Sustainable control of zoonotic pathogens in wildlife: how to be fair to wild animals?

M. Artois (1)*, J. Blancou (2)**, O. Dupeyroux (3) & E. Gilot-Fromont (1, 4)

(1) Université de Lyon, Campus vétérinaire de Lyon, VetAgro Sup, 1, avenue Bourgelat, 69280 Marcy l’Étoile, France
(2) Honorary Director General of the World Organisation for Animal Health (OIE), 11 rue Descombes, 75017 Paris, France
(3) Direction Départementale de la Cohésion Sociale et de la Protection des Populations du Cher, Cité administrative Condé, 2, rue Victor Hugo, C.S. 50001, 18013 Bourges Cedex, France
(4) Université Lyon 1, Laboratoire de Biométrie et Biologie Évolutive UMR 5558, 43, boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France

* Corresponding author: Prof. M. Artois, VetAgro Sup, 1, avenue Bourgelat, 69280 Marcy l’Étoile, France.
E-mail: marc.artois@vetagro-sup.fr
** Dr Blancou died during the preparation of this document; he was a former Director General of the OIE and an active supporter of capacity-building for Veterinary Services in wildlife health. The authors wish to dedicate this review to his memory.

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Summary
Wildlife may harbour infectious pathogens that are of zoonotic concern. However, culling such reservoir populations to mitigate or control the transmission of these pathogens to humans has proved disappointingly inefficient. Alternatives are still in an experimental stage of development. They include vaccination, medication, contraception and environmental manipulation, including fencing and biosecurity measures. This review examines the general concepts involved in the control of wildlife diseases and presents relevant case studies. Since wildlife disease control inevitably involves interfering with wildlife ecology, this is a complex goal whose attempts at realisation should be supervised by a scientific organisation. Most approaches within natural ecosystems should first be carefully tested in trials that are progressively extended to a larger scale. Finally, all measures that aim to prevent infection in humans (such as personal hygiene or vaccination) or that encourage us to avoid infectious contacts with wildlife should be recommended.

Keywords

Introduction

Animals that live in the wild can act as a reservoir, a liaison host or simply as victims of diseases transmissible to humans and domestic animals. It has long been known that the zoonotic disease rabies vanished as an infection maintained by dogs in continental Europe but instead became an infection spread by the red fox (Vulpes vulpes). Similarly, cattle have become infected with bovine tuberculosis (bTB) from an apparently new reservoir, the Eurasian badger, Meles meles, as first observed in 1971 (19) in the United Kingdom. Thus, situations arise where a wild animal population maintains and spreads a zoonotic infection. For this reason, there is growing interest in developing methods to control disease transmission from wildlife to humans or farmed animal species. Wildlife species differ from domesticated species in significant ways. They are often elusive, not always well known by zoologists, have no owners and usually no custodians and are often perceived in an emotional way by the general public (3).
In the following article, the authors focus on controlling pathogens in wildlife at their source (known as ‘release risk’, in the vocabulary of risk assessment) or where wild and domestic animal populations come into contact (‘exposure risk’). It is not the intention of the authors to discuss measures, such as personal hygiene or vaccination, that aim to protect humans as individuals against direct transmission through skin contact (e.g. tularemia); bite (e.g. rabies); inhalation of an aerosol (e.g. haemorrhagic fever with renal syndrome) or ingestion (e.g. trichinellosis). Such disease control at the source, or at the interface between wild and domestic animal populations, would circumvent the technical difficulties associated with purifying contaminated soil or water (as in the case of leptospirosis), with vector control (e.g. in West Nile fever and tick-borne encephalitis), or with protecting humans from ‘messenger hosts’ or ‘liaison hosts’, such as companion animals or domestic livestock. The transmission of microbes results from direct or indirect contact between infectious and susceptible individuals. For control purposes, there are two ways to target the infectious agent in its host: either limit the number of receptive individuals by vaccinating or killing them or treat and/or eliminate infected individuals to reduce the duration of the infectious period and the number of infectious individuals present at any given time.

When confronting the risk posed by zoonotic pathogens in wildlife, a framework for managing these communicable pathogens or parasites must be developed that is based on scientific evidence (52). In this paper, the authors review three generic control strategies that consist of prevention, mitigation and eradication. Here, controlling wildlife diseases at the source refers only to actions designed to prevent the introduction of a pathogen into a susceptible population (thus avoiding it becoming a further source population for that pathogen); reduce the prevalence of infection within the wildlife reservoir, or at least limit its effects to some acceptable level (mitigation); and, finally, to extirpate the pathogen from the source host population (eradication).

