The use of vaccines and genetically resistant animals in tick control

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Summary
The control of ticks and diseases transmitted by ticks is extremely difficult. Application of acaricides is the most common prophylactic and therapeutic control measure against these ectoparasites. The selection of tick strains which are resistant to these products, the appearance of chemical residues in milk and meat, and environmental pollution resulting from the use of acaricides pose real problems. This article deals with aspects of current work on the alternative control of ticks and places special emphasis on the development of vaccines and the utilisation of genetically resistant animals.

Keywords

Introduction
Ticks, which are ectoparasites, pose a considerable threat to humans and animals all over the world. World economic losses from ticks are estimated at United States (US) $7 billion annually, a figure which is certainly underestimated (26).

Ticks are very important vectors of diseases from both the human and veterinary perspectives. Tick-borne encephalitis viruses, bacteriae (Ehrlichia spp., Pasteurella tularensis, Borelia spp.) and the protozoae Babesia divergens and B. microti, for example, are transmitted by ticks of the genus ixodes. Boophilus spp. ticks are vectors of Babesia spp. and Anaplasma marginale; Hyalomma spp. are vectors of Theileria annulata (tropical theileriosis); Rhipicephalus appendiculatus transmits T. parva (East Coast fever) and Amblyomma spp. transmit Cowdria ruminantium (heartwater).

Ticks can also be a direct cause of illness. Salivary gland secretions of approximately 50 species of ticks are known to cause toxicoses (47, 48, 97). The best known example is tick paralysis, caused by I. holocyclus, to which thousands of domestic and farm animals along the east coast of Australia fall victim each year, and which can also be fatal in humans (96).

With their powerful mouth parts, ticks damage the skin of farm animals, which leads to reductions in the leather quality and consequently to considerable economic losses (101). Moreover, every tick bite facilitates secondary infections (bacterioses, mycoses, maggot infestations), especially in the tropics, and this aggravates the damage.

Ticks consume 1 to 3 ml of blood in the course of a complete life cycle. Where there is mass infestation, the host animals consequently suffer from anaemia and nervousness, which results in a reduction in meat and milk production. An average tick infestation of only 40 A. americanum females per cow is enough to cause a production loss of US$40 (31).

Tick control measures
The control of ticks and tick-borne diseases is extremely difficult. Even today, the most common prophylactic and therapeutic control measure against ticks is essentially the use of acaricides. In the last few decades, however, the long-term use of acaricides to control ticks has been shown to be very problematical. Therefore, there is great interest world-wide in the development of alternative control measures. Immunological approaches in particular (i.e., the development of vaccines against these parasites) are giving rise to high hopes. This article deals with aspects of current work on the alternative control of these ectoparasites, particularly the development of vaccines and the utilisation of genetically resistant animals, which could solve the dilemma of tick control by purely chemical means.

There are various methods of controlling ticks to which a varying degree of importance is attached in practice (26, 103, 123). However, none of these control measures provides complete protection from ticks and the diseases which they transmit. The feasibility of any measures to control ticks in...
developing countries, where financial resources and qualified personnel are in short supply, should also be borne in mind.

**Acaricides**

In livestock production, ticks are controlled almost exclusively through the application of an aqueous suspension of chemicals by dipping or spraying. The extensive use of acaricides incurs a great number of serious problems. These methods are very cost-intensive (between US$3 and US$20 per year per animal in Kenya) (123), and also very time-consuming. In addition, the use of acaricides encourages the selection of acaricide-resistant tick strains, so that substantial resources must constantly be used to suppress the tick population effectively. Furthermore, the possible and as yet scarcely assessable health and environmental risks which can result from the uncontrolled use of acaricides must not be overlooked. Strategic dipping could diminish the massive use of acaricides in considering the ecology of ticks. Recent developments in presentation also allow more reasonable use of acaricides: these developments include acaricide-impregnated ear tags (for ticks, such as _R. appendiculatus_, which preferentially attach themselves to this part of the body), slow-release rumen boluses and intramuscular injection (27).

