Disease management strategies for wildlife

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Summary

Three basic forms of management strategies exist for wildlife disease, as follows: prevention of introduction of disease, control of existing disease or eradication. Management may be directed at the disease agent, host population, habitat or be focused on human activities. Disease agents may be dealt with in the environment through disinfection or in the host through treatment. Disinfection and pesticides used to destroy agents or vectors are limited to local situations, may have serious environmental effects and may result in acquired resistance. Difficulty in delivering treatment limits chemotherapy to local situations. Host populations may be managed by immunisation, by altering their distribution or density, or by extirpation. Immunisation is best suited for microparasitic exogenous infections with a low reproductive rate and in populations which have a low turnover. Mass immunisation with oral baits has been effective, but this strategy is limited to a few serious diseases. It is difficult to move wild animals and techniques to discourage animals from entering an area become ineffective rapidly. The setting up of fences is feasible only in local situations. Selective culling is limited to situations in which affected individuals are readily identifiable. General population reduction has had little success in disease control but reducing populations surrounding a focus or creating a barrier to disease movement have been successful. Population reduction is a temporary measure. Eradication of a wildlife population has not been attempted for disease management. Habitat modification may be used to reduce exposure to disease agents, or to alter host distribution or density. Management of diseases of wild animals usually requires a change in human activities. The most important method is by restricting translocation of wild animals to prevent movement of disease.

Keywords

Control – Eradication – Microparasites – Macroparasites – Management – Prevention – Transmission – Vectors – Wildlife.

Introduction

The desire or need to actively manage infectious disease in wild animals is a relatively recent phenomenon, compared to health management in humans and domestic animals. In the past, occurrence of infectious disease among wild animals received little attention except when major events occurred, often involving the health of humans or domestic animals. Management of disease in wild animals is usually undertaken for some reason that will benefit humans, such as reducing or controlling zoonotic diseases, diseases shared with domestic animals, or disease conditions considered to be detrimental to species valued by humans. Interest in diseases of wild species has increased recently for several reasons including:

– emergence of zoonoses, such as Lyme disease, various haemorrhagic fevers and hantavirus pulmonary syndrome, that have been traced to wild animals

– recognition that wild animals are a reservoir for diseases, such as bovine tuberculosis and brucellosis, that may prevent the elimination of these diseases from domestic animals

– increased domestication of indigenous species, such as elk (*Cervus elaphus*) and deer (*Odocoileus* spp.), for game farming with the attendant risk of disease transmission to and from free-ranging animals

– increased awareness of risks inherent in the translocation of wild species together with their infectious diseases

– general concern about the well-being of wild populations affected by habitat degradation, fragmentation and loss

– emergence of conservation biology with intensive management of threatened or endangered species.

Concurrently, there has been a marked increase in interest in the study of population and evolutionary aspects of parasites and host-parasite relationships by ecologists. Most of such investigations have not been concerned directly with disease management, but they have provided a theoretical basis for disease management.

Infectious disease, induced by parasitic organisms, is a normal feature of the life of wild animals and the typical wild animal hosts a broad multi-species community of potentially harmful parasitic organisms. This is quite different from the situation in many human and domestic animal populations. In developed countries, infectious disease now plays a minor role in human health and the expectation is that most people will survive well beyond the age of reproduction to old age. Infectious disease is more common in intensively managed livestock than in humans but the expectation is that the great majority of domestic animals will survive and thrive until they have fulfilled their intended purpose. Thus, the farmer plans reproduction in animals to produce approximately the number needed to fit the market. In contrast, among wild animals, reproduction is far greater than necessary to maintain the population if most animals were to survive to old age. Most individuals of most species die at a young age, often before reaching sexual maturity. This high rate of mortality is caused by a variety of factors including predation, malnutrition, accidents and disease, which are interrelated and seldom act independently.

Disease management – important concepts

Two questions should be addressed early in the discussion of management of disease in wild species. The first is the desirability of altering the course of disease in free-living animals. Parasitism is a powerful ecological and evolutionary force in the natural biology of all species. For this reason, one could argue that any intervention to alter the course of infectious disease in wild animals is an undesirable intrusion. However, there is also accumulating evidence that the dynamic relationship between disease agents and host species can be disrupted severely by changes in their shared environment. Most of such environmental disruptions result from human activity and no wild animal lives in an environment that has not been modified in some manner by humans. For this reason, disease management can be viewed as an attempt to mitigate other human actions. Some authors feel strongly that this is sufficient justification for action, for example, 'When natural balances are disturbed by humans, we become ethically obligated to assume the mantle of intensive managers' (56). The second question relates to the feasibility of managing disease in free-living animals. The primary concern of most physicians and veterinarians has been the diagnosis and management of disease in individuals or small groups of individuals. Medication and treatment play an important role in this form of disease management. Management of disease in wild animals is usually conducted at the population level where individual treatment is largely impractical. This has led to scepticism about the feasibility of altering disease in free-living species. However, most advances in public health that have resulted in a great extension in human life expectancy, and in the health of domestic animals, have resulted from improved nutrition, sanitation, provision of safe drinking water and better habitation. In the first major book devoted to wildlife management, Leopold noted that in wild animals 'the real determinants of disease mortality are the environment and the population' (54). Management of environmental factors to improve nutrition, sanitation, water quality and other habitat factors, together with manipulation of host populations, is possible in many wild populations, so that management of many diseases may be feasible.

Disease management can be classified into four basic categories, namely: prevention, control, eradication and doing nothing (*laissez-faire*).

– Prevention includes all those measures designed to exclude or prevent the introduction of a disease into unaffected individual animals within a population or into an unaffected population.

– Control applies to activities designed to reduce the frequency of occurrence or the effects of an existing disease within an individual animal or a population to an acceptable or tolerable level, or to contain the spatial spread of infection. Management of this type implies that some level of disease will persist in the population and that in most instances the control measures will have to be continued in perpetuity.

– Eradication involves the total elimination of an existing disease.

– *Laissez-faire* or not attempting active management has been the most common approach to diseases of wild animals in the past, and may be the most appropriate method when the feasibility and probability of success of other options have been considered.

The choice among these four basic techniques depends upon why management is required, whether or not the disease is already present in the area or population, the availability of techniques for detecting, diagnosing and managing the disease, the availability of funding on a continuing basis for management, and the likelihood of success. Selection of the most appropriate technique requires a clear understanding of the cause and ecology of the disease, including the course of the disease in the individual, and the population biology of the parasite-host interaction.

Concepts related to host-parasite relationships have been developed that are important to consider in the planning stage of any potential disease management strategy. Three such general concepts relate to the population biology of different forms of disease. An important point in the evolution of thinking in this area was division of parasites into two broad classes based on their population biology and the nature of the interaction between the parasite and the host, rather than on conventional taxonomic status (3).

Microparasites

Microparasites are parasites that have direct and usually rapid multiplication within the host. They are generally small in size and have a short generation time compared to the life-span of the host. The microparasite group includes most viruses and bacteria, as well as many protozoa and fungi. Infections are usually transient or short-lived and hosts that recover from infection usually have immunity to reinfection that persists for an extended period. Based on these features, the host population for a microparasite can often be divided into three distinct categories, as follows: susceptible, infected and recovered-immune individuals.

Macroparasites

Macroparasites include parasites that have no direct reproduction within the definitive host. These organisms are typically larger than microparasites and the generation time is extended, often being a considerable portion of the host life-span. The group includes most helminths and arthropods. When immunity develops to macroparasites, it usually depends on the number of parasites present and is of short duration if the parasites are removed, so that infections are typically persistent and reinfection is common. The distinction between infection and disease is particularly important for macroparasites, because the pathological effects on the host, the survival rate of individual parasites in the host and the immune response all depend on the number of parasites in the individual host. Infection with a few parasites may result in no detectable harmful effect, while infection with many parasites may produce morbidity or death of the host. Categorisation of the host population is much more complex than for microparasites, because of the need to consider the distribution of the parasites within the host population and the varying degree of immunity to reinfection that occurs in individuals.

The rate at which a parasite multiplies and increases within the host population is important for disease management. The basic reproductive rate (R_o) has been defined as the average number of successful offspring that a parasite is capable of producing (4). In the case of microparasites, R_o is the average number of secondary infections produced when one infected individual is introduced into a host population in which every individual is susceptible. For macroparasites, R_o is the average number of female offspring produced throughout the lifetime of a mature female parasite which themselves achieve reproductive maturity in the absence of density-dependent constraints (4). For any parasite to be maintained within a population, R_o must equal at least 1 (i.e. at least one new infection in the case of a microparasite or one surviving female offspring in the case of a macroparasite). The greater the magnitude of R_o, the more likely the disease may spread within a population.

