INVESTIGATIONS INTO THE PARALYSIS-INDUCING ABILITY OF *RHIPICEPHALUS EVERTSI MIMETICUS* AND THAT OF HYBRIDS BETWEEN THIS SUBSPECIES AND *RHIPICEPHALUS EVERTSI EVERTSI*

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ABSTRACT

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Studies performed on sheep showed that *Rhipicephalus evertsi mimeticus* is a paralysis-competent tick species whose toxicity is either the same as, or only slightly less than that of *R. e. evertsi*. It was also proved that the paresis or paralysis induced by the *mimeticus* females is characterized by a constant incubation period which is independent of the tick infestation rate and body mass of the host, and consequently of its age. This period is entirely determined by the state of repletion of the ticks and is regulated by the date of mating. It was further proved that a precise relationship exists between an increase of engorgement or salivation activity and the intensity as well as the persistence of clinical symptoms. Thus only female ticks in the mass range of 15–21 mg are toxic. Strain-dependent differences could not be demonstrated.

The infestation rates of subspecific hybrid female ticks, and of their descendants, that are necessary to produce the respective symptoms showed no differences in toxicity. When infestations were limited to a small skin area minimum paresis could frequently not be induced, even though the actual number of ticks applied was sufficient to cause lethal paralysis.

INTRODUCTION

Dönitz (1910) described *Rhipicephalus evertsi mimeticus* on morphological grounds as a subspecies of *Rhipicephalus evertsi*. Later Nuttall & Warburton (1916) listed this tick as "*R. evertsi* var. *albigeniculatus,* Warburton, 1915 (n. var.)" and mentioned that it differed from *R. evertsi* only in having banded legs. They never formally described this subspecies though, and this name is now regarded as a synonym of *R. evertsi mimeticus*. Its distribution is mainly confined to the drier south-western regions of Africa where it replaces the less drought resistant *R. evertsi evertsi* (Theiler, 1950, 1962, 1966; Theiler & Robinson, 1954; Hoogstraal, 1956; Zumpt, 1958; Yeoman, 1967; Yeoman & Walker, 1967; Walker, Mehlitz & Jones, 1978).

The epidemiological significance of *R. evertsi mimeticus* is still very unclear. There was some suspicion that this subspecies may act either as a potential vector of *Theileria parva* and *Anaplasma* spp. (Sigwart, 1915) or perhaps have played a role in outbreaks of African horse sickness as well as heartwater of sheep in Zaire (Sace-ghem, 1918). However, such suspicions have never been verified and in the light of current knowledge, some are bound to be invalid. Schneider (1977) stated that *R. evertsi mimeticus* could transmit *Babesia bigemina* as well as babesioses in horses. Up to now, however, only the transmission of *Theileria ovis* has been proved experimentally (Neitz, 1972). The direct and especially the possible toxic effects of this tick have never been investigated. It was therefore decided to investigate the paralysis-inducing ability of female *R. evertsi mimeticus* with respect to sheep. In addition, possible population-dependent intra-subspecic differences were studied as well as the ability of *R. evertsi evertsi* × *R. evertsi mimeticus* hybrids to produce paralysis.

MATERIALS AND METHODS

Twenty-nine sheep with a mass between 20 and 40 kg and raised under tick-free conditions were used in these experiments.

They were infested during an initial experimental series with 20–60 females and the same number of male *R. evertsi mimeticus* of the Witvlei strain which originated from the Gobabis district SWA/Namibia. On some animals, ticks were simply liberated, so that they could attach where they liked, while on others the ticks were confined in cotton bags fixed to the skin.

Two other strains of *R. evertsi mimeticus,* namely Claratal (Windhoek District, SWA) and Kleinhuis (Grootfontein District, SWA), were freely fed on sheep to study possible population-dependent strain differences in their paralysis-inducing ability.

Further experiments were conducted with 20–60 female *mimeticus* plus male *evertsi* and 20–60, female *evertsi* plus male *mimeticus*, and the F_1 and F_2 generations originating from these crossbreedings. The ticks were applied to the abdomens of sheep in cotton bags fixed with Pattex glue to the skin.

In all experiments the stage of engorgement of every female tick was carefully determined by taking daily measurements of its length, excluding the gnathosoma, its greatest width at the level of the 4th pair of legs and its greatest thickness, and relating these measurements quantitatively to tick body mass values determined previously in the laboratory. The number of female ticks in the mass range of 15–21 mg necessary to induce clinically apparent levels of paresis or paralysis was determined for each experimental animal and was expressed per kg of the host's body mass. Throughout the infestation with adult ticks, recordings were made daily of each host animal's mass, rectal temperature and heart- and respiration rates as well as its condition. Different grades of clinical paresis or paralysis were judged according to the classification used for *R. e. evertsi* by Hamel & Gothe (1978), Gothe & Budelmann (1980) and Gothe & Lämmler (1982):

L I—Low degree of leg weakness with uncoordinated gait.

