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Investigation into the Critical Equilibrium Humidity, Active Atmospheric Water Absorption and Water Content of *Rhipicephalus evertsi mimeticus*

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ABSTRACT

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The critical equilibrium humidity for fully engorged nymphs of *Rhipicephalus evertsi mimeticus* was shown to be between 91% and 93.5% r.h., and for adult male and female ticks to be between 82% and 84.5% r.h. Studies on gnathosoma and idiosoma by selective exposure to differing relative humidities have shown that dehydrated adult male and female ticks are capable of active uptake of atmospheric water vapor only through their mouthparts. The percentage of water content of unfed adult male and female ticks previously dehydrated was not influenced by subsequent exposure to different relative humidities, varying similarly in both sexes, male imagines between 59.6% and 63.7%, female imagines between 59.6% and 64.4%. Analogous values (62.3% and 61.1%) were obtained for the water content of male and female imagines not previously dehydrated, which were incubated at 30°C and 100% r.h. for 7 days.

INTRODUCTION

The physiological basis for the pronounced ecological plasticity of *Rhipicephalus evertsi mimeticus* Dönitz, 1910 in meeting the challenge of critical abiotic environmental conditions in all off-host stages and surviving these for long periods of time (Kalvelage et al., 1987a,b) has not been investigated up to now. However, analogous to other tick species (Knülle and Rudolph, 1982; Needham and Teel, 1986) it can be assumed that key elements involved are the ability to maintain water balance at relatively constant levels and to quickly restore this level in response to changes in ambient relative humidity. The following investigation sought to determine how this tick species maintains

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homeostatic water content levels, by studying the critical equilibrium humidity, the interaction between ambient relative humidity and tick water content, and atmospheric water vapor uptake.

MATERIALS AND METHODS

Investigation of critical equilibrium humidity in engorged nymphs and in unfed male and female ticks

The critical equilibrium humidity is a threshold ambient relative humidity value, whereby relative humidity levels lower than the critical equilibrium humidity cause a continuous loss of water, and levels higher than the critical equilibrium humidity allow the ticks to have active atmospheric water absorption. The critical equilibrium humidity was determined for nymphs immediately after complete engorgement on cattle and for 14-day-old unfed male and female ticks of the Witvlei strain of *R. evertsi mimeticus* which had been held at 28°C and 95% r.h. before, during and after the imaginal molt.

To begin with, cleansed nymphs were held 2 days off-host at 30°C and 100% r.h., after which they were individually weighed on a microbalance (Sartorius, Göttingen). Groups of 5 specimens each were placed in perforated Eppendorf tubes, after which they were dehydrated at 30°C and 0% r.h. for 24 h and then weighed anew. Next, groups of 25 nymphs distributed between 5 Eppendorf tubes were held for 24 h at 30°C, with one group each being held at r.h. levels of 77.5%, 80%, 82%, 84.5%, 91%, 93.5% and 100% after which they were weighed anew.

The unfed adult ticks were weighed after being held for 7 days at 30°C and 100% r.h., after which they were immediately placed in an off-host environment for dehydration at 30°C and 0% r.h. for 2 days. After the dehydration process, the imagines were weighed again and groups of 10 male and groups of 10 female ticks were placed in Eppendorf tubes and held for 24 h at 30°C, and one group each at r.h. levels of 63%, 71%, 72.5%, 75.5%, 77.5%, 80%, 82%, 84.5%, 87%, 91%, 93.5% and 100%.

The r.h. levels were established and maintained in airtight desiccators using the method described by Winston and Bates (1960). The critical equilibrium humidity was determined by taking the r.h. range where the upper and lower limits caused a slight weight gain or loss, respectively.

Investigation of active uptake of atmospheric water vapor through the mouthparts of unfed male and female ticks

Six-week-old unfed adult ticks of the Witvlei strain of *R. evertsi mimeticus* were used for this investigation into active water vapor uptake through the mouthparts. Before the beginning of the experiments the imagines were held at 28 °C and 95% r.h. and then dehydrated for 48 h at 30 °C and 0% r.h. Before and after the dehydration process the ticks were precisely weighed and the results recorded.

