

BEAR MANAGEMENT AND SHEEP HUSBANDRY IN NORWAY, WITH A DISCUSSION OF PREDATORY BEHAVIOR SIGNIFICANT FOR EVALUATION OF LIVESTOCK LOSSES

IVAR MYSTERUD, Zoological Institute, University of Oslo, Postbox 1050, Blindern, Oslo 3, Norway

Abstract: During the 19th century the brown bear (*Ursus arctos*) population in Norway was reduced to remnant level. The population has since been restored and recently seems to be increasing. Concern is present for bear management in connection with sheep predation, as sheep husbandry is important throughout Norway, the stock in 1976 amounting to 1.6 million animals. The management technique now practiced combines selective hunting of troublemakers with monetary compensation for sheep killed.

The number of sheep killed by bears is insignificant compared with the total sheep mortality, and bear predation is important only locally, primarily in areas in Hedmark, Hordaland, and Finnmark counties. Ethical arguments against bears are raised in connection with observations of overkill, and a research program has been initiated to analyze predation patterns in greater detail.

Overkill by bears is not restricted to surplus killing. In most cases, small amounts are consumed from each carcass — nutritionally valuable parts such as breast fat deposits and udders. This behavior may represent extreme food selection under plentiful prey conditions and should be compared with selective grazing among herbivores. The organization of behavior in predatory mammals relevant to livestock losses is discussed.

Several grazing techniques and herding systems have been adapted to the Scandinavian forest and mountain ecosystems and are typical of vast areas covered with moraine deposits and mineral soils. During the Middle Ages, highly differentiated chalet systems were already organized in Norway, keeping and rotating herds of grazing animals under the protection of herdsmen far out in wilderness areas.

Predation by the brown bear and other large carnivores represents a traditional conflict in Norway. Bear and sheep may compete for space and plant biomass in outlying grazing areas, and the bear can become an efficient predator on sheep. Large predators have certainly been influential in the development of the chalet culture in Scandinavia; danger of predation was an important consideration when choosing localities for new chalet farms. Reinton (1955), in studies of the chalet culture in Norway, claimed that many chalet barns were originally built equally as defense against bears and as protection from inclement weather. Disproportionately strong doors and locks were distinctive features of such buildings. The practice of allowing animals to graze at night, periodically common on the European continent, was seldom practiced in Scandinavia, due, in part, to the danger of predation (Szabó 1970). Some claim that the earlier herding system in Norway was originally developed for the sole purpose of protecting livestock from predators. Most herding of livestock ceased in Norway when the numbers of predators gradually decreased in the outlying grazing areas.

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PRESENT STATUS OF SHEEP FARMING

Commercial sheep husbandry in Norway has remained small in scale, and even today small herds of sheep are kept mostly by individual farmers. Flocks of sheep are introduced without herdsmen into grazing lands, many of which are topographically rough, and most flocks are tended at rather irregular intervals. Total stock figures show the development of sheep farming in Norway from 1940 to 1976 (Fig. 1). During the war the number was kept low and figures ranges

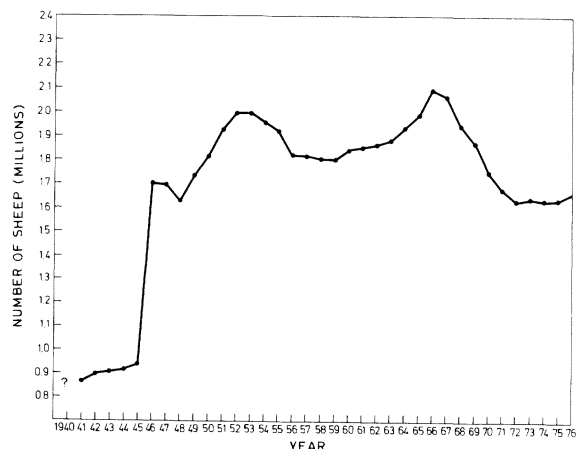


Fig. 1. Total numbers of sheep present in Norway on 20 June each year, 1940-76.

between 0.8 and 1.0 million. Postwar, however, the stock increased to 1.7 million, and since then the number has fluctuated between 1.6 and 2.1 million, with peaks during 1950-55 and 1964-68. In the 1970s, the stock remained at about 1.6 million animals, but is now increasing. The 1976 total was 1,667,488, whereas the 1974 and 1975 figures were 1,632,217 and 1,639,313, respectively, an increase of 2 percent in the latter years.

