Reports

Pheromone-Mediation of Host-Selection in Bont Ticks (*Amblyomma hebraeum* Koch)

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The bont tick, *Amblyomma hebraeum*, is the principal vector to southern African ruminants of heartwater (*Cowdria ruminantium* infection). The role of feeding male ticks, which emit an aggregation-attachment pheromone, in attracting unfed ticks to cattle was investigated. Calves infested with feeding male ticks were more attractive to unfed adult ticks than were uninfested calves. The presence of the pheromone on previously infested cattle apparently allows unfed ticks to discriminate between hosts on which these parasites have fed successfully (suitable hosts) and those on which they have not (potentially unsuitable hosts). The use of acaricides is thus unlikely to reduce bont tick populations in areas where adequate numbers of alternate (wild) hosts are present. Also, cattle so treated may lose their resistance to heartwater through lessened exposure to infected ticks.

The southern African bont tick, *Amblyomma hebraeum* Koch, is an important pest of livestock and a major vector of heartwater disease, caused by *Cowdria ruminantium*, in domestic ruminants (*1*). This disease, characterized by high mortality of susceptible animals in enzootic areas, has long been considered one of the most important livestock diseases of Africa (*2*). In addition, its establishment in Guadeloupe Island and subsequent spread to several other islands poses a threat to domestic and wild ruminants of the Americas, especially because of the presence there of actual or potential tick vectors and their propensity to use migratory birds as hosts for immature stages (*3, 4*).

Males of *A. hebraeum* are known to remain on hosts for several months (*5*) and to mate with multiple females (*6*). The attachment of unfed forms (males, females, and nymphs) is stimulated by an aggregation-attachment pheromone (AAP) that is emitted by males after a period of feeding (*7, 8*). As a result, ticks tend to accumulate on suitable hosts in clusters formed at sites (such as the belly or genitalia) where hosts groom least effectively (*9*). It is known that unfed adults of *A. hebraeum* are attracted to the source of AAP after stimulation by high concentrations of CO_2, as occurs in the breath of large mammal hosts (*10–12*). The responses to both CO_2 and AAP appear to be part of a selection process that ensures that ticks attach preferentially to hosts on which they are likely to feed successfully. Cattle on which pheromone-emitting male ticks are attached were found to be significantly more attractive to unfed adult ticks than are uninfested cattle. This host-selection mechanism may limit the effectiveness of acaricides in reducing bont tick populations in areas where untreated alternative hosts occur. It may also compound the adverse effect that the intensive use of acaricides has on the immune status of heartwater in domestic herds.

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On three occasions during the summer of 1987 the attractiveness to unfed adults of *A. hebraeum* of two Friesland steers infested with pheromone-emitting male ticks (group A) was compared with that of two similar uninfested steers (group B) at Zimbabwe's Mbizi Quarantine area in the southeastern lowveld. Group B steers had been treated at weekly intervals for at least 2 months with an organophosphate acaricide (dioxathion) until 7 days before each experiment. The observed residual effect of the acaricide was 2 to 3 days and, as males must feed for approximately 7 days before emitting pheromone (*8*), the treatment regime ensured that the treated steers were pheromone-free. All experiments were carried out in the late afternoon when soil temperatures had dropped below 30°C and there was a steady gentle breeze blowing from the southeast. The steers were sedated by intravenous injection of Rompun (0.5 ml/100 kg of body weight) and brought to lateral recumbancy with ropes.

The two group A steers were tested 100 m away from the two group B steers. Two hundred pairs of unfed, laboratory-reared adult males and females of *A. hebraeum*, which had been marked with fluorescent dusts of two different colors, were released 3 m downwind from each group. The number of attached males (unmarked) were counted before the start of the experiments. Attached, unmarked males and marked males and females were counted at the end of each experiment, 1 hour after release of the unfed ticks. The experiments were not run for

Table 1. Number of *Amblyomma hebraeum* adults attracted and attaching to parasitized and unparasitized steers 1 hour after release in three trials.

Treatment	Male ticks attached at the start			"Marked" ticks attached after 1 hour		
	1	2	3	1	2	3
Group A						
Steer 1	149	200	125	47	86	15
Steer 2	140	250	135	87	184	22
Group B						
Steer 3	2	4	7	1	1	0
Steer 4	0	0	4	0	0	2

Table 2. Number of *Amblyomma hebraeum* adults attracted and attaching to pheromone-treated and untreated steers 30 minutes after release of 100 marked males and 100 marked females.

Treatment	Pheromone-treated steer		Untreated steer	
	Male	Female	Male	Female
Marked, released ticks attached	24	12	0	2
Wild ticks attached	6	5	0	0
Marked, released ticks on steer or in immediate vicinity (<0.5 m)	14	43	3	0
Wild ticks on steer or in immediate vicinity (<0.5 m)	3	5	0	0

longer periods of time in view of the dangers of prolonged lateral recumbancy in ruminants.

