

# 12

## INTERSPECIES INTERACTION

Interactions between populations of different species can take many forms, including the following: (1) *neutralism*—a population is not affected by association with another; (2) *competition*—populations adversely affect one another in the struggle for food, living space, or other common needs; (3) *mutualism*—populations benefit one another's growth and survival and cannot survive under natural conditions without one another; (4) *protocooperation*—populations benefit by associating with one another, but relations are not obligatory; (5) *commensalism*—one population benefits but the other is not affected; (6) *amensalism*—one population is inhibited and the other not affected; (7) *parasitism* and (8) *predation*—a population adversely affects another by direct attack but is dependent on it (Odum 1959). These are summarized in relation to their effect on population growth and survival in Table 12-1.

These kinds of interactions are generally considered to be between animals, although some of them can exist between plants and animals. Amensalism, for example, occurs if free-ranging animals consume poisonous plants on the range, the consumer being inhibited by the action of the ingested toxin and the plant being unaffected except for losing that which has been consumed. The plant as a whole survives and may even be stimulated by the cropping.

This chapter deals primarily with predation, competition, and parasitism. These have been of interest to the wildlife biologist, although it may be true that other, more subtle, factors have equally as great an impact on the population dynamics of any organism.

TABLE 12-1 ANALYSIS OF TWO-SPECIES POPULATION INTERACTIONS

Type of Interaction	Effect on Population Growth and Survival of Two Populations, A and B				General Result of Interaction
	When Not Interacting		When Interacting		
	A	B	A	B	
Neutralism (A and B independent)	0	0	0	0	Neither population affects the other
Competition (A and B competitors)	0	0	-	-	Population most affected eliminated from niche
Mutualism (A and B partners or symbionts)	-	-	+	+	Interaction obligatory for both
Protocooperation (A and B cooperators)	0	0	+	+	Interaction favorable to both, but not obligatory
Commensalism (A commensal; B host)	-	0	+	0	Obligatory for A; B not affected
Amensalism (A amensal; B inhibitor or antibiotic)	0	0	-	0	A inhibited; B not affected
Parasitism (A parasite; B host)	-	0	+	-	Obligatory for A; B inhibited
Predation (A predator; B prey)					

SOURCE: Odum 1959.

Note: + indicates population growth increased; - indicates population growth decreased; 0 indicates population growth not affected.

## 12-1 PREDATOR-PREY RELATIONSHIPS

Predator-prey interactions have been studied in controlled situations (e.g., fish tanks as miniature aquatic systems) and historical ones, such as the attempts to correlate the populations of predators with populations of prey species. These populations have often been estimated by the take of trappers and hunters, and lags between the peak abundance of the predator and prey have been observed. The lynx-hare relationship is perhaps the best known example; another is the fox-pheasant.

Analytically, the ecologist is interested in the mechanisms of predation, in the factors regulating the amount of predation, and in the effect of predation on population structures and levels through time. Before considering some of the mechanisms, let us review some general characteristics of predation that have been observed among free-ranging animals.

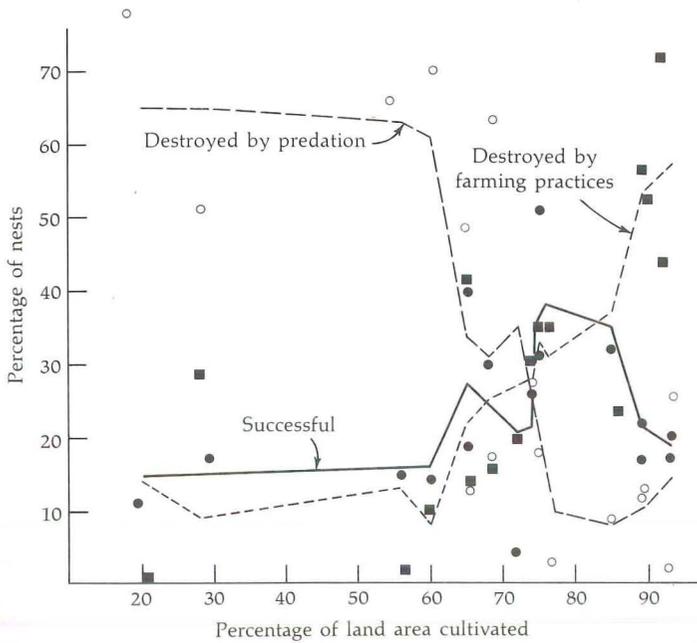


FIGURE 12-1. Relationships between percentages of nests destroyed by predation and by farming practices, total nesting success, and the percentage of land area under cultivation. The lines were drawn from three-point moving averages. (From Wagner, Besadny, and Kabat 1965.)