Manipulating the size of the host population

Manipulating the size of the host population is used to reduce the density of both the infected and susceptible individuals in a population (11). Lowering the host number should lead to a lowered incidence of infection until a threshold density is reached, at which point the infection will disappear, due to the low probability of transmission (36). Population reduction has mostly been attempted by shooting or trapping, although other methods have been used (including gassing and poisoning). Few plans to reduce host population density include an evaluation of the desired level of population decrease, and attempts to reduce large populations by culling are often offset by the effects of compensatory reproduction and immigration (12). If depopulation does not manage to permanently lower population density to below the threshold density, the infection may remain endemic, even at low incidence rates. Recent examples of rabies in foxes in Europe, bTB in badgers in the United Kingdom, and even classical swine fever in wild boar (Sus scrofa) tend to show that disease control by lethal methods is difficult to achieve in large populations of wildlife with a high turnover rate (see [11] for more details). Culling or killing animals – so-called ‘lethal control’ – is no longer perceived as the best option for mitigating the spread of wildlife pathogens to humans or domestic animal populations. For a growing number of citizens with a high level of education, lethal control is seen to impose great suffering and threaten animal demography. For these reasons, lethal control is increasingly considered unacceptable and alternatives must be developed.

In the following paragraphs, the authors examine some of the alternative methods available to control zoonotic pathogens, limiting themselves to a broad presentation of concepts and documented examples which are relevant to Veterinary Services. The interested reader will find a more detailed description of the different strategies currently being used, or at least tested, which focus on:

- the pathogen (10)
- the reservoir host (11) or
- the environment (50).

Here, the authors will successively explore the use of medical tools (such as vaccination, medication and contraception, in wild hosts) and disease control tools (divided into environmental manipulation of host habitats and protection or biosecurity measures) against the intrusion of wildlife pathogens onto farms.

Medical tools

For the sake of clarity, the authors distinguish between:

- methods that rely on immunogenic products, i.e. vaccination
- methods based on a medical therapy (either for prevention or control)
- medical tools employed to limit the population growth of a maintenance host species (contraception).
Vaccination

The concept

Both field research and mathematical modelling approaches have been used to demonstrate that, when feasible, vaccination is a valuable option. Early mathematical models of infectious disease dynamics suggest that it is useful as soon as the rate of control ensures that a sufficient proportion of the population is immune for a period of time. When achieved, herd immunity means that any given infectious specimen has a low probability of infecting a susceptible animal. If the disease is introduced into a vaccinated population, the mean number of secondary infections caused by each infected case will be lower than one, thus preventing further outbreaks from occurring \( R_0 < 1 \).

However, this scenario may be considered overly simplistic, since the practical constraints on vaccination campaigns often complicate matters. Vaccination programmes may require heterogeneous efforts over space and time to optimally deploy resources for disease control \( (1) \). Overall, vaccination is predicted to be the most efficient method in populations where host birth, host death and disease propagation rates are relatively low. Elsewhere, culling or combined strategies may be more efficient \( (9) \).

Route of delivery

A variety of approaches have been considered to deliver vaccines to wildlife. The most suitable method depends on the characteristics of the vaccine, the target species, the natural habitat where it will be deployed and the overall cost of the approach. The two main routes of vaccine administration are by injection (parenteral) and by ingestion. Injected vaccines have been tested on a number of species. These were either experimental studies or interventions with a follow-up investigation. Administering vaccine by the oral route is usually achieved with edible baits. Oral bait consists of two main components: the matrix, which comprises an attractive food; and the vaccine, which may be encapsulated within a protective capsule. Perhaps the most technically challenging aspect of bait formulation, however, is to ensure that the vaccine remains stable during processing, and while in the natural environment (usually a few days are enough). To survive passage to its destination within the target animal, the dose may require encapsulation in some protective substance or structure. Rabies vaccine is believed to allow immunisation through contact of the appropriate antigen with the oral cavity during chewing of the bait, and thus does not need to be designed to survive passage through the stomach.

Baits containing rabies vaccine were first distributed in the field by hand in Europe in the 1980s \( (7) \). This is still the case for vaccination campaigns that target specific populations, for example, during the initial stages of an outbreak. Distributing vaccine baits by hand is also the method of choice for vaccinating wild boar against classical swine fever (CSF), also known as hog cholera \( (31) \). Classical swine fever is a non-zoonotic swine disease caused by a Pestivirus \( (\text{Flaviviridae}) \). Delivery systems in general are now being increasingly subjected to economic evaluation to identify the most cost-effective solution. The cost of ground baiting was found to be consistently less than that of air baiting, for example \( (22) \).