The behavior of the ticks released downwind of group A steers was markedly different from that of the ticks released downwind of group B. The latter ticks initially remained fairly motionless at or near the site of release and then gradually dispersed in all directions; many disappeared into the litter on the surface of the soil. Ticks of group A, in contrast, immediately started to move en masse toward the steers. The group A steers also attracted wild, unfed adults (both males and females) of *A. hebraeum* from distances of more than 3 m. Wild adults that were in the immediate vicinity (within 0.5 m) of either group of steers moved to the animals.

Large numbers of the marked adults attached to group A steers and few, if any, attached to group B steers (Table 1). Males and females were attracted in almost equal numbers to the steers of group A. The majority of the marked ticks attached in the immediate vicinity of the males that were already on the animals, thus increasing the sizes of existing clusters of ticks.

To show that the group B steers did not repel ticks, at the end of the second and third replicates, 20 prefed *A. hebraeum* male ticks were placed on each animal. The ticks attached without delay. Twenty unfed ticks (10 male and 10 female) were then released onto each of the steers in the proximity of these ticks. Within 5 minutes more than 90% of the unfed ticks had begun to attach.

Finally, an experiment was performed to determine whether or not AAP alone was responsible for the attraction of the ticks to the steers. Two tick-free steers that had been dipped in dioxathion 3 weeks before the experiment and were manually freed of ticks on alternate days, thereafter were sedated as above and brought to lateral recumbancy 1 m apart. An extract of AAP was prepared by shaking 200 fed males of *A. hebraeum* in 200 ml of diethyl ether. This was poured on selected sites (escutcheon, posterior of abdomen, hind feet) of one steer, and the other steer was left untreated. After the ether had evaporated 100 male and 100 female *A. hebraeum* marked with fluorescent dust were released 3 m downwind of the two steers. After 30 minutes the number of ticks attracted and attaching to either steer was counted.

Nearly half (41 male and 57 female) of the marked ticks responded with host-seeking behavior and most were attracted to the pheromone-treated steer (Table 2). The remainder burrowed into the upper layers of the soil. Some wild ticks in the vicinity of the experiment were also attracted to the treated steer. Some of these climbed onto the steer within 13 minutes after first being sighted 9 m away. Most male ticks, released or wild, attached to the treated steer within minutes of making contact with it. Both released and wild females were slower to attach and most were found moving about the animal or in its immediate vicinity, indicating that an additional factor, possibly clasping by fed males (*5*), stimulates their rapid attachment. Approximately half the ticks attaching to the treated steer did so on areas where pheromone had been applied.

Hess and de Castro speculated that pheromone-emitting males of a related species of tick, *A. variegatum*, may "bait a host or a herd" (*13*). That this is true, at least in part, for *A. hebraeum* is shown by our results. Further, our findings confirm that the presence of pheromone-emitting males allows the unfed ticks to discriminate between hosts on which adults have fed successfully (that is, suitable hosts) and hosts on which they have not (that is, potentially unsuitable hosts). The effect is apparently to reduce mortality in populations of *A. hebraeum* caused by unfed ticks attaching to unsuitable hosts. These findings also have economic and epidemiological implications. Cattle regularly treated with acaricides may pick up fewer unfed adults (*7*) and nymphs (*8*) than untreated cattle or wild hosts. The host-selection mechanism therefore minimizes the effectiveness of acaricides in reducing bont tick populations when large numbers of suitable wild hosts are available. It will also reduce the frequency of transmission of heartwater to acaricide-treated cattle and so may adversely affect immunity within cattle herds. Exposure to heartwater is particularly important in young cattle, which gradually lose their resistance to the disease beyond the age of about 1 month (*14*). Immunity to heartwater in cattle is thought to be transient unless reinforced by repeated exposure (*1*). The chances of young calves acquiring immunity to heartwater might be increased by treating them with AAP or infesting them with male ticks, thus making them attractive to infected unfed nymphs and adults.

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The Perception of Intention

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Classical work on the perception of causality in humans is extended to the perception of intention. Two experiments explored the sensitivity of preschool children to intentional events that can be stated in terms of time and distance only. In habituation-dishabituation of attention tests, preschool children differentiated between intentional movement patterns of two balls and the nonintentional control events where the movements were desynchronized. Also, reversal of the roles of the balls produced more recovery of attention in the intentional case than it did in the nonintentional case.

EVENTS THAT LEAD TO THE PERCEPtion of causality can be stated in terms of place and time. For example, Michotte (*1*) showed that when two objects collide, provided the launching of one coincides temporally and spatially with contact by the other, the human adult perceives the relation as causal. Thus, contrary to Hume (*2*), perception of causality can be produced by even a single instance of the

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