Upland game birds and waterfowl are preyed upon by a variety of predators. The individual birds are killed by fox, coyote, house cats, raccoon, mink, lynx, bobcat, hawks, owls, and other predators in local areas. Nests are destroyed by skunks, badgers, crows, magpies, and others. Many studies of nest destruction have been made, with destruction rates varying from nearly zero to three-quarters or more of the nests. In Wisconsin, pheasant nest losses varied from 3% to 78%, with the losses inversely correlated with losses due to farming activity and the percentage of land under cultivation (Figure 12-1). Note that the losses due to predation were high under low-intensity cultivation when few nests were destroyed by agricultural practices. As cultivation increases, the rate of nest loss due to predation decreased, but that due to farming practices increased. A reversal in the rate of loss due to predation occurred when over 80% of the land area was cultivated. The percentage of successful nests was highest when 60% to 90% of the land area was cultivated, a characteristic unique to the pheasant and certainly not characteristic of other game-bird species such as the prairie chicken.

Sowls (1955) summarizes data from a variety of studies and presents data for the Delta Marsh, too. Ducklings are subject to predation by fish and turtles. Carnivorous fish are often not present in the shallow brood marshes, but ducks living on larger lakes and rivers are susceptible.

Larger animals such as deer and elk have fewer predators than do the upland game birds. Fawns and calves can be taken by coyotes, and wolves prey on deer

and moose in areas such as northern Minnesota. Wolves prey almost exclusively on moose on Isle Royal. Very high mortality of white-tailed deer fawns owing to coyote predation has been observed in Texas, with losses of about 72% of the fawns within two months (Cook et al. 1971). Mountain lions, grizzlies, and black bear prey on elk calves.

One important point to consider in evaluating predation is that intrusion by the biologist in the process of marking animals, attaching radios, checking nests, counting eggs, and so forth may result in an increase in the amount of predation. The effect of human intrusion is dependent on cover conditions and on the abilities of the predators to use human artifacts to locate prey. Crows have been known to locate nests by watching biologists working at nest sites. Merely flushing a bird from a nest leaves the eggs exposed to crow predation. Tags attached to the backs of ruffed grouse seemed to be responsible for significantly accelerated losses (Gullion and Marshall 1968). The attachment of radios, even though they may weigh but a few grams, may affect the susceptibility of the carrier bird to predation. They usually are quite inconspicuous, however, so if their weight is sufficiently low they may have less effect than colored back tags.

It is usually very difficult to estimate accurately the rate of predation on adult animals because the chances of finding the remains and determining the cause of death are very slim. One of the advantages of using a radio telemetry system to aid field work lies in the ability to locate the transmitter regularly, in order to check on the condition of the carrier animal. Sometimes the signal changes location more rapidly than the carrier animal can travel; a snowshoe hare traveling one-half mile in a minute or so clearly indicates that something is carrying it at a speed unknown to hares!

The usefulness of radio telemetry in studying predation was demonstrated by Marshall and Kupa (1963) with grouse. Mech (1967) describes the use of telemetry in predation studies of snowshoe hares (*Lepus americanus*) and cottontail rabbits (*Sylvilagus floridanus*). In one case, a snowshoe hare was killed by a red fox (*Vulpes fulva*) who was also carrying a radio transmitter. The photographed signals of both transmitters were the same because the radios were being shaken in a similar manner. The episode ended with the fox burying part of the hare and the transmitter in 10 inches of snow. Several telemetry techniques are designed specifically for the detection of mortality in free-ranging animals [see Stoddart (1970)]; temperature sensors reveal a loss of body temperature.

## 12-2 FACTORS AFFECTING PREDATION RATES

The factors affecting the amount of predation are exceedingly complex. Leopold (1933) has listed five variables that affect annual mortality due to predators:

1. The density of the game (prey) population.
2. The density of the predator population.
3. Food preferences of the predator.