**Genetic resistance**

High-performance farm animal breeds, such as cattle, which have been introduced by man into areas where ticks are endemic, often display a very low degree of natural resistance to ticks. In contrast, adaptations have developed between parasites and host in farm animals which have been native to the area for a long time, so that parasitoses have less dramatic effects. For instance, resistance to _B. microplus_ varies from breed to breed, but is generally greater within Zebu cattle (_Bos indicus_) than in European cattle (_B. taurus_). In Australia, _B. indicus_ breeds, particularly Brahman (beef) and Sahiwal (dairy) cattle, have been shown to possess a higher level of natural resistance to _B. microplus_ than _B. taurus_. crosses of _B. taurus_ and _B. indicus_ have been successfully cross-bred (73, 103). _Bos indicus_ cattle have been crossed with _B. taurus_ cattle to obtain enough of the desirable traits of the European breeds, such as body weight and milk yield (50). The Commonwealth Scientific and Industrial Research Organisation in Australia is developing the so-called 'Belmont Adaptaur', which is derived from crosses between Hereford and Shorthorn cattle. Adaptaur bulls present good resistance to the stresses of the tropics, particularly heat, _B. microplus_ ticks and internal parasites. Some Adaptaurs have extremely high resistance to ticks as they carry a gene that has a major effect on resistance, whose frequency can be increased by embryo transfer and assortative mating (36, 62). These bulls can be used as a sire breed capable of producing substantial hybrid vigour when mated to Brahman cows. The hybrids of such matings display levels of resistance to ticks and worms similar to the levels seen in Brahman cattle, and have the carcass qualities of _B. taurus_ cattle breeds.

European breeds of cattle were also imported into Africa two to three centuries ago, as a result of which, ancient breeds of _B. taurus × B. indicus_ hybrids, such as Sanga and NDama, have become well adapted to the tropical or subtropical environment. More recently, cross-breeding of _B. taurus_ with local _B. indicus_ breeds has been pursued to improve the genetic resistance of the animals to ticks and tick-borne diseases. In South Africa, the Bonsmara was bred with the objectives of repellency to ticks ( _A. hebraeum_ in particular), resistance to heartwater and ability to withstand heat stress (11). Bonsmara cattle were also more resistant to _I. ricinus_ (Karoo paralysis ticks) than Friesian cattle (_B. taurus_) (35). Indigenous breeds, namely Nguni, Bonsmara and Africander, were more resistant to _A. hebraeum_ ticks than Santa Gertrudis and Simmental (_B. taurus_) breeds (81). Nguni cattle also harboured fewer _A. hebraeum_, _B. decoloratus_ and _Hyalomma_ spp. ticks than Bonsmara and Hereford (_B. taurus_) (95).

In Ethiopia, the indigenous Mashaon oxen of the Sanga type were observed to be more resistant to _B. decoloratus_ than crosses between Africander and Sussex oxen (34). In Ethiopia, indigenous breeds (Arsi and Boran) harboured less _A. variegatum_, _B. decoloratus_, _R. evertsi evertsi_ and _H. marginatum rufipes_ ticks than crossbred Boran × Friesian or European cattle (94). Horro and Boran cattle are also less infested with _B. decoloratus, A. cohaerens_ and _R. praetextatus_ ticks than crosses with European cattle breeds (3).

To build up an immunity against ticks, therefore, an animal must first of all have some contact with these ectoparasites. In some cases, a naturally acquired immunity to ticks could be increased by genetic selection in farm animal breeds (11, 25, 100). Brahman cattle (_B. indicus_) carry less _R. appendiculatus_, _A. hebraeum_, _R. e. evertsi_ and _H. m. rufipes_ ticks than Simmental cattle. The resistance correlated with gamma globulins levels and the number of eosinophils in the blood of the cattle. Consequently, a part of this phenomenon is probably a consequence of acquired resistance.

**Ecological measures**

Ecological measures within the grazing area also afford some degree of biological control over ticks (123). The formation of tick niches can be avoided by means of controlled grassland farming and pasture rotation, as well as by the choice of forage plants. The erection of fences restricts the exchange and introduction of ticks from wild animals. The operation of tick traps using aggregation pheromones could also be included under biological control measures (51), but in practice these traps are rarely employed.

**Immunological methods**

An extremely attractive way of controlling ticks would be to introduce resistance to these ectoparasites through immunisation. In the last few years, great progress has been made in the field of immunisation against ticks, as a result of
which a vaccine against B. microplus is now available (120). A similar vaccine has been produced in Cuba (76). In the context of immunisation against ticks, being well informed about the immunological interactions between hosts and the ectoparasites is clearly important.

