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Feeding Pattern, Mating and Oviposition in Female *Haemaphysalis longicornis* Neumann (Acari: Ixodidae)

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The feeding pattern, mating and oviposition were examined in the female cattle tick, *Haemaphysalis longicornis.* Females of the bisexual race needed mating to complete engorgement and oviposition : in the absence of a male, the females extended the time of feeding and failed to engorge and detach. One male was capable of mating with at least 6 females. Mating seemed to occur at the earliest on the 3rd-4th day after commencement of feeding when the volume of the female reached over 10 mm^3. The feeding rate of the females of the parthenogenetic race was lower than that of the bisexual ones up to the 4th day in the feeding stage. However, both the mean engorged weight (mg) and the mean duration (days) of the feeding period were not significantly different between the two races. There wes a positive correlation between the total number of deposited eggs and the fed female weight in the bisexual race. The egg production efficiency varied with the body weight. The theoretical minimum body weight for oviposition was 28.4 mg, and mating seemed not always to be needed for oviposition.

INTRODUCTION

In ixodid and argasid ticks, blood-sucking is so harmful to their hosts and so important to tick reproduction that studies on the relationship between feeding and reproduction have been extensive (Oliver, 1974), and mating is necessary for most ticks before they will complete oogenesis and oviposition (Diehl et *al.*, 1982).

Haemaphysalis Zongicornis Neumann, the most dominant species on Japanese pastures, has both bisexual and parthenogenetic races (Kitaoka, 1961; Hoogstraal et *al.*, 1968). For the bisexual race occurring in Korea, detailed works have been carried out (Kang, 1981a, b). The ecological and physiological investigations on the tick in Japan, however, have been made chiefly on the parthenogenetic race, and there have been no studies on mating.

Therefore, the purpose of the present study was to clarify the feeding pattern in the females of both races, the impact of mating on tick feeding and oviposition, and the effect of the quantity of blood meal on oviposition in the bisexual race.

MATERIALS AND METHODS

1. Feeding experiments

Female and male ticks of bisexual *H. Zongicornis* were collected by flagging on a

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pasture at Kujū highland, Ōita Prefecture. Three feeding experiments were designed using the following female vs. male ratios ; 20 females and 20 males (experiment 1), 10 females and 1 male (experiment 2) and 10 females only (experiment 3) were fed on the ears of the rabbits under laboratory conditions. The body length, width and depth of the females were measured using a caliper (with 0.05 mm precision) at the same time every day up to detachment, and then the volume was estimated by the stereometry of a spheroid ($\pi/6 \times$ length $\times$ width Xdepth). Unfed and fed body weights of the females were weighed on a Metller electric balance (AE 160) to the nearest 0.1 mg.

In addition, 11 parthenogenetic females (Okayama strain) which came from colonies maintained at the National Institute of Animal Health, Tsukuba, Japan, were followed as above during feeding.

2. **Oviposition**

Fifty-five females of the bisexual race at various stages of feeding were removed from cattle on the Kujū highland and transferred to a dark incubator kept at 25°C and 95% RH after measurements of their body weight. The total number of deposited eggs was counted and the number of eggs laid per mg of body weight was calculated for each female which oviposited.

In order to examine oviposition of females fed without males, 7, 9 and 9 females were removed from the rabbit on the 6th, 9th and 12th day in the feeding stage, respectively, and then were treated as mentioned above.

RESULTS

1. **Feeding pattern in the female of the bisexual race**

1) *Experiment 1 (Fig. 1)*

In the unfed stage, the mean volume (±SD, N = 20) of the females was 1.1 ± 0.2 mm^3 (1.6 ± 0.2 mg). On the 4th day in the feeding stage, the mean volume of the females (12.2f9.0 mm^3, N = 15) increased 11 times as large as that in the unfed stage. On the 5th day, 1 female died, 2 females enlarged rapidly and completed engorgement and detachment, and the remaining 12 females gained in a little volume (13.3f4.3 mm^3). Subsequently, 2, 5 and 5 females detached on the 6th, 7th and 8th day, respectively ; the mean engorged body volume of the above 14 females reached 211.7f33.3 mm^3 (266.3 ± 35.4 mg), being 192 times larger than that in the unfed stage, and the duration of feeding averaged 6.9 ± 1.1 days.