L II—Intermediate degree of leg weakness with moderate to high degree of swaying of the body and folding-in of the limbs; strong mobility disturbance.

L III—High degree of leg weakness; although the animal attempts to get up it cannot stand upright, but it still attempts to crawl forwards.

T.P.—Complete paralysis, with animal lying permanently on its side and no further attempts to rise. Lifting of the head still possible; grinding of the teeth.

T.P. (d)—Complete paralysis ending in death.

RESULTS

a. *Paralysis-inducing ability of female* R. evertsi mimeticus

When infestation with *R. e. mimeticus* (Witvlei strain) took place in enclosed bags, no paralysis could be induced in 9 sheep even with high infestation rates [up to 2,3 ticks/kg sheep body mass (SBM)].

Furthermore the engorgement of these ticks, was independent of the rate of infestation and was characterized by initial small increases in mass from 7,2 mg on Day 1 post-infestation (p.i.) to 8,4 mg, 9,6 mg, 11,1 mg and 17,3 mg respectively up to Day 5 p.i. This was followed by a period of higher engorgement rates, with mass increases of 41,0 mg, 162,6 mg and 409,0 mg respectively up to Day 8 p.i. Finally a mean repletion mass of 897,5 mg was reached after a mean of 9,8 days. During the experiment the sheep showed no changes in general condition and motility and their body temperatures, heart- and respiration rates remained within normal limits.

In an experiment where the ticks were allowed to attach where they liked all 3 sheep infested with the Witvlei strain showed symptoms of either paresis or paralysis. The clinical manifestation produced by ticks in the mass range of 15–21 mg were similar in all 3 animals. Only ticks in this phase of engorgement could be compared with regard to the appearance and development of the clinical symptoms.

The infestation rates of ticks which have reached a mass of 15–21 mg per kg SBM could be directly correlated with the degree of clinical manifestation. To produce a medium degree of leg weakness, 0,35 and 0,29 ticks/kg were required, while 0,75 ticks produced a lethal paralysis (Table 1). Repletion of female ticks was completed after a mean of 10,2 days, when they reached a maximum mass of 781,4 mg (Table 2). Throughout the whole period of the infestation, the rectal temperatures of the sheep remained constant with a mean of 39,5 °C. Their heart rates were not influenced by the paresis or paralysis. However, the respiration rates of sheep which exhibited an L II degree of paralysis increased from 20–24 before the infestation to 36–42 at the height of the reaction. In the sheep which became completely paralysed, the respiration rate increased to 70 per minute and also changed from abdominal to costo-abdominal.

Similar results were obtained with the other 2 strains of *R. evertsi mimeticus* (Claratal & Kleinhuis) when the ticks were allowed to attach freely on sheep. In these instances 0,87 and 0,81 ticks/kg SBM induced a total paralysis (Tables 1 & 2).

b. *Paralysis-inducing ability of* mimeticus *females crossbred with* evertsi *males*

Similar to the previous experiment, neither paralysis nor paresis could be induced when *mimeticus* females fed simultaneously with *evertsi* males in enclosed bags. The 3 sheep used in this experiment were infested with a total of 0,2; 0,9 and 1,9 ticks/kg SBM respectively. However, when only the ticks with a mass of 15–21 mg per kg SBM are taken into consideration, the infestation rate was 0,04; 0,22 and 0,25 ticks/kg SBM respectively. In all 3 sheep the engorgement masses of the female ticks were more or less 6,9 mg, 6,8 mg, 7,8 mg and 10,2 mg respectively during the first 4 days of the infestation. On the 5th day p.i., their mean mass was 22,8 mg. This

increased during the following 4 days from 57,5 to 376,7 to 489,5 to 636,0 mg. A mean maximum mass of 793,9 mg was obtained after a mean of 9,5 days of engorgement. All 3 sheep were unaffected during the infestation period with respect to their rectal temperatures and heart and respiration rates. When a similar experiment was conducted with 1 sheep on which the ticks were allowed to attach freely, a low degree of leg weakness was noted. The infestation rate was 0,61 ticks with a mass of 15–21 mg/kg SBM in this instance (Tables 1 & 2).

c. *Paralysis-inducing ability of F₁ females resulting from female* mimeticus *crossed with male* evertsi

In contrast to homozygous *mimeticus* females, F₁ females resulting from crosses between female *mimeticus* and male *evertsi* were capable of producing paralysis when they were fed in an enclosed area.