The host population size required for a disease to become established and to persist is also an important factor when considering disease management strategies. The size of the host population has a direct effect on the likelihood of parasite transmission and, hence, on the magnitude of R_o. Every parasite requires a minimum number or density of hosts to become established. The population threshold for establishment is often referred to as 'N_T' and at this level, $R_o = 1$. In very general terms, the magnitude of N_T varies inversely with the efficiency with which a parasite is transmitted. In other words, the more efficiently a parasite is transmitted, the smaller the population required for its persistence. This can be illustrated by considering infectious diseases of canids. Many microparasites, such as canine distemper virus, produce transient disease with a short period during which transmission may occur, do not persist for long in the external environment and require close contact among individuals for infection. Although canine distemper spreads rapidly in a susceptible population, this type of parasite has relatively inefficient transmission over the long term and a large host population is required for R_o to remain ≥ 1. When canine distemper is introduced into a naïve population, some infected individuals may die and other infected animals recover and become immune. Thus, the number of susceptible individuals in the population decreases. If the population is not large enough to give birth to sufficient new susceptible animals to replace those that died or have become immune, R_o will fall below 1, and the disease will die out. In contrast, many macroparasites, such as helminths, have a very long life-span in the individual host, and the transmission stages are persistent in the environment or in intermediate hosts. Transmission is efficient and the threshold density of hosts needed to maintain the parasite can be small. Thus, parasites such as intestinal tapeworms, are able to maintain themselves in small populations among which there is infrequent contact between individuals, as is common in carnivores.

Infectious agents can also be classified in another manner that is useful in considering disease management. Yekutiel divided agents into endogenous and exogenous groups (103).

Endogenous agents

Endogenous agents are those that are often present in the body without causing obvious disease, or that are ubiquitous in the external environment and that cause disease only under special circumstances. Such agents, also called opportunistic or facultative pathogens, often produce non-specific infections of the respiratory, alimentary, urinary and reproductive systems in animals compromised by other factors.

Exogenous agents

Exogenous agents are not present in the body of healthy individuals but are acquired from outside sources, usually from other animals. They tend to produce well-defined disease shortly after introduction into the body and most do not survive for an extended period in the external environment. This simple division is useful because, in general, the more potential sources that exist for a disease agent, the more difficult it will be to reduce or eliminate the disease. Thus, endogenous diseases are more difficult to eliminate than exogenous diseases. Yekutiel concluded that eradication, even on a local basis, would only be possible for strictly exogenous diseases in humans (103).

Although the magnitude of R_o and N_T are not known for most diseases in wild animals, the goal of management is often to reduce R_o to <1, so that the disease will die out. This might be done in several ways, for instance by attacking the agent directly, by blocking transmission among animals, or by reducing the population of susceptible individuals below N_T. The concepts discussed above provide guidance on which type of management is more likely to be successful in reducing or eliminating a disease. Based on these general principles, one can conclude in advance that:

– diseases with only one source are more easily controlled than those that have multiple sources

– immunisation is more likely to be effective in dealing with diseases caused by microparasites than for those caused by macroparasites

– management of disease caused by macroparasites might be directed at maintaining low levels of infection in the animals to protect them against damaging heavy infections

– population reduction is more likely to be effective as a management strategy for diseases with inefficient transmission than for diseases that will persist at very low population levels

– population reduction is unlikely to be effective as a management strategy for a parasite that occurs in several species, because the disease may persist in the target species although the population is below N_T, if the parasite is maintained in other more numerous species.

Indigenous or exotic agents

Finally, infectious agents may be classified as indigenous or exotic (alien) agents. In the case of indigenous agents, an evolutionary tolerance has generally developed between host and parasite over millennia, resulting in relative 'endemic stability'. This stability may be disrupted by human-induced changes, such as habitat degradation, fragmentation or loss. In the case of alien agents entering an ecosystem, the wildlife populations are frequently immunologically naïve, resulting in destructive outbreaks of disease.

Different types of disease will require different disease strategies and different methods may be employed at specific points in a management programme. The various management techniques available have been divided for discussion into reactive, pro-active and population density management. Within each, the basic elements of prevention, control, eradication and *laissez-faire* apply.

Reactive disease strategies

This group of techniques is applied in circumstances in which a disease is present in an area or population of animals, and the desire is to either reduce its impact (i.e. contain and control the disease), or to eliminate it completely. Management can be aimed directly at the disease agent, at reducing transmission, or at preventing access to the disease agent.

Disease agents can be 'attacked' within the host animal, free in the external environment, or in some vector or alternate host. If the disease has only one vertebrate host, or transmission is limited to some identifiable part of the external environment, attack on the agent may be a feasible strategy. The more potential sources that exist for the agent, the less likely management directed at the agent *per se* will be successful.

Destruction of the parasite within the vertebrate host through use of drugs such as antibiotics or anthelmintics is commonly used to control disease in humans and domestic animals. A disadvantage of this approach is that the parasite may already have caused injury to the host before treatment. There is no reason to believe that this method would not also be useful in wild animals, if appropriate drugs could be delivered to the individuals. However, the basic problem lies in finding a method of delivering treatment to the animal. It is for this reason that treatment has limited application in wild animals except, perhaps, in isolated groups such as endangered species in which affected individuals can be identified and captured for treatment. For example, Bornstein *et al.* reported that sarcoptic mange was treated successfully in a small population of Arctic foxes (*Alopex lagopus*) in Sweden by capture, treatment and release (15). Similarly, individual red grouse (*Lagopus lagopus scoticus*) were captured on British moors and treated with an anthelmintic to reduce infection with the nematode *Trichostrongylus tenuis* (28, 49). Treated females produced significantly more young than did untreated females. This experimental treatment was conducted on study areas up to 800 ha in size, but the feasibility of using the technique more extensively has not been reported.

A programme to control psoroptic mange in a small remnant population of desert bighorn sheep (*Ovis canadensis nelsoni*) in New Mexico illustrates several problems in using individual animal treatment as a method of disease management (53). When the disease was recognised in 1978, the population contained 200-250 animals but declined to <70 by 1979. The decline was thought to be due to mange. Initially, acaricide was placed in bags over salt blocks in the hope that the sheep would be dusted with acaricide while using the salt. However, sheep avoided the bags. (Techniques used to deliver treatment to domestic species may fail in wild animals because of differences in behaviour). Next, as many of the sheep were captured as possible, dipped in acaricide solution, held in captivity for 10 to 14 days, re-dipped, and then transferred to a holding area where they were maintained for about a year until released. The cost to capture and treat each sheep was about US$2,000 (53). (This type of treatment is feasible only for small numbers of highly valued animals. Often, as in this situation, the entire population cannot be captured for treatment.) This treatment apparently was successful in removing mites, although no sensitive diagnostic technique was available to detect low-level infections. Only 59% of the treated animals survived treatment. (Capture and handling of wild species for treatment may result in unacceptable mortality.) Animals that could not be captured were injected remotely with anthelmintic by airgun from a helicopter. The programme was judged to have been successful in controlling but not eliminating the disease; however, mange recurred and treatment was changed to capture of visibly affected sheep for treatment. It was concluded that continued annual treatment would be necessary (70). In this example, the agent was a macroparasite with features of an endogenous agent, in that lightly infected sheep had no clinical signs. Even if treatment was successful in eliminating mites from individual sheep, recovered animals would not have long-lasting immunity and re-infection could be expected. The NT for this parasite is probably very low, so that the parasite could persist in a very small population, with a few infected individuals serving as a reservoir for reinfection of treated animals.

A study by Murray *et al.* is important in the discussion of individual animal treatment as a management option, because it provides detailed information on the efficacy of anthelmintic treatment in reducing parasites in a wild population (65). Snowshoe hares (*Lepus americanus*) were captured and treated bimonthly with the anthelmintic ivermectin. The prevalence and intensity of infection with five nematodes and one species of tick were compared between treated and untreated hares over a 27-month period. Treatment significantly reduced the mean prevalence of infection by four of the nematodes and the mean intensity of infection by three nematodes but some treated hares showed no reduction in either prevalence or intensity of infection compared to control animals. Treatment reduced the prevalence of two nematodes for about 50 days and longer for two other species. Treatment had no effect on the tick *Haemaphysalis leporispalustris*. Based on the large variation in effect among individuals and the short duration of effect, Murray *et al.* stated that it 'remains questionable to what extent anthelmintics may be used for the conservation or management of wild populations' (65). Considering the difficulty in delivering drugs repeatedly, they concluded that 'it may never be possible to successfully implement long-term nematode control in free-ranging populations exclusively via chemotherapeutic drugs'.