4. The physical condition of the game and the escape cover available.
5. The abundance of "buffers" or alternative foods for the predator.

None of these factors are stable over time. The density of the game population varies, depending on the conditions affecting productivity and on the reproductive potential of the species. Quail and pheasants have greater annual variation in population density than do large mammals such as deer, elk, and moose. Densities vary with the season also; many more birds are present in a given habitat just after hatching than during the incubation period. Further, the mobility of the birds is considerably less during incubation than after hatching. Incubating females spend most of the time on the nest where they are usually concealed by cover. The chance of a predator locating such a bird is probably less than when the bird is actively rearing the brood. Thus there is an actual density (this is difficult if not impossible to determine) and there is an apparent density, or a population level that appears to exist based on direct or indirect observations of the individuals. Keep in mind that the density apparent to a human driving along a road or spending a few hours in the field is different from that apparent to a predator living in the habitat. Further, the visual environment of the predator is different from that of a human since it may be looking through vegetative cover from a lower height or it may be looking down into the vegetation as it flies. Also, predators can detect the presence of prey by scents and sounds that humans are not aware of. These kinds of considerations were discussed in Chapter 2.

The food preferences of a predator are a complex summation of the previous experiences of the predator, the chemical interactions through taste and the digestive processes, the abundance of any food that could be eaten, and other factors that work together with any or all of these. It is difficult to determine the relative importance of these factors; the analytical ecologist should first concentrate on studying the effects of different combinations of foods in the diet rather than the causes of these combinations.

The physical condition of the prey species and the escape cover available vary greatly on a seasonal basis. Further, they frequently vary together, with a decline in the physical condition of the animal coinciding with a decline in the amount of cover available owing to snow accumulations, plant decadence, and other factors that change the mechanical, thermal, and optical characteristics of cover. A reduction in the density of the cover may force an animal to travel farther to reach sufficient cover. The distance to this cover becomes more critical as the animal's physical capacity for travel is reduced, thereby compounding the interaction between cover and predation. As the vegetation resumes growth in the spring, the animal's condition improves, too, increasing its ability to escape.

The importance of "buffers" or alternative foods available to a predator is closely tied to Leopold's third variable. If there is a variety of prey species or alternate foods available (such as berries for fox and coyote), the predator's diet is likely to be varied. As hunting conditions worsen, the predator is forced to eat fewer kinds of foods and more of each kind.

The term "buffer" species has generally been applied to species other than the prey under consideration. From a functional biological point of view, a buffer can be a member of the same species as the prey under consideration. If the prey species is polygamous, such as the pheasant, the shooting of cocks only, for example, is not considered detrimental to the total pheasant population. If, however, there is a shortage of other buffer species available, then the cocks may become buffers for the hen population. This may not be of much significance during periods in which populations are large, but it could be important when the pheasant population is at or below a minimum threshold for a rapid rate of increase. Leopold suggests that this kind of relationship is worth considering by pointing out that different prey-predator abundance ratios warrant different considerations.

Rates of predation alone do not permit an analysis of the effects of predation in an analytical ecological context. In the absence of sound biological information on rates and their effect in relation to the total ecology of a species, it is beneficial to evaluate the effect of different predation rates in relation to different reproductive rates by simulation, resulting in an understanding of the balance between productivity and mortality of animals in different age, weight, and reproductive classes. There are realistic limits within which to confine the analysis; predation, for example, can vary from zero to 100% of the prey population. Biologically reasonable rates are found somewhere between those two extremes, and an analysis of rates at intervals between zero and 100% in relation to reproductive rates at intervals between zero and the maximum reproductive potential of the animal will provide insight into the relative importance of predation to different population densities. If a time element is added to this analysis, both seasonally and over several generations, further insights are gained into long-range trends. These considerations are discussed in Chapter 19. They are a part of a population model that starts with the smallest possible working model and progresses toward the most "real" model possible. This is different from a common procedure in population ecology in which masses of numbers are accumulated in the field and an equation(s) is derived without an understanding of the important factors causing those numbers to vary.