At present, agricultural experts advocate the economic policy of increasing sheep production in Norway. A prognosis for 1990 predicts 1,993,000 animals. One of the national goals is to reduce the importation of certain meat products and fodder, thus becoming more self-sufficient through better utilization of national resources. There are few ecological or biological arguments against a strategy of self-support, which includes increasing use of local outlying grazing areas above the present level of sheep production.

LOSSES AND COMPENSATIONS

Sheep losses compensated for as bear depredations in Norway during 1966-75 are shown in Table 1. As can be seen, the yearly compensated loss fluctuated between 30 and 240 animals. The losses are presently small in relation to the total sheep stock. Sheep losses are, however, generally restricted to certain small areas, the most important found in Finnmark (Wikan 1970, 1972), Hordaland (Elgmork and Mysterud 1976), and Hedmark (Myrberget 1968; Mysterud 1974, 1975a, 1975b) counties. Some losses also occur in Oppland and Buskerud (Elgmork 1976b), Sør Trøndelag, Nordland, and Troms counties. Economic compensation, which does not represent actual market value, is awarded for sheep that can be documented as

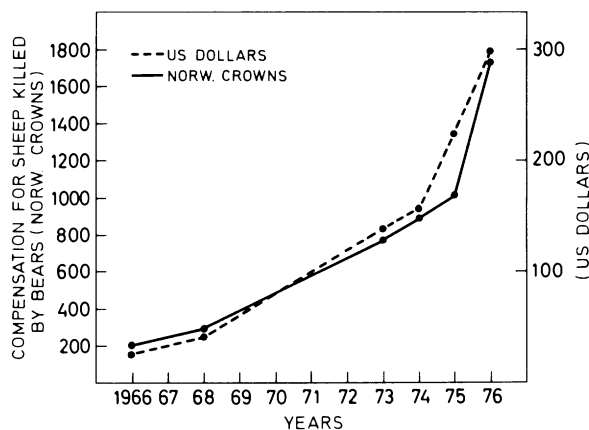


Fig. 2. Economic compensation awarded per sheep for ewes killed by brown bears in Hedmark County, 1966-76. Amounts given are in Norwegian crowns (solid line). U.S. dollar equivalents (stippled line) are based on current exchange values.

killed by bears. Fig. 2 gives some examples of calculated prices per sheep for ewes killed in Hedmark county in recent years.

One way to influence sheep producers in a positive direction has thus been to adequately compensate their economic losses. A future strategy could be to increase this compensation to profit level.

STATUS OF THE BEAR POPULATIONS

From an original population consisting of several thousand animals, the brown bear was relentlessly shot in Norway during the 18th and 19th centuries and reduced to a remnant level. The approximate annual kill around 1850 averaged 225 individuals. Hunting statistics indicate a steady population decline from 1850 to 1925 throughout the country (Myrberget 1969). By the beginning of the 20th century, the population had been

Table 1. Numbers of sheep compensated for as being killed by bears, by county, in Norway, 1966-75.

Year	Counties									Total
	Hedmark	Oppland	Buskerud	Hordaland	Sør-Trøndelag	Nord-Trøndelag	Nordland	Troms	Finnmark	
1966	39	4	4	0	190	0	0	0	0	237
1967	12	5	0	0	0	0	0	0	78	95
1968	40	6	0	0	0	0	0	0	122	168
1969	0	0	17	0	0	0	0	0	58	75
1970	0	6	3	0	0	0	0	0	26	35
1971	0	0	18	0	0	0	0	0	51	69
1972	0	0	19	0	32	0	0	0	0	51
1973	63	0	21	0	0	0	0	3	0	87
1974	32	0	0	31	0	0	117	0	0	180
1975	48	5	0	69	0	13	0	0	87	222
Total	234	26	82	100	222	13	117	3	422	1,219

greatly reduced, and between 1920 and 1930 it was at a minimum. In about 1940, Olstad (1945) believed that resident populations were present only in the Vassfaret area in Oppland and Buskerud counties (Elgmork 1976a) and in South-Varanger in Finnmark. However, recent investigations have shown that remnant populations have also survived in other areas (Mysterud 1977). Myrberget (1969) estimated the population at 25-50 animals in 1969, but it must now be roughly estimated at more than 100 individuals. Decreasing trends have changed during the latter half of the 20th century, and the populations now seem to have entered a period of increase. The total number of bears killed has remained at a stable level since 1940; the distribution of the kill by counties is shown in Table 2. Since