The rate of body volume increase per day in the females (Table 1) increased gradually up to the 4th day. After that, although the rate increased remarkably in the females which were fated to engorge and detach rapidly, it was low in the remaining females.

2) *Experiment 2 (Fig. 2)*

In the unfed stage, the volume of the females was 1.0 ± 0.1 mm^3 (N = 10). Four females died before attachment, and the remaining 6 females were follwed up ; out of them, 3 females engorged and detached each on the 5th, 6th and 8th day in the feeding stage, 2 on the 10th day, and 1 on the 11th day. The volume of 4 females which were found with a male attached to their ventral surface was 5.0, 12.5, 26.6 and 39.1 mm^3 at the time of mating. Subsequently the 4 females rapidly engorged and detached within

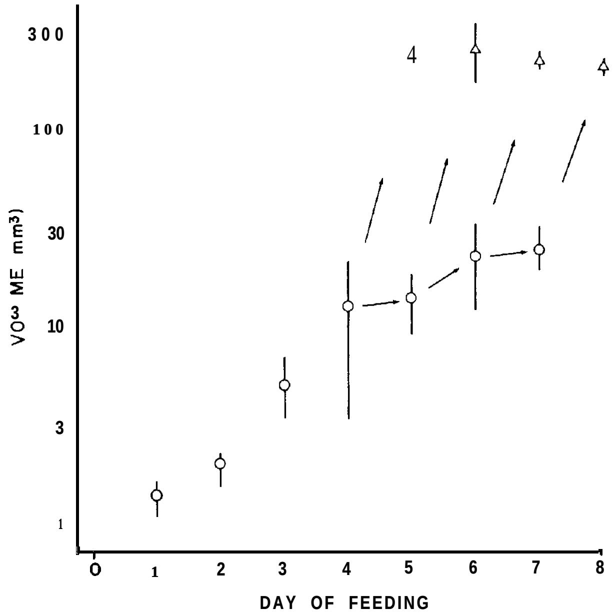

Fig. 1. Changes in the volume (log-transformed values) of the, bisexual female of *Haemaphysalis longicornis* in the experiment 1 (N ; females 20, males 20). Open square, circles and triangles indicate the mean volume of the females in the unfed, feeding and detached stages, respectively : vertical lines represent standard deviations. Arrows show the course of feeding.

Table 1. Daily changes in the rate of body volume increase in the females of the bisexual and parthenogenetic race of *Haemaphysalis longicornis* from commencement of feeding to engorgement and detachment.

	Body volume increase per day (%)							
	Days after attachement							
	O - l	l - 2	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8
Bisexual (Experiment 1)								
Feeding	25.0→	43.0→	152.8→	150.4→	9.1→	60.8→	9 . 1	–
Detached	–		–	–	↘ 1768.9	↘ 1704.2	↘ 876.2	↘ 737.1
Parthenogenetic								
Feeding	7.9→	6.0→	68.1→	125.3→	265.3→	178.0	–	
Detached			–		–	↘ 833.0’	243.5	

Arrows indicate the course of feeding.