The appearance, intensity and extent of this paresis were, as in the case of pure *mimeticus* females, directly proportional to the infestation rate of females in the engorgement mass range of 15–21 mg. Of the 3 sheep used in this experiment no clinical signs appeared in the 1 sheep which were infested with only 0,12 ticks/kg SBM while infestations of 0,7 and 1,78 ticks produced a high degree of leg weakness and total paralysis (Table 1). In the case of all 3 sheep the engorgement of female ticks followed the same pattern and was independent of the degree of clinical manifestation (Table 2). As in the case of female *mimeticus*, the body temperatures and heart rates of sheep infested with the F₁ generation stayed constant and within the normal range. However, the respiration rates of affected sheep increased from 18–27/min before tick infestation to 61/min when medium leg weakness was present and 71/min in the case of total paralysis, during which breathing became mainly costo-abdominal.

d. *The paralysis-inducing ability of F₂ females resulting from female* mimeticus *crossed with male* evertsi

Female ticks of the F₂ generation fed in an enclosed bag also induced a similar degree of paresis to that produced by the F₁ generation. One sheep with an infestation rate of 0,16 toxic ticks per kg SBM did not contract the disease, but another that received 0,68 ticks became paretic and showed a medium degree of leg weakness (Table 1). As in the case of the non-affected animal, the mass of ticks during the first 4 days of the engorgement period changed only slightly, from 9,1 to 9,1 to 10,0 to 12,3 mg. It then increased, parallel with the appearance of the first clinical signs, and reached 22,5 mg on the 5th day p.i. Together with a medium degree of leg weakness, the mean tick mass increased to 71,2 mg on the 6th day p.i. Between days 7–9 p.i., as the clinical signs declined, tick masses increased from 130 to 262 to 366,5 and finally to 766,9 mg after a mean of 10 days engorgement.

The respiration rate of the sick animal increased from 22 before infestation to 32–34 during L II. It also showed heavy breathing mostly of the costo-abdominal type. The body temperatures and heart rates did not change in any of the other animals during the infestation.

e. *Paralysis-inducing ability of* evertsi *females mated with* mimeticus *males*

R. e. evertsi females which were mated with *mimeticus* males showed a somewhat higher ability for inducing paralysis than the pure-bred or crossbred *mimeticus* females. The different degrees of paralysis were also dependent on the infestation rate with ticks in the engorgement phase of 15–21 mg. The total number of female *evertsi* ticks per kg SBM (0,7; 0,7 and 0,9) were almost the same in the 3 experimental sheep. However,

TABLE 1 A comparison between the maximum degree of paresis and the infestation rate of engorging females with a mass of 15–21 mg as well as the total infestation/kg sheep body mass of different *Rhipicephalus evertsi mimeticus* strains and *mimeticus/evertsi* hybrids

Strain/hybrids	Incubation period (days)	Maximum degree of paresis	Infestation rate during engorgement phase of ticks with a mass of 15–21 mg/kg sheep body mass	Total infestation rate/ kg sheep body mass
a) Witvlei	7	L II	0,35	0,9
Witvlei	7	L II	0,29	1,6
Witvlei	5	T.P. (d)	0,75	1,9
a) Claratal	6	T.P.	0,87	1,24
Kleinhuis	6	T.P.	0,81	1,15
b) *mimeticus* ♀♀ *evertsi* ♂♂	—	—	0,04	0,2
	—	—	0,22	0,9
	—	—	0,25	1,9
	5	L I	0,61	0,9
c) F_1	—	—	0,12	0,9
	5	L III	0,7	1,0
	5	T.P.	1,78	2,6
d) F_2	—	—	0,16	0,9
	5	L II	0,68	1,7
e) *evertsi* ♀♀ *mimeticus* ♂♂	—	—	0,14	0,7
	6	L II	0,22	0,7
	5	T.P.	0,58	0,9
f) F_1	4	T.P.	1,5	1,5
	6	L III	0,57	1,5
g) F_2	5	L II	0,41	1,48

TABLE 2 Mean mass of females (mg) of different *Rhipicephalus evertsi mimeticus* strains and *mimeticus/evertsi* hybrids during engorgement

