The role of sheep in the epidemiology of foot-and-mouth disease and proposals for control and eradication in animal populations with a high density of sheep.

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Summary

This paper highlights the role of sheep in the epidemiology of foot-and-mouth disease (FMD), drawing on examples from disease episodes in which sheep or sheep products have been implicated as the source of infection both in transboundary epidemics and spread within countries.

Disease control strategies are proposed, based on the epidemiology of FMD in sheep, and directed at achieving specific objectives under different situations where sheep are the dominant species in the livestock population.

Clinical signs of FMD in sheep

The clinical signs of foot-and-mouth disease (FMD) in sheep under natural conditions have been described by Zaikin (1959) and Littlejohn (1970) and are illustrated in the AVIS multimedia suite (AVIS 1999). It is of considerable epidemiological importance that the clinical signs of FMD in sheep are frequently mild or inapparent (Geering 1967; Donaldson and Sellers 2000).

The role of sheep in the transboundary spread of FMD

Sheep have often been implicated as disseminators of FMD virus, both between and within countries. Examples of the involvement of sheep in the transboundary spread of FMD virus include: the introduction of FMD into Canada by sheep imported from the UK in 1875 (Krystynak 1987); the 1978 and 1983 type A epidemics in Morocco (Donaldson 1999); and the 1994 type O epidemic in Greece (Tsaglas 1995). Infected sheep imported from South America were the most likely cause of the 1978 epidemic in Morocco (Dr H G Pereira, personal communication; Bakkali 1982). In the 1983 Moroccan epidemic infected sheep from Spain entered Morocco through the Spanish enclave of Ceuta and caused a chain of outbreaks extending from the north of the country to Agadir in the southwest. Clinical disease was identified only in cattle but a serological survey showed that many sheep and goats had also been infected (Donaldson A I - unpublished results). The 1994 type O epidemic in Greece was linked to the smuggling of sheep from Asiatic Turkey onto the Greek island of Lesbos (Tsaglas 1995). FMD was not diagnosed initially on Lesbos, however, when sheep were transferred to mainland Greece cattle became infected and the disease was
recognised. Yet another example of transboundary spread was the North African epidemic of 1989-92. The epidemic started during the winter of 1989 in Tunisia and then swept westwards into Algeria and Morocco. The majority of the spread was attributed to the uncontrolled movement of large numbers of sheep, especially around the time of religious festivals when there was a surge in the demand for sheep meat (Samuel et al. 1999).

Excretion of FMD virus by sheep

Although FMD in sheep is often clinically silent, the amount of FMDV excreted by infected sheep is significant, especially in the very early stages of infection during the viraemic phase. Burrows (1968) found virus in oesophageal-pharyngeal samples, blood, milk, rectal swabs, preputial swabs and vaginal swabs for up to 5 days before a clinical diagnosis of FMD could be made. The usual mechanism by which infection is transmitted from sheep to other species, most commonly cattle, is thought to be the aerogenic route i.e. infectious droplets and aerosol particles excreted in the breath of infected sheep being inhaled by cattle. This is the consequence of several determinants: firstly, sheep and cattle are often grazed together or are brought into close proximity at markets; secondly, infected sheep excrete considerable quantities of FMD virus in their exhaled breath from around 1 day before they show signs of disease and for up to 4-5 days later (Sellers and Parker 1969; Donaldson et al. 1970); and thirdly, cattle are highly susceptible to infection by airborne FMD virus (Donaldson et al. 1988).