One important consideration when developing baits for wildlife is the potential for legal restrictions on the use of certain substances (such as antibiotics, e.g. tetracycline, or biological dyes, e.g. Rhodamine B) in the environment. This is especially likely to be a factor where exposure to non-target livestock cannot be ruled out.

The vaccine

The required properties of a vaccine vary according to the pathogen and the host characteristics. In the case of rabies, CSF or bTB, the vaccine must be delivered as a live modified organism or a live vector \( (e.g. \text{vaccinia virus}) \), since the immune reaction can only develop if the vaccine antigen comes into contact with immunocompetent cells through the oral mucosa. This poses a substantial challenge for oral delivery in particular, because to ensure that the immune response is sufficient to confer protection, the immunising pathogen must remain viable during formulation, storage and deployment in bait. The vaccine must also retain viability in the host up to the point of immune induction \( (16) \).

The efficacy of vaccination in wildlife

Data demonstrating the efficacy of a vaccine destined for use in wildlife are most frequently generated from studies using captive animals that are vaccinated and subsequently challenged with the pathogen. The results of such studies may be supplemented with controlled field trials, and both form the basis for the claims made for the vaccine in its summary of product characteristics, the wording of which may be restricted and prescribed by licensing authorities.

Vaccine efficacy should be evaluated by the decrease of the microbe prevalence in connection with an increase of the seroprevalence rate in the population, to assess that no other side effect can influence this outcome. However, the animal sampling used to test efficacy, i.e. its representativeness, must represent the target population.

To prove the feasibility of such methods, the main case study of immunising free-range wildlife against a zoonotic pathogen remains the control of rabies, both in Western Europe and North America. Following appropriate vaccine baiting, the incidence of rabies diminished by about...
60% each year in France until 1996, when it was finally eliminated (6). Targeting the European red fox resulted in the near-complete elimination of rabies from Western and Central Europe (38, 43). An investigation of the relative cost-effectiveness of rabies oral vaccination versus fox culling concluded that the former became economically beneficial after four years, and that culling had only ever resulted in a transient break in the occurrence of the disease, whereas oral vaccination resulted in elimination (5).

Similar strategies have since been used to control rabies in other species in Europe, the United States and Canada (see 10, for a comprehensive review). As a result of these success stories, vaccines have become more widely considered as an option for controlling diseases in wildlife.

The available body of evidence demonstrates the potential value of vaccination in making a significant contribution to the future management of disease in wild mammals. Several issues concerning single efficacy and mass immunity still need to be addressed. Nevertheless, it is likely that, in the near future, vaccination will play an increasing role in the management of other serious wildlife diseases, in addition to rabies and CSF, with bTB looking to be at the top of that list.

**Medication**

Large-scale use of direct medication has rarely been considered for free-living wildlife, except for exceptional circumstances where there has been a serious threat to human health, or to highly valued wildlife. The available literature in this field is limited.

Direct medication requires the use of regulated drugs, and official authorisation would be necessary for their use in wild animals. Such drugs may be expensive and may need to be deployed by qualified professionals, causing potential costs to grow substantially if the disease is not rapidly eradicated. Possible undesirable side effects of direct medication include the persistence of harmful residues of veterinary drugs in the environment and in non-target species. In addition, evolutionary effects, such as the emergence of drug-resistant disease strains and inhibition of selection for resistant hosts, could potentially lead to more extreme epizootics in the future.

An important and successful example of treating (captive) wild mammals was conducted in the National Wildlife Research Centre of Taif (Saudi Arabia), when an outbreak of tuberculosis due to Mycobacterium bovis was discovered in a herd of Arabian oryx (Oryx leucoryx). Treatment with antimycobacterial combination therapy was successful in producing tuberculosis-free oryx calves, suitable for release into the wild (24).

**Fertility control and contraception**

Alongside therapy and immunisation, which aim to limit infection or exposure, medical tools can also be used to control animal host populations (29, 45). The aim is to reduce, in a sustainable way, the growth of an animal population by delivering, with appropriate tools, either a drug (a compound interfering with the hormone balance affecting fecundity), or an antigenic protein able to disturb the production of gametes or their fusion inside the genital tract (sperm or ovule) to reduce fertility. When this is employed in wildlife management, it has been mostly to control pest animal populations (46). The use of contraception to control diseases remains theoretical (4, 33).