removal to solve the problem of stock-killers. The technique now being tested includes shooting only troublemakers through ordinary hunting — careful removal of predatory bears at the time and place of the problem, preferably only the individual actually involved. The removal of troublemakers is undertaken by small groups of hunters from the local areas who are paid for their efforts by the federal government. The personnel of each hunting group is selected by the local game management unit and approved by the wildlife administration. The hunters are not professionals, but hunt only when stock-killers appear in their area.

In 1968, 1969, and 1970, permits to remove stock-killers during the protected period prior to 15 June were given to Sør-Varanger municipality, Finnmark

Table 2. Hunting statistics for brown bears in Norway, 1940-76. (Based partly on Myrberget 1969.)

Years	Counties										Total
	Hedmark	Oppland	Buskerud	Telemark	Sogn og Fjordane	Sør-Trøndelag	Nord-Trøndelag	Nordland	Troms	Finnmark	
1940-49	2	1	4	1	1	0	2	4	0	1	16
1950-59	4	0	1	0	1	0	2	10	0	5	23
1960-69	5	0	0	0	0	1	1	3	0	11	21
1970-76	2	0	0	0	0	0	1	0	2	6	11
Total	13	1	5	1	2	1	6	17	2	23	71

1970, 11 bears have been removed from the populations. Methods of removal include legal hunting (3), shooting of stock-killers (4), self-defense killing (1), and poaching (3).

PROTECTION AND MANAGEMENT OF BEARS

Since 1940, measures to protect the brown bear have been as follows: During 1940-41, the species was protected during the denning period from 1 November to 15 May. During World War II, 1942-45, bears were given total protection. After the war, the protection was removed except for the period 1 November-15 May. In 1966, this protection was extended to 15 June in Troms and Finnmark counties, primarily to prevent hunting with snowscooters (Myrberget 1969). On 28 May 1971, the bear was given total protection in Oppland and Buskerud counties, but not until 11 May 1973 was the species given total protection throughout the country. It is legal, however, to kill bears attacking humans and livestock, regardless of protection laws.

A significant political pressure for removal of bears stills emanates from interests connected with sheep and reindeer (*Rangifer tarandus*) husbandry. The federal wildlife administration is attempting to use selective

County, and 1 bear was shot in 1968. During 1973, total protection was enacted and the first permit to remove a stock-killing bear was issued in Trysil, Hedmark County, where a subadult male was shot (Mysterud 1975b). In 1975, Trysil municipality was given a new permit, but no bear was killed. In 1976, 11 permits to remove 8 different bears were issued in 8 municipalities in Hedmark (8), Sør-Trøndelag (2), and Finnmark (1) counties. Seventeen hunting groups were formed, 2 in municipalities which did not receive permits. One subadult male was shot in Trysil municipality by the collective efforts of the 15 hunting groups that were in operation. Thus, only 3 bears have been removed by authorized hunters during the period 1968-76; this low efficiency has led to a discussion on different bear-hunting techniques. Removal of specific killers is considered the most selective and efficient means of contending with the predator problem (Cain et al. 1972), and it will be important to develop an efficient strategy for future removal of troublemakers. In spite of the acknowledged hazards to livestock, opinion polls, even from counties with the greatest losses of sheep, show that a majority are in favor of preserving a bear population.

SHEEP-KILLING PATTERNS OBSERVED IN BEARS

Much more data are needed from detailed studies of which individual bears develop into stock-killers before we can evaluate the long-term consequences of their removal from the population. Hedmark County, where the bear population has long been notorious for killing sheep and where some damage to sheep flocks is more or less constant (Mysterud 1975a), has been selected for studies, and data on sheep-killing bears have been collected since 1968 (Mysterud 1974, 1975b, unpublished data). The investigations so far have shown that sheep predation incidents in the area can be roughly grouped into 3 categories:

- (1) Sheep killed by adult male bears and used as a regular food source by the male and/or associated family group resident on or near sheep grazing pastures.
- (2) Sheep killed, often in numbers, by subadult males that have established home ranges on the grazing areas. Such individuals may develop into habitual sheep-killers and troublemakers.
- (3) Occasional sheep killed by straggling or transient bears, most often of little significant to the total kill.