### 12-3 ENERGETIC CONSIDERATIONS

*Life* was defined in Chapter 1 as a process consisting of the orderly rearrangement of matter with the expenditure of energy. Everything an animal does "costs" something in terms of energy, and predation is no exception. There are some generalizations about predation that provide background for understanding the variations in rates of predation by different predator-prey combinations. A large predator must consume more very small prey than larger prey. In other words, a fox needs to consume more mice than pheasants to satisfy its nutritional requirements. This assumes that the prey are eaten, and killing is not just a form of displacement behavior. The cost of catching the prey becomes an important consideration when evaluating the predation rate necessary for meeting the

nutritional requirements, since these requirements vary in part in relation to the cost of catching. Thus if it is harder to catch mice than pheasants, relatively more mice must be caught to meet the extra energy demand. If mice are easy to catch, the predator may be better off energetically by eating several small mice rather than spending more energy trying to catch one large pheasant.

The spatial distribution of prey is an important factor in determining the cost of predation. Game birds are widely distributed during the nesting season, for example, and will most likely be more difficult to locate and capture than when a group of them is confined to a small patch of cover in the winter. After hatching, there is a high density of birds within the brood radius, and it is likely to be less costly for a predator to locate and catch one member of the brood than if only single birds were available.

Weather conditions affect the behavior patterns of predator and prey differently. Storms affect the distribution of both predator and prey, the condition of each, and the rate of predation. Snow as a mechanical barrier affects the usefulness of cover. Deep snow covers the living area of many potential prey such as mice. Snow is a barrier to travel, although frequently it is a greater barrier to the larger predator than the smaller prey. Some prey are larger than the predator, however; moose are larger than wolves, for example. The effectiveness of snow as a barrier varies in relation to both of these animals. Loose fluffy snow may be a mechanical barrier to wolves but not to moose. Deep snow with a crust strong enough to support a wolf may not support a moose, and the prey are much more easily caught. Very cold weather may cause white-tailed deer to reduce their activity, but it may not affect wolves. Pheasants may not feed in open fields during high winds, but fox may be less affected.

Mech et al. (1971) describe several accounts of the hunting behavior of wolves. The most interesting characteristic observed was a fairly short chase after white-tailed deer. The wolves appeared to have as much or more difficulty in snow than the deer at times, and the wolves would stop to rest after only several hundred yards of chase. After the radio-tagged wolves were successful in killing a deer, they remained in the vicinity of the kill for one to seven days, depending on how recently they had eaten.

Predators are frequently credited with catching the weaker animals. This has been demonstrated in predator-prey relations between wolves and moose, caribou, bison, and other prey [see Mech (1970)]. The recent study by Mech and Frenzel (1971) on the age, sex, and condition of deer killed by wolves in northern Minnesota shows that wolves tend to prey on old, debilitated, or abnormal deer. This generalization should not necessarily be applied to all predator-prey relationships since the manner in which the predator hunts may affect the opportunity of the prey to utilize its physical capacity for escape.

The difficulty in catching a prey depends on its ability to escape owing to its physical condition and abilities as well as the condition of the cover. Thus it may be harder for a predator to catch a rabbit in thick brush than a pheasant in a field if both stay on the ground. If the pheasant flies when it detects the predator, it may become immediately unavailable if the predator is confined to the ground.

Some birds can fly faster than others, however; it may be more efficient for the predator to pursue a grouse, which has a shorter flight distance than a pheasant. The behavior of predators may change with variations in hunting conditions. According to Nellis and Keith (1968), lynx (*Lynx canadensis*) had daily cruising distances of 3.0 miles and 5.5 miles in two successive winters in Alberta, and their success in catching snowshoe hares dropped from 24% to 9%, respectively. The authors attributed this change to different snow conditions. No significant differences were observed in the number of kills, although the kill per mile traveled was lower in the second of these two winters. This indicates that they tried harder when hunting conditions were poorer because of snow conditions. They caught less food during the less successful (relatively) year, which may indicate a higher utilization of each kill under poor hunting conditions.

Differential survival of individual prey (ruffed grouse in this case) that can be related to behavioral or physiological characteristics has been noted by Gullion and Marshall (1968). Male grouse survived four months longer when they used transient drumming logs not used by a predecessor than those that replaced earlier drummers on perennial logs. This indicates that the raptorial predators focused on a physical object in the habitat that elicited a perennial behavioral response, waiting in ambush for the grouse to use it. The actual attack occurs when the grouse are en route to or from the log. The few males observed to live to an old age in the Cloquet Forest (Minnesota) all occupied transient logs. The relationship between body size and predation habits has been analyzed by Rosenzweig (1966; 1968). He has pointed out that larger predatorial carnivores (secondary consumers) tend to eat larger prey. The exceptions to this include the secondary consumers that are also primary consumers, such as the black bear. They are larger than mountain lions or wolves, but they prey on smaller animals. The difference can be explained by their consumption of a considerable amount of vegetation also. Thus the body size of a predatory carnivore appears to be related to both the size of the prey and the level of utilization of nonprey foods.