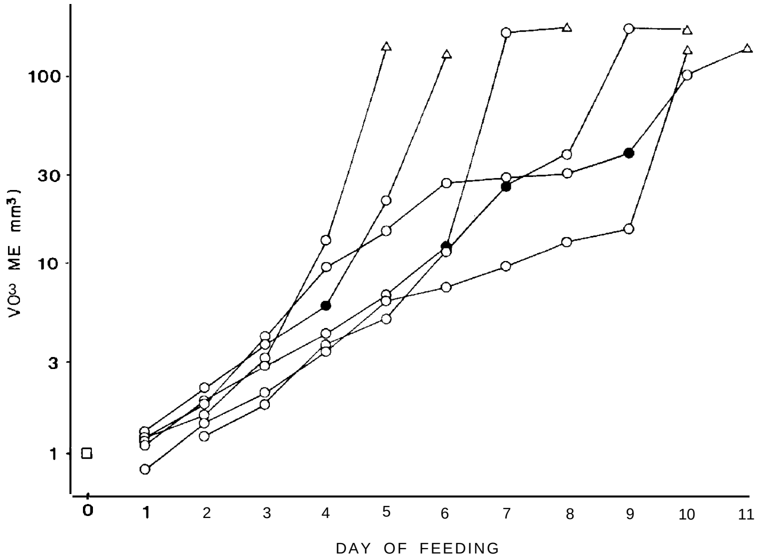

Fig. 2. Changes in the volume (log-transformed values) of the bisexual female of *Haemaphysalis longicornis* in the experiment 2 (N ; females 10, male 1). Because 4 females died before their attachment, the data on the remaining 6 females are presented. Open square shows the mean volume of unfed females. Open circles indicate the volume of fed females and closed ones represent the volume when the females are found with a male attached to their ventral surfaces. Open triangles give the volume of detached females.

additional **2** days later. The volume of the above 6 engorged females was 153.1f20.9 mm^3 (193.8 ± 38.6 mg).

3) *Experiment* 3 (Fig 3)

The mean volume of the females in the unfed stage was 1.0 ± 0.2 mm^3 (N = 10). On the 5th day in the feeding stage, 2 females dies, and the volume of the remaining 8 females (3.9f0.5 mm^3) increased 4 times over that in the unfed stage. On the 11th day, 2 females died, and the surviving 6 females remained attached to the host, gaining in volume (17.4±10.8 mm^3) 17 times over that in the unfed stage ; no female engorged.

2. **Feeding pattern in the female of the parthenogenetic race**

As shown in Fig. 4, the mean volume of the 11 females in the unfed stage was 1.4±0.2 mm^3 (2.0±0.2 mg). On the 5th day in the feeding stage, 1 female died, and the surviving 10 females increased the volume (22.1±20.3 mm^3) 16 times larger than that in the unfed stage. On the 6th day, 1 died, 4 engorged and detached and 5 continued feeding. On the 7th day, 2 died and 3 detached after engorgement. The volume and the duration of feeding in the above 7 engorged females averaged 208.7f29.6 mm^3 (249.1 ±38.3 mg) and 6.4 ± 0.5 days, respectively.

The rate of body volume increase (Table 1) tended to accelerate during the period from commencement of feeding to detachment, but the rates on the 0-1st and 1st-2nd day were very low and the rate on the 5th-6th day was a little inferior to that on the 4th-5th day.

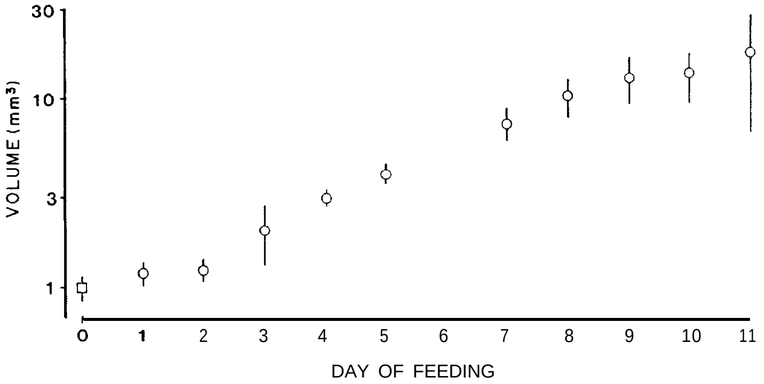

Fig. 3. Changes in the volume (log-transformed values) of the bisexual female of *Haemaphysalis longicornis* in the experiment 3 (N ; females 10, male 0). Open square and circles indicate the mean volume of unfed and fed females, respectively. Vertical lines represent standard deviations.

