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INTRODUCTION

The interrelationships of man and animals have become increasingly complex as human populations have increased. Man's demands for additional food, fiber, and timber have led to more intensive use of the lands and waters. As a result, most habitats for wild creatures have become so altered that many forms have suffered large population reductions. Other animals, finding these alterations to their liking, have established new balances and substantially increased in density, often coming into conflict with man's interests and welfare.

Obtaining enough food, clear water, and clean air, and satisfying man's needs for leisure, recreation, and aesthetic values, necessitates a sound ecological understanding of the problems of managing vertebrate pests. And because of the continuum of complex interactions that exist among living things, this requirement is not easily satisfied. Unfortunately, man's "progress," by definition, means alteration; and whenever the new balance or equilibrium (which animal populations establish following any manipulation of the original environments) either threatens the existence of a desired environment or results in a direct pest to man, artificial control or manipulation of the densities of such vertebrate populations then becomes necessary.

This paper briefly introduces the subject of vertebrate pest control, integrates and interprets some important ecological principles of control methodology, and intercalates these discussions with analysis of the biological backlashes and other ecological interactions that may be created whenever troublesome species of vertebrates are controlled by biological means. Insight in this area must be deepened if we are to fulfill our primary objective of learning how to manage a healthy environment in perpetuity. One important merit of biocontrol is that most people accept carefully planned ecological dislocations in nature more readily than they do the repugnant and hazardous aspects of eliminating nuisance vertebrates with poisonous materials.

Man is inevitably faced with conflicting ecological interactions, both from his pests and from the procedures he uses for alleviating the depredations of wild animals. In other words, since man is an integral part of the balance of nature, he needs greater insight into the factors that regulate the stability and productivity of modified ecological communities if he is to learn how best to cope with the dislocations he creates in nature. The ecosystem is the basic unit of structure and function that must ultimately be dealt with. It is kaleidoscopic in character, however, and such changing scenes and patterns are not easy to deal with since the ecosystem has many hierarchal levels and is like a quasi-organism, with its modus operandi consisting of factors that appear to be irreducible wholes.

The balance of nature is the dynamic adjustment — survival of the fittest — which occurs between organisms and other components of the ecosystem. At best, and only in the remotest areas, man is still concerned with only semi-naturalistic situations. By definition, in true natural situations no creatures are labeled "pests." Also, it is axiomatic that man will come into conflict with other phases of the environment around him, just as all wild animals also have numerous other species that are pests to them (Howard 1967).

Obviously, a keener insight is needed into the factors that regulate the productivity and stability of vertebrate communities. It appears that the essential logics of applied ecology, in this instance the control of vertebrate pests, will be determined in the future from new concepts about the complex biological entities involved -- not the quantification of biological measurements. Quantification per se is no longer as important as it used to be (except for facilitating the publication of the research). The complexity of ecosystems largely prevents elegant explanatory constructs for the time being, and this restricts effective use of sophisticated computerized language. At the moment, in this specialized field of applied ecology the prime research objective should be to discern the correct entities, for we are now in an era of conceptualization. Even though measurements are essential to permit class-conceptualization in logical order, measurements are no longer very profound by themselves.

Since vertebrate species become pests simply because they are well adapted to prevailing habitat conditions, biological control, in particular making the habitat unsuitable to the species in question (when such can be accomplished), is a much more desirable and effective procedure for controlling the offending animals than just attempting to destroy or otherwise remove individual animals. Biological control perhaps finds one of its principal advantages in that carefully planned ecological dislocations in nature are far more acceptable to most people than are the elimination of nuisance vertebrates with poisonous materials.

Even though biological control has not been developed to the same sophistication and effectiveness with vertebrates as with certain insects and mites, it still behooves us all to exploit every ounce of its potential effectiveness now. Actually, biocontrol of vertebrates is being practiced considerably more than most people realize. To appreciate this, merely visualize how many cultural and agricultural practices could easily be altered to create more serious pest problems, and even create new pests from species that are now quite innocuous.

DEFINITION OF BIOLOGICAL CONTROL

There are two broad approaches to reducing the density of troublesome populations of rodents, birds, predators, and other vertebrates. They are biological control and "conventional" methods of control. Control of vertebrates biologically implies the use of a biological process. This can be accomplished in several ways. One is by use of a biological agent such as a chemosterilant which disrupts successful breeding of the pest species; in another method a predator or disease may be used to increase the mortality rate. In addition, for the purpose of this paper an important form of biological control is intentional alteration of the pest's environment so as to increase mortality, reduce natality, or cause a significant dispersal from the affected area. Habitat modification may reduce food and cover or increase natural predation or debilitating diseases.

So-called "conventional" control methods, which are not considered further in this discussion, encompass such procedures as poisons, exclusion by barriers, chemical repellents, frightening devices (shape, motion, color, light, odor, and sound), shooting, traps and snares, stupefacients, anesthetics, wetting agents, electric shock, and bounty payments.

It is important that biological control as used herein be defined at the outset, for the reader might otherwise argue, with justification, that some of the conventional methods mentioned above might also be considered as biological control. Their role in this paper, however, is restricted to the ways in which conventional means might be utilized in integrated control to augment the effectiveness of certain biological control procedures. Another reason for defining biological control, as used in this paper, is that many entomologists have a different interpretation. Their usage has the average layman visualizing biological control of either weeds or invertebrates (and unconsciously projecting it to include vertebrates) as being the introduction of host-specific pathogens, parasites, or predacious invertebrates. Please note, however, that this viewpoint does not include habitat manipulation as a form of "biological control." Some entomologists (Stern et_al 1959) suggest that the term "biological control may apply to any species whether it is a pest or not, and regardless of whether or not man deliberately introduces, manipulates, or modifies the biological control agents." Their definition of biological control is as follows: "The action of parasites, predators, or pathogens on a host or prey population which produces a lower general equilibrium position that would prevail in the absence of these agents."

For the purpose of this paper the biological control of a vertebrate pest is defined as being an attempt to reduce the population density of a pest species (i.e., increase mortality, reduce natality, or cause a significant emigration) either by increasing predation, manipulating the conditions of the habitat, introducing or stimulating epizootics, or by the application of antifertility agents.

Even though relatively little knowledge is presently available on the utility of biological control methods in regulating undesirable population densities of vertebrate animals, this approach does show promise, especially in conjunction with integrated control. Integrated control, as used herein, places the primary dependence upon natural regulating forces and "biocontrol," and only initially and sparingly intercalates various "conventional" means of reductional control of the target species, and then only when absolutely necessary. Obviously of paramount importance is a keener insight on these non-pesticide approaches to controlling certain mammals, birds, and other vertebrate pests in order to avoid the incipient hazards of pesticides and to create self-regulatory ecological units. There is a need for ecological concomitance -- the living with natural forces -- and the development of more ecological and sophisticated approaches of integrated control. After all, vertebrate pest control is applied ecology, i-e., management of the behavior of individual animals and regulation of population levels, not the destruction of individuals per se. Therefore, all animal control should be based on prudent translation of the ecological laws of nature into an effective integrated management policy. What is really sought in vertebrate pest control is a reduction of troublesome populations to a tolerable level; in fact, the primary objective of vertebrate control should be the alleviation of damage, including the destruction of vertebrates only when that is a necessary adjunct to the alleviation of damage.

DYNAMICS OF VERTEBRATE PESTS

Vertebrate populations are plastic and dynamic, constantly fluctuating in density within limits imposed by their genetic constitution and the characteristics of the environment. Their density is primarily the consequence of self-limitation and the suitability of habitat condition (Howard 1965a), which man can often do little about, since, out of necessity, he must continue modifying his environment — at least until the human birth rate is checked. The interacting population stress factors that limit vertebrate densities include emigration, predatton, shelter, food, disease, social interaction, and various vicissitudes of 1ife.

Broadly speaking, the three basic self-limiting procedures that counteract the innate ability of vertebrate pests to produce an even greater surplus of offspring are the interaction of compensatory mortality, reduction in natality, or emigrations. At different times under special conditions, any one of these forces can play the dominant density-regulatory role. Toxic chemicals are utilized to provide compensatory mortality, and the antifertility action of estrogens provides a reduction in natality. What is needed, if biological control (including antifertility agents) are to be effective without drastic habitat modifications or use of pesticides, is some self-accelerating method of control that forces populations down by eroding their homeostatic capability.