The whole predator-prey complex of interactions is very challenging to the analytical ecologist. The approach to predator-prey analyses should be made within the confines of natural laws governing the energetics of the interactions, including both nutritive and thermal considerations. Such an approach will provide insight into the mechanisms operating, after which behavioral constraints and other characteristics that have developed over time can be considered.

**TROPHIC LEVELS.** The idea of trophic levels in interspecies interactions is a valid one. Herbivores eat plants, carnivores eat herbivores, and secondary carnivores eat the carnivores that feed on herbivores. Different levels of efficiency can be attached to the different trophic levels [see Odum (1959)]. There is a "loss" of energy in going from a lower to a higher trophic level. This results in "pyramids" that depict reductions in numbers, biomass, or energy from the lower to the higher level. These representations are fine for depicting general principles, but the drama associated with spatial and temporal factors is lost. None of the animals living in an ecosystem can depend on the average biomass or energy transfer from one

trophic level to another to survive; each must meet its needs on a day-to-day basis. Some of these needs may be met by the mobilization of body reserves, or they may be met by daily feeding and other regulatory behavior.

As Rosenzweig (1968) points out, some species are both primary and secondary consumers, so they are at two different trophic levels at the same time. This characteristic permits an animal to "regulate" its energy efficiency by going to the lower trophic level, that is, toward the primary productivity level when food is scarce and to levels above primary productivity when hunting conditions are favorable. Changes in weather conditions, seasonal changes in animal behavior and activity, and seasonal changes in plant phenology can cause these shifts to occur.

The timing of the shifts may be of considerable significance to both predator and prey. The arrival of spring may make a difference to the predator as it shifts from one prey species to another, and changes in phenological characteristics may result in an abundance of alternative foods that could replace the prey. The latter seems to be the situation in Texas where the timing and abundance of the berry crop has a significant effect on the amount of coyote predation on fawns (Knowlton, personal communication).

Differences in population and biomass parameters for moose on Isle Royale have been presented by Jordan, Batkin, and Wolfe (1971) (Figure 12-2). Note that the population can decrease but the standing crop can increase during part (April-August) of that time. The transfer, or total live weight of animals dying each month and hence available to predators, remains fairly constant. While these dynamics through time are occurring, moose of different ages play distinctly different roles in population and biomass dynamics (Figure 12-3). The population in July includes more animals that are one year old or younger than any other age class, but the highest standing crop can be attributed to the six-year class. The transfer by death is highest in the one-year class, lowest in the three-year class, and rises to a secondary peak in the twelve-year class. Figures 12-2 and 12-3 combined illustrate how multidimensional the population characteristics are in space and time. The averaging of all these factors into single values for each year and all moose would result in the loss of considerable information.

When factors affecting the productivity of both predator and prey fluctuate greatly, a greater departure from the average is noted and productivity increases or decreases greatly, depending on whether the combination of circumstances has a positive or negative effect. It is these kinds of fluctuations that result in population fluctuations over an ecologically short time span of just a few years, but a long enough time span to cause significant changes in legislation regulating hunting and the activities of game biologists and managers. Thus it is particularly important for the biologist and the manager to understand the cause of short-term fluctuations in order to predict and explain the biology of the current situation. It is hoped that this would result in the institution of appropriate policy that would eliminate undue political and economic pressure, which often results in wresting decision-making authority from resource biologists and managers and placing it in the hands of political groups.

Predator control has always been a controversial topic among biologists and sportsmen. Disagreements have often been caused by a lack of understanding of the impact of predators on game populations in relation to social and economic factors. Predator removal *can* result in higher prey populations according to Chesness, Nelson, and Longley (1968). They found that the cost of predator control per pheasant chick hatched on a controlled versus an uncontrolled area was \$4.50, a rather high figure. The effectiveness of predator control was demonstrated by Balser, Dill, and Nelson (1968) also; 60% more ducklings from about one to three weeks of age were counted in the area with intensive predator control.