Field observation of predation patterns in the study area has shown that the usual pattern of bear predation is that 1 or a few sheep are killed at a time and are either consumed or cached for future consumption. However, situations can arise in the outlying grazing areas where a number of sheep are killed within a relatively limited time and space. In 1 case from Hedmark, 26 of a herd of 28 sheep were killed during 1 night. Other overkill incidents occurred in 1973 and 1976 (Mysterud 1975b, unpublished data). The number of sheep struck down by the predator, in some cases clearly exceeding the immediate or short-term need for prey biomass, and multiple kills and unconsumed carcasses seem to be reported in almost every study of predator losses (Rowley 1970, Henne 1975, Dorrance and Roy 1976, Nesse et al. 1976). Little seems to be known about the biological significance of such killing patterns. This observed phenomenon will therefore be explored and explained in a theoretical discussion of the general organization of mammalian predatory behavior.

SURPLUS KILLING

One well-known type of overkill reported among mammalian predators is surplus killing of prey (Kruuk 1972, Curio 1976). Surplus killing is defined as the

behavior of a predator that kills without either itself, its young, or members of its social unit attempting to consume the prey, although they have free access to the carcass and the prey is among their potential food species (Kruuk 1972).

Surplus killing occurs primarily in closed, artificial conditions, for instance when a fox (*Vulpes* sp.) gets into a henhouse or mink (*Mustela vison*) into a hatchery pond. Such events are sometimes described as killing "orgies," a phenomenon exceptionally detrimental to domestic livestock if they have no means of escape (Fox 1971, Nesse et al. 1976). Young and Goldman (1946) mention a case where a puma (*Felis concolor*) entered a sheep pen and, in the course of 1 night, killed 192 sheep. Blocking of escape routes by fences may be an important factor in explaining surplus killing, but it also occurs in unfenced natural ecosystems. The phenomenon applies to mammalian predators in general; under conditions where normal anti-predator reactions of the prey are blocked, surplus killing seems to be released. Among bears, several examples of surplus killing have been described for the polar bear (*Ursus maritimus*). Even Nansen (1924) called attention to the fact that polar bears killed far more young seals than they consumed (Lønø 1970). Perry (1966) mentioned 1 case in which a polar bear killed 21 narwhals (*Monodon monoceros*) enclosed by ice in a small pond, and Freeman (1973) reported multiple kills of beluga (*Delphinapterus levae*) by a solitary bear.

During field investigations into high densities of small rodents, large numbers of lemmings (*Lemmus lemmus*) and other small mammals such as shrews are often bitten to death but left uneaten (Mysterud unpublished data). One attempted explanation of this has been that lemmings, for example, contain substances that make them less coveted as prey (Hagen 1952, Andersson 1976). However, under other conditions, large quantities of lemmings are consumed by the same predator.

During certain winter conditions, prey species may tramp through snowpack while a predator walks upon it. Surface structure of snowpack seems to be extremely important in some predator-prey relationships; and on certain types of crusts, examples are known where brown bears have killed a number of moose (*Alces alces*) (Hellgren 1967, Wikan 1970). However, the carcasses were not left completely uneaten; the predation therefore represents killing pattern no. 2 discussed below.

The caribou-hunting behavior of American Indians and Eskimoes, summarized by Kelsall (1968), may

also be explained as surplus killing. During certain incidents, when natives are faced with large numbers of caribou and have plentiful ammunition, they frequently seem to go berserk and fire blindly into the animals until ammunition or caribou are gone (Kelsall 1968:221).

Surplus killing has been assumed to occur only in extremely rare cases (Curio 1976). This is probably a correct assumption when comparing the surplus-kill percentage with the usual consumption killing. When it does occur, however, it may be of quantitative importance to the group or population affected. Dorrance and Roy (1976) have, during their investigations on sheep losses to predators in Alberta, Canada, reported that the probability of predation was lower in confined flocks — those kept in pens or sheds throughout the year — than in free-ranging flocks. But when predation did occur in confined flocks, it was particularly severe. As a result, predation losses were highest in confined flocks and lowest in range flocks. Conclusions concerning the ecological significance of this behavior should therefore not be drawn until field investigations provide information on the frequency of this form of killing.