The dehydrated ticks were then immediately immobilized in a double chamber, whereby the front portion of the tick was hermetically sealed off from the idiosoma. To accomplish this the area of the basis capituli where the pedipalps, chelicerae and hypostome attach was sealed off with Parafilm (American Can Company, Connecticut, U.S.A.) and in addition to this with paraffin (solidification point 42–44 °C; Merck, Darmstadt, F.R.G.). In one of the isolated compartments of the chamber an r.h. level of 93.5% was maintained, while in the other compartment a level of 15% was maintained. While the tick as a whole was held for 24 h at 30 °C the mouthparts were exposed to 93.5% r.h. and the idiosoma to 15% r.h., after which the imagines were weighed. In the second part of the experiment the humidity levels were reversed in the two chambers for 24 h after which the ticks were again weighed. As the final experiment in this investigation, the mouthparts were exposed to 15% r.h. and the idiosoma to 93.5% r.h. for 48 h, the ticks being weighed before and after exposure. An increase in weight in the dehydrated male and female imagines was taken as an indicator of atmospheric water vapor uptake, and the percentage of weight increase was used to determine the extent of uptake.

In each series of experiments 5 male and female ticks were used. The r.h. levels were established and maintained using the method described by Winston and Bates (1960), whereby for 0% r.h. concentrated sulfuric acid, for 15% r.h. a saturated LiCl solution, and for 93.5% r.h. a saturated KH_2PO_4 solution were used.

Water content of unfed male and female ticks after exposure to differing relative humidities

For the investigation into the relationship between relative humidity level and water content, 2-week-old unfed male and female adult ticks of the Witvlei strain of *R. evertsi mimeticus* were used. These ticks were held before, during and after the imaginal molt till the start of the experiments at 28 °C and 95% r.h. The ticks were dehydrated for 24 h at 30 °C and 0% r.h., after which groups of 10 male and groups of 10 female imagines were immediately placed in environments with differing r.h. levels for 3 days. One group each was exposed to r.h. levels of 63%, 71%, 72.5%, 75.5%, 77.5%, 80%, 82%, 84.5%, 87%, 91%, 93.5% and 100%, all at a constant 30 °C. Furthermore, one non-dehydrated group was exposed for 7 days to a r.h. of 100% at 30 °C. Upon completion of the exposure phase the imagines were weighed. The ticks were then placed in 4-cm × 2.5-cm rolled-edge glass containers which were sealed with perforated aluminium foil and dried for 24 h in a hot-air sterilizer (Memmert, Schwabach) at 120 °C. The desiccated ticks were immediately weighed and the water content percentage was calculated using the weight differences. The r.h. levels were established and maintained in airtight desiccators using the method described by Winston and Bates (1960).

RESULTS

Critical equilibrium humidity of engorged nymphs and unfed male and female ticks

After the 24-h dehydration of the fully engorged nymphs, which caused a weight loss of between 2.1% and 3.3%, and the exposure thereafter of 25 specimens each at various relative humidity levels ranging from 77.5% to 100% at 30 °C, weight gains of 0.6% and 1.2% could only be obtained at a relative humidity level of 93.5% and 100%, respectively. Relative humidity levels of 91% and below caused a loss of weight of between 0.7% and 1.9%; therefore the threshold between water loss and uptake of atmospheric water vapor lies between 91% r.h. and 93.5% r.h. (Table 1).

In male ticks, the dehydration process caused a weight loss of between 2.1% and 3.8%. However, after 24-h exposure of 10 ticks each at different relative humidity levels ranging from 63% to 100% r.h., a weight gain of 0.4% was registered beginning at a relative humidity level of 84.5%. As the water-vapor saturation level of the air increased, weight gains also increased continuously from 1.8% at 87% r.h. to 3.2% at 93.5% r.h., to finally reach a maximum of 3.4% at 100% r.h. (Table 1).

The weight loss data of the female imagines was consistent with that obtained from the male ticks. After dehydration the weight loss varied between 1.5% and 6.6%; the first weight gain also occurred at 84.5% r.h. and increased from 1.8% at 87% r.h. to 2.5% at 93.5% r.h. to reach a maximum at 2.7% at 100% r.h. Therefore, the critical equilibrium humidity lies between 82% r.h. and 84.5% r.h. in both male and female adult ticks (Table 1).

Active uptake of atmospheric water vapor through the mouthparts of unfed male and female ticks

As Table 2 shows, the body weight of dehydrated adult ticks only increased after selectively exposing the mouthparts to 93.5% r.h. for 24 h. The weight gain ranged from 1.3% to 4.4% in female imagines and 1.8% to 3.3% in male ticks. When the idiosoma was exposed to 93.5% r.h. and the mouthparts to only 15% r.h. for 24 h, the body weight remained the same or decreased. Even when the period of exposure was increased to 48 h, a positive change in body weight occurred only if the mouthparts were exposed to a relative humidity level of 93.5%. This gain ranged from 1.9% to 4.3% in male imagines and from 1.1% to 2.5% in female ticks (Table 3). In comparison, when the idiosoma was

TABLE 1

Average weight of fully engorged nymphs (N) and unfed male and female ticks of *R. evertsi mimeticus* before and after dehydration at 30°C and 0% r.h. and after a 24-h incubation of dehydrated ticks in different humidities varying between 63.0% r.h. and 100% r.h.