Available methods are derived from the field of human birth control (8), but some come from domestic animal reproduction control (25). For extensively free-living populations, contraception can only be delivered through a spontaneously spreading vector-engineered micro-organism or bait (8, 26, 51). Nevertheless, both approaches pose environmental safety and technological problems (2, 37). They have been tested in a number of mammal species, both in experimental trials and limited field studies (15), but the practical problems posed have not yet been sufficiently resolved to allow their extensive use over large areas. Nevertheless, the prospects are encouraging for these products, when used in combination with more traditional tools to control infectious pathogens or parasites in wildlife (42).

**Efficiency and safety of medical control of a pathogen**

While vaccination and other therapies are often seen as attractive because they do not harm living animals, these control options might have potentially detrimental side effects. Medical products, bait compounds and methods of deployment can be potentially harmful to target or non-target species. Attenuated ‘live’ vaccines can induce infection in species for which the vaccine has not been developed. It is essential that the potential negative effects of direct medication and vaccination are always thoroughly and systematically evaluated before their use in free-ranging wildlife.

It is an ecological axiom that parasites and pathogens can influence an ecosystem’s structure and processes and so the control of pathogens in natural systems can have far-reaching consequences. For example, where a pathogen limits host abundance, vaccination may lead to an increase in host populations, which will, in turn, have an impact upon the rest of the ecological community. It has been speculated that oral vaccination of foxes against rabies in Europe has facilitated the expansion of echinococcosis,
although the role of rabies in limiting fox populations is not proven (14). It is thought that some pathogens may effectively mediate competition between species (28), in which case vaccination might theoretically enable a previously suppressed host species to become dominant.

Furthermore, microbes (whatever they are, viruses, bacteria or fungi) and parasite species are part of natural biodiversity. We may wish to consider whether their comprehensive eradication is desirable in terms of retaining biodiversity and in view of the possible long-term effects of microbe or parasite extinction.

Environmental tools for disease control

Environment manipulation

The host-pathogen relationship is determined not only by the species involved, but also by the environmental conditions. The characteristics of soil, climate and vegetation and the presence and spatial distribution of resources and other species, such as predators, all influence the dynamics of the host-parasite system (50). As a consequence, modifying local environmental conditions may contribute to controlling the transmission of zoonoses, generally in combination with other tools. The primary aim of environmental management may be either to render local conditions unfavourable for a vector, a host, or the pathogen itself, or to limit contacts between the source population and the target.

Reducing the availability of resources and shelter is the first tool to limit populations of pathogens, vectors or hosts. Specifically, managing water availability has been one of the most useful tools, through drainage, controlling water points or limiting vegetation. This strategy has long been used for malaria, where transmission depends on the freshwater and plant community that provide the mosquito’s habitat (40). The identification and control of water points has also been used during recent chikungunya epidemics (20).

Manipulating the predators, microbes or parasites of a host population, or even of the other species present in the environment, may theoretically help to mitigate disease propagation. Generally speaking, reinforcing populations of predators is thought to reduce the host population and thus pathogen transmission. Moreover, the presence of other pathogens in hosts, specifically when they are phylogenetically unrelated, may have a facilitating effect for disease transmission, possibly through indirect, immune-mediated interactions (34). Species that are not part of the pathogen life cycle may thus influence the host-pathogen dynamics through a complex network of relationships, and variations in their abundance is expected to influence propagation. However, due to the complexity of these interactions, manipulating the density of other species would also be expected to have indirect, possibly short-term effects, along with undesirable consequences, and no attempt has yet deliberately been made to control pathogens in this way.

When clustering of animals is identified as a cause of disease expansion, it may be useful to change the spatial distribution of the host population by dispersing hosts or preventing their access to specific clustering points. Dispersing the hosts can be achieved by changing the feeding strategy. For example, in Michigan, baiting and feeding white-tailed deer (Odocoileus virginianus) have both been banned in counties where deer are infected by bTB, to avoid local aggregation around feeding points. A decrease in bTB prevalence has been subsequently observed, although eradication has not been achieved (17). Practically speaking, however, manipulating the behaviour and spatial distribution of hosts may prove difficult. For example, techniques used to frighten or repulse animals generally lose their effectiveness fairly rapidly; moreover, frightening the animals will disperse them and may spread the disease. Reducing supplementary feeding is rarely sufficient if not accompanied by a change in the form of food distribution (44). Alternatively, it is possible to create new habitats to attract animals outside an at-risk zone, for example, by planting attractive food sources (50).

