peoples to capture a variety of species. This may well have been one beginning of paddock rearing.

It may be that domesticability, as with zoo breeding, rests upon the selection of rare behavioural genotypes from within a population heterozygous for wildness, and cultivating these for man's use. Research on this aspect of wild-living large ungulates merits further attention, in view of the growing interest in cultivating wild species for the more efficient use of rangelands.

Apart from tameability, the response of wild species to fences or other means of directing or confining populations is important at some levels of management. This aspect of behaviour is still largely known at the empirical level. Jumpers, such as Odocoileine deer and impala, are more difficult to confine than caribou, muskox, pronghorn antelope and other species which seldom jump. The response of various species to such abnormal experiences as electric fences has been recorded for few large mammals, though there is a wealth of zoo experience.

## 6. SOCIAL CONSTRAINTS UPON HARVEST AND MANAGEMENT

In parks and reserves, as in game farms, it is important that surplus members in a population be removed with as little disturbance as possible to those that are to remain. It is frequently desirable to be selective in the harvest as for instance to take predominantly young males, in polygamous species, or old males no longer able to maintain a position in the breeding hierarchy.

The behaviour studies reported here contain a number of features that can be used to accomplish these ends of management. There are also behavioural features that must be given serious consideration in the drafting of harvesting plans.

Owen-Smith (Vol. 1, Paper 15, p. 351) suggests maintaining 'vacuum' areas into which the displaced sub-adult white rhinoceros would move and from which they could be removed without disturbing the resident adult animals.

The bachelor herds of oryx, giant sable and other species of similar behaviour offer opportunity for removal of the desired portion of that category, unless they are merely temporary resting herds of otherwise reproductive males. The exact composition of bachelor herds in each species must be known, if the behaviour is of possible use in accomplishing removal of surplus animals.



### (a) The role of the aged in the maintenance of tradition

The general desirability of harvesting predominantly from males where a population experiences heavy predator pressure, should not overlook the need to maintain a proportion of adult males adequate to support the breeding pattern of the species and to assure the preservation of the traditions of the species. Geist (1971a) has indicated the importance of the older members of both sexes as the essential custodians of such traditions as the location of winter and summer ranges, fawning grounds, escape terrain and specially secure areas where infrequent severe weather threatens survival. This is of particular significance in species such as bighorn sheep in which the older males are the preferred trophy.

Bergerud (Vol. 2, Paper 29, p. 570) has documented the importance of tradition in the Newfoundland caribou when he reports that groups of captive reared animals, or of animals captured elsewhere and released into suitable habitat, failed to establish essential patterns of migration.

Another matter of importance that has a behavioural input concerns the design of harvest routines so as to remove animals from each of the harvestable demes or geographical units of the population. Thus in a species such as the Uganda kob, where each male breeding ground has its satellite herd or herds of mixed age and sex (Buechner, Vol. 2, Paper 49, p. 865), if effective reduction of the population is the objective then each of these demes should be included.

Elephant populations present unique constraints. Laws (Vol. 2, Paper 26, p. 520) maintains that the most effective technique to be used in a reduction programme is one that concentrates on the killing of entire matriarchal groups. In this way there is no dissemination of 'wildness' through the remaining population which would arise if there were experienced survivors of these family parties. He points out that where indiscriminate shooting of elephant has been practised, the results can be seen in the development of large herds of very wild animals which are difficult to control and can cause damage disproportionate to the size of the population.

Yet another constraint is the previously mentioned requirement to protect the female with a newborn young from disturbance that will impair the bonding between the two. Furthermore, we have little evidence to reveal the success of orphans in growing up and establishing themselves as fully-equipped members of their 'society'.

Learning and tradition are inescapable when a species enters a new range and, if it is to survive, it must weave together the seasonally-changing feed resources and the alterations in temperature, rainfall and snow accumulation into a viable life style. This becomes of particular importance in the re-introduction of species to areas formerly inhabited successfully. Choice of the genotype to be reintroduced, and careful selection of the most appropriate time of the year and the segment of the range upon which the animals are to be released, are important derivations of this acknowledgment.

One of the areas where behaviour can make a real contribution is in developing species-specific techniques for the reintroduction of species. An excellent illustration of this approach is the experiments reported by Bergerud (Vol. 2, Paper 29, p. 581). In introducing caribou to a new range he used fawns which were led through the area they were to inhabit. Later he added wild fawns which learned the habitat from those already 'introduced' to it. In short, he not only introduced caribou to the area but also introduced the area to the caribou, thus re-creating home range knowledge.

This becomes particularly demanding where the newly transplanted animals must learn to find and to know both a summer range and a winter range in widely separate places. Failure in this is the reason so many re-introductions of bighorn are unsuccessful in establishing new centres of dispersal.

Spinage (Vol. 2, Paper 33), Gauthiers-Pilters (Vol. 2, Paper 28) and Baskin (Vol. 2, Paper 27) write that female waterbuck and camels form a permanent attachment to the birth place of their first calf. Mendelssohn (Vol. 2, Paper 40, p. 736) states that in gazelles it is the gravid females that appear to be the colonizers of new terrain. They go there to fawn and return thereafter. This may be a widespread principle and if so could be made use of in increasing the predictable results of re-introduction or introduction.

Geist (Vol. 1, Paper 10, p. 238) draws an important contrast between species of northern and southern origin in their conversion of vegetation. He points out that the species from areas with great seasonal fluctuation in feed supply will tend to concentrate such biological events as rutting and birth into short periods and to store energy as fat. On the other hand, species from areas of relatively constant carrying capacity will have a more diffuse biological calender and convert feed more generally into protein than to fat. This would be a consideration in the choice of species for game ranching.