Treatment of individual animals can and should be used to reduce the risk of translocating disease agents in wild animals being moved to new environments; however, it must not be relied upon as the sole method of preventing transfer of disease agents. For example, the nematode *Elaphostrongylus cervi* was introduced to Australia (73) and the tick *Dermacentor albipictus* was introduced to New Zealand (42) with cervids that had been treated prior to translocation. Part of the problem in this regard is that the drugs that might be used have often not been tested extensively in wild animals, or against parasites of wild animals, so that their actual efficacy is unknown.

Widespread or mass medication has been attempted for a few human diseases, including malaria and schistosomiasis. Development of acquired resistance by the parasite to the chemical used is a definite risk in any programme that is dependent upon continued and widespread use of chemotherapy because of the selective pressure for resistant organisms. The other major problem with this technique lies in delivery of the treatment to the individual, even in humans. There have been very few attempts to use mass treatment in wild animals. Anthelmintics were used to control *Protostrongylus* spp. lungworms in bighorn sheep (*Ovis canadensis*) on a few occasions (85). Sheep were accustomed to consuming bait to which anthelmintics could be added. Treatment was timed to kill larval parasites in pregnant females and reduce transplacental infection of lambs *in utero*. It was also hoped that treatment would reduce the number of adult worms carried by sheep and, hence, environmental contamination with larvae. While the survival rate of lambs from treated ewes was much higher than that of lambs born to untreated ewes (85), treatment did not eliminate lungworms from the population nor did it deal with the underlying problem of too many sheep concentrated on small areas of heavily contaminated habitat. Miller reported that anthelmintic therapy had failed to prevent epidemics of pneumonia in bighorn sheep populations in Colorado (61). The same method of baiting was used to deliver antibiotics to groups of sick sheep during a pneumonia outbreak (33) but the effectiveness of this treatment is unknown. Qureshi *et al.* reported that anthelmintics could be delivered to free-ranging white-tailed deer (*Odocoileus virginianus*) using a baiting system (76). The objective in this case was to control transmission of the liver fluke *Fascioloides magna* among deer and thus prevent contamination of pasture and infection of cattle. Over a three-year experimental period, the prevalence of the parasite in treated deer on a 391 ha study area was reduced to 8.7% compared to 72% on control areas. The feasibility of applying this technique over larger areas is unknown, as is the risk of acquired resistance if the anthelmintic were to be used repeatedly over a wide area.

If a disease agent is localised in a specific site in the external environment, it may be possible to destroy it there and reduce or prevent infection. Collection and disposal of carcasses of animals that have died of disease is a method that has been employed frequently for disease occurrences in wild animals. Friend and Franson provide detailed instructions on methods for collecting and disposing of carcasses of small animals (birds) (35). Disposal of carcasses to reduce contamination and transmission seems intuitively sound, because carcasses may contain infectious organisms. However, there are no quantitative data to indicate the degree of carcass sanitation required to reduce the incidence of any infectious disease. The effectiveness of carcass sanitation has been studied in regard to avian botulism. While botulism is not an infectious disease, toxin formed within bird carcasses propagates the disease, mimicking an infectious process, so the results of studies may be relevant for infectious conditions. Reed and Rocke found that sentinel ducks (*Anas platyrhynchos*) in experimental pens containing carcasses were significantly more likely to develop botulism than were ducks in pens with no carcasses (77). This confirmed that carcasses are an important source of toxin and that complete removal of all carcasses would be a sound management technique. In natural situations, it may be difficult or impossible to find and remove all carcasses. For instance, only 6% of duck carcasses placed in a Texas marsh were detected by searchers (93) and 32% of marked carcasses were recovered in carcass collections during a botulism outbreak in Saskatchewan (21). The proportion of carcasses collected during clean-up operations during an intensive study of botulism in prairie Canada ranged from <10% on large, heavily vegetated lakes to approximately 60% on intensively searched small wetlands. In this study, there was no improvement in survival of radio-marked ducks on lakes with carcass clean-up compared to similar lakes on which no carcasses were collected (T. Bollinger, personal communication). The value of carcass sanitation is likely to be disease- and site-specific. It will vary with the persistence of viable infectious agents within carcasses, the amount of contact between live animals and carcasses, and the dose of organisms required for infection, as well as the ease with which carcasses can be found and the effort devoted to carcass collection.

Disinfection and other forms of sanitation are used frequently in human and veterinary medicine. Disinfection has been used in a number of circumstances involving infectious diseases of wild animals, including treating waterholes associated with the transmission of anthrax (71), disinfecting wetlands where avian cholera (37, 84) and duck plague (68) were occurring in waterfowl, liming to destroy parasite eggs around artificial feeding sites used by hares (88), and disinfection of soil enriched by bird droppings in which the fungus *Histoplasma capsulatum* was known to grow (101). The effectiveness of disinfection in reducing or preventing infection seldom has been evaluated, however, Skrjabin reported that lungworms (*Protostrongylus* spp.) were eliminated from hares after three years of liming around feeders, while hares in untreated areas remained infected (88). Disinfection is only practical in situations in which the agent or transmission of the disease occurs in a very limited area. Another potential problem is that the chemicals required may have undesirable environmental effects that preclude their general use. Disinfection should be considered as a component of the management programme for situations in which wild animals have to be concentrated, such as at artificial feeding or watering sites.

Habitat modification to destroy agents or to interfere with disease transmission is potentially of great value in diseases affecting wild animals. Application of these methods requires a thorough knowledge of the ecology of the disease to be effective, and there are few specific examples available of the successful use of this type of management for diseases of wildlife. The ‘tools’ for this type of management are often similar to the axe, fire and plow that Leopold suggested could be used to ‘doctor’ wild animal diseases (54). Fire is a powerful tool for habitat manipulation and has been used occasionally in disease management. Pienaar burned vegetation in areas where anthrax occurred to destroy the bacterium and to facilitate finding carcasses (71). Under experimental conditions, burning reduced the number of ticks parasitising young wild turkeys (*Meleagridis gallopava*) (50) and prescribed burning of forests is effective in reducing populations of several species of tick (1). Seip and Bunnell (87) reported that Stone’s sheep (*Ovis dalli stonei*) grazing on ranges burned annually passed less lungworm larvae than did sheep using unburned range, but why this occurred and the significance of this observation are unclear. Habitat manipulation of another type was performed to reduce water-borne transmission of *Pasteurella multocida* among eider ducks (*Somateria mollissima*) in the St Lawrence River, Canada (102). Avian cholera occurred repeatedly among nesting birds on one island while it did not occur among birds on adjacent islands. The problem island was heavily shaded by very dense shrub cover and had poor drainage with standing water, from which *P. multocida* was readily isolated. The unaffected islands were open, grassed and well-drained. It was hypothesised that transmission was occurring in association with the standing water, so the shrubs were cleared, the standing water was drained and grass was planted. The island continues to be used by breeding eiders and avian cholera has not occurred at high levels since the habitat was modified. Waterholes were modified in dry areas of California to reduce the occurrence of necrobacillosis among deer (83). The objective was to prevent concentration of animals in areas composed of ‘mud, contaminated by droppings’ that were heavily contaminated with the causative bacterium. It was thought that animals became infected by walking through the mud at these sites and subsequently developed pododermatitis (footrot). Management consisted of filling and covering some waterholes, reducing overflow from water tanks to reduce muddy conditions, and creating new clean water sources.

Habitat modification is more often directed at either the vertebrate or invertebrate hosts of disease than at the causative agent *per se*. For example, fire may have more value as a method for influencing animal distribution than in destroying disease agents. Pienaar felt that burning helped to limit geographical spread of anthrax by keeping animals in the outbreak area to graze on the regrowth that occurred after the fire rather than dispersing to new areas (71). Environmental manipulation may range from simple, localised changes, such as filling tree holes to prevent their use by breeding mosquitos that transmit viral diseases (62), locating woodpiles and rockpiles away from dwellings to reduce contact between humans and rodents that carry hantaviruses and *Yersinia pestis*, and mowing lawns around dwellings to reduce tick transmission of Lyme disease from wild animals to humans, to widespread landscape alterations. An example of the latter type was the clearing of riverine vegetation that formed essential habitat for tsetse flies (*Glossinia* spp.) as part of a programme to control diseases transmitted between wild and domestic animals (38). Habitat modification may be used to disperse animals away from known disease sites, for example by draining wetlands where outbreaks of botulism and avian cholera occur and fencing waterholes to prevent access during anthrax outbreaks. This is often most effective when suitable new alternative habitat is created. Habitat modifications may also be used to encourage animals to use areas of lower risk. Skrjabin described construction of artificial watering sites to control infection of moose (*Alces alces*) by a damaging trematode (probably *Parafasciolopsis fasciolaemorpha*) (88). This parasite is transmitted by snails that were abundant in wet areas used by moose in dry years. Ponds were dug in peat bogs where the snails were absent because of the acidity of the soil and water. Moose using these ponds were parasitised much less commonly than those using natural, less acidic, waters.