Naturally acquired resistance to ticks

Tick feeding induces a complex array of host immune responses involving antigen presenting cells, T lymphocytes, B lymphocytes, antibodies, complement, basophils, mast cells, eosinophils and a number of bioactive molecules (16, 17, 106, 110, 115). Acquired resistance to hard ticks (Acari: Ixodidae) may be expressed in ticks as follows:

- reduced engorgement weight
- increased duration of feeding
- decreased numbers of ova
- reduced viability of ova
- blocked moulting and the death of engorging ticks (110).

Host grooming is an important factor in limiting tick infestation (8).

As early as 1939, Trager showed that guinea-pigs become immune to Dermacentor variabilis as a result of pluri-infestation (98). Since this pioneering work, acquired immunity to ticks has been studied most extensively using laboratory animals (guinea-pigs, rabbits or mice) and cattle (17, 115). Resistance acquired by laboratory animals is often more intense than that observed in natural hosts (83), although laboratory mice infested with immature stages of I. ricinus constitute an exception (67). However, some wild rodents (Clethrionomys glareolus, for example) acquire immunological-based resistance to ticks (29).

The ability of many cattle breeds to acquire a resistance after repeated contact with ticks has been known for a long time (115, 110). The B. microplus cattle parasite-host system has been studied from an immunological perspective most extensively in Australia. Acquired resistance or susceptibility of cattle to Hyalomma spp. ticks has been studied in Morocco (89), resistance to H. anatolicum anatolicum and R. evertsi has been studied in Sudan (64) and resistance to R. appendiculatus has been studied in western Kenya (65).

Ticks are pool feeders. After the chelicerae and hypostome have penetrated the skin of the host, a local inflammation develops in which the host neutrophils participate. The feeding pool is formed by the destruction of the tissue and blood vessels beneath the rostrum tip (14). The ticks feed from this pool: in adult ixodids, two feeding stages can be distinguished. During the first stage (five to seven days), ticks consume predominantly blood cells and broken-down host tissue and there is an approximately tenfold increase in weight. Only in the last 12 to 24 hours do the females suck large amounts of blood, and during this period the weight of the tick increases by up to 150 times (compared with an unfed female). The salivary glands, which undergo dramatic morphological and functional changes in the course of blood feeding, are extremely important for normal nutrition (58). Most ixodids secrete cement through the salivary glands, which strengthens the attachment of the rostrum to the skin (59). The salivary glands also play a vital role in excretion and osmoregulation (32, 59). In addition, salivary gland secretions are of great importance in tick immune evasion mechanisms (83). Tick saliva contains pharmacologically active molecules that possess anti-haemostatic, vasoactive and immunosuppressive properties (62, 84, 114). These pharmacologically effective components prevent, for example, the aggregation of blood platelets, T-cell activation and the binding of the third component of complement (C3). By inactivating the pain mediator, bradykinin, and oedema-forming factors such as anaphylatoxin, the generation of pain is prevented together with the tendency to scratch, which could lead to the removal of the parasites (83). On the other hand, vasoactive amines maintain the blood and cell flow to the rostrum by dilation of the local vessels. Nevertheless, contact between tick and host over several days provides ample opportunity for innate and specific acquired (adaptive) immune defences to affect the tick. Tick countermeasures against host immune defences target those pathways shown to be important in the expression of acquired immunity to ticks (110). Tick suppression of host immune defences probably enhances the ability of tick-borne pathogens to establish effectively in the host.

The hosts are confronted with a large number of potential antigens through the secretions of the tick salivary glands. For example, a chromatographic fraction enriched with a 65 kiloDalton (kDa) protein isolated from I. ricinus salivary gland extracts (SGE) induced a specific in vitro dose-dependant T-cell proliferation (41). Langerhans cells in the skin trap antigens and also interact with a variety of cell types through an array of cytokines (90). These cells are amongst the first to be exposed to immunogens in the skin, and from here they migrate to draining lymph nodes (57), to be transformed into dendritic cells in the paracortical area of the draining lymph nodes and then to function there as antigen-presenting cells for T lymphocytes (71, 72). In BALB/c mice repeatedly infested with nymphal I. ricinus ticks, lymphocytes from lymph nodes draining the tick attachment site produced significant levels of tumour necrosis factor α (TNF-α) and granulocyte-macrophage colony-stimulating factor (GM-CSF) when stimulated in vitro with concanavalin A (Con A) or anti-cluster of differentiation antigen 3 (CD3) antibodies (39). GM-CSF induces the maturation of epidermal Langerhans cells in vitro by maintaining their viability and inducing high expression of class II MHC antigen molecules (52). Migration of these cells from the skin to the regional lymph nodes and their accumulation in these secondary lymphoid organs are controlled by TNF-α (23, 24).