**(b) The role of the separate senses in establishing critical distance**

Critical distance, the distance at which animals will flee from stimuli recognized as dangerous, certainly differs between species and upon competing stimuli. A classic example is the strong inherited behaviour of muskox toward wolf-like creatures, including sled dogs, that so many hunters have used to permit themselves to get close to the animals while hunting them.

Deane and Feely (Vol. 2, Paper 51, p. 885) comment on the importance of presenting the automobile and man to ranched game in circumstances that will not increase the critical distance. Here reference to the important paper of Parker and Graham (1971) provides many useful data and ideas. If the automobile-man combination becomes a source of alarm, hunting becomes so difficult as to be uneconomical. This thus becomes a limiting factor in the economics of game ranching.

Dean and Feely emphasize that it is important to restrict hunting to short, well spaced intervals. It should be compensated for by harmless activity by day and night. A further concern is the reduced carcass quality caused by fear of man at the time of killing.

In most of the open-ground ungulates discussed in this symposium, it is inferred that vision is the primary initiator of alarm reaction. There are no studies specifically directed to exploration of the relative importance of sight, hearing and olfaction in modifying behaviour. The successful management of a variety of species can be influenced importantly by such information adapted to management procedures.

**(c) Structure and dependence relationships within groups**

All the major constraints in this category have been referred to already in other contexts. The need to protect the mother and neonate from disturbance; the uncertain survival status of the orphan; the role of the territorial male in the orderly distribution of the population over its range and the effective reproduction of the herd; the possible role of the male in inducing ovulation at times appropriate to the seasonal cycle in food supply (demonstrated in hogs but perhaps operative in other species also); the role of the harem male plains zebra in defending all members of his harem from attack by predators, are all in this category.

**(d) Sex ratios and reproductive efficiency**

The traditional hunting patterns in North America, more than in most parts of the world, concentrate upon removal of the males. Where trophy hunting is important as a recreational pursuit, the pressure is further concentrated upon the mature or old males. In territorial species these are critical to effective maintenance of the breeding pattern. Furthermore, as stated above, the older animals are the custodians of important traditions. Where males and females occupy different ranges seasonally, as is the case in many northern and mountain species, the loss of tradition by either sex could lead to the failure of the population.

In species such as the moose, where there is prolonged courtship and pair association prior to breeding, the sex ratio required to assure full reproductive participation of the females depends upon density of the population.

Obviously in pair forming monogamous species an even harvest of the two sexes is important and techniques that lead to a differential pressure on either sex should be avoided.



## 7. BEHAVIOUR AND THE TECHNIQUES OF RESEARCH

The researcher must be fully aware of all behavioural characteristics of the species he is studying that may contribute to or bias his results. Thus the daily activity of animals, seasonal or local movements and differential distribution of the sexes can bias census or facilitate it. Sex- or age-specific behaviour can alter death rates, as can patterns of territoriality. This can involve displacement of young into vulnerable peripheral habitats and exposure of territorial males to increased predation or greatly increased energy demands.

Many studies now require the marking of individual animals for later recognition. Plainly marking of newborn young can have two possible consequences that may endanger survival. One is the inhibition of appropriate bonding between mother and young, both by the disturbance itself and by the introduction of man odour and a strange device (the tag) into the sensitive relationship. Such considerations should enter into the decisions concerning when, during the critical period, the operation should take place. Ideally it should be postponed until this period is complete and the bond likely to be well established.

Elsewhere in this review I have commented upon the great differences between different wild ungulates in their amenability to restraint and handling. These differences can be important in the selection of a species for a specific research study.

## 8. BEHAVIOURAL CONSTRAINTS UPON NON-CONSUMPTIVE USE

One of the most rapidly increasing uses of wildlife is tourism or the study of wild creatures as a hobby. Inasmuch as all such man-animal contacts are potential sources of disturbance, some cautions can be derived from the studies reported here. Of first importance is protection of the mother with newborn young from disturbance (Lent, Vol. 1, Paper 1, p. 44).

Another constraint arises from the desirability of protecting the traditional breeding grounds of such lek-species as the Uganda kob, that may be easily accessible, from frequent disturbance by tourists that could lead to its abandonment and the loss of the satellite population.

Similarly, the searching out of the concealed young of *abliegen* species can lead to their exposure to added predation dangers. Such problems suggest a need to proscribe some areas where young are traditionally born and concealed, and even to limit the territory of automobile use in park areas to the roadways or to buses operated by the unit rather that private or hire vehicles. Intensive use of some areas by car-driving tourists is inducing erosion and reducing carrying capacity of the ranges.

I refer again to my remarks earlier in this paper about the need to habituate animals to people and the artifacts that normally accompany people. It is equally urgent to introduce people to animals in park areas. Where animals are accustomed to people it is important that people behave so as to be readily recognizable as such. The quadrupedal sneak attempted by some observers and would-be photographers makes the individual more like a predator than a man and introduces disturbance, to the detriment of both participants.

In general the papers presented to this symposium reconfirm the principle that animals strive to live in a predictable habitat and when this is altered in any way react in a manner likely to restore predictability. A thorough knowledge of species-specific behaviour allows the manager to adjust management practices to fit his objectives. Unfortunately these objectives are seldom stated in precise terms. Only when there are clearly stated objectives for conservation of wildlife in National Parks, for sport hunting, for game ranching or in the search for solutions to the conflict between wildlife and industry, can full advantage be taken of existing knowledge of animal behaviour. Only then, also, can the research be designed to extract new knowledge.

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