Before attempting to exploit the full potential of biocontrol of vertebrates, one should also have knowledge about the dynamics of vertebrate populations and understand fully both the advantages and consequences of creating biotic imbalances intentionally. Changes in the composition of habitats can lead to other problems, such as a dispersal of the troublesome species into new niches. Many vertebrates have been able to alter their normal food and cover requirements to take advantage of the artificial habitats created by man.

All biotas, but some more than others, apparently have vacant niches, even in faunas that are otherwise well-balanced. This is borne out by the irregular pattern of success and failure of animal introductions throughout the world. Vertebrates are often acclimatized without any apparent reduction in the densities of other species of vertebrate animals. And, the wider the tolerance of an animal, the greater will be the number of suitable niches available for its survival without any immediate genetic differentiation being required.

When a farmer replaces a native vegetation with nonnative types of forage or cultivated plants (developed in breeding experiments) while of necessity ignoring factors such as natural selection by native animals, he may alter the habitat to such an extent that the native wild animals can no longer exist there. In other instances, the alien forage or crop may stimulate certain native mammals and birds to become so numerous that they may completely destroy the crop locally. The introduction of alien species may likewise result in the destruction of certain types of native vegetation. The probability that introduced animals will disrupt the natural stability of their new habitats depends upon many factors. If native animals are present that are closely related to those being introduced the chances are much less that the stability of the habitats will be weakened. That is why many species of big game ungulates introduced into the United States have not upset the stability of habitats and become serious pests, as occurred in New Zealand.

The density of any particular species of mammal, or of the total vertebrate components of the biomass, at any particular moment often appears to be influenced intrinsically not as much by a fluctuation in the amount of primary production as it is by variously inherited behavioral traits of the vertebrates involved and by intraspecific stresses (psychological, competition for food or mates, territoriality, weather, disease, or other vicissitudes of life). Animal populations have considerable powers of self-limitation, which prevent the severe overpopulations that would otherwise destroy the species. Self-limitation counteracts their innate ability to produce a surplus of offspring. Even though members of a species become their own brake to counteract their great reproductive potential, the upper density limits may be raised or lowered within certain ill-defined parameters whenever man modifies the environment. Individual animals often starve to death, die of disease, or are killed by storms, but populations of wild vertebrates do not completely exhaust all of the food over a sizable area, causing all of the occupants to starve. And, similarly, if provided food ad libitum, the populations will stop increasing when a certain equilibrium density is reached. It is this level of density that somehow triggers complex, self-limiting controls. This is Nature's way of preserving the species.

Faunal diversity provides a limited degree of natural control, i.e., it increases the capacity for continuous self-regulation of species with respect to their environment. When there is considerable diversity of fauna and flora, living things and systems then appear to be endowed with a self-regulating feedback mechanisms which guarantees their sustenance, adaptiveness, and perpetuation in a dynamic continuum. Just how the social behavior and bio-energetics of a species controls population density is not well understood, but individual animals as well as populations are dynamic in structure and behavior; they are not static units. The best example of how diversity in fauna and flora provides biological stability can be found in the tropics, where insect epidemics and extensive defoliation of vegetation are consequently a rare phenomenon. By way of contrast, compare this situation with extreme cyclic irruptions of herbivorous lemmings in the arctic tundra, where these rodents periodically denude their habitats. There is no question but that biological diversification results in greater stabilization of the environment and increased biological control. The reason that habitat diversification often cannot be the biological control procedure employed is because reduced diversity (even monoculture, e.g., much of today's agricultural practices) also leads to greater control of nature for the benefit of man. Economics prohibit doing otherwise because the modern home-maker does not wish to buy diseased fruit and vegetables or to pay higher prices for food products.

Perhaps the main reason some vertebrates are difficult to control is that they have high tolerances, low requirements, and quantitative resilience. Pest species of vertebrates often have steep population growth curves. To push these populations off the top of the classical sigmoid growth curves by biocontrol or any other means, onto the precipitous slope will be of no avail unless the control effort is unrelenting or something else counteracts the various biotic factors that nurture the growth curve and survival rate.

Biocontrol (for vertebrates in particular, the manipulation of habitat conditions) should not be employed a priori, because, if done improperly, the treatment can create more problems than it cures. In fact, it can cause more problems than the use of poisons. With repeated poisoning of vertebrate pests there is concern about the possibility of subtle and undesirable physiological and behavioral responses, or of carcinogenic and mutagenic effects on both the target species and on nontarget populations. However, when a habitat is modified, there is little doubt but what it will produce more pronounced interactions with other species of animals than would usually result from population reductions caused by either chemosterilents or toxicants. Observations indicate that natural biomes have a well-established, stable, animal-soil-vegetation complex which usually is not delicately balanced. A natural change (e.g., by disease) or man-caused change (e.g., by shooting), in the density of a native species of browsing, grazing, seed-eating, or predatory mammal does not precipitate a dramatic "balance-of-nature" type chain reaction of responses by other components of the biological community. Such chain reactions usually are the consequences of the introduction of alien plants or animals, farming, grazing, logging, man's use of fire, or natural catastrophic events (Howard 1965b), all of which amount to a significant habitat modification. And the main way that our native biotas have been degraded and fragmented is by the alteration of habitats. Take the coyote as an example. The coyote started out as a lonely predator of prairie dogs and rabbits in the Great Plains and other western parts of the United States, excluding Alaska. Then man came along, with lambs and chickens, and while he spread his civilization into the coyote's habitat, the coyote backtracked along man's trail. Now the coyote is found living almost anywhere from California to Maine and in Alaska.

Before man's use of biocontrol for vertebrates can come into full bloom, answers must be obtained to some difficult problems. For example, it will be necessary to learn what the interacting factors or forces are that enable a community composed of dynamic populations of many species to share the components of the environment in which they live so as to produce a relatively stable biota. But, out of necessity, to advance the understanding of basic ecological principles it also will be essential to limit such investigations to a manageable number of factors. An ecosystem has many hierarchal levels and is like a quasi organism, with its modus operandi consisting of constant changes in the production, storage, modification, utilization, and loss of energy; hence, perhaps its determining factors are irreducible wholes, which necessitate a holistic analysis in the development of concepts.

PREDATION

The use of natural enemies (predators) to control pest populations of vertebrates is not a simple procedure. The role played by vertebrate predators as enemies of pest vertebrates (e.g., rodents, rabbits, and birds) is not a phenomenon easily interpreted, even empirically. Before discussing potential methods of employing predators of pest forms of mammals and birds as a means of biocontrol, we must analyze some of the basic predator-prey interactions to learn to what extent native vertebrate predators are determinants of the population density of native species of vertebrate prey.

It has been my observation that the combined predation pressure by native hawks, owls, snakes, and carnivores usually establishes a greater, not lesser, seasonal and annual density of species of vertebrate prey than would otherwise exist. The magnitude of the natural vertebrate densities in existence for long periods over large areas is largely determined by the suitability of other aspects of the habitat and by self-limitation resulting from intraspecific stresses used in the broad sense (psychological, competition for food or mates, territoriality, weather, disease, or other vicissitudes of life), not by interspecific relationships between predators and their prey. Another weak point concerning the effectiveness of native predators in controlling pestiferous mammals and birds is that the predators concerned are not host-specific; in general usually being opportunists, taking what is most readily available. One way they may stimulate their prey to become more abundant is by feeding on the weak and unfit, thus tending to increase the average vigor and adaptiveness of their prey. Predators are also self-limiting, usually reproducing much more slowly than their prey, and often prey on other predators. Furthermore, even when predators actually do temporarily depress a vertebrate prey population, they do not necessarily reduce it to a density acceptable to man's needs.

It should be pointed out that in this discussion we are not concerned with the need of controlling predators to increase the density of a vertebrate prey which man intends to prey upon (harvest), such as lambs or chickens, or the product of fish hatcheries or game farms, or of any other situation where man makes such heavy demands on the prey species that he does not wish to share many individuals with natural predators. Man, of course, is the ultimate predator, and through his intelligence he has devised means whereby he can easily reduce the populations of many vertebrate prey species to a very low level -- in a few cases even to extinction. In his blind predaciousness and ecological ignorance, he has sometimes done just that.

My hypothesis -- "that vertebrate predators usually do more to increase population densities of field rodents than they do to depress them" -- implies that, without predation, self-limitation stress factors come into play at lower density levels, and that these forces operate as population controls more drastically than does predation. This predator-prey theory also implies that natural selection has enabled native predators to stimulate their natural prey populations to exist at the ecologically optimum density. Optimum density here refers to the total number of individuals that the habitat can support on a sustained yield basis.