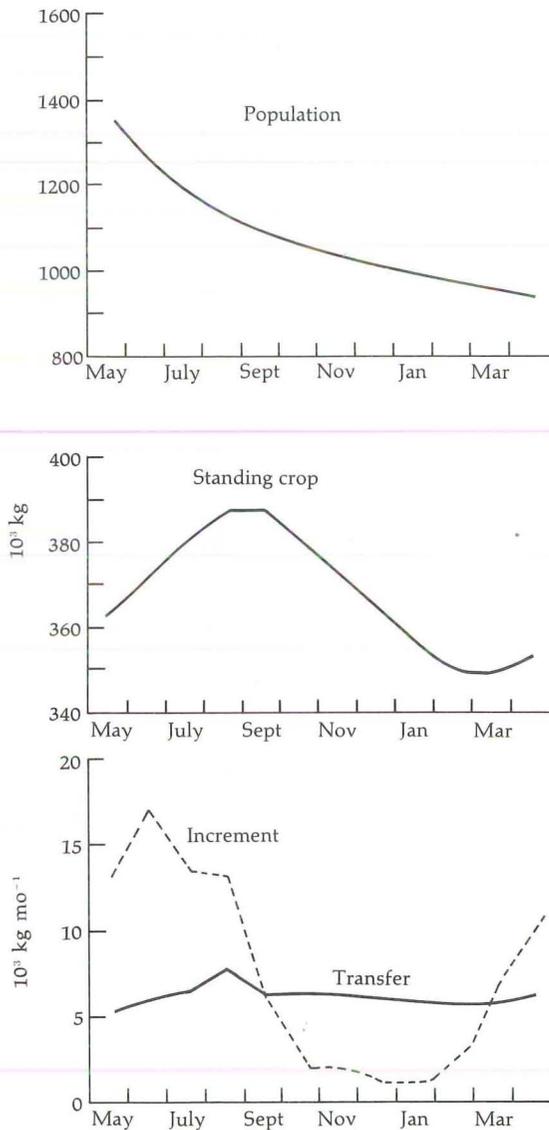


FIGURE 12-2. Monthly levels of population and of biomass parameters computed for the Isle Royale moose herd. Standing crop is the live weight of the population; increment is the total live weight gained each month; and transfer is the total live weight of animals dying each month. (From Jordan, Batkin, and Wolfe 1971.)

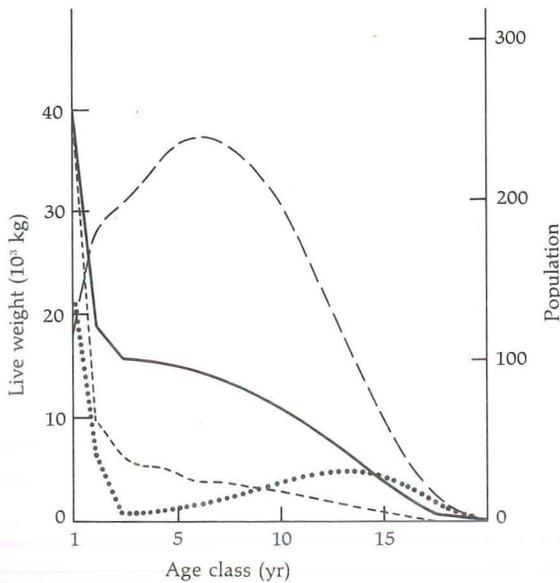


FIGURE 12-3. Numbers and biomass parameters computed for each age class of the Isle Royale moose herd. Population (solid line) is the number present in July; standing crop (long-dashed line) is total live weight in July of the population; annual increment (short-dashed line) is the year's total of live-weight gains; and annual transfer (dotted line) is the year's total of live weight on moose dying. (From Jordan, Batkin, and Wolfe 1971.)

The entire predator-prey complex needs to be studied with considerable attention given to the roles of all potential predators over time. The biology of predator-prey interactions should be studied first, after which social and economic considerations can be appropriately added.