Strain/hybrid	Days after infestation									
	1	2	3	4	5	6	7	8	9	10
a) Witvlei	7,7	7,7	9,5	10,4	10,8	22,2	39,1	156,4	416,6	764,4
Witvlei	7,7	7,7	10,1	10,3	11,6	20,6	51,2	183,4	388,6	781,4
Witvlei	8,1	8,2	8,6	9,9	15,4	26,8	Ticks removed			
a) Claratal	8,0	8,6	8,0	9,0	13,2	26,4	Ticks removed			
Kleinhuis	8,0	8,0	8,6	10,1	12,2	17,7	Ticks removed			
b) *mimeticus* ♀♀ *evertsi* ♂♂										
(3 negative sheep)	6,9	6,8	7,8	10,2	22,8	57,5	376,7	489,5	636,0	1 040,5
(Sheep B 11)	8,2	8,2	8,9	11,1	16,6	65,3	463,2	811,0		
c) F_1	7,8	8,4	9,1	11,1	19,9	34,0	203,1	252,7	691,0	793,9
	8,2	8,4	9,0	10,3	17,8	85,6	223,4	741,4		
	7,8	8,6	9,2	11,4	18,6	66,4	228,2	432,6	808,9	
d) F_2	9,1	9,2	10,3	11,3	33,3	74,6	228,5	335,2	396,4	803,8
	9,1	9,1	10,0	12,3	22,5	71,2	130,0	262,0	336,5	766,9
e) *evertsi* ♀♀ *mimeticus* ♂♂	7,6	8,8	8,8	13,2	39,8	126,2	603,2	827,9	865,6	
	8,2	8,3	8,5	9,7	12,6	35,7	161,3	540,6	622,9	867,5
	9,9	9,6	10,7	12,0	20,2	36,0	135,5	534,4	630,4	816,5
f) F_1	8,1	8,3	8,7	30,4	85,5	558,3	913,4			
	8,1	8,7	9,3	9,9	20,3	72,8	209,4	500,3	920,9	
g) F_2	7,1	7,9	8,9	13,7	25,1	81,8	488,0	574,3	1 077,1	

when the infestation rate of the ticks between 15–21 mg only are taken into account it was shown that the sheep with 0,22 ticks showed a medium degree of leg weakness while that with 0,58 ticks/kg SBM showed a total paralysis. One sheep with 0,14 ticks/kg SBM showed no symptoms (Table 1).

The course of engorgement was independent of the infestation rate in that the mass of engorging ticks did not increase noticeably during the first 4 days of engorgement. However, these values increased, parallel with the development of clinical signs, from 20,2 and 35,7 on Day 5 and 6 p.i. to reach a maximum of 816,6 to 867,5 mg after a mean of 10,5 to 10,7 days p.i. respectively (Table 2). As in the case of an infestation with *R. e.*

mimeticus females, the rectal temperatures and heart rate did not change but the respiration rates of the sick animals increased from 20–24/min before infestation to 37 with L II paralysis and to 72 in the case of total paralysis. At the same time the breathing became laboured.

f. *Paralysis-inducing ability of F_1 females produced by female* evertsi *mated with male* mimeticus

F_1 females resulting from female *evertsi* mated with *mimeticus* males showed a similar paralysis inducing ability in the 2 test sheep both qualitatively and quantitatively, as was the case with the progeny of *evertsi* females which had been mated with *mimeticus* males. When the infestation rates with ticks between 15–21 mg

are taken into account, 0,57 ticks/kg SBM produced a high degree of leg weakness while 1,5 ticks produced total paralysis. The mean tick masses, as in the other series, only changed slightly during the first 4 days of the engorgement period. From Days 4 and 5 onwards these values increased continuously to reach a maximun of 913,4 mg and 920,0 mg after 7,4 and 8,8 days respectively. (Table 2). The body temperatures and heart rates remained normal during the course of paresis, but the respiration rate increased from 20–28/min before infestation to a mean of 54 when L II paralysis was reached and 76 during total paralysis.

g. *Paralysis-inducing ability of F_2 females produced by* evertsi *females mated with* mimeticus *males*

Only 1 sheep was used in this experiment and the ticks were fed in an enclosed area. The toxic potential of this F_2 generation closely resembled that of the F_1 generation as an infestation rate of 0,41 ticks in the toxic phase per kg SBM produced a medium degree of leg weakness (Table 1). The mean mass of an engorged female was 7,1; 7,9; 8,9; 13,7 & 25,1 mg on Day 1–5 of the infestation respectively. It increased from 81,8 mg on Day 6 to 488,0 and 574,3 after Days 7 and 8 respectively. After the complete recovery of the animal on Day 9 a mean engorgement mass of 1077,1 mg per female was reached (Table 2). Throughout the infestation the rectal temperature and heart rate stayed normal but the respiration rate increased slightly from 24/min before infestation to a mean of 34 when L II paralysis was reached.