The term 'vectors' is used here to mean invertebrates that carry or transmit an infectious agent between vertebrates. Vectors may be either required or a facultative part of the ecology of a disease. Manipulation of vectors is an important part of the management of many diseases in domestic animals and humans. This has usually been done by attempting to reduce the population of the vector species. Some general features of vectors should be considered when vector control is contemplated, as follows:

– prevalence of infection in the vector is usually extremely low compared to that in the vertebrate host (i.e. the great majority of the vector population is not infected)

– the life-span of most vectors is very short, and they often have the ability for very rapid increase, so that populations may rebound rapidly after reduction

– the activity of many vectors is highly seasonal and is affected by weather, so that they may be available for control only during a restricted period

– species responsible for disease transmission often comprise only a tiny proportion of the population of similar species that may be harmed by any control programme.

The introduction of highly effective pesticides led to a belief that many diseases could be controlled or eliminated by vector population reduction using these chemicals. However, two major problems were recognised early and continue to limit the effectiveness of this management method. The first is that many compounds suitable for killing vectors are broad-spectrum poisons with serious environmental side-effects that limit their usefulness. The second is that acquired resistance develops rapidly in vector populations following the repetitive use of chemicals. For these reasons, chemical control of vectors has often been unsuccessful.

There have been few attempts to control vectors that carry disease of wild animals, except in the case of zoonotic diseases. Insecticides, including DDT (dichloro-diphenyl-trichloro-ethane), carbaryl and permethrins, have been used to control fleas involved in transmission of *Yersinia pestis* among wild rodents (10, 11, 36), including intervention in outbreaks of plague among black-tailed prairie dogs (*Cynomys ludovicianus*) (36), the principal prey of the endangered black-footed ferret (*Mustela nigripes*). General area-wide distribution of insecticide for this purpose has been unsuccessful and acquired resistance has been observed (10). Even targeted application of insecticide to burrows resulted in a 'significant problem' … 'through killing nontarget insect species with associated ramifications to the ecosystem' (36). Copper sulphate was used to kill aquatic snails that were the intermediate host for the liver fluke *Fascioloides magna* in the former Buffalo National Park, Alberta, Canada (94). Pybus concluded that this technique was successful in eradicating the fluke, but that 'considering the great environmental impact of such methods, they are unlikely to be used in a modern situation' (75). Several acaricides have been used extensively on lawns around homes in some areas to reduce populations of *Ixodes dammini*, the tick that transmits Lyme disease from wild animals to humans (91). In general, it appears that pesticides are most useful when used in a very selective manner in small areas and in combination with other methods including environmental manipulation and biological controls.

Pro-active management

This group of techniques includes those intended to prevent introduction of a disease agent into an area where it does not occur, and those designed to protect individual animals from either infection or disease.

Infectious diseases have a geographic range that is determined by the presence of adequate suitable host animals, i.e., a host population $\geq N_T$, and by a variety of environmental factors that allow transmission of the infectious agent. The geographic range of a disease can be viewed as being constrained by an ecological 'barrier' that consists of many components. The range of an infectious agent may increase and new areas may be colonised as a result of natural phenomena that alter the ecological barrier, such as increased rainfall or changes in vegetation, or in response to human-induced changes. Humans may alter ecological barriers allowing a disease agent to extend its range or completely circumvent existing barriers. Examples of the former type range from global effects, such as climatic warming, to local effects such as irrigation providing new habitat for disease vectors, concentrating animals through features such as artificial feeding, or by altering other environmental factors that change the distribution and abundance of animals. Ecological barriers are circumvented by direct translocation of infectious agents or more commonly through moving animals together with their disease agents.

Management to prevent movement of an infectious disease and its spread into new areas should be viewed as a process of protecting or supplementing natural ecological barriers, or of replacing natural barriers with artificial barriers. As it is difficult or impossible in the long-term to prevent natural changes, this type of management is usually directed at human-induced changes and consists of modifying human behaviour. This may include altering existing activities as well as considering the possible consequences of new activities on disease during the planning stages. Reducing or preventing global changes such as climatic warming go far beyond management of disease in wild animals, but local ecological barriers may be managed.

The most direct form of barrier management are measures designed to prevent the translocation of disease agents and/or disease vectors. Translocation of wild animals is a common management tool and has been used both to introduce new species and to restore extirpated populations. However, there are many historical examples of translocation of diseases of wildlife. Some of these were intentional, such the introduction of myxomatosis and rabbit haemorrhagic disease into Australia, but most were inadvertent, for instance the introduction of both the causative agent and the vector mosquito of avian malaria into Hawaii, introduction of *F. magna* with elk from North America to Europe, translocation of raccoon rabies northwards in the United States of America (USA), and introduction of nematodes of the genus *Elaphostrongylus* in cervids moved from Europe to other continents. In the past, the rigours of transport and the time required to move animals served as an unintentional barrier to translocation of disease agents, since many hosts, vectors and disease agents failed to survive the trip. However, the risk of such introductions has increased dramatically because of developments in transportation. The short travel time between any two points on the globe at present is often less that the incubation period for many infectious diseases.

The potential for disease movement through animal translocation and reintroduction has been discussed by several authors (8, 23, 24, 39, 45, 66, 102). Any animal translocation contains two types of risk, as follows:

a) that the introduction of exotic disease with the animals may adversely affect indigenous animal populations at the release site, and

b) that diseases present in the indigenous animals at the release site may have adverse affects on the translocated animals.

Corn and Nettles referred to the latter as a 'reverse risk' (23). In the light of these two types of risk, animals should never be translocated without a thorough understanding of the potential disease agents present at both the site of origin and the release site. A critical factor that must be considered in any proposed translocation and release of wild animals is that living animals cannot be sterilised. At least some of the microfauna that occur in and on any animal will be moved with the animal. Davidson and Nettles used the term 'biological package' to describe the animal, together with its infectious agents and parasites that it moved (24).

Corn and Nettles proposed a protocol to reduce the disease risk associated with translocation of elk in North America (23). The protocol contains five components that are applicable to any proposed translocation or reintroduction of wild animals, as follows:

1. Evaluation of the health status of the source population. This should include a complete review of all available information on the health of the source population, as well as testing of a significant sample of the population for specific diseases, using serology and necropsy where appropriate.

2. Quarantine of the animals that are to be moved to allow testing and observation. To be effective, the quarantine period must be at least as long as the maximum incubation period for any known disease of concern.

3. Physical examination and diagnostic testing of animals to be moved. While this will reduce the risk of disease transfer, it must be remembered that no pre-movement test is likely to be 100% effective in detecting every infected individual.

4. Restriction on translocation from certain areas or populations where specific diseases are known to occur. This is particularly appropriate for diseases for which there is no reliable live animal test (e.g. chronic wasting disease of cervids).

5. Prophylactic treatment of the animals to be moved. Chemotherapy will reduce the likelihood of transferring certain disease agents, but treatment is unlikely to be 100% effective in removing infectious agents from infected animals. This is particularly true for wild species for which there is usually little or no information available on appropriate dosage of drugs, or the efficacy of the drugs that might be used.

In addition, the health status of animals at the release site must also be evaluated. This should include a review of all species, including domestic animals, that might be susceptible to disease agents that could be introduced with the translocation, as well as species that might carry agents that could potentially harm the introduced animals.

Despite all of these precautions, there is always a risk in any movement of animals that disease agents that are currently unrecognised may be translocated, become established, and cause disease problems in the new area.

The development of effective vaccines and mass immunisation has had dramatic effects on many infectious diseases of humans and domestic animals. There is no reason to think that immunisation would not be similarly effective in wild animals, if appropriate vaccines were available and could be delivered to the animals. Although the use of immunisation has been restricted to a small number of diseases of free-living animals, there is good evidence that it may be very effective under certain conditions.