#### 12-4 MAN AS A PREDATOR

Man as a biological species is at different trophic levels. Different cultures and societies are oriented more toward being either primary consumers or secondary consumers, and some individuals are entirely vegetarian or primary consumers. The hunting instinct is strong in man, and the hunting tradition is present even after intensive agriculture reduces the need for hunting as a source of food. The ecological role of man at the present time may necessarily include hunting, if some populations of animals are to be maintained in balance with the supply of resources.

The incompatibility of man and wolf or man and mountain lion, for example, has resulted in a lack of natural predators necessary to maintain a balance between the consumer and the supply of resources. The prohibition of hunting in national parks has demonstrated the need for natural predators, since populations of elk, for example, have increased beyond the ability of the resources to support them. Programs to reduce the number of elk have been attempted for many years in some areas because the herd is too large for the food supply. Trapping is often resorted to when a serious food shortage develops on a range, but the removal and release of weakened animals is usually not a desirable way to handle the problem. Trapping and transporting wild ruminants is costly and often results in mortality due to shock and the effect of other stresses on the animals.

A hunted animal is more wary than an unhunted one; Behrend and Lubech (1968) have observed this for white-tailed deer in the Adirondacks. Increased wariness is a desirable thing ecologically, but resort owners and their clientele often prefer the tamer, more abundant animals. Thus a social problem is superimposed on the basic biology of the situation. The important point to remember is that man should be primarily responsible to the biology of the organism and of the ecosystem, and social, economic, and political considerations should remain secondary.

#### 12-5 PARASITES AND PATHOGENS

A large number of parasites and pathogens have been found living on and in free-ranging animals. Many short reports describing lesions, tumors, aberrant behavior, and other abnormalities have been published. Diagnostic work is usually done coincidentally with the collection of other biological information such as that gathered at checking stations during the hunting season. Treatment of free-ranging animals is not feasible because they are not under the control of man. The control of diseases in wild populations is usually by natural attrition when the number of carriers reaches such a low point that transmission is interrupted. Disease control by natural means can be accelerated by reducing the carrier population through hunting, trapping, or other means.

Several publications have appeared that describe various characteristics of the epidemiology of different parasites and diseases. A small book entitled *Diseases of Free-living Wild Animals* by McDiarmid (1962) is organized according to the taxonomy of the pathogens, with short descriptions of diseases due to bacteria, fungi, viruses, protozoa, rickettsiae, and true neoplasms of viruses associated with tumor formation. Different hosts known or suspected to be carriers are discussed for each kind of pathogen.

A book on diseases transmitted from animals to man (Hull 1963) includes discussions of the role of both domestic and wild animals as carriers. Thirty-two authors contributed to this edition of the book, each discussing their subject within a format of their choosing.

Another book (McDiarmid 1969) is a collection of papers on a variety of diseases that were considered at a symposium sponsored by the Zoological Society of London. In his foreword, Dr. McDiarmid points out how general world interest in diseases of wild animals has been amply demonstrated in the 1960s but that some countries still do not devote much attention to diseases in relation to wildlife ecology.

Davis and Anderson (1971) have edited a book on parasitic diseases of wild mammals. It is interesting to note that this book is also a collection of papers by several authors. It appears that no single ecologist with a deep interest in wildlife diseases has written a comprehensive treatise on the role of diseases in wildlife ecology. The analytical treatment of diseases as a factor affecting productivity,

complete with models relating the effect of pathogens and parasites to productivity, is an exciting prospect in wildlife ecology.

Individual ecologists may often ignore diseases as a vital part of ecological relationships. This may be because ecologists are generally not prepared to detect the effect of diseases on productivity. The ecological effects of diseases on the structure of a population owing to relative effects on different members of that population, the changes in productivity because of changes in population characteristics, and the effect of diseases and parasites on the physiology and behavior of an individual as well as its relation to other species deserves careful analytical attention.

A recent but pioneering attempt to use the systems approach in the analysis of a host-parasite interaction is described by Ractliffe et al. (1969). Their model has three principal components, including (1) a parasite control mechanism, (2) a parasite population, and (3) a mechanism for haematocrit regulation. Host-parasite interactions were simulated, using data from field observations, which illustrated how such a simulation model can provide the basis both for selecting the specific variables that should be studied and for estimating the quantitative nature of the variables.