A steep decline in virus excretion from sheep occurs around the fourth or fifth day of clinical disease, the time when a circulating antibody response first becomes detected and presumably results from immune clearance (Gibson et al. 1984; Pay 1988; Cox et al. 1999). Thereafter the potential for sheep to transmit infection declines dramatically. Sheep, like other ruminants, may become carriers. Around 50% of convalescent sheep may become persistently infected for up to 9 weeks, and a small number of animals may carry virus for up to 9 months (Burrows 1968; McVicar and Sutmoller 1969; Salt 1993). Carrier viruses isolated from sheep have been found to have retained their pathogenicity for sheep, pigs and cattle (Khukhorov et al. 1973; McVicar et al. 1968). Carrier sheep held under experimental conditions have generally failed to transmit FMD but there are a couple of reports of transmission of sub-clinical infection. In Germany carrier sheep did not transmit infection to in-contact cattle but sub-clinical infection did result in one in-contact sheep (Geering 1967). Similar experiments in India failed to transmit infection from carrier sheep to in-contact sheep submitted to physical or chemical stress (Sharma 1978). There are apparently no authenticated examples of carrier sheep being the origin of outbreaks although it has been speculated that they may have been the source of the 1983 outbreak in Denmark (Dr E Stougaard, personal communication).

Sheep products and the spread of FMD

Sheep products have been the origin of FMD outbreaks. For example, contaminated frozen lamb (Aon-the-bone®) from Argentina was blamed as the source of the 1967-68 UK type O
epidemic, the largest ever recorded in the UK with a total of 2,364 outbreaks (Anon 1969). This experience led the UK authorities to radically change the regulations for the importation of meat from South America. These included a ban on all imports of unprocessed sheep and pig meat. Beef was accepted provided it was de-boned and the pH checked post-mortem to ensure that it was sufficiently acid to inactivate FMD virus. Additional requirements were imposed to ensure that cattle destined for slaughter were fully vaccinated. These procedures, though viewed at the time by South American exporters as being very labourious and expensive, allowed the trade in beef to continue without compromising the security of the UK. The success of the policy over many years persuaded countries in other parts of the world to follow suit and had a major impact in the global liberalisation of trade in beef.

**Immunisation of sheep and evidence that FMD infection in sheep can be self-limiting**

Sheep can be readily immunised against FMD with vaccines formulated either for routine prophylactic or emergency use. Potent, oil-formulated, emergency vaccines can induce a protective immunity in sheep against challenge by airborne homologous FMD virus within 4 days of vaccination (Barnett and Cox 1999; Cox et al. 1999). In circumstances where the objective is to create an immune belt, for example when ring vaccination is implemented around an outbreak or when a buffer zone is established to protect a disease free area, then the vaccination of the sheep in the population is essential. However, experience from Kenya and Uruguay suggests that the vaccination of sheep in control programmes in endemically infected countries or zones is not justified and that a more effective strategy is to use available vaccine in the cattle population to achieve the highest possible coverage in that species. In Kenya, where the cattle population was routinely vaccinated but suffered occasional outbreaks, Anderson et al. (1976) found in follow-up investigations that there was an almost complete absence of virus carriers in both the sheep and goat populations, although there was close contact with clinically infected cattle. It was, however, evident from the high proportion which were seropositive that they had been exposed. Similarly, before the eradication of FMD in Uruguay, where the sheep to cattle ratio is 2.6:1 and the two species often graze together, the vaccination of sheep was abandoned as being both impractical and uneconomical. Instead, available vaccine was used to increase the vaccination coverage of the cattle population. This strategy was highly successful - outbreaks declined to zero in the cattle population and there was no evidence of the continued circulation of virus in the sheep population.

It can be concluded from these findings that in mixed cattle-sheep populations where the cattle are immunised but suffer occasional outbreaks that infection in the sheep will be self-limiting i.e. the \( R_0 \) value will fall to less than 1.0 and so infection will not be sustained. \( R_0 \), the basic reproduction rate, may be defined as the number of secondary cases arising from a single primary case in the absence of any constraints on the spread of infection (Macdonald 1952). Therefore, if \( R_0 > 1 \) each primary case will, on average, result in more than one secondary case and infection will spread through the population. Conversely, if \( R_0 < 1 \), each primary case will, on average, produce less than one secondary case and infection will die out (see Haydon et al. 1997).
Even in mixed cattle-sheep populations where the cattle are fully or partly susceptible, there is circumstantial evidence that infection in the sheep can be self-limiting. In the Greek 1994 epidemic a total of 95 outbreaks occurred over a five month period. The morbidity rate in sheep flocks declined during the course of the epidemic. At the start serological results showed that around 65% of sheep in positive flocks had seroconverted but later in the epidemic this dropped to around 5% (Mackay et al. 1995). Total stamping-out was employed at the start of the epidemic but changed to partial stamping-out later (Tsaglas 1995).