Average weight (mg) of ticks																
Before dehydration			After dehydration			Weight loss (%)			Incubation of dehydrated ticks in (% r.h.)	After incubation			Change of weight			
N	♂♂	♀♀	N	♂♂	♀♀	N	♂♂	♀♀		N	♂♂	♀♀	N	♂♂	♀♀	
16.8	6.38	7.56	16.2	6.19	7.29	3.0	3.0	3.6	100	16.5	6.40	7.49	+1.2	+3.4	+2.7	
16.6	5.17	7.17	16.2	5.06	7.06	2.4	2.1	1.5	93.5	16.3	5.22	7.24	+0.6	+3.2	+2.5	
15.3	5.59	6.45	14.9	5.38	6.23	2.6	3.8	3.4	91.0	14.7	5.43	6.38	−1.3	+0.9	+2.4	
15.3	5.61	6.72	14.8	5.43	6.53	3.3	3.2	2.8	87.0	14.6	5.53	6.65	−1.4	+1.8	+1.8	
16.8	5.22	7.85	16.3	5.09	7.49	3.0	2.5	4.6	84.5	16.0	5.11	7.51	−1.8	+0.4	+0.3	
16.3	5.96	6.66	15.9	5.74	6.50	2.5	3.7	2.4	82.0	15.6	5.69	6.44	−1.9	−0.9	−0.3	
14.4	5.96	7.28	14.0	5.80	7.04	2.8	2.7	3.3	80.0	13.9	5.78	6.96	−0.7	−0.3	−1.1	
14.4	5.56	7.40	14.1	5.38	7.14	2.1	3.2	3.5	77.5	13.9	5.34	7.06	−1.4	−0.7	−1.1	
	6.28	7.27		6.12	7.06		2.5	2.9	75.5		6.09	7.02		−0.5	−0.6	
	5.65	6.14		5.48	5.78		3.0	5.9	72.5		5.44	5.74		−0.7	−0.7	
	6.30	6.56		6.06	6.27		3.8	4.4	71.0		6.02	6.16		−0.7	−1.8	
	5.77	7.57		5.62	7.07		2.6	6.6	63.0		5.56	6.94		−1.1	−1.8	

TABLE 2

Weight of unfed male and female ticks of *R. evertsi mimeticus* before and after dehydration at 30°C and 0% r.h., and after 24-h selective exposure (SE) of the mouthparts in 93.5% r.h. and 15% r.h.

Body weight of ticks (mg)							
Sex	Before dehydration	After dehydration	Weight loss (%)	After SE[a]	Change (%)	After SE[b]	Change (%)
♂♂	6.3	6.0	4.3	6.2	+3.3	6.2	0
	6.4	6.0	6.3	6.2	+3.3	6.1	−1.6
	6.0	5.7	5.0	5.8	+1.8	5.7	−1.7
	4.3	4.1	4.7	4.2	+2.4	4.2	0
	6.5	6.2	4.6	6.4	+3.2	6.3	−1.6
♀♀	8.1	7.8	3.7	7.9	+1.3	7.8	−1.3
	8.2	7.8	4.9	7.9	+1.3	7.9	0
	7.1	6.8	4.2	7.1	+4.4	7.0	−1.4
	8.1	7.8	3.7	8.0	+2.6	7.9	−1.3
	9.4	9.0	4.3	9.2	+2.2	9.2	0

[a]Mouthparts in 93.5% r.h., idiosoma in 15% r.h.
[b]Mouthparts in 15% r.h., idiosoma in 93.5% r.h.

TABLE 3

Weight of unfed male and female ticks of *R. evertsi mimeticus* before and after dehydration at 30°C and 0% r.h. and after a 48-h selective exposure of the mouthparts at 93.5% r.h. and the idiosoma at 15% r.h.