The purpose of immunisation is to render the individual resistant to an infectious agent. This resistance may be of two types. It may prevent the animal from becoming infected, or it may prevent the development of disease. It is very important to distinguish between these two forms of resistance, because animals immunised with a vaccine that prevents disease but not infection may still be able to transmit the causative agent. The objective in immunising animals may also be of two types. In some instances, the objective is to protect the individual from the disease. For example, immunisation was used to prevent anthrax in roan antelope (*Hippotragus equinus*) in Africa (27) and bison (*Bison bison*) in Northern Canada (20). *Bacillus anthracis* is present in the soil and there is little or no direct transmission from infected individuals to susceptible members of the population so that the aim in these programmes was to prevent animals from dying of the disease rather than to reduce transmission of the causative agent. In contrast, immunisation of wild carnivores including foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*), is designed to reduce transmission of the disease within the population, although immunisation also protects the individual. Obviously, a vaccine that prevented development of disease but not infection and transmission would be less suitable than one that prevented infection, if the goal is to reduce transmission. Immunisation designed only to protect the individual animal is likely to be of limited usefulness in free-living animals except in circumstances, such as management of endangered species, where the cost of delivering vaccine can be justified. The remainder of the discussion will deal with mass immunisation designed to reduce transmission.

When the goal is to decrease transmission of a disease, immunisation is used to reduce the proportion of susceptible animals in the population. In diseases caused by microparasites, the population can be sub-divided into susceptible, infected and resistant components and that immunity induced by infection or immunisation tends to be long-lasting. In contrast, immunity in diseases caused by macroparasites depends on the number of parasites present, is short-lived when no parasites are present, and reinfection is common. For these reasons, immunisation is more likely to be effective as a management strategy for reducing transmission of diseases caused by microparasites than of diseases caused by macroparasites.

The proportion of the population that must be immunised to have a significant effect on disease transmission is related to R_o, the reproductive rate of the disease. In general, the proportion of the population that must be immunised must exceed $1\text{-}1/R_o$(2), so that a large proportion of the population must be immunised in those diseases in which each infectious individual results in infection of many susceptible members of the population. Because R_o is related to population density, in general, the greater the population density, the larger the proportion of the population that must be immunised for disease control. Populations with a high recruitment rate and rapid turnover have a high proportion of new susceptible animals and may require high rates of immunisation to be effective.

An important factor in any immunisation programme is the average age at which susceptible animals are exposed to the disease agent. To be successful, immunisation must occur prior to infection, so that the average age of immunisation must be younger than the average age of infection in the population. In general, diseases in which animals are exposed at an early age will be more difficult to control through immunisation than diseases with a later average age of exposure. Diseases that are transmitted vertically from dam to offspring, or in which transmission occurs before there is any opportunity for immunisation, e.g., transmission before emergence from the den, are probably not amenable to management through immunisation. In some diseases there may be only a narrow window of time during which immunisation would be effective between the decline of maternal (passive) immunity in young animals and the average age of infection. Cassier *et al.* experimented with immunisation of female bighorn sheep to protect their offspring from pasteurellosis (19).

The other essential features of any immunisation programme relate to the characteristics of the vaccine and the ability to deliver the vaccine to a sufficiently large proportion of the population. Desirable features of a vaccine include the following requirements:

– it produces no significant disease in the host or non-target species

– it stimulates long-lasting protective immunity (preferably after a single exposure because of the difficulty of delivering repeated doses of vaccine to wild animals)

– it is protective against all varieties of the causative agent in the area

– it is incapable of reversion to a pathogenic form

– immunised individuals can be differentiated from animals recovered from natural infection

– it is inexpensive and stable.

Wobeser has discussed requirements of vaccines in detail (102).

In most situations related to wild animals, it is not practical to capture and handle individual animals for immunisation; however, this may be possible for small numbers of highly valued animals or in other special circumstances. For instance, De Vos *et al.* (27) used a helicopter and dart gun to vaccinate individual roan antelope to protect them from anthrax and Cassier *et al.* (19) vaccinated bighorn sheep captured with a helicopter and netgun. Rosatte *et al*. (80) reported that trapping, vaccinating and release of skunks and raccoons was an effective method of controlling rabies in an urban environment, and this technique also was used to create barriers to the spread of raccoon rabies in Ontario, Canada (81). Elk have been immunised for brucellosis on feeding grounds in Wyoming, USA, using a 'biobullet' (89). Between 1965 and 1977, almost 28,000 bison in northern Canada were rounded up in corrals with helicopters and vaccinated against anthrax (96). The effectiveness of the latter programme has not been assessed.

The most effective method for mass immunisation of wild animals is through distribution of oral vaccine that is effective when ingested with a bait. For this purpose, vaccines must have features in addition to those listed earlier. First, the vaccine must produce immunity when ingested. Second, because the vaccine is placed in the environment, it is imperative that it must be non-pathogenic for non-target species that might inadvertently ingest the bait. Third, the vaccine must be stable and retain its immunogenicity for as long as possible under adverse environmental conditions. Given the different food preferences and foraging habits of the different species, extensive testing is usually necessary to develop a bait that is very attractive to the species being targeted and less attractive to non-target species (31). Baits consumed by non-target animals are wasted and it may be difficult to deliver sufficient baits to the target species if there is strong competition with many non-target animals (92). The appropriate bait density for a particular situation must be discovered through testing in which the proportion of the target population consuming one or more baits and the proportion of the population developing protective immunity are measured. The frequency of baiting required varies among species, and among locations for the same species (58). As the R_0 is not known for diseases of wild animals, and is highly variable from situation to situation, it is not possible to predict the proportion of the population that must be immunised to control a disease. Oral vaccination, using a variety of vaccines, baits and methods of delivery, has been successful in eliminating rabies from foxes in several European countries and in Ontario, Canada (58). This method may be practical for other diseases in which the high costs for vaccine and bait development and testing, and the relatively intense effort required for bait delivery can be justified.

In summary, immunisation is best suited as a management strategy for microparasitic exogenous infections that have a low reproductive rate, in populations with a low turnover rate and in which the average age of infection occurs later in life. Capture and handling of animals for parenteral administration of vaccine is likely to be practical only for valuable species on small areas or under other unusual circumstances. Mass immunisation with oral vaccines delivered in bait may be effective, but its use is likely to be limited to a few serious diseases, because of the cost of developing, testing and delivering appropriate vaccine-bait combinations.

Population density management for disease management

Populations of host animals can be manipulated in several ways, with the objective of reducing disease transmission or eliminating the disease agent from a population. The techniques can be divided into four broad categories, as follows:

– alteration of animal distribution

– selective removal of diseased animals from the population

– general reduction in population density

– elimination or eradication of the total population that may have been exposed to the disease.

These categories can be considered as a series of steps in which the intensity of the action, the violence on the population, and the probability of public resistance increase with each step.

The objective in changing the distribution of animals for disease control is usually to reduce contact between susceptible and infected animals, or between susceptible animals and some specific geographical feature where transmission occurs. This technique is applicable only where the disease is limited to an identifiable area or site. A common recommendation in the face of a localised disease outbreak or epizootic, particularly among highly mobile species such as birds, is to disperse the animals away from the site. This technique has been employed to manage outbreaks of avian botulism (67), and to move waterfowl away from an outbreak of duck plague (68) and whooping cranes (*Grus americana*) away from an avian cholera epizootic (104). Pienaar discouraged vultures from using waterholes and destroyed vulture roosting sites to prevent contamination of waterholes with *Bacillus anthracis* carried from carcasses of animals dead of anthrax (71). Meagher described attempts to relocate bison in the Yellowstone National Park as part of a programme to manage brucellosis and prevent transmission to cattle (60).

It is extremely difficult to move wild animals out of their established range. Techniques used to frighten or haze animals rapidly lose their effectiveness with continued use (59) and animals will return or repopulate areas quickly unless the habitat can be made unattractive or suitable alternative habitat is made available. New attractive habitat may have to be created. For example, Parrish and Hunter flooded new wetlands to facilitate moving birds away from a botulism outbreak (67). Dispersal of animals into new areas also may create other management problems in the new area.

The value and efficacy of animal dispersal as a disease management strategy has never been evaluated in any type of controlled study of a wildlife disease. This technique is best suited for dealing with non-infectious diseases, such as localised toxin spills, in which there is no risk that moving the animals will also move the disease agent and establish new foci of disease. When dealing with infectious disease, there may be a risk that some of the animals dispersed will be infected and that these may establish new foci of infection and, hence, expand the geographical range of the disease. If the disease to be managed is known to have a very restricted distribution, or is a newly discovered disease, dispersal of animals from the known areas of infection should not be attempted because of the risk of extending the range. However, if the disease agent is known to be widespread, and the occurrence of clinical disease is dependent on some environmental factor limited to a particular site, dispersal may be an appropriate strategy. The first major outbreak of duck plague among wild birds in North America provides a good example of the dilemma associated with dispersion. That outbreak, in which about 10,000 mallards (*Anas platyrhynchos*) and several hundred Canada geese (*Branta canadensis*) died, occurred in mid-winter on a small area of open water in a refuge in South Dakota (68). Although this was the first major epizootic of duck plague recognised among wild waterfowl in North America, and the disease was considered at the time to be exotic to North America, a decision was made to disperse the birds rather than to try to contain the disease. Although there is no evidence that the dispersal of potentially infected birds resulted in widespread dispersion of the particular virus found at the outbreak site, containment and depopulation would probably have been a more sound strategy (102). Friend and Franson concluded that 'As a general rule, animal dispersal is not recommended when infectious disease is involved, unless it can be assured that the population being dispersed will not infect other wildlife' (35).