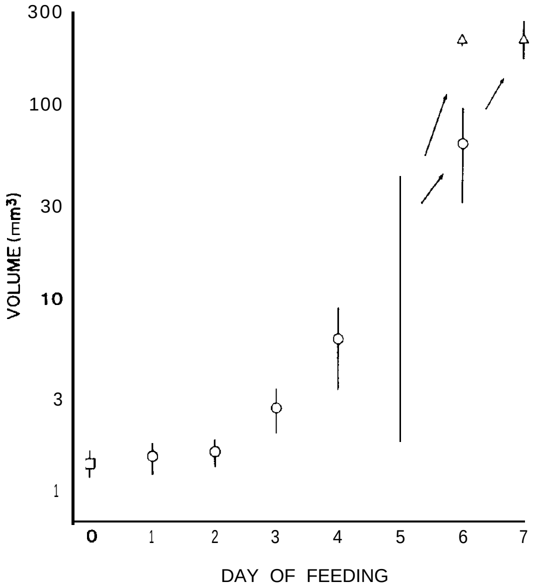

Fig. 4. Changes in the volume (log-transformed values) of the parthenogenetic female of ***Haemaphysalis*** *longicornis* from commencement of feeding to detachment (N ; females 11). Open square, circles and triangles indicate the mean volume of unfed, fed and detached females, respectively : vertical lines represent standard deviations. Arrows show the course of feeding.

3. Oviposition

1) Oviposition ability of females removed from cattle

The number of eggs laid by 55 females of the bisexual race was plotted against log-transformed values of the fed weight (Fig. 5), where the lowest weight of a female was 2.1 mg and the highest was 303.0 mg. Twenty-one females weighing 27.6 mg and less failed to lay eggs, but the other 34 females oviposited (preoviposition period, 6.5±

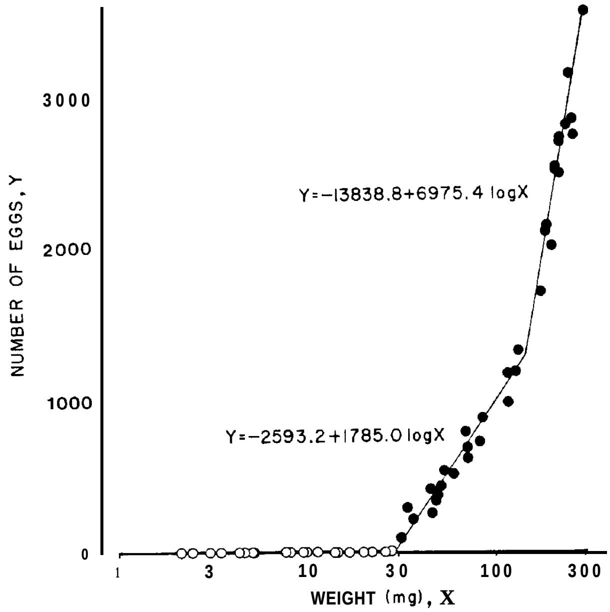

Fig. 5. Relationships between the total number of deposited eggs and the postfed body weight (log-transformed values) of the bisexual female of ***Haemaphysalis longicornis***. Open and closed circles indicate oviposition failure and success of partially engorged females, respectively. The regression lines are expressed by two equations joining at the weight of 146.8 mg, from which the theoretical minimum weight for oviposition (X intercept) is calculated at 28.4 mg.

Table 2. Egg production efficiency according to both the-body weight and the number of deposited eggs per mg of the body weight in the females of the bisexual race of *Haemaphysalis longicornis*.