Body weight of ticks (mg)					
Sex	Before dehydration	After dehydration	Weight loss (%)	After 48-h selective exposure	Weight change (%)
♂♂	5.5	5.2	5.5	5.3	+1.9
	5.1	4.8	5.9	5.0	+4.2
	5.7	5.5	3.5	5.7	+3.6
	5.6	5.1	8.9	5.2	+2.0
	4.9	4.6	6.1	4.8	+4.3
♀♀	5.7	5.1	10.5	5.2	+2.0
	9.6	9.1	5.2	9.2	+1.1
	7.1	6.7	5.6	6.8	+1.5
	8.6	8.1	5.8	8.3	+2.5
	7.0	6.5	7.1	6.6	+1.5

TABLE 4

Weight of unfed male and female ticks of *R. evertsi mimeticus* before and after dehydration at 30 °C and 0% r.h., and after 48-h selective exposure of the mouthparts in 15% r.h. and the idiosoma in 93.5% r.h.

Body weight of ticks (mg)					
Sex	Before dehydration	After dehydration	Weight loss (%)	After exposure of mouthparts in 15% r.h. and the idiosoma in 93.5% r.h.	Weight change (%)
♂♂	4.2	4.0	4.8	3.9	−2.5
	5.6	5.3	5.4	5.2	−1.9
	6.0	5.6	3.3	5.7	−1.7
	5.8	5.5	5.2	5.3	−3.6
	5.3	5.0	5.7	4.9	−2.0
♀♀	7.9	7.4	6.3	7.2	−2.7
	8.1	7.7	4.9	7.6	−1.3
	8.5	8.0	5.9	7.8	−2.5
	7.8	7.5	3.8	7.3	−2.7
	9.3	8.9	4.3	8.8	−1.1

TABLE 5

Average weight of unfed male and female ticks of *R. evertsi mimeticus* before and after 24-h desiccation at 120 °C, and the absolute (abs.) and percentage water content after incubation in different relative humidities

	♂♂				♀♀			
Relative humidity (%)	Weight before desiccation (mg)	Weight after desiccation (mg)	Water content (abs., mg)	Water content (%)	Weight before desiccation (mg)	Weight after desiccation (mg)	Water content (abs., mg)	Water content (%)
63	5.39	2.18	3.21	59.6	6.51	2.53	3.98	61.1
71	5.77	2.16	3.61	62.6	6.00	2.22	3.78	63.0
72.5	5.27	1.93	3.34	63.4	5.42	1.93	3.49	64.4
75.5	5.92	2.20	3.72	62.8	6.82	2.57	4.25	62.3
77.5	5.19	1.94	3.25	62.6	6.80	2.65	4.15	61.0
80	5.56	2.14	3.42	61.5	6.83	2.75	4.08	59.7
82	5.40	2.09	3.31	61.3	6.29	2.54	3.75	59.6
84.5	4.93	1.92	3.01	61.1	7.07	2.74	4.33	61.2
87	5.41	1.99	3.42	63.2	6.58	2.49	4.09	62.2
91	5.30	1.95	3.35	63.2	6.40	2.38	4.02	62.8
93.5	5.19	1.92	3.27	63.0	7.16	2.72	4.44	62.0
100	5.32	1.93	3.39	63.7	7.96	3.21	4.76	59.7
100 (7 days)	7.58	2.86	4.72	62.3	6.28	2.44	3.84	61.1

exposed for 48 h to the higher level of relative humidity the ticks lost weight, from 1.7% to 3.6% in male ticks and from 1.1% to 2.7% in female imagines (Table 4).

Water content of unfed male and female ticks after exposure to differing relative humidities

The water content of unfed male and female adult ticks, calculated by determining the percentage difference between the weight of the tick before and after 24-h desiccation at 120°C, was not influenced by dehydration and the exposure to varying relative humidity levels which followed (Table 5). The water content varied similarly in both sexes between 59.6% and 63.7% in males and between 59.6% and 64.4% in female imagines. Analogous values were determined for male and female adult ticks exposed for 7 days to 100% r.h. at 30°C without previous dehydration. In males the water content was 62.3%, in females 61.1%. The absolute water content was higher in females as a result of their greater initial weight.