This concept is not new. As Scott (1958) pointed out, Forbes (1880), in writing about birds, asserted that "annihilation of all the established 'enemies' of a species would, as a rule, have no effect to increase its final average numbers" and, in a later paper (Forbes 1882), he also stated that excessive populations *are* "in one way or another, self-limiting." According to Huffaker (1958), "density-induced autoinhibition or intraspecific competition in the broad sense is the only true governing or equilibrating mechanism." Specific mortality factors like predation seldom persist long enough to have an appreciable effect on the over-all density of prey populations; instead, the mortality level may precipitate natural population responses tending to offset it (Errington 1956). For the most part, predators feed on prey that already has a poor life expectancy, and even excessive predation can be compensated for by accelerated reproduction. Accrued evidence indicates that much predation, even when conspicuous and severe, may operate in an incidental fashion rather than as a true depressant (Errington 1946). Rodents, hares, and grouse all decreased in numbers at the very time when 22 species of their avian and ground predators were thought to be controlled (Crissey and Darrow 1949). Pocket gopher numbers showed no correlation with the presence or absence of coyotes (Robinson and Harris 1960). "Voles probably exemplify a general law that all species are capable of limiting their own population densities without either destroYing the food resources to which they are adapted, or depending upon enemies or climatic accidents to prevent them from doing so" (Chitty 1960). "Instead of competing directly for food, animals compete for conventional substitutes, e.g., territory or social position, which are capable of imposing a ceiling density at the optimum level, and can prevent it from rising to the starvation level which would endanger future resources" (Wynne-Edwards 1959). It seems obvious that the predators of lemmings in Alaska, as reported by Pitelka (1958), were largely opportunists exploiting prey that could not have survived anyway; the predators only delayed, hence perhaps magnified, an already inevitable rodent population crash. Predation may be considered a beneficial service for most prey species, and for some species it may even be important to survival (Latham 1951). The rabbit plague in West Wales leaves no doubt that, wherever "skimming" a population by trapping was introduced, "the rabbit population increased by leaps and bounds" (Hume 1958).

The concept that predators usually do more to stimulate numbers of vertebrate prey than to depress them requires a proper appreciation of both the period and the size of area involved. Unless otherwise stated, the period is a long one, including many generations of the species; it does not apply just to part of the normal lifetime of specific individual vertebrates. Likewise, each area involved is large enough to support entire populations of both the predator and prey species; the hypothesis is not concerned with small areas containing only a few individual territories or home ranges.

Pearson (1966) made a very intensive study over a 3-year period analyzing the frequency with which rodents (mainly Microtus californicus and Reithrodontomys megalotis) appeared in the droppings of carnivores feral cats, raccoons, gray foxes, and skunks) on a 35-acre study area. On the basis of the thoroughness and the timing of the carnivore predation, and on the absence of cycles in an island population of Microtus free from carnivores, he postulates that carnivore predation is an essential part of the regular cycle of abundance of Microtus, lemmings, and other microtines. His theory does not imply that the carnivores destroy the top of the mouse cycle, but rather that they bring the cycle down to very low levels after something else has helped to remove the peak mouse population.

Natural selection has seen to it that both the vertebrate prey and their predators require each other if they are to exist in nature in optimum densities. It is the author's hypothesis that predators usually cannot permanently depress vertebrate population densities; instead, they usually increase the vigor and reproductive success of the prey enough that they eventually more than replace any individuals that the predators may destroy. Since predators have evolved under natural selection, predation must in some way favor keeping their food supply (the prey species) at the maximum density inherently permissible under self-limitation and remaining within the thresholds of security of the ecosystem. It seems likely not only that the average population density would be less, but that the cyclic peak densities (irruptions) of most species would also be less, not more, if there were no natural predators to assist in precipitating such cycles. Without predation as a continuous or periodic stimulus for prey populations to increase in numbers, the self-limiting factors of population controls apparently come into play before the density of such populations has attained what the habitat could support under the influence of sustained predation.

One way in which predators may bring about a higher density is by maintaining a younger age class within the prey population. Younger but reproductively mature individuals of at least some species may have smaller home ranges and less-defended territories, yet reproduce as rapidly as older animals. Many types of stimuli can prompt vertebrates to increase their numbers. Game managers have been proclaiming for some time that the proper intensities of fishing and hunting can result in an increase in fish and game. The livestock operator learned long ago that adequate harvest is essential to maintain a maximum carrying capacity of sheep or cattle.

If a deer herd is protected from all natural predators as well as from hunters, it will "become to some extent self-limiting after it develops an over-population" and its productivity and population density will then decline (O'Roke and Hamerstrom 1948}. Darling (1937) pointed out how "antisocial behavior" limits red deer. The Wisconsin Conservation

Department has shown that liberal hunting regulations increase the deer herd (Dahlberg and Guettinger 1956). In the western United States the development of overpopulated big-game herds is correlated positively with an increase in the total numbers of hunters (Rasmussen and Doman 1947). Control of predators was once credited with a pronounced population increase and subsequent die-off in the early 1920's in protected deer of the Kaibab forest, in northern Arizona, but a closer look at the factors responsible seems to indicate otherwise. According to Lauckhard (1961), "Game men are now convinced that the removal of cougar from the Kaibab had nothing to do with the boom and bust of the deer herd. The deer increase apparently was the aftermath of some habitat changes."

Many bird and mammal predators are attracted to areas that support concentrations of palatable prey species, but, once the surplus or excess prey disappears, the remaining prey is largely inaccessible to predators living in that area. As a consequence, predators that are highly mobile may well leave such areas if they are not too involved in breeding responsibilities, and they may become pestiferous predators in their new habitats. It is common knowledge that insectivorous birds often disappear from areas following insect control operations, as a consequence of loss of food supply (e.g., see Couch 1946; DeWitt and George 1960; Rudd and Genelly 1956). Less mobile animals like fish in a stream, may succumb if the insect fauna is artificially depleted. Even though it is virtually impossible to separate analytically all influencing factors in these situations, a number of studies have shown that loss of food supply following spraying operations has contributed materially to fish die-offs (Cope 1960; Cope and Springer 1958; Graham and Scott 1959; Kerswill 1958). A similar phenomenon occurs when rodents are removed. Their predators, the hawks, owls, snakes, and carnivores, must then move to new localities or suffer malnutrition (Howard 1953)

Natural Predators

The previous remarks about predation make a fairly strong case that natural predators are not effective regulators of populations of vertebrate prey species. The answer is not that simple, however, and bona fide exceptions to the aforementioned hypothesis can undoubtedly be found. Nevertheless, it is apparent that in analyzing the regulatory mechanisms involved in the control of vertebrate prey species by natural enemies, much more insight is needed on basic behavior, ecology, and host-parasite and predator-prey interactions.

Regarding natural predators, it should be pointed out that the unquestionably high esthetic value of natural predators cannot be emphasized too strongly. Also, since natural predators *are* a dynamic component of ecosystems, their numbers should never be manipulated artificially, either up or down, without first employing considerable ecological wisdom in the process. And we must all be quick to confess that many significant questions concerning the potential importance of natural predation in controlling troublesome species of vertebrates are yet to be resolved.

Perhaps the most thorough study of predation by hawks and owls on a rodent population in one township was conducted by Craighead and Craighead (1956). They "conclude that the total weight of food required by a raptor population and the number of prey animals killed during a year are of such magnitude that raptor predation must be recognized as an effective biological control; furthermore, that the way in which raptor predation acts on collective prey throughout the year to effect this prey reduction strongly suggests a precise regulatory force." As a matter of semantics, I am not sure they are correct in saying that raptor predation is "an inexpensive form of control" of noxious prey species, while also contending that "under natural conditions no one prey species can draw enough predation pressure to keep its population at a dangerously low level," because, before most vertebrate pests can be considered "controlled," they must be reduced below a dangerously low level so that they cannot promptly build up again.