Parasites (and pathogens) may affect an animal directly by diverting energy through the parasite system or by causing a metabolic constraint that upsets the metabolic efficiency of the host. The energy requirements of *Haemonchus contortus*, a roundworm found in the abomasum of sheep, deer, and other ruminants, were calculated and compared with the energy requirements of deer at different levels of productivity (Moen, unpublished data). These calculations showed that the number of parasitic worms necessary to cause an energy drain equal to that of normal productive functions was too great for the space available in the abomasum. Thus the effect of the energy drain was not the dominant cause of death but contributed to it by increasing the total energy requirements at a time when energy supplies were limited.

A more significant effect of *Haemonchus* and other parasites is their effect on the metabolic functions of various systems of the body. *Haemonchus*, for example, is apparently related to erythrocyte levels (Whitlock and Georgi 1968), which in turn are related to oxygen transport efficiency and the susceptibility of the host to a variety of other decimating factors. Productivity functions, the maintenance of homeothermy in cold environments, and sustained activity are three obvious metabolic functions that require oxygen transport.

Another example of the physiological effect of parasites may be seen in the relationship between deer, moose, and the roundworm *Pneumostrongylus tenuis*. This parasite is carried by white-tailed deer with little or no known effects. However, infected moose suffer a neurological disease that results in aberrant behavior, including reduced fear of man and a decrease in muscular coordination, which is manifested externally but caused internally. The result is death for the moose; large moose populations may not be found in areas with large deer populations because deer are carriers of a parasite that is potentially lethal for moose.

## 12-6 COMPETITION

The most powerful forces in the life of an animal may be exerted by members of its own species, but other species interact with the animal in several ways. They compete directly or indirectly for the available material and energy within the space that they share. The extent of this competition depends on how much their operational environments overlap. Long-term adaptations often tend to minimize direct competition. For example, subtle differences in food preferences may develop.

The ranges of wild ruminants often overlap. Mule deer, white-tailed deer, elk, and moose can be found in the same general area. There may not be much competition for food, however. In the summer, for example, deer eat a mixture of browse and herbaceous plants, while elk are primarily grazers. Moose and deer feed on both aquatic and terrestrial plants, but the larger size of the moose permits it to feed in areas that deer cannot reach.

The restricted winter range is often the site of the most direct competition among species. Elk may forage on woody browse at that time, competing directly with deer. Moose and deer forage heavily on woody browse during the northern winters, competing directly for those species that both prefer.

Snow depths can affect the amount of competition for food. Moose are not bothered much by depths of 20 inches, a critical depth for the deer. Snow characteristics that are related to cover types seem to affect the distribution of moose and deer in the winter; Telfer (1970) observed little competition between the two species because of the different effects of snow cover on their distribution in New Brunswick. Only 1% of the area was shared by the two species.

Direct competition for food may exist between wild animals and domestic stock. In general, competition is less intense when both the wild and the domestic animal populations are low, permitting each to select its most preferred forage. As populations increase, competition between the groups increases.

Indirect competition is a more subtle type of interspecies interaction. Small mammals such as mice, rabbits, prairie dogs, ground squirrels, gophers, and others affect the growth of forage without competing directly with livestock or game animals for some of the aerial parts. These animals consume the roots and early growth of grasses and forbs, and their absence can result in higher forage yields.

Another form of indirect competition takes place between livestock and game birds and waterfowl. Overgrazed pastures are of little value as nesting cover. Stock ponds with muddy banks devoid of vegetation are not suitable for waterfowl. This kind of competition can be reduced by carefully regulating the number of livestock using an area, with fences for confining access to water to specially prepared areas with proper slope and substrate.

## 12-7 CONCLUSION

The relationships between an individual free-ranging animal and members of its own species and other species are very labile, varying in both time and space. The keen observer recognizes many of these relationships, mentally integrating

them into a system that may be biologically realistic but difficult to explain. After all, the human mind is a kind of computing system, but without a single common program format. An analysis of behavioral interactions is difficult because of a lack of definitive units to quantify these relationships. Thus this chapter and Chapters 10 and 11 have been somewhat general, with brief indications of how such analyses might be approached.

Having progressed from physical to physiological to behavioral interactions thus far, let us now turn to an analysis of interactions involving all of these. The analyses described in the remainder of this text are representative of what can be done in analytical ecology. Many other analyses can be made, of course, and students with backgrounds in basic sciences are urged to develop further analyses of additional interactions present in the ecosystem.

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