Circulating immunoglobulin G (IgG) antibodies to tick salivary gland antigens, which are induced by tick feeding, have been detected in several host animals (16, 110). By
D. andersoni immunity observed after a single infestation with surrounding the tick bite (105). The almost absolute histamine-rich basophils concentrate particularly in the area was partially broken down after treating the guinea-pigs with very well-developed resistance of guinea-pigs, in which Histamine also seems to be mainly responsible for the involvement of humoral factors in the acquisition of immunity against ticks could be shown (13). This immunity, even though weakened, has also been transmitted passively to cattle against B. microplus (86).

The complement system is involved in the development of immunity against ticks. The acquired resistance to D. andersoni larvae in guinea-pigs was inhibited by lowering the C3 component with cobra venom factor (111). C3 is deposited in the dermo-epithelial junction near the location of the tick bite (7). Activation of the complement system in the vicinity of the tick bite could locally attract basophils (102). In rabbits, the C3 level in the serum rises sharply after reinfestation with adult I. ricinus (75). Ticks fed on plu-infested rabbits consume more C3 than those on hosts infested for the first time, and also digest haemoglobin with difficulty.

Pathogens have developed methods to modulate successfully the complex network of cytokine-cell interactions (66). Therefore, the fact that ticks can modulate host cytokine elaboration is not surprising (39, 40, 77, 78). An immunohistochemical analysis of skin cryostat sections at 72 h post I. ricinus nymph-attachment on BALB/c mice revealed that CD4+ T cells outnumbered CD8+ T cells in all infestations (69). Seventy-two hours after tick attachment in primary infestation, some infiltrating cells in the skin gave positive test results for interferon-γ (IFN-γ) and interleukin-4 (IL-4) messenger RNA (mRNA), but not for IL-2 mRNA (68). In skin sections of reinfested mice, mRNA coding for IFN-γ, IL-2 and IL-4 were detected in infiltrating cells. Cells which gave positive results for IL-4 mRNA were lower in number than those showing positive results for IFN-γ and IL-2 mRNA. A significant decrease in the number of IL-4 mRNA-positive cells was noted in the tertiary infestation. These cytokine findings may correlate with observations showing the occurrence of a slight cutaneous delayed-type hypersensitivity in tick-infested mice (67).

Cutaneous reactions at tick attachment sites on cattle and laboratory animals expressing acquired resistance contain infiltrates of basophils and eosinophils (4, 5, 14). Basophil infiltration was described as a cutaneous basophil hypersensitivity response (4). This phenomenon, which is a form of delayed-type hypersensitivity (30), is probably mediated by T helper cells 1 (Th1) lymphocytes (70). The infiltration of basophils is more pronounced in guinea-pigs than in rabbits (14). Similar conditions are also present after the infestation of cattle or rabbits with H. a. anatolicum (43, 44) or A. americanum (18, 19).

In the infested skin, homocytotropic immunoglobulins bind to Fc receptors on mast cells and basophils (13). Tick antigens complex with these antibodies to cause the release of bioactive molecules (15). Degranulated mast cells and basophils are found at tick-bite sites, and a greater number of degranulated cells are observed during reinfestation (14). These cells, as well as infiltrating eosinophils, release histamine, leukotrienes, prostaglandins, eosinophil major basic protein, enzymes and other biologically active molecules at the bite site, which probably contribute to acquired resistance (110). In cattle infested with B. microplus, the release of histamine causes a skin irritation which leads to increased scratching; in this way, some of the ectoparasites are actively removed from the host (63). A positive correlation has been established between the skin histamine concentration and the degree of resistance acquired by cattle against B. microplus (117). Histamine also seems to be mainly responsible for the very well-developed resistance of guinea-pigs, in which histamine-rich basophils concentrate particularly in the area surrounding the tick bite (105). The almost absolute immunity observed after a single infestation with D. andersoni was partially broken down after treating the guinea-pigs with histamine antagonists (105).
The preceding remarks underline the great complexity of the inflammatory and immunological reactions which are involved in the interactions between ticks and their hosts.