One must be careful how one appraises the pros and cons of the value of vertebrate predators. For example, one author (whom we will not cite since his views have probably changed) reasoned that the destruction of 110,495 coyotes in one year in the western United States was a serious mistake. He said that, if they had not been taken through control, they would have justified their existence, theoretically, by killing and consuming the entire mouse population from 33,000,000 acres, and that the removal of the mice by the coyotes would have saved a considerable amount of forage. The fallacy in this line of reasoning is, of course, that both the time factor and the reproductive potential of rodents are overlooked. The rodents would have been reproducing during the entire year, quickly compensating for those eaten by the coyotes. The coyotes also would have been having pups during the period when they were being destroyed. No matter how many coyotes are present, they do not seem to be able to decrease, let alone eradicate, their food supply. Natural selection has evolved a situation wherein predators are favored most, when they can stimulate the development of the maximum possible prey population. At best, predators act only on the symptoms of most vertebrate pest problems; they cannot treat the disease, which is the condition of the habitat. "

"Birds are common targets of predaceous mammals and carnivorous birds. ... in the best study of its kind, Tinbergen (1946) showed that European sparrow hawks took a large percentage of house sparrows during a given year (perhaps 50 percent). Nevertheless, he could not conclude that the population was importantly impaired from year to year. Moreover, in other areas of England and the Low Countries where sparrow hawks have been assiduously removed, there seems to be no compensating increase in house sparrow populations. . . . Irrespective of a bewildering welter of apparently conflicting data and views, it seems likely that predators are not a dominant influence in the control of most mammalian populations. . . . Some mammals, like some birds, can be extraordinarily effective hunters. . . . But even among these skilled hunters, the victims seem most frequently to be the handicapped - - the immature, the wanderer, the ill-adapted. The removal of such prey may conceivably result in more vigorous prey populations rather than less" (Rudd 1964).

Introduced Predators

It has been demonstrated that one or more introduced predators in a localized situation, e.g., house cats, can sometimes depress, and keep depressed below environmental capacity, a confined population of rats or house mice for as long as the diet of the cats is supplemented periodically with other food. When house cats living about a farm house or barn are forced to subsist entirely upon what is available to them in the form of wildlife, they can do so only if the habitats of the wild animals are sufficiently favorable that the cats are unable to destroy the populations of mice and rats which are their food supply; otherwise, the cats also would die or be forced to disperse. "Cats have a great advantage over human beings in the control of rat populations at a very low level: they do not seem to get bored! The psychological problem of such maintenance work may to that extent be helped. . . . From these and certain other instances, it is concluded that if a sufficient number of cats (say four) is introduced after complete rat extermination has been done, and if part of their food is supplied as milk, they will maintain the immediate area of the farm buildings rat-free. They will not necessarily clear a farm of an existing rat infestation. The quantity of cats is probably more important than their quality. To keep cats on this scale is certainly more expensive in human food (used for the cats), than if human servicing was used for rat clearance, but it supplies a useful and efficient source of additional labor, which has the important attribute of maintaining the efficiency of control at very low rat densities" (Elton 1953). It should also be recognized that having cats around a household or farm means that certain species of birds will not be able to nest successfully in the same area.

Alien predators introduced for biological or entomophagous control of insects can occasionally reduce the density of a localized population of a species of prey that evolved in the absence of that predator, although purposely introduced vertebrate predators usually have not been as effective in permanently reducing the population densities of their newfound species of prey as was anticipated by those who introduced them.

McCabe (1966) cites a personal communication from W. W. Dykstra that "The U. S. Fish and Wildlife Service has had some success in controlling herring gulls in the Boston Harbor area near the Logan Airport. On small islands where only gulls were breeding, foxes and raccoons were liberated. These predators, of one sex only, reduced the reproduction on the test islands by as much as 95 percent." The predators were trapped and removed after the food supply had been exhausted.

"During the period 1910-1930 an area of 600 hectares of the Frisian island of Terschelling was planted with young trees. Much damage was done to these plantations by water voles, Arvicola terrestris terrestris (L.). For the biological control of this pest 102 weasels, Mustela nivalis L., and 9 ermines, Mustela erminea L., were introduced in 1931. The weasels disappeared within 3 years, the ermines on the other hand increased strongly and had to be controlled in turn. They exterminated the water voles within 5 years and reduced the population of the rabbit, Oryctolagus cuniculus (L.), on the island to an extremely low level." Soon the ermine commenced feeding on sparrows, starlings, terns, shellducks, curlews, other waders, poultry, tame ducks, and even turkeys. "After 1939, however, a state of natural balance seems to have established itself, the ermines, though still common, are by no means a pest anymore."

Dogs, either tethered or running free, can be utilized to frighten away coyotes and smaller predators from poultry, deer from small paddocks, etc. At several Canadian and European airfields, trained falcons have been employed to reduce the numbers of birds, which are a potential hazard to aircraft operation.

The intentional introduction of predators to control troublesome species of vertebrates, obviously, should not be undertaken until after all potential ecological consequences have been carefully scrutinized. Introduction of a predator onto a very small island or other isolated locality might result in complete extermination of a certain kind of vertebrate prey, but in most situations an introduction of alien predators into a new ecosystem is not only perilous but may prove to be catastrophic, because the predators of vertebrate pests are not host-specific. Tragic examples include introduction of the mongoose into Hawaii to control rats, the fox into Australia to check rabbits, and New Zealand's introduction of weasels, stoats, and ferrets in the mistaken belief that they would control the rabbit. All of these introduced predators not only failed to accomplish their mission but have themselves become troublesome predators. "Failure resulted because two ecological contingencies were not recognized; (l) that predators are usually versatile and rarely obligate, particularly out of native habitat; and (2) that predation by one species alone is only rarely a population regulator of vertebrate animals" (McCabe 1966).

HABITAT MODIFICATION

Whenever food supply, shelter, or other factors of the habitat are changed, the animals reflect the change in some way. Habitat selection is an important intrinsic factor favoring the localization of populations; hence, vertebrate species that have become a pest have usually done so because they are so well adapted to the prevailing habitat conditions. The basis for biological control is to discover a means of modifying existing biotic conditions so as to reduce specific pest populations by causing emigration, starvation, or debilitation of some type that results in lowered natality and/or increased mortality.

Yet, isn't it a bit incongruous that making the habitat intolerable to a pest population is generally considered a much more desirable control procedure than selective destruction of the target species with pesticides or other conventional control means? From the ecosystem point of view, the use of a relatively specific pesticide is far better than any intentional modification of a habitat. Any habitat manipulation that effectively reduces the troublesome status of a population of vertebrates will most likely alter the entire ecosystem, i.e., effect the species composition and density of all other kinds of vertebrates and invertebrates living in that ecosystem, far more drastically than could result if the same degree of control was achieved by some relatively selective "conventional" control method. This is because the most important factor determining the presence or absence of any animal in a given locality is the suitability of the habitat to that species, not inter-specific competition. Also, since many of the pest vertebrates have been able to adapt successfully to modified environments, any habitat modification may create new and unsuspected problems stemming from other species of vertebrates.

If one is willing to accept the ecological consequences, many kinds of vertebrate pest problems can be greatly alleviated by modifying the habitat. Orchards or other trees near a vineyard invite greater bird depredations. The removal of oak trees and cottonwoods adjacent to walnut and almond orchards reduces losses to crows, magpies, woodpeckers, jays, and gray squirrels. Woodlots in close proximity to cultivated fields often increase pest problems to agriculture, regardless of whether hawks and owls take up residence in the trees. Clean farming that eliminates cover along fence rows and field margins is generally frowned upon by conservationists. It pays off, however, where bird attacks on rice are prevalent (Neff and Meanley 1957). Restricting to a minimum the storage of grain in field shocks prevents rodents from building up to pest proportions. It hardly needs elaboration here that removal of the nesting, shelter, and roosting places can significantly reduce many types of vertebrate pest problems.

A dramatic example of how important an alternate or buffer food can be in helping reduce crop damage by troublesome vertebrates is found in one solution to waterfowl depredations. Ducks and geese, which can be very destructive to many kinds of crops (Biehn 1951), can be frightened away from valuable grains, vegetables, and pasture land if waterfowl refuses are available in the general vicinity to provide adequate resting areas and sufficient food to hold the birds until the crops are harvested. Otherwise, various herding and frightening devices are much less effective.

In some special instances, vegetative barriers can be planted. A 16-foot strip of rye sown around the edges of a barley field on a wildlife refuge reduced jackrabbit damage to the barley (Lewis 1946). Since the jackrabbits do not relish rye, they apparently did not enter far enough to discover the barley.

Indirect control of moles through reduction of the food supply, though comparatively expensive, is useful on lawns and golf turfs (Marsh 1962). The same technique can be used to discourage skunks from digging in lawns for grubs and other insects (Merrill 1962).

Sanitation has long been recognized as an effective means of controlling rats and mice biologically. The rat problem in Baltimore was greatly reduced when a program of food and cover destruction was undertaken (Emlen 1947).