DISCUSSION

Rhipicephalus evertsi mimeticus is able to effectively withstand critical off-host environmental conditions for long periods of time while maintaining its viability (Kalvelage et al., 1987a,b). Its distinctive ecological plasticity is based upon the capability, at least in regard to the capacity to compensate for water losses, to produce water catabolically or anabolically as well as by passive or active atmospheric water vapor resorption (Freda and Needham, 1984; Needham and Teel, 1986). Active uptake of water by drinking has also to be considered, especially in microhabitats where condensation occurs and offers a frequent and reliable source of water (Needham and Teel, 1986; Splisteser and Tyron, 1986). The homeostatic maintenance of its water balance is crucial for the survival of the tick and is probably based primarily, or even exclusively, on the combined action of active and passive water resorption, coupled with a reduced metabolism owing to inactivity of ticks as well as a relatively impermeable integument. If these mechanisms are viewed separately, it must be concluded that active water absorption, which is related to critical equilibrium humidity, plays a minor role in *R. evertsi mimeticus* and only shares in maintenance at high relative humidity levels.

The critical equilibrium humidity, also known as critical equilibrium activity (Freda and Needham, 1984; Needham and Teel, 1986) is defined as a threshold ambient relative humidity, whereby a continuous loss of water results at lower humidities and a maintenance of water steady-state by uptake of atmospheric water vapor at higher levels. The presented data shows that this level is not obtained until the fairly high relative humidity of 91–93.5% in nymphs, and in unfed male and female imagines a relative humidity of between 82% and 84.5% has to be reached. These values do not, or only slightly, differ from those values obtained from other ixodid tick species (Knülle and Rudolph, 1982; Jaworski et al., 1984) that populate drier or more humid habitats than *R. evertsi mimeticus*. However, the degree of ecological restriction and specific classification according to the off-host environment populated in the approximately 800 described tick species is an essential species characteristic which cannot be explained by the relatively uniform equilibrium humidity. Possibly, the species differences can be explained by differences in passive integumental water absorption below the critical equilibrium humidity as well as differences in the water permeability of the integument, at least in regard to the humidity and temperature tolerance of *R. evertsi mimeticus*. Passive water absorption, as has been shown by investigations of *Amblyomma americanum* (Freda and Needham, 1984; Needham and Teel, 1986) is much more important in the maintenance of water steady-state even at critical humidity levels with a 66–77% participation, and even functions at levels below the critical equilibrium humidity. At the same time, however, it must be considered that in highly dehydrated ticks the critical equilibrium level can be adjusted to much lower levels (Knülle, 1966; Gaede and Knülle, 1987).

If these species-specific integumental differences are taken into account, *R. evertsi mimeticus*, with a weight loss of 1.5–6.6% after 24-h dehydration at 30°C and 0% r.h. in the imagines and 2.1–3.3% in engorged nymphs, is in contrast to other species such as the humidity-sensitive *Ixodes ricinus* which can lose up to 50% of its weight in female ticks after 24-h exposure to 25°C and 0% r.h. (Lees, 1946); this tick is more efficient in regard to its integumental water retention, and can almost be classified in the same group with the desert-living *Hyalomma asiaticum* which only loses 0.6% of its body weight at 26°C and 0% r.h. (Balashov, 1960).

Further support for the assertion that *R. evertsi mimeticus* has a highly effective integumentally controlled water-balancing system is provided by the results on the water content of unfed male and female imagines. After dehydration for 24 h at 30°C and 0% r.h., and the following 3 days of exposure to different r.h. levels ranging from 63% to 100% r.h., their water content varied from 59.6% to 64.4% for males and females. This barely deviates from the results obtained from ticks held at constant 30°C and 100% r.h., the results being 62.3% and 61.1% for male and female ticks, respectively. The similarity in results obtained from ticks which were dehydrated and held at a relative humidity below the critical equilibrium humidity, and ticks which were held at relative humidity levels far in excess of the critical equilibrium humidity, allows the conclusion that in contrast to other ixodid species (Sauer and Hair, 1971; Chi-Yen et al., 1973; Hair et al., 1975), *R. evertsi mimeticus* can even balance its water content in relative humidity levels below the critical equilibrium humidity. The exact modus operandi of this equalization at low water vapor saturation levels has not yet been explained; however, it is apparent from other experiments carried out (McMullen et al., 1976; Rudolph, 1976; Rudolph and Knülle, 1978; Knülle and Rudolph, 1982; Freda and Needham, 1984; Needham and Teel, 1986) that it cannot be the result of active water vapor uptake from the atmosphere by the mouthparts of the tick. Passive water absorption at subcritical-equilibrium humidity levels can be essentially assumed for all tick species with certain species-specific differences (Needham and Teel, 1986). However, if and to what degree the water permeability of the integument can explain the extraordinary temperature and humidity tolerance of *R. evertsi mimeticus* must still be examined experimentally, particularly in regard to the critical transition temperature which is evidenced by a sudden and distinct rise in cuticular permeability.

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