The Kenya Veterinarian 18(2) (1994) 470-472

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THE BIOLOGY OF THE TRANSMISSION DYNAMICS OF *THEILERIA PARVA*

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East Coast fever (ECF), Corridor disease and January disease of cattle are caused by the sporozoan, *Theileria parva*, which is transmitted transstadially by the main tick vector *Rhipicephalus appendiculatus*. This means the larvae and nymphae become infected by feeding on a piroplasm positive animal and *T. parva* is transmitted by the resultant nymphae and adults respectively. Theileriosis caused by *T. parva* is considered through its range to be a most economically important disease. In this paper, the transmission of the *T. parva* parasite which drives the epidemiology of theileriosis is considered in relationship to the biology of the tick and the *Theileria* parasite.

TICK POPULATION DYNAMICS AND TRANSMISSION

The transmission dynamics of *T. parva* is greatly influenced by the population dynamics of *R. appendiculatus* which is quite variable in different parts of the tick's distribution. In the Lake Victoria Basin, the ticks can undergo up to 3 generations per year and all instars can be present infesting host throughout the year. In drier areas of eastern Africa, only one generation a year may occur. In eastern Africa, the transmission of *T. parva* can occur all the year around but can be seasonal in its dynamics due to prolonged dry periods which reduces the activity of the *R. appendiculatus* ticks. Hence, in eastern Africa, the distribution and seasonal dynamics of *R. appendiculatus* is therefore controlled by climatic conditions which in turn controls the seasonal dynamics of *T. parva* transmission.

In southern Africa, the seasonal dynamics of *R. appendiculatus* shows a different pattern due to the occurrence of behavioural diapause in adult ticks. Diapause is a complicated phenomenon to study since all ticks have the ability to enter quiescence. The difference between diapause and quiescence is that diapause is a predetermined state of low activity and metabolism usually initiated, maintained and terminated by changes in day length and other factors and is under neurohormonal control, whereas quiescence is a reversible state of inactivity which is controlled by environment thresholds of temperature and humidity. The end result is that only one generation of ticks is possible per year, as during diapause, ticks will not quest for a host. The seasonality of the tick instars is very marked in southern Africa with adults for example in Zimbabwe showing a peak in January. Hence, the adult ticks after moulting in southern Africa enter diapause which is only broken in middle December by a critical day length of 13.2 hours in Harare, Zimbabwe. The effect of diapause is that the egg, the stage most susceptible to desiccation, hatches during the unimodal rainy seasonal or shortly afterwards. This has a major effect on the transmission dynamics of *T. parva* as 95% of all cases of January disease can be attributed to the relatively short time the adults are active. The other cases can be probably attributed to nymphal challenge occurring later in the year.

A major question is what happens in the intermediate zone between southern Africa and equatorial eastern Africa. In Eastern Province of Zambia, it appears that ticks can either enter diapause or not dependant on the time of the year of the nymphal moult (Berkvens, 1990). In Central Malawi, the ticks appear to enter diapause but it is not known what happens in southern Tanzania. Although recently we have obtained further insight on the effects of diapause the full implication on the dynamics of *T. parva* transmission have yet to be elucidated. What effect, for example, does a 6 month diapause in the adult ticks have on the survival of *T. parva* parasites?

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COMPETENCE OF DIFFERENT STOCKS OF RHIPICEPHALID TICKS FOR THE TRANSMISSION OF *T.PARVA*.

Recent studies have shown that there is considerable difference in the competence of different stocks of *R. appendiculatus* for the transmission of *T. parva*. The competence of each tick stock may not be the same for each *T. parva* stock. It has been reported that *R. zambeziensis* was a better vector of *T. parva* derived from African buffalo (*Syncerus caffer*) in South Africa or derived from cattle in Zimbabwe than *R. appendiculatus*. Recent experiments using stocks of *R. appendiculatus* and *R. zambeziensis* from Zambia, Zimbabwe and Kenya for the transmission of *T. parva* stocks from Kenya and Zimbabwe found considerable differences in the vector competence between the tick stocks which was not the same for the two stocks of *T. parva*. The observed variations in vector competence of *R. appendiculatus* stocks could explain differences in epidemiology of *T. parva* throughout its range. It is likely that the tick population is important in selecting the *Theileria* parasites in a particular area since some strains of *T. parva* may be transmitted more efficiently than others.