In some situations there is every reason to believe that the intensity of undesirable browsing of young conifers by deer might be substantially reduced by increasing the amount and availability of alternate and more preferred species of browse. Such an increase in food supply will not necessarily result in a corresponding increase in deer numbers, nullifying this benefit. Of course, the most logical way of managing temporary deer problems related to forest regeneration is by liberalizing the bag limit and the hunting season.

Some of the noxious forms of vertebrates, especially those in urban areas, can be controlled by carefully regulated practices that cause a minimum of adverse side effects (undue hazards to health, injury to nontarget species, or residues on agricultural commodities), but control practices against species which attack agricultural crops, stored foods, rangelands, and forest trees present more difficult problems (Swift 1964). These instances require a great deal of additional ecological knowledge. What is needed for effective biocontrol of vertebrates is some self-accelerating method of control that forces populations down by eroding their homeostatic capability (Watt 1964).

"The search for bird-resistant varieties of cereal grains is a field of biological study likely to yield long-lasting results, even though early results have been somewhat disappointing. . . . Cultural practices and habitat manipulation may also be relied upon to alleviate bird damage in some situations" (Besser 1962). One reason why biological control of birds has been difficult is the ecological versatility of the species that have become pests.

"The use of effective bird-resistant varieties of crops, while not at present a reality, may yet prove to be one of the more promising means of combating bird depredations in the future," according to DeGrazio (1964), who cites some research results. Three blackbird-resistant varieties of grain sorgum (Northrup King 120, Northrup King 125, and Adkins-Phelps 614), although growing alongside heavily damaged corn field, had less than one percent damage. A tight-husked hybrid variety of corn that was thought to be bird-resistant, however, sustained heavier damage than surrounding corn because it was slow in maturing, being still in the vulnerable dough stage after the other varieties had begun to harden.

An example of how habitat modification can reduce a vertebrate pest to a low level is provided by Keith et al. (1959). Aerial spraying of weedy, mountain rangeland in western Colorado with a herbicide (2, 4-D) resulted in the following changes one year after treatment: The pocket gopher population was reduced 87 percent, the production of perennial forbs was reduced 83 percent, and grass production was increased 37 percent. This decrease in gophers was probably due to the decrease in forbs available to them. Gophers do better on forbs than on grass, and the spraying changed their diet from 82 percent forbs to 50 percent, and from 18 percent grass to 50 percent. In unpublished U. S. Department of Interior, Fish and Wildlife Service Reports of 1946-1948, M. W. Cummings found that up to 90 percent of the gopher population on Grand Mesa, Colorado, was removed by weed control with herbicidal sprays (Cummings 1962).

Of the many examples of how habitat modification either creates or controls various species of field rodents, only a few are cited here. Land-use is habitat alteration, and when the habitat is changed man must expect some undesirable things along with the good. The establishment of alfalfa or other irrigated pastures creates a favorable habitat for pocket gophers and meadow mice; but at the same time this altered habitat becomes inhospitable to a large number of other kinds of rodents. Even light grazing by cattle on California annual rangeland is enough to make the habitat more suitable to ground squirrels.

Control of European rabbits in New Zealand has probably been greater from extensive applications of lime and superphosphate fertilizers than from toxicants, because rainfall there is equally distributed through out the year and the veqetative response to fertilization produces such a rank growth of grass that such habitats become unsuitable to this rabbit (Howard 1958). A dense stand of herbaceous vegetation favors meadow mice, but mowing or grazing by livestock makes it no longer favorable. Cultural practices in apple orchards sometimes require a sod-type of ground cover with the addition of heavy mulches around tree bases, and this favors meadow mice. Prunings piled around the base of the trees as a buffer food often minimizes mouse damage except during severe winters (Fitzwater 1962). The bare habitat produced temporarily by range improvement practices of converting brushlands into grassland, greatly favors some species of rodents, which then become a serious pest until the herbaceous vegetation is well established. Cutting timber improves the habitat for certain rodents, deer, and rabbits, creating serious silvicultural problems until new seedlings are established and have grown out of the reach of troublesome species of vertebrates.

DISEASES

Disease can be looked upon as the result of forces of ecology; for epizootics that from time to time locally decimate populations of some kinds of vertebrates do so as a result of a dynamic relationship between three principal factors: the effect on the host species, the agent of disease, and the current environmental conditions. The way disease affects the dynamics of vertebrate populations is largely ecological and not a mere interplay between the host and the agent. It is because of these ecological forces that disease becomes a potential biological controlling factor. But "under any situation, an epidemic is only a temporary phase, and it can only be understood when it is related to preceding and succeeding events" (Jones 1964).

Before the implantation of disease-causing organisms can become an important tool in the control of vertebrates, more knowledge is needed on the complete ecology of such epizootics and on the associated inherent hazards of artificially manipulating the dynamics of such disease agents. I would like to quote a few basic rules that must be taken into consideration regarding the role of disease in vertebrate control, from a paper by Herman (1964). It is a concise description of the basic problems involved.

1. The applicant organism must be demonstrated to be highly pathogenic to the prospective subject species. Usually, a disease which occurs normally in the subject species is not a potential applicant, or it would already be doing an adequate job. Thus, the applicant is more likely to be an organism exotic to the subject species.

2. The potential killing power, residual duration, and ultimate resistance must be anticipated. One should strive for as complete knowledge as possible concerning long-range consequences to the total population and survival of the subject species.

3. The applicant organism must be host-specific. We cannot, for example, introduce into blackbirds a disease that would be a threat to other birds, livestock, or man.

4. The applicant organism must be available. Not only is it necessary for sufficient supply of infective material for the initial implant, but the natural environment must be favorable for its perpetuation if the desired impact is to be achieved. If a vector or intermediate host is essential, it must be present in the environment.

5. If initiated, the control program should be monitored in every detail to ensure its progress in the direction anticipated without adverse detrimental side events not anticipated.

"In searching for natural foci of disease agents in wildlife, it is logical to study habitat types which have a large and relatively stable wildlife population. In such foci one does not expect to observe diseases in the reservoir wildlife hosts, but if the viruses, rickettsia, bacteria, or fungi set up chains of infection in aberrant hosts, this may result in epidemics of disease, sometimes having a high mortality" (Johnson 1964). Peak populations of wildlife *are* reached in altered environments and successional changes in the vegetative cover. It is during these situations when disease agents in wildlife are apt to spread to new hosts and start epidemics. But, of course, intentional introduction of exotic species of animals or plants into an environment just to precipitate epizootics among the native pest vertebrates is not a procedure to initiate recklessly. Yet, there may be sophisticated ways developed for modifying the habitat to increase the incidence of certain fairly specific pathological mortality factors in pest vertebrates.

The number of different kinds of significant debilitating diseases which may cause numbers of wildlife to succumb is quite large. And much larger still is the number of kinds of parasites and other pathogens involved. The specific diseases of man known to be derived from wildlife are many. For example, in just the state of California we find: "rabies, Western encephalitis, St. Louis encephalitis, Colorado tick fever, Rocky Mountain spotted fever, relapsing fever, Q-fever, plague, tularemia, murine typhus, lymphocytic choriomeningitis, psittacosis, leptospirosis, salmonellosis, and toxoplasmosis. A variety of bacterial infections may be contracted from wild animals, notably those caused by Pasteurella pseudotuberculosis, Pasteurella multocida, Bacillus anthracis, Erysipelothrix rhusiopathiae, Clostridium tetani, and Listerella monocytogenes. Certain of the fungus diseases, such as coccidioidomycosis and histoplasmosis, are derived from exposure to wildlife habitats. California virus has been isolated from arthropods collected in California and Rio Bravo virus from bats. Serological tests have shown that these viruses may produce infection in man. During field studies of arthropods, small mammals, and birds in California and Oregon, several viruses have been isolated which may prove to be of importance as disease agents, i.e., Modoc virus, Turlock virus, Kern Canyon virus, Hart Park virus, and two yet-unnamed Viruses isolated from Microtus montanus meadow mice" (Johnson 1964).