Enforced separation of infected and susceptible animals has been used to prevent transmission of diseases between wild and domestic animals, and in a few instances to separate wild animals from humans to reduce transmission of a zoonotic disease. For instance, game-proof fences have been used in Africa to separate African buffalo (*Syncerus caffer*) infected with foot and mouth disease, bovine tuberculosis and theileriosis from domestic cattle (44, 51), and wild pigs (*Phacochoerus aethiopicus* and *Potamocheorus porcus*) infected with African swine fever from domestic pigs (51). Limited fencing across travel routes was attempted to prevent bison potentially infected with brucellosis from leaving the Yellowstone National Park and coming into contact with cattle (60). The fences in the latter instance were ineffective because the bison rapidly developed detours to circumvent the fences. Fencing to exclude deer resulted in a marked reduction in the number of larval and nymphal *Ixodes dammini* ticks on small experimental areas in a region where Lyme disease was endemic, leading Stafford to conclude that fencing of 'moderate tracts of land' could be an effective component in reducing risk of Lyme disease (90). Fences are not feasible for diseases transmitted by highly mobile vectors, or for diseases in which small animals are involved as potential hosts of the disease. For example, Stafford found that rodents introduced ticks through deer-proof fences (90). Fences are relatively expensive to construct, require continual maintenance and periodic replacement, may require extensive habitat disruption for their construction, may seriously disrupt the movement of wildlife not affected by the disease, and are subject to failure. Some forms, such as electrified fences, may not be acceptable in areas where human contact is likely. For management of infectious diseases that may pass between wild and domestic species, double-fencing with an animal-free exclusion zone is usually required to prevent close contact between animals. The fence must be sufficiently robust and impermeable to prevent movement of all species that might be involved in disease transmission or sympatric species that are known to challenge and break fences. For instance, 2-m high fences are sufficient to confine game farm elk but do not prevent the entry of wild deer (*Odocoileus* spp.) into the pens. This became a concern when chronic wasting disease, that affects both deer and elk, was discovered in elk on game farms. Enforced separation, using methods such as fences, has relatively little application in management of infectious disease among free-living animals, except in very local situations, but may have an important function at the interface between wildlife and traditional agriculture.

Another management technique aimed at reducing or eliminating a parasite from a population is to selectively remove infected individuals. 'Selective culling' or 'test-and-slaughter' has been used successfully as part of the management strategy for several diseases of domestic livestock. There are a number of requirements that limit the application of selective culling for use in wild animals. It is only appropriate for situations in which:

a) the entire population can be examined

b) infected individuals can be identified (i.e. a sensitive and specific test is available)

c) infected individuals can be readily captured (repeatedly) for testing

d) animals known to be free of the disease can be isolated from the untested portion of the population, and

e) removal or sacrifice of a portion of the population is acceptable or tolerable.

Primarily because of the need to capture, handle and hold individual animals, this method has not been used widely in wild animals. Test and removal was used in conjunction with calfhood vaccination to eradicate brucellosis from a captive herd of bison in Elk Island National Park, Alberta, Canada (96). Facilities were available in this situation to handle the animals repeatedly. All of the original group of animals eventually tested positive and were destroyed, but some of their offspring remained free of brucellosis and provided the nucleus of a new herd. Selective killing of visibly affected individuals was used, together with chemotherapy through treated salt blocks, to control sarcoptic mange in chamois (*Rupicapra rupicapra*) (72). Test-and-slaughter was rejected as an option for elimination of brucellosis and tuberculosis from a free-ranging population of bison in Wood Buffalo National Park, Canada, for many reasons, including the impracticability of capturing over 3,000 wild bison in a 44,000 km^2 wilderness, the difficulty in holding test-negative animals so that they would not be exposed to infected individuals that had not been tested, the lack of highly sensitive tests, and the likelihood of a high rate of injury and mortality associated with capture and handling (102). Because of the requirements for success, selective culling is unlikely to be a common method of disease management in wild animals. It might be used as an alternative to total population elimination in situations where it is imperative to conserve genetic diversity while eliminating a disease.

The reverse of selective culling is being used in northern Canada to develop a population of bison free of brucellosis and tuberculosis, beginning with a wild source herd in which both diseases occur at high prevalence. In this approach, rather than selecting individuals infected with the disease for disposal, individuals with the least likelihood of being infected are selected from the herd and retained. Intensive searches are performed to locate neonatal calves within the free-living herd. The calves are removed to an isolation facility, treated intensively with antibiotics, and reared in pairs to reduce the potential loss should an infected individual be recognised. The animals are tested repeatedly during rearing to maturity, and their offspring will be used as the foundation of a new herd free of the diseases. The plan is to remove the free-ranging disease herd prior to reintroducing disease-free animals to the wild. Similarly in South Africa, the breeding of African buffalo that are free of foot and mouth disease, theileriosis, tuberculosis and brucellosis is currently being successfully practised, to supply 'clean' buffalo to conservation areas outside the disease endemic zones (12).

Reducing the population of animals within an area has been attempted frequently as a method to manage disease in wild animals. Population reduction is based on epidemiological theory that predicts that for directly transmitted infections, the per capita rate of disease transmission and the prevalence of disease will increase with increasing population density. Although usually not stated in these terms, the goal is to reduce the population to a level at which R_O approaches 1, so that the incidence of the disease is reduced, or to below N_T at which point R_O = <1, and the disease will die out. Population reduction is most likely to be effective for diseases in which there is only a single source of infection, and unlikely to be effective for diseases that occur in several species or that have multiple sources of infection. Population reduction is more likely to be effective as a management strategy for diseases with inefficient transmission, than for parasites such as many macroparasites, that are transmitted very efficiently. The degree of population reduction required or desired is sometimes expressed in relation to carrying capacity, which is the density of population at which birth and death rates balance or at which the population is at an equilibrium. While populations are never likely to truly achieve an equilibrium, and there will be different equilibrium points under different circumstances, the concept of carrying capacity is useful as a reminder that the population size is a balance between the removal of animals from the population by all causes, including the disease itself and the depopulation effort, and recruitment to the population through reproduction and immigration. The more intense the depopulation effort, the lower the reproductive rate of the animal, and the less recruitment that occurs through immigration, the greater the likelihood of effective population reduction.

Population density could be reduced either by decreasing the number of animals within an area or by increasing the area available for the same number of animals. Populations of many wild species have been compressed because of habitat degradation and loss but, in most cases, there is little or no effective manner of increasing the amount of available habitat. If unoccupied suitable habitat is available, 'surplus' animals could be removed from one site and translocated to another. This method was used to reduce population density of bighorn sheep as a preventive measure to reduce the likelihood of outbreaks of pneumonia (86). In most instances, population density is reduced by removing animals. Normally this is done by killing animals, i.e. by increasing the mortality rate, but a population could also be reduced by decreasing reproduction. Control of reproduction has been attempted for pest species and there is interest in developing reproductive control methods in a few disease situations (29), but there is no information available on the actual use of this form of population reduction for disease management among wild species.

Population reduction can be of three general types, namely: focal around a specific site, locally extensive in an area to create a barrier, or generalised over a broad region. All three forms have been used for disease management. The first two are only appropriate for diseases that are localised and in which the distribution is well known or where a very localised effect is desired. Wobeser reviewed a number of such projects and identified some general features of population reduction programmes (102), as follows:

– Population reduction has usually been aimed at carnivores, and species considered as pests, rather than at game species or species considered beneficial by the public. This reflects the difficulty in convincing the public of the need for killing 'desirable' species. This aversion may be reduced if there are multiple reasons for population reduction. Deblinger *et al.* described reduction of a deer population on a site extending over 567 ha that was performed with the aim of preserving vegetation, improving deer condition and reducing risk of Lyme disease in people in the area (26).

– Population reduction has been more effective in preventing entry of disease into an area than in dealing with established disease. For example, there are several instances in which intensive local depopulation of carnivores in advance of a spreading wave of rabies was successful in preventing spread into areas free of the disease. These include depopulation of vampire bats (*Desmodus rotundus*) to prevent infection of cattle in Argentina (34), depopulation of foxes in Switzerland (99) and Denmark (64), and depopulation of striped skunks in Alberta along a 30-km strip parallel with the border with Saskatchewan and Montana (40). In these examples, control was possible because the disease was moving in a single direction. Geographical barriers that precluded lateral movement of the disease aided in some situations.