EXTREME FOOD-SELECTION KILLING

Overkill phenomena other than true surplus killing, where no part of the animal would be eaten (Kruuk 1972), have been observed. Sheep carcasses investigated in most overkill incidents in Hedmark are not without small eating marks (Mysterud unpublished data). In such cases, the breast of the animal is opened in a stereotyped way, and breast fat deposits and/or parts

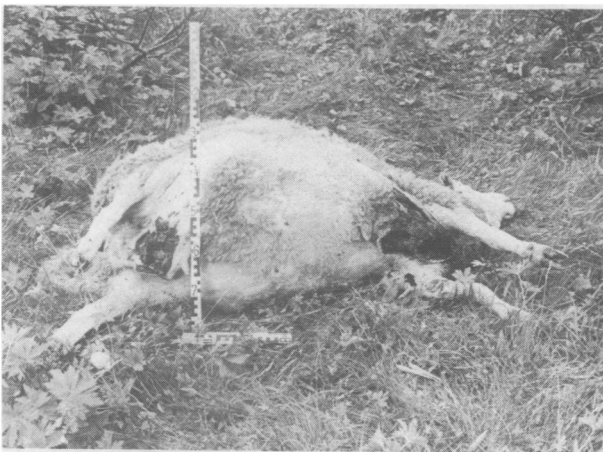


Fig. 3. A ewe killed by a raiding bear in Hedmark, southern Norway, 1976, showing the consumption marks typical of extreme food selection on sheep. The bear has cut the hide, exposed the breast, and consumed the fat deposit together with small amounts of udder. Instead of eating more from this carcass, other nearby ewes were killed and the selective eating pattern repeated.

of the udder are removed (Fig. 3). These incidents may represent extreme food selection as defined by Stenseth and Hansson (1977): a selection of small but nutritionally valuable parts of the animal. Such killing is also part of human hunting behavior, exemplified by the killing of caribou by northern Indians for removal of tongues (Kelsall 1968). High sheep density may well represent an ecological situation where individual bears develop optimal eating habits — “grazing” on sheep udders and breast fat deposits. This preference constitutes a combination of high-energy fat storage and udder tissue rich in proteins, minerals, vitamins, etc., and represents a nutritionally balanced intake. If this “organ grazing” constitutes extreme food selection, whole carcasses should not be considered as units when a predator’s eating behavior is considered. This eating pattern may be better compared with selective grazing among herbivores that remove specific parts of plants. Field studies of a variety of species show that herbivores usually select plant items so that the net gain of metabolizable energy is maximized, as shown by Stenseth et al. (1977) for the field vole (*Microtus agrestis*). The breadth of the food niche of field voles has been shown to vary with the density and quality of all available food items. With the more extreme organ selection and smaller amount consumed per sheep, a larger number of animals must be killed to meet a bear’s food requirements.

It is not the purpose of this paper to present a detailed model of this behavior, but it is not difficult to theoretically describe such biological phenomena by simple, continuous functions, presented here in 3 steps.

When disregarding certain factors, the average amount consumed from each carcass may be described as a function of sheep population density. The number of animals killed per unit time (z) multiplied by the amount, measured in weight (v), consumed from each carcass satisfied the food requirement of the bear. If this requirement is a rough constant, K , and the prey animals can be regarded as “homogeneous food,” then

$$zv = K. \text{ Hence, } v = \frac{K}{z}, \text{ which expresses a hyperbola.}$$

Obviously the homogeneity assumption is an oversimplification, but one might reasonably present the function $v(z)$, shown in Fig. 4.

The number of animals killed per unit time (z) may be assumed to be an increasing function of the sheep population density (x). Such a functional response curve, modified from Holling (1959), is denoted by $z(x)$, and it can have 1 of several forms. In Fig. 5, an arbitrary illustration of such a function is shown. If we