Body weight (mg)	Number of deposited eggs per mg of body weight	Egg production efficiency
Feeding		
less than 28.4	0	Non-oviposition
28.4 – 146.8	8.4 ± 1.9	Partial oviposition
146.8 – 303.0	11.3 ± 0.9	Almost complete oviposition
Engorged and detached*		
142 – 235	12.5 ± 0.8	Complete oviposition

*Yano *et al.* (1985)

0.8 days ; oviposition period, 17.4k3.4 days) and egg numbers increased with gaining weights. A positive linear correlation existed between the total number of deposited eggs and the weight of the females ; however, the regression lines were expressed by two equations, joining at 146.8 mg according to the method of Takai and Akiyoshi (1981). The number of deposited eggs per mg of the body weight averaged 8.4± 1.9 (± SD, N = 20) in the females weighing less than 146.8 mg, and 11.3±0.9 (N = *14)* in the females weighing more than 146.8 mg (Table 2). Both the numbers were significantly different from each other ($P<0.01$). The theoretical minimum body weight for oviposition was calculated at 28.4 mg using the regression line

2) *Oviposition ability of females fed without mules*

The mean body weight of the females which were removed from the rabbit on the 6th day in the feeding stage (29.4±5.9 mg, N = 7) was significantly lighter ($P < 0.05$) than that on the 9th day (43.3±11.8 mg, N=9) and that on the 12th day (45.3±17.5 mg, N= 9). The mean body weight of 25 females used for the experiment was 40.2±14.3 mg. Out of them, 13 females averaging 36.0± 16.9 mg failed to oviposit. The remaining 12 females (3 on the 6th day, 5 on the 9th day and 4 on the 12th day) oviposited, whose mean body weight was 44.7± 9.7 mg. The preoviposition period, oviposition period and the number of deposited eggs per mg of the body weight did not significantly differ among the above three feeding stages, being 10.4±2.8 days, 11.8±4.5 days and 4.6f2.1 eggs, respectively. There was no positive correlation between the total number of deposited eggs and the fed body weight. Parthenogenesis did not occur in this case.

DISCUSSION

In *H. longicornis*, differences in body weight, number of eggs laid (Kitaoka, 1961) and number of chromosomes (Oliver *et al.*, 1973) between the bisexual and parthenogenetic races have been reported. The present study revealed the following difference in the feeding pattern between both races. The bisexual female gradually increased the feeding rate and reached an almost constant volume up to the 4th day in the feeding stage, and subsequently it slowly ingested a blood meal ; mean while once the female mated, it engorged rapidly and detached. The parthenogenetic female ingested a blood meal slower than did the bisexual female up to the 4th day, but subsequently had a rapidly increasing feeding rate. In both races, however, the mean engorged body weight (266.3 mg for the bisexual race, 249.1 mg for the parthenogenetic race) and the mean duration of feeding (6.9 days for the former, 6.4 days for the latter) were not significantly different from each other ($P > 0.05$).

Mating in ixodid ticks (Metastriata) is indispensable for rapid and complete engorgement by females (Oliver, 1974 ; Diehl *et al.*, 1982). In this connection, the relative engorgement state (RES) ratio ($W^{1/3}/SI^{1/2}$; W, weight ; SI, scutal index= scutal length x width) has been regarded as an index to the quantification of engorgement. In feeding by *Dermacentor variabilis* females, the RES ratio in unmated females which were fed for 11 days does not attain that in the mated, fully engorged and dropped ones (Obenchain *et al., 1980).* The feeding experiments in the females of the bisexual race *H. longicornis* proved that the presence of males was necessary for complete engorgement and detachment. Provided that mating took place when a female and a male faced each other, it seemed to occur at the earliest on 3rd-4th day after female attachment, when the female volume was 10 mm^3 and over. A male of this tick was able to mate with at least 6 females.