Immunosuppression
As mentioned earlier, tick saliva contains immunosuppressor factors. This could interfere with the development of acquired or artificially induced resistance. In laboratory animals, tick feeding impaired the ability of lymphocytes obtained from infested hosts to proliferate in vitro in the presence of the T-cell mitogen Con A, while responsiveness to the B lymphocyte mitogen Escherichia coli lipopolysaccharide was not changed or increased (40, 107). Pure-bred B. taurus cows and calves infested up to four times with ten female and five male D. andersoni displayed reduced in vitro proliferative responses of peripheral blood lymphocytes to the T-cell mitogen phytohaemagglutinin (PHA) during the third and fourth exposures (113). Proliferative responses to PHA were reduced by up to 47%, when compared with cells from uninfested controls. Pure-bred B. taurus cattle infested with B. microplus also demonstrated consistently reduced in vitro lymphocyte responses to PHA, when compared with lymphocytes from uninfested cattle (53).

The anti-tick immune response is thus often characterised by a reduction in the response of mammalian host lymphocytes to Con A and PHA stimulation. This has been suggested to result from a decrease in IL-2 production caused by tick saliva components. In fact, prostaglandin (PGE₂) from I. dammini saliva seems to reduce T-cell line production of IL-2 by direct contact (85). PGE₂ inhibits lymphokine production by T helper 1 (Th1) cells, but there is no effect on Th2 cells (10). Recent observations show that the reduction of IL-2 production by murine spleen cells is due to a 5 kDa protein contained in saliva of I. dammini tick rather than to PGE₂ (99). Another protein which inhibited T lymphocyte proliferation in the presence of Con A has also been isolated from the salivary glands of D. andersoni (9).

Female D. andersoni SGE were assessed for ability to alter the elaboration of cytokines by normal murine macrophages and T lymphocytes stimulated with mitogens (77). Macrophage cytokine IL-1 elaboration was significantly suppressed by SGE, and TNF-α production was also reduced. Macrophages collected from uninfested pure-bred B. indicus and B. taurus were suppressed in their ability to elaborate IL-1 and TNF-α by the same SGE (78). T lymphocyte elaboration of IL-2 and IFN-γ was also inhibited. IL-4 production was not changed in vitro by the presence of SGE (R.N. Ramachandra, unpublished observation). Supernatants of lymph node cells from uninfested control animals. The ability to produce anti-SRBC antibodies returned to normal levels when animals were immunised four days after termination of blood feeding. Rabbits infested with adult R. appendiculatus demonstrated a suppressed ability to develop an antibody response to bovine serum albumin when immunised during the peak stages of tick feeding (33).

Tick immunisation
Two strategies are presently pursued in the development of vaccines against ticks, as follows:

a) the first approach is to mimic a naturally acquired immunity. The aim is to characterise and isolate those antigens to which a host is exposed during a normal infestation which may be the trigger for the development of immunity;

b) the second approach is based on the idea of directing the immune reactions to 'concealed antigens', which cannot be recognised by the immune system of the host during a natural infestation (116). This approach has been pursued above all in Australia, by research teams concerned with tick immunisation (74, 116, 118).

With the first approach, particular attention was paid to the characterisation of salivary gland antigens (18, 115). This organ obviously introduces the tick host to a large number of foreign substances which could have an immunogenic effect. Since the pioneering work of Trager (98), many attempts have been made to immunise laboratory animals and cattle with crude or partially defined SGE or cement (12, 20, 92, 93, 104). However, the level of immunity obtained in such experiments was at best only as high as that following natural tick infestation, and was often lower. After immunisation with salivary gland antigens, there are often hypersensitivity reactions of the skin at the site of the tick bite which are contra-indicated in a vaccination (109).

Rabbits pluri-infested with I. ricinus build up antibodies which recognise a 25 kDa integumental tick protein, and the antibody titres against this protein are particularly high in animals with strong levels of resistance (87). In the African cattle tick R. appendiculatus, a corresponding 20 kDa protein was found with which the antibodies against the 25 kDa of I. ricinus cross-reacted. The protective properties of the 25 kDa antigen were confirmed in experimental vaccination of rabbits with this 25 kDa protein (16). The resistance obtainable from immunisation, however, was less than that which occurred after pluri-infestation. The 20 kDa protein also confers some protection against R. appendiculatus in cattle (88).
Protection against ticks could also be induced with extracts of other tick organs (109). A particularly high degree of resistance was obtained in guinea-pigs following immunisation with extracts of either the midgut and reproductive system (antigen 1) or all the internal organs (antigen 2) of *D. andersoni* females (6). Calves immunised with antigen 1 also became immune to *D. andersoni*. In addition, as had happened with guinea-pigs, only a few eggs were laid and hardly any larvae hatched out. A clear resistance in rats was also obtained with midgut extracts of *D. variabilis* (1). Immunisation against midgut antigens, therefore, seemed very promising.