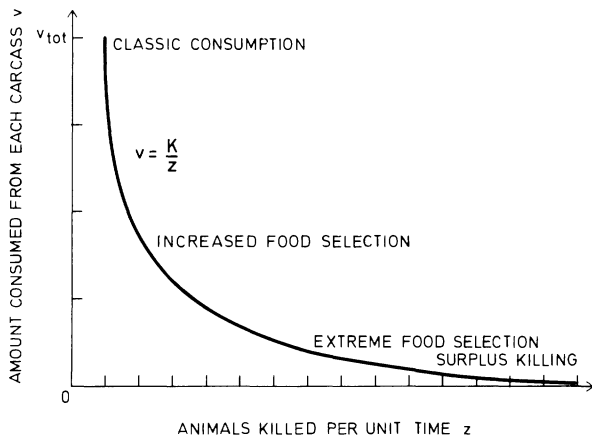


Fig. 4. One basic relationship in predation incidents on sheep is the amount eaten from each carcass (v) as a function of the number of animals killed per unit time (z). The function runs from classic consumption, where 1 animal is killed and completely consumed ($z = 1, v = v_{tot}$), to surplus killing, where many animals are killed which are not consumed ($z \rightarrow \infty, v = 0$). Between these values, increased selection of prey parts develops with increasing z , a phenomenon denoted as extreme food selection ($z \rightarrow \infty, v \rightarrow 0$).

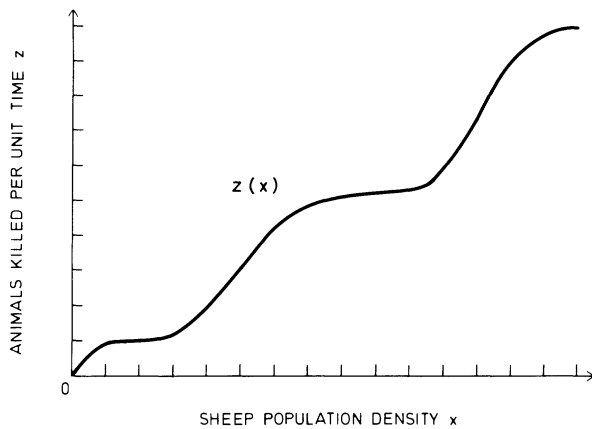


Fig. 5. Functional response curve $z(x)$ for bear-killed sheep, where x denotes sheep population density and z is the number of animals killed per unit time. The function $z(x)$ can have several forms; an arbitrary example is given here.

combine the curves in Figs. 4 and 5, we see that the weight or percentage consumed from each carcass becomes a decreasing function of x (Fig. 6). The higher population density (x) means more animals killed per unit time (z) and a smaller amount (v) eaten from each carcass. This function, denoted by $v(z(x))$, can have several forms, of course; only 1 example is illustrated in Fig. 6. It must be pointed out that the $z(v)$ functions actually depend on several other factors, not included as arguments in the function. Of special interest is the relative ease with which a bear can capture a sheep. This factor perhaps stem from some sort of optimization between the energy required to eat and digest most or all of an animal, compared to the energy expended in capturing an animal. On pastures with high sheep den-

sity, bear search, hunt, chase, and capture efforts are, of course, all minimized.

Let us explore in some detail the succession of elements organized as part of the predatory behavior sequence relevant to an understanding of this last statement.

THE PREDATORY BEHAVIOR SEQUENCE

Restricted definitions of the concept of predation in

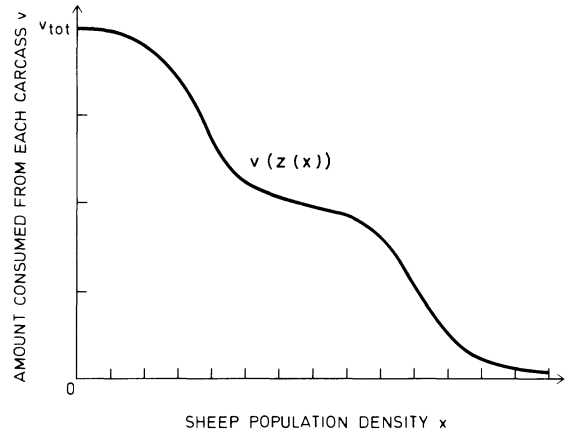


Fig. 6. Amount eaten from each carcass (v) as a function of sheep population density (x). The function is expressed as $v(z(x))$, where z is the number of animals killed per unit time (cfr. Figs. 4, 5). The function $v(z(x))$ can have several forms; only 1 example is given here.