Quoting further from Herman (1964): "There is a tremendous volume of published data on the occurrence of potential disease-causing organisms in wild birds. Most of it relates to discovery of new parasites and their taxonomy. Case reports, histories of prevalence or frequency of specific diseases in limited areas or summaries of such reports are rare. Details of pathogenesis or pathology, or a clarification of life cycles, that tell of disease potential or mode of infection are even rarer. Epizootics occasionally have been recognized in wild bird populations, but the causes often remain unidentified. In contrast, there are many case reports for single individuals; these only suggest a potential for losses and are not evidence of actual epizootics. . . . Epizootics in which large numbers of birds die of a diagnosed cause have been recognized in very few cases. The most dramatic is botulism which causes extensive losses among birds, particularly waterfowl. Development of the disease is related to habitat contamination; a toxin is produced by the growing botulinus bacterium and the birds get sick from consuming this toxin. The bacteria grow best in the absence of oxygen and thus the disease occurs in association with decaying animal or plant matter which produce conditions ideal for such growth. Outbreaks have been reported primarily among waterfowl, shorebirds, pheasants, and poultry. . . . Bacteria of the Salmonella group are among the chief causes of disease losses among captive birds, such as poultry. These bacteria are pathogens of the intestines and cause disease, often fatal in a wide variety of animal hosts . . . Salmonella infections have been reported from starling, rusty blackbirds and cowbirds in New Jersey . . . Potentially they could cause extensive losses among wild birds but, to date, no severe outbreaks have been noted in North America. Encephalitis is a virus-caused disease which has had much publicity in recent years. . . . English sparrows and pheasants are the only species of our wild birds known to have died from encephalitis. . . . Pox, another virus infection frequently recognized in birds, is manifested by the development of small tumors (up to the size of a pea), usually on the beak or feet. . . . The so-called Rous sarcoma virus appears to be connected in some way with the occurrence of Leukemia, a disease which takes a large toll in poultry and is known to occur in wild birds as well. In a survey we have been conducting on blackbirds, we have uncovered at least 65 species of parasites, either by our own examinations or from reports in the literature. All of these parasites must be considered to be potential pathogens, even though we have not yet uncovered evidence of disease that can be attributed to any of them. Each must be studied experimentally to determine mode of infection and the circumstances under which it can be harmful or fatal to the host. The main point I wish to bring out here is that none of these parasites are host-specific to the blackbirds and they can be expected to be found in at least a variety of passeriform birds if not in most species of birds. Parasites are likely to be more narrowly host-specific than bacteria or viruses, but even with parasites the range of infective hosts can usually be expected to include most of the passeriform species."

The classical example of a disease agent's being used intentionally to control a wild animal population is provided by the story of myxomatosis in Austral is (Fenner and Ratcliffe 1965), where results were truly fantastic before the virus became attenuated and qenetic resistance appeared in the rabbit population. Quoting further from Herman (1964): "Prior to release of the myxoma virus (causative agent of myxomatosis) many experiments had been performed to test its control potential. It had been demonstrated that the virus is nearly always lethal to wild and domesticated forms of the European rabbit (Oryctolagus cuniculus). Further, it had been demonstrated that all common domesticated animals, as wel1 as representatives of the native fauna (mostly marsupials) and the introduced hare (Lepus europaeus, were refractory.

"Early experiments with myxoma virus did not portend the later success. . . . The importance of mosquitoes as vectors of the disease was not known when these initial field tests were made. Transmission of the virus was reported to be mechanical. Australian investigators have shown that a number of blood-sucking arthropods are capable of transmitting the infection but that mosquitoes are the chief vector. The vector has been referred to as a 'flying pin'; in other words, its mouth parts become directly contaminated with the virus rather than by the virus developing or multiplying within its body. Thus, any arthropod which would feed on a lesion on an infected rabbit and then bite a susceptible host would transmit the virus by contamination.

"An interesting series of events also occurred in Europe. A French doctor, desiring to reduce the native rabbit population on his walled estate in France, released the virus and dramatically reduced his local population. Since this virus can be transmitted by free-flying arthropods, the wall around his estate was no barrier and the disease spread through much of Europe and also to the British Isles. The kill of the native rabbits was as dramatic as it was in Australia. The gains to agricultural interests have been great, but the sportsman lost his most important trophy, and the numerous people who kept a few rabbits in the backyard as a source of food lost this supply of supplementary protein.

"For completeness of the myxoma story, I must point out that for several decades outbreaks of myxomatosis have occurred among commercial rabbitries in California. Our native cottontails are presumably the reservoir of infection. The cottontails are susceptible to the virus but develop no characteristic lesions, manifestations of the disease, or fatalities."

Davis and Jensen (1952) reported on experimental attempts to introduce an epizootic among wild rats living naturally on a farm in Maryland. Into this population, which preliminary studies had indicated was free of any Salmonella, they inoculated a bacterium, Salmonella enteritidis, which is considered highly pathogenic to rats. It causes extensive intestinal involvement and is transmitted in contaminated feces from infected animals.

Herman's (1964) analysis of this experiment is as follows: "Although Davis and Jensen did not fully explore the population changes, it was certain that the population doubled during the interim of their study, and thus the induced Salmonel1a could not be considered effective in lowering the population. They point out that their data show clearly that an organism of potential pathogenicity may have no measurable effect on population size, mortality or reproduction. They emphasize that their data indicate the complexity of disease phenomena and warn against hasty conclusion about the role of pathogens in population management." Only limited success has resulted from a commercial bacterial rodenticide called "Ratin," which has a short shelf-life.

According to Herman (1964): "There undoubtedly have been many unreported attempts to control wildlife populations with disease-causing agents. It is known that as early as the 1880's Pasteur recommended the introduction of a bacterial pathogen to reduce the rabbit population in Australia; in fact he sent one of his assistants to Australia with cultures of the organism. However, cautious government officials vetoed the project.

"A number of years ago I was told of a 100 percent successful project to eliminate the wild pig population on a privately owned island off the coast of California by the introduction of hog cholera virus. But to my knowledge this event was never documented. More recently, similar attempts (personal communication from Schroeder 1964) to eradicate native swine on another island off the California coast with this virus yielded disappointing results. While it was demonstrated that the disease was well established in a few animals there was little spread and the investigators concluded that the use of live cholera virus in depopulating wild swine is not satisfactory. Because of the repercussions that might occur from potential dangers of introducing a disease into a population, it is only subsequent events, such as resulted from the release of myxoma virus by the French doctor, that bring these attempts to the attention of the public or even the scientific community.

"An epidemic (involving man) or epizootic (involving animals) is a complex phenomenon. Its full understanding requires a thorough knowledge of the biology of the causative agent and associated organisms, of the definitive host and vectors; and of the transmitters of intermediate hosts if they are involved. It also involves a knowledge of the interrelations of various hosts that may become a part of the complex, plus data on ecology, environment, behavior, food supply, immunology, pathology, and more."

CHEMOSTERILANTS

Antiferti1ity agents have been largely unexploited in regulating the population levels of troublesome species of vertebrates, and there is prodigious need for a safer, more effective, and generally acceptable means of reducing artificially the reproductive rates of native and introduced species of mammals, birds, reptiles, and fishes. If harmful populations of pestiferous vertebrates can be effectively suppressed with an economically efficient application of reproductive inhibitors, the need for toxic chemicals would be lessened, thus reducing the contamination of biotic environments.

Chemosterilants cannot change the general equilibrium position of pest populations permanently, so repeated applications are required to restrain the populations from again increasing beyond the economic density threshold. Chemosterilants will not be a panacea for all rodent control needs, but they will probably become a valuable adjunct to integrated control of pest species, with a conscious harmonizing of the use of antifertility agents with other biological and conventional control methods. A combination of sterilants and conventional methods will probably make synergistic effects possible, with the degree of control greatly exceeding the sum of the independent effects of each method.

When reproduction can be suppressed economically, this procedure is far superior to attempts to regulate population densities by increasing one or more mortality factors. If the objective is to develop safe, selective, effective, and acceptable means of regulating densities of vertebrate populations, a logical first approach is to find a means of suppressing reproduction rather than increasing mortality rates through the use of pesticides. As Balser (1964a) pointed out, "it may be more practical to prevent animals from being born than to reduce their numbers after they are partially or fully grown and established in a secure environment. Increasing one or more mortality factors often results in a compensating increase in reproduction or survival or both. This reduces the effectiveness of any control program. By suppressing reproduction, the compensating increase in reproduction may be overcome, while survival may be increased in the remnant population. Movement or ingress which occurs when animals are removed from a population may be lessened by occupation of territories by treated coyotes."

Wetherbee (1964) wrote: "Birth control should not be viewed as the panacea for pests, however. By definition vertebrate pests are weeds — organisms with high tolerances, low requirements and quantitative resilience. The vertebrates that we classify as pests have very steep population growth curves. Populations of many of the vertebrate pest species are probably at or near the leveled off top of the classical sigmoid growth curve. To artificially push them off the plateau, by biogenetic control or any other means, onto the precipitous slope of the sigmoid growth curve is of no avail unless the biogenetic control effort be unrelenting or else it be accompanied by a concurrent control of the biotic requirements that nurture the growth curve and survival rate. A half sterilized bacterial culture doesn't remain sterile for long, neither does a reproductively inhibited population of dump fed rats."