Research teams in Australia achieved the breakthrough in the development of vaccines against ticks (121). Based on the work of Allen and Humphreys (6), an approximately 70% reduction in the number of ticks was obtained by immunising cattle with extracts derived from female *B. microplus* (56, 60). This level of resistance is substantially higher than that which follows pluri-infestation. Immunisation led to the death of adult ticks, whereas immunisation following pluri-infestation affected mostly larval stages. Hypersensitivity reactions do not seem to play any special part in the immunity, but after immunisation serious histological damage was found in the midgut epithelium of ticks. Red cells transit into the haemolymph (2). In the search for, and characterisation of, the midgut antigens responsible for this resistance, 3.3 mg of protective antigenic material was obtained from a total of 1,368 g of adult *B. microplus* ticks (119). Over 90% of ticks show visible damage after vaccination with these antigens. A membrane-associated glycoprotein was identified as the protective component (118). To use this Bm86 antigen on a larger scale, sequencing and cloning of the protein was performed in *Escherichia coli* (79). The recombinant antigen produced in this experiment also gave the desired protection. The research teams in Australia also obtained data on the mechanism of immune effectors (2, 61). Immunoglobulin G, with or without complement, is sufficient to cause the damage in the tick gut. The Bm86 antigen is localised in microvilli membranes of the midgut epithelium and is probably associated with endocytosis (61). The vaccine has been tested in the field, has been taken through the full registration process and is now in commercial use in Australia (22, 120).

A protein, Bm91, was further identified as a protective vaccine antigen from the tick *B. microplus* (55). This protein contains regions of very strong amino acid sequence similar to mammalian carboxypeptidases or angiotensin-converting enzymes. The addition of the Bm91 antigen enhanced the efficacy of the vaccination compared to the efficacy using Bm86 alone (122).

**Conclusions**

The spectacular success of the research teams in Australia is an impressive example of the effectiveness of immune prophylaxis against ticks. However, this work now stimulates the further development of vaccines against other tick species and other ectoparasites (121). Attention is drawn to the importance of the concept of immunisation against concealed antigens. Nevertheless, even by optimistic standards, complete protection from ticks cannot be expected to result from vaccination without the use of other control measures. Several tick species occur in practice in the same area, and these can differ widely in their biology. Today, the prophylactic and therapeutic control measure against ticks is essentially realised by the use of acaricides. The future lies more in integrated measures to control ticks, i.e., in a combination of classical and modern methods which incorporate chemical, ecological, genetic and immunological aspects of tick control.

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Utilisation de vaccins et d’animaux génétiquement résistants pour lutter contre les tiques

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Résumé
Il est extrêmement difficile de lutter contre les tiques et les maladies qu’elles transmettent. L’application d’acaricides est la méthode prophylactique et thérapeutique la plus fréquemment utilisée contre ces ectoparasites. La sélection de souches de tiques résistantes à ces produits, l’apparition de résidus chimiques dans le lait et la viande et la pollution due aux acaricides posent de véritables problèmes. L’auteur donne un aperçu des travaux en cours sur des méthodes alternatives d’élimination des tiques, tout en mettant particulièrement l’accent sur l’élaboration de vaccins et l’utilisation d’animaux génétiquement résistants à ces parasites.

Mots-clés

El uso de vacunas y de animales genéticamente resistentes para el control de las garrapatas

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Resumen
El control de las garrapatas y de las enfermedades que éstas transmiten es un campo extremadamente difícil. La aplicación de acaricidas es la medida de uso más corriente para el control profiláctico y terapéutico de esos ectoparásitos, aunque ello no deja de presentar ciertos inconvenientes, como la selección de cepas resistentes de garrapatas, la aparición de residuos químicos en la leche y la carne o la contaminación del medio ambiente resultante del uso de los fármacos. El autor aborda diversos aspectos de las actuales investigaciones sobre formas alternativas de control de las garrapatas, haciendo especial hincapié en la elaboración de vacunas y el uso de animales genéticamente resistentes.

Palabras clave
References