DISCUSSION

These investigations have proved that *R. e. mimeticus* can induce paralysis in sheep. Its toxicity in comparison to that of the nominate subspecies *evertsi* is clinically similar. This was demonstrated by the finding that corresponding degrees of paralysis were produced by approximately the same infestation rates of ticks/kg SBM. In addition the paresis and paralysis induced by these tick subspecies are characterized by very constant periods of time between tick infestation and these initial clinical manifestations. This is analogous to the results obtained with the nominate subspecies *evertsi* (Hamel & Gothe, 1978; Gothe & Budelmann, 1980; Gothe & Lämmler, 1982) and other ixodid species [Todd, 1914; Bruce, 1925; Ross, 1926, 1932, 1934a, b, 1935; Gregson, 1936, 1958, 1959, 1962, 1973; Mail & Gregson, 1938; Davidson, 1941; Hughes & Philip, 1958; Emmons & McLennan, 1960; McLennan & Oikawa, 1972; Goodrich (cited by Sutherland, 1974); Doube, Kemp & Bird, 1977; Goodrich & Murray, 1978; Stone, 1979; Stone, Doube, Binnington & Goodger, 1979; Stone, Cowie, Kerr & Binnington, 1982; Binnington & Stone, 1981; Wilkinson, 1982]. This incubation period is completely independent of the rate of tick infestation and of the mass of the host animal, and thus of its age. It is exclusively dependent on the engorgement of the female ticks and is regulated by their mating dates. An exact parallel exists between the mass increase of the females during engorgement (viz. with the activity of their salivary glands) and the development as well as the persistence of clinical symptoms. Similarly, the intensity of the clinical symptoms are directly proportional to the infestation rate and therefore probably also to the size of the toxin inoculum. They are, however, indirectly proportional to the body mass of the animal, which as a rule is correlated with the age of the animal. Because of its similarity to *evertsi* paralysis, especially regarding the constant time interval between the beginning of infestation and the first manifestation of symptoms, one can also define *mimeticus* induced paralysis as a toxicosis.

For the same reason one can also postulate that when the toxin is introduced dynamics and kinetics are partially initiated and actively influenced by the successful transfer of spermatophores during mating. In addition, the toxin most probably only becomes pathogenically active in female ticks with body masses in the range of 15–21 mg. As in the case of *evertsi*, strain-dependent differences in toxicity could not be demonstrated for *mimeticus* (Gothe & Bezuidenhout, 1986).

By analogy with *evertsi* paralysis (Gothe & Lämmler, 1982), it can be concluded that the toxic phase of *mimeticus* females is most probably limited to a very short period of a few hours only during the continuation of engorgement by individual ticks which have already reached a mass of not less than 15 and not more than 21 mg. This state is normally reached after 5–6 days p.i. The 2 subspecies of *R. evertsi* were also found to be biologically convergent and not sexually isolated (Gothe, Gold & Kraiss, 1985).

It was established that the toxicity of *mimeticus* females after consubspecific mating was almost equal to that of *evertsi* in that 0,75–0,87 ticks/kg SBM compared to 1,1 ticks/kg for *evertsi* were necessary to produce total paralysis (Gothe & Budelmann, 1980). In addition there was no difference regarding the toxicity of females resulting from intersubspecies crossbreeding as well as their filial generations, compared to those induced by *mimeticus* and *evertsi* subtypes. It may thus be expected that tick paralysis may be present in hybridizing zones, assuming that the area of infestation is always guaranteed to have a large number of potent ticks. In most instances where infestations took place in a small enclosed area of the skin only it was impossible to induce even a slight disorder in motility in highly susceptible sheep despite the fact that the tick numbers themselves were high enough to cause, at least in some cases, lethal paralysis. It is not clear what mechanism is responsible for the decline or total blocking of the effects of the toxin. It may be the result of a venous insufficiency caused by the attachment of the cotton feeding bags. They may cause a partial prevention of venous back flow and therefore limit the toxin distribution to the target organ. Possibly, also, locally produced vaso-active substances may influence the function of the veins as transport vessels.

On the other hand, one must also consider the decrease of about 50 % in the pathogenicity of female *evertsi* after preinfestation with adult male ticks (Gothe & Budelmann, 1980). The feeding of ticks in an enclosed area ensures fast detection of female pheromones by males and thus results in early mating (Schniewind & Gothe, 1982). The subsequent process of engorgement was shown to be sortened and the toxic phase therefore passed quicker. This may result in reduced toxin production and/or secretion.

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