COMPARATIVE TRANSMISSION OF *T.PARVA* BY INSTARS OF *R. APPENDICULATUS*

Recently, we have been able to compare the vector competence of nymphal, adult female and male ticks. When the larvae and nymphae are infected by feeding on acute *T. parva* infected cattle at the same time female ticks invariably develop higher infections than male ticks and adult ticks higher infections than nymphae. There is often not such a great difference in prevalence of infection but the intensity and abundance of infection is much higher in female ticks. It would appear that this is due partially to the structures of the salivary glands in the different instars. These salivary gland arrangements correlate with relative abundance or intensity of *T. parva* infection in the salivary glands. The implication for transmission is that it would be expected that milder infections would be transmitted by nymphal ticks than by adults. The adult male is not such a competent vector as the female because it has a lower abundance of infection and feeds in a less regular manner than the female.

SOURCE OF INFECTION FOR TICKS

In recent years, it has been found that the carrier state in *T. parva* infections is widespread in the field so an understanding of the relative ability of carrier animals to infect ticks compared to cattle undergoing acute infections is important. In the case of adult ticks resulting from nymphae fed on carrier cattle or buffalo, the infection rates are extremely variable and it appears that some stocks of *T. parva* produce a more efficient carrier state than others. The extreme cases are *T. parva* (Muguga) stocks on the one hand, which have yet not been shown to produce a carrier state, and buffalo on the other hand, which can remain efficient carriers for years. Larvae are much less efficient in picking up infection from carriers than nymphae. This appears to vary between *T. parva* stocks since infection can usually be detected in nymphae fed as larvae on *T. parva* (Marikebuni) carrier cattle but was not detected in nymphae fed as larvae on *T. parva* (Kiambu 5). It can be concluded that as cattle remain carriers in the field for a considerable period, often for years, the carrier animals are paramount in maintaining *T. parva* infection and that nymphal/adult transmission is more important than larval/nymphal transmission. However, it should be remembered that more larvae infest cattle than nymphae (possibly at a ratio of 10 to 1), and their transmission cycle is shorter.

SURVIVAL OF *T.PARVA* INFECTION IN TICKS

After the early work showed that paddocks in South Africa remained infected with *T. parva* for less than 15 months, there have been very few studies on *T. parva* survival in ticks under natural conditions. In the Kenya highlands, various studies have shown that *T. parva* survival in adult *R. appendiculatus* is altitude dependent, and was at least 19 months at 2100 m altitude, 18 months at 1800 m and 15 months at 1600 m altitude, times approaching the longevity of as the ticks themselves. It was found that *T. parva* in nymphal ticks survived for approximately 11 months at 1800 m altitude. At the Kenya Coast, it was found that *T.*

parva survived in adult ticks for 9 months. The survival of *T. parva* in the salivary glands of nymphal and adult *R. appendiculatus* appears to be density dependent, with highly infected ticks showing a high mortality of parasites that ticks with lower infection levels.

MODELLING THE TRANSMISSION OF *T.PARVA*

An important component of modelling the transmission of *T. parva* is the modelling of population dynamics and the climatic suitability for *R. appendiculatus*. The models created so far are climatic based and tend to be quite adequate for eastern Africa (Sutherst, 1987; Byrom & Gettinby, 1992; Perry et al., 1992). To make these model more accurate in central and southern Africa, a component accounting for diapause in adult *R. appendiculatus* would have to be incorporated. Two transmission models have been constructed for eastern Africa using detailed data from the Trans-Mara, Kenya (Medley et al., 1992). A method of estimating the rate of infection to cattle of *T. parva* at the endemically stable state was developed and empirical estimates of all the parameters used in the model are available. The degree to which animals recovered from theileriosis (the "carrier state") are able to transmit the infection to nymphae or larvae is a crucial determinant of infection in a herd. The impact of two methods of control influencing transmission were investigated, infection and treatment immunization and reduction of tick feeding by acaricide control.

Improved biological understanding of tick populations and their *Theileria* parasites will allow the development of transmission models which will be more widely applicable and as described in this paper this information is being obtained. The definition of survival of parasites in ticks and the role of different instars and tick populations in *T. parva* transmission will allow the construction of more accurate models. It is hoped that the combination of individual models can be incorporated into epidemiological models for *T. parva* infection in the near future which would be useful for formulating improved control measures.

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