Finally, the spatial distribution of the population can be changed to separate the source population from the target through fencing. Fencing has the advantage of not disturbing the wildlife population within (or outside) the fenced area, while rendering contacts with the target difficult. However, fences also increase spatial fragmentation, which is often considered undesirable for conservation purposes (18). The use of fencing is limited, due to practical considerations and undesired effects, with most examples located in South Africa and Australia. Fences first entail high costs for their construction and maintenance. Fenced areas should be large enough to contain all the elements that are necessary for the wild population to survive, including water resources and areas suitable for reproduction and dispersal or migration, if they are needed. Above all, the fence must be able to prevent all at-risk contacts. For example, direct contacts are still possible when a single fence is built (49).

The prerequisite for effective environmental management is that our knowledge of the system is sufficient to anticipate all the consequences of proposed actions. According to the patterns of disease transmission, environmental management may significantly help in reducing disease risk but, alone, is rarely sufficient.
Protection and biosecurity

Isolating animals

Defensive disease prevention consists of isolating safe specimens, or a safe population, to prevent them from being exposed to a contaminated population. Several measures could be implemented, such as confinement, quarantine or movement control. For example, poultry confinement is used when migratory birds, which could be potential carriers of the highly pathogenic avian influenza H5N1 virus, are present in an area where poultry are given outdoors access. This avoids direct contact with wild birds and indirect contact with their excrement, and so prevents disease transmission to breeding birds or even farmers (39).

Compartmentalisation and zoning

On the same principle, based on the separation between safe and infected animals, the World Organisation for Animal Health (OIE) has developed two new concepts, called ‘compartmentalisation’ and ‘zoning’, to separate domestic from wildlife populations. Zoning and compartmentalisation are procedures implemented by a country that wishes to define sub-populations of distinct health status for disease control. Zoning applies to an animal subpopulation that is defined primarily on a geographical basis. In the event of disease outbreaks, a single containment zone, which includes all cases, can be established to minimise the impact of the disease on the entire country.

The concept of compartmentalisation, developed in 2005, is based more specifically on the setting up of a ‘compartment’, in which several establishments (e.g. parent hatchery, production farm, slaughterhouse, processing plant and feed mill) are linked by production pathways and have a common biosecurity management system. Both compartments and zones contain an animal subpopulation with a distinct health status for a specific disease (21, 41) and require regular surveillance of this subpopulation (e.g. periodical blood sampling to detect antibodies).

The concept of zoning is widely understood all over the world and is commonly used in animal disease eradication (23), for example in cases of foot and mouth disease and Newcastle disease (which are, respectively, a Picornavirus and a Paramyxovirus infection of animals with very limited zoonotic potential). Nevertheless, the concept of compartmentalisation seems to be better suited to controlling zoonotic pathogens in wildlife, in that:

- domestic livestock can be raised in an area where there are infected wildlife, and
- wild animals can also be protected from domestic animal diseases, thanks to the biosecurity measures put in place in the compartment.

The objective is to prevent the transmission of the disease from infected animals to safe domestic or wild animals and, by extension, to humans (47).

The recognition process takes a long time and requires significant investment in terms of time and money (27, 53, 54). Thus, both a precise definition of the standard of compartmentalisation required and harmonisation between countries appear essential at the international level to facilitate its implementation. A specific regulation on compartmentalisation, currently being developed by the European Union (23), OIE (27, 57) and European Commission (21), will certainly help to clarify the procedure of recognition in the years to come. Particular attention should be paid to these concepts, as they could be one of the best solutions to prevent the risk of transmitting zoonotic pathogens to and from wildlife in the future.

Discussion

During recent decades, at least in Europe, several trials have been made to control the reservoirs of zoonotic pathogens by reducing the size of the maintenance host population to less than a minimal threshold, below which these pathogens vanish. Culling or any lethal control is only achievable when there is no overall threat to the survival of a species, or a single population. In addition, the tools used to limit the growth of the reservoir population must be safe for the whole ecosystem and acceptable from a welfare point of view.

When drugs, medicines or vaccines are being considered, the environmental safety of these methods should be examined through a process of preliminary evaluation, together with their practical feasibility and long-term sustainability. Habitat manipulations or fencing can efficiently control or limit exposure to environmental pathogens or can constrain the movement of infectious animals. However, while habitat manipulation may be efficient as a preventive measure, it often has significant side effects by disturbing the ecological balance of ecosystems.