– Population reduction has been more effective for focal occurrences than for widely disseminated disease. Radial depopulation within a 5-km radius was used when raccoon rabies occurred in Ontario, Canada. This was accompanied by trap-vaccination and release of raccoons within an additional 5- to 10-km zone, and general aerial baiting with vaccine over a larger area (81). It was believed that population reduction was the most effective way to deal with animals that might be incubating rabies near the index cases, since vaccination is not effective in animals in the late stage of the disease. The apparent success of this local action is in contrast to many reports of the apparent failure of general population reduction of carnivores to deal with enzootic rabies (14, 25, 30, 57, 59).

– Population reduction without habitat modification to make the area less attractive to the species (or to lower the carrying capacity) is a temporary measure. The speed with which a population recovers depends on the extent of reduction, the size of the area which influences the amount of recruitment through immigration, and the reproductive rate of the species. Population recovery is highly species- and site-specific. As examples, Waltermire found that a population of Richardson's ground squirrels (*Spermophilus richardsoni*) reduced by 90% in spring for plague control recovered to about 52%-64% of the pre-control level by mid-summer but some degree of reduction persisted for one year (98). Bögel *et al.* estimated that European fox populations reduced to 20%-30%, 40%, 60% and 80% of the original population would recover to original densities within four, three, two and one year(s), respectively (13). Everard and Everard estimated that poisoning killed 33%-66% of mongooses (*Herpestes auropunctatus*) in some areas of Grenada, but that the population recovered in some locations within nine months (30).

– There has been a trend away from attempted wide-scale depopulation to population reduction on a local level.

– Population reduction projects tend to be supported well while disease is highly evident, but lose support and funding when the prevalence of disease decreases. This may allow recrudescence of disease.

If population reduction is to be used for disease control through either focal reduction around individual cases or to create a barrier to disease movement, effective surveillance and rapid reporting of cases are necessary, so that control can be applied in the correct location. This is a serious limitation on the technique because intense surveillance usually is not available for wild species. It is particularly unreliable for small or inconspicuous species but even for medium-sized and large animals the 'normal' reporting rate of diseased animals is very poor. For example, the reporting rate for foxes dying of rabies in Europe was estimated at 2%-10% (5). The reporting rate is likely to be even lower for unexpected disease occurrences. Hone and Pech estimated that the probability of an individual diseased feral hog being reported was <0.0015, should foot and mouth disease occur in Australia (48).

The size of the population reduction zone or barrier is critical. If it is too small, infected animals will be missed or will move across the barrier; if it is too large, the effort to remove animals may be so diluted that insufficient animals will be removed. (For instance, if the radius for population reduction is 2 km, the area in which population reduction must be performed is about 12.5 km^2, whereas if the radius is increased to 5 km, the area = 78 km^2, requiring >6-fold more effort.) The size of the area must be based on the expected travel distance or home range of the species and these will be highly variable in different habitat types. Animals infected with some diseases (e.g. rabies), may move considerably greater distances than normal animals in the same area (82). Muller suggested that a control zone 60-100-km wide was needed for foxes in Denmark (64), Lord used a depopulation zone 15-km wide for rabies control in vampire bats (55), and a zone 5-km wide was used for rabies management in striped skunks (40) and raccoons (81) in Canada.

Reduction of the population density within a restricted area may have to be accompanied by other actions to prevent the influx of susceptible animals from the surrounding area because local population reduction 'may be counter-productive if the subsequent contact rate is increased because of immigration of susceptible animals' (46). Hone and Bryant proposed a technique that might be employed to control foot and mouth disease in feral pigs around a focal outbreak in cattle (47). In the model, intense depopulation would be conducted in the central zone at the same time as a pig-proof fence would be constructed around a perimeter to prevent both immigration and emigration. Rosatte *et al.* used a similar zone approach to deal with an incursion of raccoon rabies into Ontario (81). Intense trapping and euthanasia of trapped raccoons and striped skunks was performed within 5 km of the initial cases. At the same time, raccoons and skunks were captured in a second radial zone 5 to 10 km from each case. These animals were vaccinated, tagged for identification and released. This was supplemented by aerial application of oral vaccine baits over a broader area surrounding the cases.

It is very important in focal depopulation around isolated cases of disease to be able to apply intense population reduction pressure rapidly. For instance, Pech and Hone suggested, on the basis of a model, that it would be necessary to eliminate >95% of the feral pigs within an area in less than 21 days to be successful in controlling a local outbreak of foot and mouth disease (69). Rosatte *et al.* identified the existence of a detailed contingency plan which could be implemented immediately, and the rapid deployment of staff, as the keys to success of a programme to control raccoon rabies in Ontario, Canada (81).

The degree of population reduction required to prevent a disease from spreading or to lead to its extinction is unknown for most diseases. The value is likely to be highly variable in different locations, even for diseases that have a single host. For instance, rabies remained enzootic in Ontario at a fox population density which was thought to result in the disappearance of the disease in Europe (97). The following examples are intended only to illustrate the degree of population reduction that has been suggested as appropriate in different circumstances. Waltermire estimated that a ground squirrel population would have to be reduced by at least 90% for effective management of plague (98). Roberts suggested that *Mycobacterium bovis* infection could be eliminated from a brushtail possum (*Trichosurus vulpecula*) population in New Zealand by reducing and maintaining the population at 43% of its carrying capacity (79). Fornes *et al.* estimated that they removed about 95% of the vampire bats in advance of a spreading wave of rabies (34), and Rosatte *et al.* estimated that 83% to 91% of raccoons were killed in the zone around the initial cases of raccoon rabies in Ontario (81). 'Virtual elimination' and approximately 80% reduction of deer populations on two small areas in Massachusetts resulted in reduction in the number of *Ixodes dammini* ticks in both areas and a reduction in the incidence of Lyme disease in humans on one site (26).

In general, mass population reduction over large areas has only been attempted for the most serious of diseases. Evidence from early attempts is difficult to interpret. In many cases, notably those involving rabies referred to earlier, general population reduction was considered to have been ineffective. There have been suggestions that attempted depopulation of coyotes (*Canis latrans*) might increase natality and decrease natural mortality to potentially offset the planned population reduction (22). In situations in which a disease disappeared from an area following population reduction, there were no detailed studies to determine the actual contribution by population reduction. Examples of such programmes include massive killing of deer in California during an outbreak of foot and mouth disease (16), and in Florida as part of a cattle fever tick eradication programme (41) and killing of many foxes in Spain following a local incursion of rabies (6). An incursion of rabies into the province of Alberta led to a massive depopulation of carnivores between 1952 and 1954. The disappearance of the disease was credited to the population reduction, together with control and vaccination of dogs (7); however, the same epizootic died out in the neighbouring provinces of British Columbia, Saskatchewan and Manitoba without any organised programme of wildlife depopulation (95).

The longest-running programme of non-selective culling of a wild population for disease control is the effort to reduce or eliminate *Mycobacterium bovis* infection in brushtail possums as a source of infection for cattle in New Zealand. The principal method used for more than 40 years has been aerial distribution of baits containing sodium monofluoroacetate (1080) (43). Some general features of this programme are worth noting. There has been no evidence of acquired physiological resistance to 1080, although it has been used on up to 2.5 million ha annually; however, a significant proportion of possums survive poisoning operations for a variety of other reasons (43). Infection among possums is not uniformly distributed; the highest prevalence occurs in habitats capable of supporting the highest density of possums (18). Large- scale, short-term reduction of possum populations seldom has been effective because, without follow-up control of possums, the incidence of tuberculosis in cattle regained its previous level (9). Sustained long-term reduction of possum populations to about 22% of the pre-control density resulted in a major reduction in the incidence of tuberculosis in cattle and the prevalence of tuberculosis in possums (17). Caley *et al.* suggested that if the level of possum population reduction was sufficient, tuberculosis could be eradicated from the population (17).