Similarly, the 1989-92 North African epidemic began with a high attack rate, severe disease among adult animals and a high mortality rate among lambs. However, as the epidemic progressed the rate of mortality declined to a negligible level and serological investigations detected only small clusters of seropositive animals in several flocks, suggesting that attack rates within flocks had also fallen. In comparison with the epidemic in Greece these changes occurred more slowly and were more closely associated with the implementation of control measures such as vaccination (Samuel et al. 1999).

**Laboratory investigation of the possibility that FMD infection in sheep can be self-limiting**

Experiments are currently in progress at IAH, Pirbright designed to test the hypothesis that FMD outbreaks in sheep populations may be self-limiting. The progression of disease and infection is being monitored as virus is transmitted from inoculated donor sheep through groups of recipient sheep serially exposed by contact. The aims are to quantify the parameters relating to virus transmission and virulence and to determine whether these determinants change with serial passage. It has been found that the dose of virus administered to donor sheep was critical and influenced their ability to transmit infection and the severity of disease in both them and recipient in-contact animals. The results have demonstrated that the relationship between the dose of virus, the quantity of virus replicated, the infectiousness of the host and the rate of contact is complex (Gareth Hughes, unpublished results). The influence of the strain of virus and host genetic factors are additional parameters which should be examined to obtain a more complete picture.

**Variation in virulence of sheep-adapted strains of FMD virus**
While host genetic factors are probably major determinants in the wide variability of the severity of clinical signs manifested by sheep during FMD outbreaks it is likely that some of the effect is due to inherent differences in the pathogenicity of the field strains involved. There are numerous reports from the field of strains causing severe disease in sheep. For example, the SAT 1 serotype during 1962-63 epidemic in the Middle East (Mackowiak 1970; Nazlioglu 1972) and the A22 serotype in Iran (Hedjazi et al. 1972). In Botswana the SAT 1 virus strains were very virulent in sheep and goats, whereas the SAT 3 strains were not (Falconer 1972). The strain which caused the 1989-92 epidemic in North Africa was very virulent in sheep. The start of the epidemic in Tunisia coincided with the lambing season and over 50,000 lambs succumbed. Cattle were also affected but the morbidity rates were low and there was almost no mortality in that species. When the disease spread into Algeria and Morocco sheep were predominantly affected. In Algeria the attack rates for the different species were: sheep 95%; goats 3%; and cattle 3%. In Morocco the rates were: 92.7%; 7% and 0.3%, respectively. The decline in the attack rate for cattle late in the epidemic was attributed in part to the fact that in Morocco the cattle had been vaccinated previously, this was not the explanation for Tunisia where the cattle had not been vaccinated before the start of the epidemic (Samuel et al. 1999).

A feature common to the majority of these epidemics was that the strains of virus were exotic to the country or region, the productivity losses among the sheep population were high, mostly due to lamb mortality, and so a strong case could be made on economic grounds for vaccinating the sheep population. By contrast, in situations where strains of low virulence are circulating, for example when strains are endemically present, the lambs are likely to be protected by maternal antibody, the economic losses will be lower and so the argument for vaccinating the sheep will be weaker.

**Proposed strategies for control and eradication**

Based on the foregoing information a series of actions are proposed for the control and eradication of FMD in animal populations with a high density of sheep (Table 1).

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**References**


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