Many scientists have postulated that a given number of sterile individuals in a population exerts a much greater biological control pressure on that population than removal of that same number of fertile individuals. This concept that those that remain not only fail to contribute to the next generation but meanwhile compete for space and food and social order is correct biologically, since it is based on the population principles of density dependence and the sigmoid growth curve; but it is of little importance to the farmer or other individual who may be troubled by a vertebrate pest. Also, it will be necessary to determine whether the sterile individuals still behave as fertile individuals socially. Should they lose all aggressiveness and become submissive individuals, it is conceivable that they might then be ignored in the normal territoriality and peck order of the group, so that the population threshold might be increased. Since Vertebrates are long-lived in comparison to insects, and since, once they become a pest problem, it is usually not possible to wait out the life span of the noxious individuals involved, antifertility agents will probably prove most helpful in maintaining populations of vertebrates at a low level after they have been brought there by other means.

Birds

Davis (1959) found that triethylene-melamine (TEM) inhibited testicular recrudescence in starlings, causing the testis to become merely an interstitial organ, and concluded that the use of a gametocide promises to add sensitivity to control measures. In a field test on red-winged blackbirds, this cytocide inhibitor of meiosis did cause a measurable reduction in hatchability and the number of nestlings produced per nest (Vandenbergh and Davis 1962). Of great significance is their observation that TEM had no discernible effect on pairing or other mating behavior. Behavior changes also did not appear in rats administered TEM (Bock and Jackson 1957). One difficulty in using TEM on the red-winged blackbirds is that it had to be made continuously available to the birds during the breeding season. "While TEM on the basis of Davis[1] work presently has the highest candidacy for operational use against male birds (in spite of negative findings that we have experienced when the compound is used on sexually active male birds), Enheptin (2-amino,5-nitrothiazole) also has potential for special purposes. This compound tested at the Massachusetts [Co-operative Wildlife Research] unit has no effect upon rats but has differential potencies among bird species" (Wetherbee 1964)

In Elder's (1964) 4-year search for a practical oral contraceptive for controlling nuisance birds, viz, pigeons, most substances that were effective in inhibiting ovulation in other animals proved to have little effect on pigeons, even in nearly lethal doses. The compounds he tested included tranquilizers, gametocides, antithyroid compounds, hypophyseal inhibitors, insecticides, fungicides, and coccidostats. "Practical results were obtained with anticholesterol compound SC-12937 (22, 25-diazacholestanol dihydrochloride). When this compound constituted 0.1 percent of the diet for 10 days in early November, no eggs were laid for 3 months, full fertility among some birds was not reached for 6 months, and some remained anovulatory for 12 months. Following spring feeding, ovulation was almost completely inhibited for 3 months, and after 6 months remained 75 percent inhibited." Provera at 0.1 percent or more in the diet and arasan at 0.35 percent inhibited ovulation without severe debilitation of the birds, but the effect was lost as soon as the materials were withdrawn from the diets.

Nichols and Balloun (1962) also have shown that anticholesterol compounds can reduce egg laying. According to Wetherbee (1964): "These hypocholesterolemic agents [SC-12937 and SC-11952] seem to be the most potent female gametocides available to date for the control of over-populations of birds. They are new, and more research is needed in their possible side-effects not to say in the economics of their industrial production and techniques of selective administration."

Six valuable review papers by Wetherbee et al_. (1962) — focused upon sterility either as reproductive failure deliberately induced, reproductive failure incidentally discovered, or sterility mechanisms postulated — are the following, on Recent Findings in the Inhibition of Avian: (l) Sperm Sustentation, by R. D. Crawford; (2) Ova Sustentation, by P. F. Consuesra; (3) Embryogenesis, by M. J. Landy; (4) Oogenesis, by R. G. Somes, Jr.; (5) Spermatogenesis, by B. C. Wentworth; and (6) Embryo Sustentation, by R. P. Coppinger. In a subsequent paper on Vertebrate Pest Control by Biological Means, Wetherbee (1964) reviews some of the significant pest control points brought out in the six seminar papers.

The transovarian deposition of colored dyes into yolks of hens' eggs has been recognized for a long time by poultry scientists (Denton 1940). Recently, however, Wetherbee et al. (1964) showed that an oil-soluble dye, Sudan Black B, fed to laying adult female birds not only labeled the yolks with discrete layers of black, providing positive evidence that the female had fed on treated bait, but also adversely affected the hatchability of such eggs when fed in low concentrations. After conducting extensive tests with the little Japanese quail (Coturnix coturnix), they found that almost all fertile eggs failed to hatch that were laid for 10 days after females were fed as little as 500 mg of Sudan Black B per kg of feed in a single acute dose. When laying females were fed levels lower than 20 mg/kg, the yolks of all eggs laid for about one week were discolored; hatchability was adversely affected only at levels of Sudan Black B of 167 mg/kg and above. They reported a very broad margin of safety between effective dose in inhibiting hatch and lethal dose (only 25 percent mortality occurred at 16,000 mg/kg). "The likelihood of secondary effects on predators eating the adults or the dyed eggs is remote, as only a small fraction of the low dose ingested finds its way to the yolk; most passes out the digestive tract" (Wetherbee 1964).

Quoting further from Wetherbee (1964): "The hormonal balance which regulated the formation of spermatozoa in the testis has been a natural site of attack for reproduction prohibitionists. The administration of prolactin is antagonistic to gametogenesis and also inhibits gonadotropic hormone secretion (Bates et al_. 1937). However, proteinaceous hormones cannot be administered orally, and it is impractical to capture and inject animals from any appreciable fraction of a wild population. Diethylstilbestrol (DES)-induced capons that used to be available on the poultry market bear testimony to the effectiveness of the hormonal approach to sex reversal, but those capons were produced by implantation of long-lasting hormonal pellets under the skin. The ingestion of hormones (the ethinylated steroids are more effective orally than the nonethinylated) is ineffective unless continued over an extended period and most of these hormones are prohibitively expensive.

"In chickens a great many drugs and feed contaminants have a statistically noticeable effect on hatchability of eggs. Gossypol found in crude cottonseed oil or meal was found to reduce hatchability by Bird (1956). The oil of the fava olive and cyclopropene fatty acids found in many mavalaceous plants (Sterculi foetida) suppress hatchability. . . . Any of the nutritional or pharmacological agents that affect quality of yolk, albumen or shell tend to depress hatchability. We have already mentioned the fungicide Arasan causing the production of soft-shelled eggs, that will not sustain embryos. For one reason or another scores of these candidate compounds have been eliminated from our screening tests with the quail (C. coturnix); either they are not available commercially, or they are too expensive to produce, or they are apparently detoxified, or as with Arasan have a taste disagreeable to the bird (Arasan is actually used as a bird repellent!). Elder (1964) working with the pigeon reports parallel experience.

"Emulsified oil, sprayed over the eggs of the herring gull in Maine and Massachusetts was used by the United States Fish and Wildlife Service from 1934 to 1953. This pioneer embryocidal programme was a move in the right direction, but economical and sophisticated methods and tools had not been developed at that time."

<u>Mammals</u>

In 1965, Mr. Rex E. Marsh and the author became interested in determining the feasibility of utilizing an antifertility agent in suppressing population levels of troublesome species of rodents. Mestranol, an estrogen, was the best candidate material we could find for rodents, although we plan to confirm this by comparing it with any other potential and promising material that should come to our attention. Estradiol 17B, a most active naturally occurring compound, is not active by the oral route.

We are convinced that mestranol, and perhaps other antifertility agents, have a distinct role in future control operations, but, of course, a clearer insight on some of the fundamental principles and concepts involved is still needed.

According to Wetherbee (1964), "the antioestrogen U–11, 55A, a diphenylindene derivative made by the Up john Company. . . . and related compounds, except for frank oestrogenic agents, were the most potent oral mammalian antifertility agents reported up to 1963 (Duncan, et_ al_. 1963)."