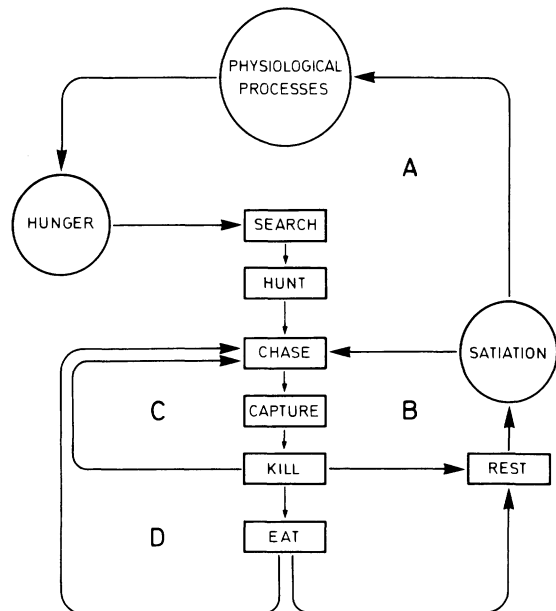


Fig. 7. Organization of specific behavioral patterns associated with predation by large mammals. Loop A describes classic killing-and-consumption predation, B and C surplus killing, and D extreme food-selection killing. All patterns have been observed in areas where brown bears prey on sheep.

most textbooks generally include the killing and eating of animals (Hassel 1976), but Curio (1976) has argued that "eating" should be avoided. Curio (1976:1) defined predation as "a process by which an animal spends some effort to locate a live prey and, in addition, spends another effort to mutilate or kill it." For our purpose it is advantageous to further break down the definition. In the simplified model presented in Fig. 7, separate behavioral elements, each assumed to have its specific threshold motivation, have been identified in the organization of predatory behavior. All of the observed patterns of predation associated with large carnivores can be explained by this model.

Classic killing-and-consumption predation follows the sequence shown in loop A of Fig. 7. *Hunger* provokes *search* for prey, and the *hunt* is then initiated. The predator may locate fresh scent trails (olfactory stimulus), or may hear (auditory stimulus) or sight (visual stimulus) the prey. Different strategies have been developed for approaching or surprising the prey. In certain species, the location of prey culminates in the predator *chasing* the prey in the attempt to capture it. Specific behavior patterns have been developed in all species to *capture*, *kill*, and *eat* the prey. *Rest* is usually induced or associated with a period of *satiation*, and after assimilation of the food, hunger is again induced. *Search* → *hunt* → *capture* → *kill* → *eat* is thus an idealized and simplified behavior sequence, almost dogmatically described for most mammalian predators. However, Kruuk (1972) has observed in the African wild dog (*Lycaon pictus*) that both satiated and resting animals can be stimulated to hunt anew by the sudden appearance of prey near them. A chase will then release the components *capture* and *kill*, but not necessarily *eat* (Fig. 7, loop B). Thus, chasing seems to be motivated differently from killing and eating (Kruuk 1972). Fox (1971) suggested that the prey-killing response of canids has a very high satiation level and that prey-killing can therefore continue beyond the nutritional needs of an individual simply because the prey is available and vulnerable. However, another study of sheep-killing by coyotes (*Canis latrans*) under captive conditions showed that food deprivation had no discernible effect on the killing behavior but did influence feeding activity on kills. The observations directly suggested that hunger is not always the primary motivation for predatory behavior (Connolly et al. 1976).

During surplus killing incidents, it seems that environmental conditions can release behavior sequences of the type *chase* → *capture* → *kill* → *chase* → *capture* → *kill* → *chase* → . . . (Fig. 7, loop C). In fenced areas

and other enclosures, the release of such a sequence may be explained simply by blockage of the normal flight reaction of the prey. The predator becomes linked up in a continual C-loop: As one animal is killed, a new stimulus to chase is immediately received. The stimulation to stop hunting is difficult to isolate (Grant 1972).

Extreme food selection might similarly be described by the sequence *chase* → *capture* → *kill* → *eat* → *chase* → *capture* → . . ., with only small, nutritionally valuable parts eaten after each kill (Fig. 7, loop D).