The most severe form of population reduction is total extirpation of a species from an area. Eradication of a wild species has been suggested as a method that might be used should a serious animal disease, such as foot and mouth disease become established in a disease-free area, (47, 69) and was proposed as the method of choice for eliminating brucellosis and tuberculosis from bison in and around Wood Buffalo National Park in Canada (32). However, the author is aware of only two published reports of eradication having been used for disease control in a free-living species and both were on a very local level. Gershman *et al.* eradicated the surviving eiders, gulls (*Larus* spp.) and terns (*Sterna hirundo*) on islands off the coast of Maine following an outbreak of avian cholera among eiders (37). Pursglove *et al.* used a wetting agent sprayed from aircraft to immobilise over 6,000 American coots (*Fulica americana)* in a group experiencing avian cholera (74). The birds were then collected and killed. The efficacy of these actions is questionable. Eradicaton of the eiders did not prevent subsequent occurrences of the disease among the eider population in the area (52). Montgomery *et al.* (63) believed that mortality in an outbreak among coots similar to that described by Pursglove *et al.* (74) declined because of population reduction caused by the disease and migration. There are very few reports in which intentional eradication of a wild species has been accomplished for any purpose. The elimination of muskrats (*Ondatra zibethicus*) from Great Britain by trapping (100) stands as an example that extirpation may be possible.

The potential for eradicating a population of large animals, such as might be considered during an incursion of foreign domestic animal disease, has been tested on two occasions in Australia. Feral pigs on a 50 km^2 area were first poisoned with 1,080 baits and then live pigs were hunted from helicopters. Hone concluded that 'eradication would be almost complete, but probably not entirely so' using these methods (46). Neither the rate of recruitment through immigration from the surrounding countryside nor the cost to maintain depopulation of the area were reported. Ridpath and Waithman tested the feasibility of eradicating feral water buffalo (*Bubalus bubalis*) on a 389 km^2 area (78). Using a combination of helicopter round-ups, shooting from helicopters, and shooting from the ground, more than 97% of the population was removed over a 3.5 month period. These experiments illustrate a fundamental problem with extirpation. As the population is reduced, the effort required for further reduction escalates markedly and elimination of the final few animals may be extremely difficult. It may also be very difficult to determine when and if extirpation has been accomplished. These experiments were conducted on small areas (equivalent to circles with a radius of about 4 and 11 km, respectively) on which intense management pressure could be exerted and maintained. In contrast, Hone and Pech estimated that foot and mouth disease might have spread within the feral pig population to cover 10,000 km^2 to 30,000 km^2 prior to the first case being diagnosed (48). Based on their experimental trial, Ridpath and Waithman concluded that 'eradication of buffalo from their entire range would be an unrealistic objective, both economically and practically' (78).

Total eradication of a population of wild animals that may have been exposed to a disease, as has been the case in emergency control operations in domestic animals, is probably impossible, at least in the short-term.

Conclusion

Management of disease in wild animals must be based on sound knowledge of the biology of the disease agent and the species affected, and particularly of the population ecology of the disease process. The initial step in any management programme is to clearly define its objective. This might be to prevent introduction of a disease, to reduce the frequency of occurrence or effect of a disease, or to eradicate an existing disease. When the objective has been defined, potential techniques for reaching the objective can be considered, together with their advantages and disadvantages. It is also important to consider in advance the required and available resources for management. Management may include techniques to manipulate the disease agent or its vectors, the host animals, other aspects of the environment, or human activities. It is very important that management programmes include a continuous monitoring process, so that the effectiveness of techniques can be measured, and new methods can be introduced if current methods are ineffective. Programmes should be sufficiently flexible to change with evolving circumstances as the programme proceeds and several methods may need to be applied either simultaneously or sequentially during a programme. Public education is a valuable component of many management programmes; both to gain public support through demonstrating the need for management and to change human activities that influence the disease.

In general, it is easier to prevent the introduction of new diseases than to control or eradicate existing diseases. Short-term specific measures, such as treating individual animals, disinfection, or dispersing animals from focal areas of infection, are expensive, transient in effect, limited to small areas, and may have little effect on the general health of the population. Long-term non-specific techniques, such as habitat improvement, may reduce disease over time as well as having other beneficial effects. Many of the techniques that have been used to manage disease in wild animals are of unproven effectiveness.

■

Stratégies de gestion des maladies de la faune sauvage

G. Wobeser

Résumé
Il existe trois grandes stratégies de gestion des maladies de la faune sauvage : la prévention, la lutte contre les maladies existantes et l'éradication. Les mesures de gestion peuvent s'appliquer à l'agent pathogène, à la population hôte, à l'habitat de l'hôte ou aux activités humaines. Face aux agents pathogènes, on peut agir à deux niveaux : la désinfection de l'environnement ou le traitement de l'hôte. La désinfection et l'utilisation de pesticides pour détruire les agents ou vecteurs sont limitées à des situations locales ; elles peuvent être nocives pour l'environnement et induire l'acquisition de résistances. Les difficultés liées à l'administration d'un traitement limitent la chimiothérapie à des foyers isolés. La gestion des populations hôtes peut reposer sur la vaccination, sur la modification de leur répartition ou de leur densité, ou encore sur leur extirpation de la zone. La vaccination est la méthode la plus indiquée contre les infections exogènes dues à des microparasites présentant un taux de reproduction peu élevé et chez des populations qui se renouvellent lentement. La vaccination de masse au moyen d'appâts oraux s'est révélée efficace, mais cette stratégie se limite à quelques graves maladies. Il est difficile de déplacer les animaux sauvages et les techniques visant à dissuader les animaux de pénétrer dans une zone deviennent rapidement inefficaces. La mise en place de clôtures n'est possible que dans certaines zones limitées. L'abattage sélectif se limite aux cas dans lesquels les individus affectés sont immédiatement identifiables. La réduction d'une population en général s'est révélée peu efficace pour lutter contre les maladies ; en revanche, on a obtenu de bons résultats en diminuant les populations se trouvant à la périphérie d'un foyer ou en créant une zone tampon pour éviter la propagation d'une maladie. La réduction des populations est une mesure temporaire. L'éradication d'une population d'animaux sauvages à des fins de gestion sanitaire n'a jamais été tentée. En revanche, il est possible de modifier l'habitat pour réduire l'exposition aux agents pathogènes ou pour changer la répartition des hôtes ou leur densité. La gestion des maladies des animaux sauvages implique habituellement une modification des activités humaines. La principale méthode consiste à limiter les mouvements d'animaux sauvages pour prévenir la diffusion des maladies.

Mots-clés
Éradication – Faune sauvage – Gestion – Macroparasites – Microparasites – Prévention – Prophylaxie – Transmission – Vecteurs.

■

Estrategias de gestión de enfermedades de la fauna salvaje

G. Wobeser

Resumen
Para gestionar las enfermedades de la fauna salvaje caben tres tipos básicos de estrategia, a saber, prevenir la introducción de la enfermedad, controlar la enfermedad ya presente, o erradicarla. La estrategia de gestión puede centrarse en el agente etiológico, las poblaciones o hábitats del animal huésped o las actividades humanas. Cuando se opta por atacar el agente patógeno, cabe

recurrir a la desinfección (para contener su presencia en el medio natural) o al tratamiento (para eliminarlo del organismo de los huéspedes). El uso de desinfectantes y plaguicidas para destruir el agente o sus vectores se limita a zonas reducidas, ya que esos productos pueden tener graves efectos ambientales o inducir la adquisición de resistencias. La dificultad de administrar tratamientos farmacológicos limita también este expediente al ámbito local. En cuanto a las poblaciones del huésped, cabe inmunizarlas, modificar su distribución o densidad o simplemente extirparlas del lugar. La inmunización es el mejor método para microparásitos exógenos con una tasa de reproducción baja y para poblaciones huéspedes que se renuevan lentamente. Aunque se han demostrado fructíferos, los métodos de inmunización masiva con cebos de comida sólo se aplican a unas pocas enfermedades de especial gravedad. Desplazar a los animales salvajes no resulta fácil, y las técnicas para ahuyentarlos de una zona concreta pierden eficacia con rapidez. La colocación de vallas sólo es factible en áreas reducidas. El sacrificio selectivo se reserva a los casos en que resulta sencillo detectar a los individuos afectados. Aunque la reducción general de poblaciones no ha sido muy útil en la lucha contra enfermedades, la reducción alrededor de un foco infeccioso o la creación de barreras al movimiento de la enfermedad, en cambio, sí han dado buenos resultados. La reducción de una población es en cualquier caso una medida temporal. Nunca se ha intentado erradicar una población de animales salvajes como medida de gestión sanitaria. La modificación del hábitat es un posible expediente para reducir la exposición a agentes patógenos o alterar la distribución o densidad de las poblaciones huéspedes. Por regla general, la gestión de enfermedades de la fauna salvaje requiere introducir cambios en las actividades humanas. El método más importante es el de restringir el traslado de animales salvajes para evitar que una enfermedad se desplace.

Palabras clave

Control – Erradicación – Fauna salvaje – Gestión – Macroparásitos – Microparásitos – Prevención – Transmisión – Vectores.

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