It has been said that minimum engorgement weight required for ixodid ticks to oviposit is about 10% of their normal engorgement weight (Balashov, 1972). In the bisexual *H.* Zongicornis, the minimum weight of 28.4 mg for oviposition corresponded to 10.4% of the mean engorgement weight. On the other hand, the proportion of the oviposition threshold engorgement weight to the unfed weight seems to vary with species : for instance, about 10 and 11.9 times in *D. variabilis* and *Rhipicephalus* ***sanguineus,*** respectively (Diehl et ***al.,*** 1982), 11.5 in ***Ixodes*** *ricinus*, ***5.2*** in *Dermacentor pictus*, ***9.1*** in *Rhipicephalus turanicus*, ***6.8*** in ***Hyalomma*** *asiaticum* and 6.5 in *Hyalomma anatolicum* (Balashov, 1972). In ***H. Zongicornis,*** the proportion was 17.8 times. Such differences may reflect the disparity in the efficiency of ixodid egg production.

A linear relationship exists between the weight of fully engorged ticks and the number of deposited eggs, and the efficiency of egg production has been expressed as the number of deposited eggs per mg of female fully engorged weight (Diehl et ***al.,*** 1982). In accordance with the concept of Kitaoka and Yajima (1958), the egg production efficiency in the feeding females of the bisexual race of ***H. Zongicornis*** was classified by the number of deposited eggs per mg of body weight (Table 2). In relation to this, complete oviposition (12.5± 0.8 eggs, N = 10) occurs in the detached females (142-235 mg) (Yano et al., 1985).

In the absence of mating, some incompletely engorged females of metastriate ixodids may lay a small batch of eggs ; such behaviour is exceptional among non-parthenogenetic ticks (Diehl ***et*** *al.*, 1982). For instance, only 1 out of 10 females of *Amblyomma americanum* fed without males oviposits a few eggs (Brown and Stenner, 1982). The females of *Boophilus annulatus* and ***B.*** *microplus* confined without males have normal repletion weights and lay healthy-appearing egg masses, but eggs produce few larvae (hatch ratio < 0.01%), meaning a low degree of parthenogenesis (Thompson ***et al.,*** 1980). As for the natural mating and artificial stimulations, it has been stated that the stimulus for rapid engorgement of female ***D.*** *variavilis* involves receiving the spermatophore and/or its contents (Pappas and Oliver, 1972), and various mechanical and chemical treatments in ***A.*** *americanum* provide stimulations for further feeding and oocyte growth maximally to the stage 3 of Balashov (1972) (Oliver ***et al., 1975).***

In ***H. Zongicornis,*** the Weonseong strain of this species from Korea has been proved bisexual, because no larva emerged from the eggs produced by the females fed without males: the mean fed body weight of 12 females examined is 71.84 mg; the mean preoviposition period, ovipositon period and the number of deposited eggs per mg of the body weight at 25°C and 85.0% RH are 10.83 days, 11.16 days and 7.8 eggs, respectively (Kang, 1981b). Also in the present study, 48 per cent females (12/25) fed without males oviposited : our results for the above two periods coincided with those of Kang (1981b). Accordingly, the female ticks of the bisexual race of ***H. Zongicornis*** appear not always to need mating for egg production and have an ability to oviposit eggs by feeding stimuli alone, suggesting that such an ability might have become a factor in the establishment of parthenogenesis. In the absence of mating, however, imcompletely engorged females were inferior to normally mated and engorged females in the oviposition performance : the preoviposition period (10.4 days on an average) was prolonged, the oviposition period (11.8 days) was shortened and the number of deposited eggs per mg of body weight (4.6 eggs) decreased, compared with 6.0 days, 23.3 days and 11.8 eggs, respectively in the latter females at 25°C and -100% RH (Yano et ***al.***, 1987).

In conclusion, the feeding pattern in the female *H. longicornis* varies between the bisexual and parthenogenetic races. The bisexual pattern is markedly influenced by the presence or absence of mating and its timing, and oviposition occurs at the minimum weight of ***28.4*** mg. Female ticks of the bisexual race do not always need mating for oviposition, and oocyte growth and egg production are under the control of the quantity of blood meal.

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