That one or several behaviors can be smoothly linked together is a matter of efficient adaptation in different species when thresholds are low. Even the *capture* behavior in the model is sometimes observed separately from *killing*, for instance when polar bears play and throw young seals in the air (Perry 1966) or young cats capture mice and play with them without killing them. In some cases, extreme organ selection has been observed on sheep which have not actually been killed (Mysterud unpublished data). The survival of such animals may be explained as shock-bite recoveries (Mysterud 1975b), general shock recoveries, incomplete killing due to human disturbance, incomplete killing behavior by young animals, or eating performed without killing. From purely biological arguments, it is not unlikely that, under certain circumstances, handling of prey animals becomes so easy that a behavioral sequence following a modified D-loop, *chase* → *capture* → *eat* → *chase* . . . (Fig. 7), could develop where there is a net gain of energy by omitting killing. There is also the possibility that prey-killing may have evolved as part of the eating process and that specific killing bites or methods are lacking. Henne (1975) has reported 2 instances in which coyotes fed on sheep before they died, and the same has been observed with coyote predation on mule deer (*Odocoileus hemionus*) (Cahalane 1947) and elk (*Cervus canadensis*) (Robinson 1952). A restricted concept of predation could be used synonymously with killing behavior defined, for instance, as the removal of live prey animals from populations. But even this definition will not be specific, as killing is also an element of intraspecific competition (Curio 1976).

DIFFERENTIAL RATE IN MAMMALIAN PREDATION

The predatory strategies of mammals may be organized so that removal of prey animals can be described at different rates, dependent on environmental factors relating to escape behavior, etc. Consequently, mammalian predator pressures may be far more effi-

cient than supposed from estimates of whole carcass consumption, and the speed at which prey animals are eliminated may be maximized under various circumstances. Naturally this may be of significance in both artificial and natural situations where the population of prey animals is excessive and the number of predators too few to control prey populations through eating procedures. In most situations, stability of prey populations can probably be maintained in part through the pressure exerted by maintaining classic consumption killing. The most important effect of the mechanism of differential rate operating through extreme food-selection and surplus killing may be in systems where a large surplus of cyclic animals regularly must be killed off, which is usually the case in large areas of the northern hemisphere. This mechanism is also important for any population that undergoes irregular fluctuations.

In the construction of models describing predator-prey relationships, differential predation rates of these types will complicate the description of predation efficiency due to erroneous estimates of prey removal drawn from energy arguments, which are most often based on consumption of the whole prey animal. That is, when calculating the needed prey number based on energy and nutritional demand per individual predator and multiplying by the estimated size of the predator population, there is strong evidence that prey removal might be underestimated. From investigations of bears and sheep in Hedmark, it is already clear that such simple evaluations cannot be used in connection with sheep-bear relationships.

WHAT ARE THE FUTURE RESEARCH NEEDS?

In regard to predation and livestock, the only conclusion one can draw from literature is that much more research is needed (Jobman 1972). This discussion proposes that predatory behavior as a strong selective force and control mechanism for surplus population numbers might be more biologically significant than tissue-eating and the associated transfer of matter and energy in ecosystems emphasized in energetic contexts

(Cringan and Harris 1972). Predation pressure exerted by large carnivores may be of prime importance in development of role play, space use, and social evolution, in both prey and predator species, expressed by Edmunds (1974:14) as an "armed race" between predator and prey, both of which constantly develop new behavioral patterns involving both gene pools. Prey removal rates in husbandry — differential livestock loss sizes — are an important field of study in evaluation of these evolutionary consequences.

For livestock production it is basic to realize (1) that evolutionary behavioral equilibria in open systems exist before the introduction of flocks of animals whose behavior or social structure is not adapted to the prevailing ecosystem. Sheep and domestic reindeer, the 2 most important rangeland species in Norway, often graze in socially unstructured aggregates and periodically graze within fenced areas, making them highly vulnerable. (2) The majority of domestic animal species have greatly reduced locomotive capacity compared with wild animals. Production of sheep is today guided by commercial aims such as quantity and quality of wool and meat, and natural defense and/or escape mechanisms have been generally bred out in exchange for increased productivity or increased ease of managing the animals (Howard 1974, Klebenow and McAdoo 1976). More detailed knowledge of predator behavior should bring parameters of prey behavior patterns, social structure, locomotor capacity, etc., within the scope of livestock research to minimize losses.

Ecosystem management which aims at maintaining predator and livestock populations within the same space, therefore, needs a knowledge of predator-prey relationships for development of good predator management programs and estimation of optimal livestock densities and tolerable loss sizes. However, an understanding of the predator behavior sequence and livestock removal rates ought to be regarded as of utmost importance, whether we are to introduce more sheep into the habitat of a small bear population or into the habitat of an increasing bear population. At present, these 2 alternatives seem to be the only realistic choices in Norway.

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