Recently, the OIE has promoted the concepts of zoning and compartmentalisation, which can be applied to control wildlife pathogens, such as avian influenza. This approach has triggered studies to improve biosecurity (or bio-protection) of settlements of domestic animals against the intrusion of wildlife disease carriers. Similarly, limiting human exposure to these pathogens (or to their vectors, namely, infected animals) can be as effective as vaccination, for example in the cases of Lyme disease and tuberculosis.

The current zoonotic risk presented by wildlife should not be exaggerated. With regard to the dangers reported in the
EU, human disease directly linked to wildlife hosts remains of far less significance than many other risks. Nevertheless, the individual consequences of exposure to some of the zoonotic wildlife pathogens (rabies, echinococcosis, haemorrhagic fevers, viral encephalitis) can be lethal. The low probability of occurrence set against the seriousness of the disease resulting from exposure renders the risk assessment particularly difficult to balance. In such cases, risk assessment should be regularly updated through appropriate general or targeted surveillance.

Conclusion

In today’s world, more than ever, there is no barrier between human and animal medicine. Most human infectious diseases are of zoonotic origin and many, if not most, of the emerging diseases have originated from wildlife reservoirs (30). Severe acute respiratory syndrome (SARS) illustrated the short epidemiological link between remote colonies of horseshoe bats (Rhinolophus sp.) infected by a coronavirus in Malaysia and a serious disease infecting citizens of large cities, such as Hong Kong and Toronto (35). The concept of ‘one world, one health’ invites us to consider that controlling or mitigating the risks associated with infectious diseases of veterinary and/or public health importance has something to do with the health of wildlife and ecosystems (32, 48). Various approaches can be tested to break the connection from a wild infectious source and various targets in the ‘domestic’ world.

Nowadays, wild species are considered as being of great value, whether or not they can be used as a resource (13). It becomes difficult and, moreover, counterproductive simply to naively destroy the animals that maintain and spread pathogens (11). Nevertheless, in some instances, culling reservoir populations may be considered in a restricted area for a short term. However, generally speaking, all alternative options should be exhausted first, as far as the management of a zoonotic disease is concerned.

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Lutter durablement contre les agents pathogènes zoonotiques présents dans la faune sauvage sans léser les animaux sauvages

M. Artois, J. Blancou, O. Dupeyroux & E. Gilot-Fromont

Résumé

Les animaux sauvages peuvent héberger des agents pathogènes infectieux ayant une dimension zoonotique. Néanmoins, l’abattage de ces populations hôtes en vue d’atténuer ou de maîtriser la transmission à l’homme de ces agents pathogènes s’est avéré une mesure décevante et inefficace. Des solutions alternatives sont actuellement à l’étude. Parmi les mesures envisagées figurent notamment la vaccination, les thérapies médicamenteuses, la contraception et l’aménagement de l’environnement grâce à la mise en place de clôtures et de mesures de biosécurité. Les auteurs examinent les concepts généraux régissant
Control duradero de los patógenos zoonóticos en la fauna salvaje: ¿cómo tratar decentemente a los animales salvajes?

M. Artois, J. Blancou, O. Dupeyroux & E. Gilot-Fromont

Resumen
Los animales salvajes pueden albergar patógenos infecciosos de importancia zoonótica. Sin embargo, el sacrificio de esas poblaciones de reservorios con el fin de mitigar o contener la transmisión de tales patógenos al ser humano ha resultado poco eficaz, y por ende decepcionante, y las posibles soluciones alternativas, como la vacunación, la medicación, la contracepción o la modificación de las condiciones ambientales, por ejemplo con cercados o medidas de seguridad biológica, aún están en fase experimental. Los autores examinan los conceptos generales ligados a la lucha contra las enfermedades de los animales salvajes y exponen estudios monográficos de interés al respecto. Se trata de un objetivo complejo, puesto que esa lucha supone forzosamente interferir en la ecología de la fauna salvaje, por lo que toda tentativa en ese sentido debería estar sujeta a la supervisión de un organismo científico. Convendría someter a prueba cuidadosamente la mayoría de las intervenciones en ecosistemas naturales mediante ensayos realizados a una escala progresivamente mayor. Por último, hay que recomendar todas las medidas que apunten a prevenir la infección del ser humano (como la higiene personal o la vacunación) o alienten a las personas a evitar todo contacto infeccioso con animales salvajes.

Palabras clave
References