A small concentration of estrogen or a larger amount of androgen can exert an action at the hypothalamic-pituitary areas in new-born rodents in such a way that their future ability to produce ova or sperm and sex hormones is essentially lost. Barraciough (1961) thinks the physiological mode of action is through the crippling of pituitary growth. This is the area where the highly potent estrogen, mestranol, and other estrogens are most effective in creating sterility in rodents. Estrogens in the rat can also cause abortion and in other ways interfere with pregnancy (in contrast to little effect with humans). Mestranol (developed by Syntex Corporation) is a highly effective sterilizing agent in rats. When administered to the very young rodent (up to about 10 days of age), either by subcutaneous injection, by gavage, or through the milk of a treated dam, both males and females are irreversibly sterilized throughout life. When the steroid is administered to normal adult females in minute quantities, a serious impairment in ovulation, fertilization, and implantation follows (Anon.). At this time, mestranol appears to be a promising oral rodent antifertility agent.

As pointed out by Linhart and Enders (1964), diethylstilbestrol is inexpensive, fat-soluble, stable under extremes of temperature, and importantly to vertebrate control, effective when taken orally. Estrogen could be distributed in the field in effective baits during the breeding season of foxes and other pest species. By inhibiting reproduction, it should result in lowered densities of the species in question. Diethyl stilbestrol has been shown to depress reproduction in dogs (Jackson 1953), mink (Travis and Schaible 1962), and other species.

Biweekly testicular biopsy failed to reveal any adverse effects on spermatogenesis when 50 mg of diethylstilbestrol were given to male foxes (Linhart and Enders 1964). However, subsequent biopsies did not measure any possible loss of libido or retardation of spermatic development of less than 2 weeks' duration from these males being dosed with this synthetic estrogen. As Jackson (1959) points out, since antifertility effects may be produced without obvious histological damage, alterations in fertility should be the primary concern, with testicular histology used as an ancillary investigation.

When silver fox vixens were force-fed single doses of 50 mg of a synthetic estrogen, diethylstilbestrol, those given the estrogen any time ranging from 9 days before mating to not more than 10 days after mating, but not so if fed it earlier or later, failed to produce offspring (Linhart and Enders 1964). The diethylstilbestrol was dissolved in a few drops of ethyl alcohol and mixed with 10 cc of melted tallow. The mixture was then force-fed to anesthetized (ether) vixens by a syringe and an 8-inch copper tube inserted into the esophagus.

Acceptance by wild red and gray foxes (Vulpes fulva and Urocyon cinereoargenteus) of baits for administering antifertility agents was field-tested in New York in 1961-1963 (Linhart 1964). Foxes, dogs, and crows, in that order, consumed the baits most frequently. Other wild and domestic species took baits only occasionally. "The results suggest that the possibility for finding a 'superbait' is not promising," but additional trials were recommended. "Development of a bait which would repel dogs but be readily taken by foxes does not seem likely because of the close kinship between the two. ... If control of fox abundance through baits containing an antifertility agent is to be practical, a high proportion of a fox population must consume the baits to achieve a significant reduction in productivity." This study also pointed out the importance of having the subjects accept the bait at the proper phase of their breeding season.

Intensive research on the use of antifertility agents in management of mammalian predator populations has been conducted by Balser (1964a, 1964b) and his associates at the Denver Wildlife Research Center at the U. S. Fish and Wildlife Service. Balser points out that not only will a wide variety of agents be required but, more importantly, detailed knowledge is needed on a variety of techniques of application, proper timing, dosage, and the dispersal of baits. In many instances he thinks the problems of application far outweigh the development of a suitable drug.

Balser (1964a) also points out that "Applying antifertility agents in a bait to species having one litter per year is much simpler than application to those which produce several litters a year. The latter may require drugs that produce permanent sterility to make baiting practical; otherwise bait would have to be repeatedly applied or continuously available. For species breeding once a year, whether monestrus or polyestrus, agents must be selected that will block reproduction for the entire breeding season rather than result in delayed breeding after the effects of a drug wear off. Blocking reproduction in species such as the raccoon (Procyon lotor) and striped skunk (Mephitis mephitis), which go into dormancy or hibernation, precludes the use of agents that interfere with follicle development. In the north, these animals are believed to breed shortly after movement begins in the spring. These animals must either be treated during breeding and gestation, or some way must be found to interfere with reproduction before they go into hibernation.

Animals that do not normally breed their first year (partly true in the case of the coyote) have a lower reproductive potential which increases the vulnerability to antifertility agents and prolongs the effects on the population. Where population reduction of the black bear (Ursus americanus) is necessary and an adequate hunting harvest is not possible, summer or fall baiting with antifertility agents may prove practicable. This situation exists in the Pacific Northwest where extensive bear damage occurs on timber.

The breeding season of coyotes in most cases is not concurrent with the smaller carnivores but precedes them. This adds greatly to the selectivity of this method. Selection of bait carrier, dispersal of baits, and choice of baiting sites are all expected to minimize the effects of associated species and increase selectivity for the target species. An added advantage is the non-lethal effect on domestic dogs that frequent control areas.

"Concerning the effect of stilbestrol on future reproduction, foxes, mink, and dogs have produced successful litters the year following administration of this drug. Indications are that stilbestrol would not have lasting effects except in cases where an extreme overdose causes damage to ovarian tissue."

"A further question is raised about possible delayed breeding that would negate the effects of antifertility agents. This is true of progestational agents as used in dogs and humans and may be true of stilbestrol when administered prior to ovulation during follicle development. Two of our penned coyotes ovulated 30-45 days after administration of a single 100-mg oral dose of stilbestrol when given about 3 weeks before the normal peak of estrus. However, in coyotes, when stilbestrol is administered after ovulation to interfere with implantation or gestation, new follicles cannot be raised until corpora of either pregnancy or ovulation become non-functional. This prevents the coyote from recycling before the next breeding season."

"Results of the field trial indicate that a wild coyote population can be successfully treated. Whether similar results can be obtained under a wide variety of conditions will be determined in future field trials."

SUMMARY

Biological control of vertebrates is applied ecology, *i.e.*, it is the regulation of population levels, not necessarily the destruction of individuals. Actually, all animal control, even "conventional" methods of vertebrate pest control, should be based on a prudent translation of the ecological laws of nature into an effective management policy. Unfortunately, vertebrates are relatively long-lived, so troublesome populations usually cannot be tolerated until they die of natural causes due to some biological control procedure. Therefore, the greatest likelihood for effective application of biological control of existing pestiferous vertebrate populations is by means of integrated control, where biological control is done concomitantly with an initial population reduction produced by some conventional control method.

Biological control of a vertebrate pest implies an effective reduction in density of the pest that has been caused by intentionally modifying biotic elements of the pest's environment. If successful, the induced biotic reduction of the population will produce economic control by reducing the pest's density below the economic-injury level to the economic threshold, where, should the population density start to increase, there would be "sufficient time for the initiation of new control measures and for these measures to take effect before the population reaches the economic-injury level" (Stern et al. 1959). The governing mechanisms incorporated in biocontrol include predation, habitat manipulation, diseases, and antifertility agents.

The potential role of natural and introduced predators of vertebrate pests is discussed at some length. Introduced predators, such as house cats supplemented with milk, appear to have more utility in vertebrate control than do natural predators, which are more likely to stimulate their prey species to increase in density than to depress them. Since natural predators are a dynamic component of ecosystems, their numbers should never intentionally be artificially manipulated, either up or down, without first obtaining considerable ecological knowledge about the consequences.

When one is willing to accept the ecological consequences, many kinds of vertebrate pest problems can be largely alleviated by modifying the conditions of the habitat. Support for this statement is the fact that the most important factor determining the presence of animals in a given locality is the suitability of the habitat to the species in question. However, it must be recognized before habitats are intentionally manipulated to control vertebrates that any artificial alteration of the physical conditions of habitats will alter the entire ecosystem more drastically than could result if members of specific species of animals were removed by some host-specific control method.

Before disease-causing organisms can become an important tool in the control of vertebrates, it is essential that we have a keener insight on the complete ecology of such epizootics and the inherent hazards associated with artificial manipulation of the dynamics of such agents. The complexity of disease phenomena should serve as a warning against any hasty assumptions about the role of pathogens in population management. At present, various frightening devices, repellents, exclusion by barriers, electric shock, stupefacients, and anesthetics show much greater utility in the field of vertebrate pest control.

Even though, at the moment, insight into chemosterilants must be much greater before antifertility methods can be widely applied to control the birth rate of troublesome populations of vertebrates, it is a challenging and promising field of research with mammals, birds, reptiles, and fish. A combination of sterilants and conventional control methods would probably have synergistic effects (the degree of control greatly exceeding the sum of the independent effects of each method). A variety of promising birth control materials and procedures for birds and mammals are discussed.

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