

STUDIES ON TICKS OF VETERINARY IMPORTANCE IN NIGERIA: INTRINSIC FACTORS INFLUENCING OVIPOSITION AND EGG-HATCH OF *AMBLYOMMA VARIEGATUM* UNDER NATURAL CONDITIONS

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Abstract. During the peak of rains of 1983, 1984 and 1985 in the forest zone of Nigeria, female *Amblyomma variegatum* engorged to various weights were subjected to different experiments for the purpose of observing the intrinsic factors which influence oviposition and egg-hatch under natural conditions. Two types of oviposition patterns were observed. New terms were introduced to quantify the relationships between the daily weight loss and daily number of eggs oviposited by a tick. These terms are "actual mass", "convertible blood mass", "oviposition efficiency" and "mass conversion rate". A major advantage of adopting the "oviposition efficiency" and "mass conversion rate" is that they relate directly to the measure of the metabolic activity utilized by the tick for the process of oviposition. The entity "convertible blood mass" also enables recognition of individual capability in the utilization of blood mass for oviposition. Investigation on the relationship of weight of eggs with sequence of oviposition showed that eggs were heavier when few eggs were laid than when numerous eggs were oviposited. The heaviest eggs were laid towards the end of oviposition. Two types of relationship were found to exist between the sequence of oviposition and the eclosion period of eggs. Adult *A. variegatum* engorged to more than 2.49 x were affected by immersion in water for longer than 7 days. Such ticks died without ovipositing and the water in which they were submerged became dark-red. Eggs immersed in water for periods ranging from 1-7 days hatched in about the same number of days as control eggs and their viability in terms of percent-hatch was not affected.

Research on the egg-stage of ticks has been generally neglected. Studies on this stage are however desirable because it is the only immobile stage in the tick's life history and the numbers laid by the engorged female tick and the proportion which hatches are crucial for the propagation of the ticks' generation. Most of the previous works were conducted in the laboratory and directed towards the oviposition pattern in relation to daily weight loss of the ovipositing tick (Drummond et al. 1971, Balashov 1972, Bassal and Hefnawy 1972, Londt 1977, Dipeolu and Ogunji 1980). There are fewer works on tick oviposition conducted under natural conditions (Branagan 1973, Dipeolu 1983a) and they have shown that extrinsic factors such as relative humidity, temperature and moisture influence the oviposition pattern of engorged ticks. Earlier works in Nigeria (Dipeolu 1983b, 1984) have also shown that the season of the year and the field environment in which the ticks oviposit are important extrinsic factors as ticks were found to produce greater numbers of eggs during the peak and end of rains and when placed in the shade. Of all these extrinsic factors, the effect of excessive moisture on oviposition and egg-hatch is the least studied. Sutherst (1971) suggested that the effect of heavy rains is the silting up of mass of eggs. Amoo (1984) found that the vitality of eggs of *Boophilus decoloratus* and *B. geigyi* flooded with water for up to 48 hours was not affected and their engorged females laid eggs after flooding with water for 24 and 72 hours, respectively.

Apart from the widely-reported correlation between the state of engorgement and number of eggs laid, there is no other intrinsic factor which has been shown to influence oviposition. Furthermore, the correlation of weight of egg mass and the number of eggs contained in the mass have been a problem in experiments involving tick oviposition. Australian workers (Wagland 1975, Sutherst et al. 1979) for example, equated 0.1 g of eggs of *B. microplus* to about 1000 eggs without consideration of the sequence of oviposition of the egg mass and this procedure was adopted by Amoo (1984) for eggs of *B. decoloratus* and *B. geigyi*. In this paper, we report the intrinsic factors which influence the oviposition of engorged *A. variegatum* and we show the relationship between the weight of a batch of eggs, the sequence of its oviposition and the number of eggs in the batch.

MATERIALS AND METHODS

The experiments were conducted between July and October of 1983, 1984 and 1985. These months represent the periods of peak of rains (July and August) and end of rains (September and October) in the forest zone of Nigeria. These periods are characterized by oviposition of large numbers of eggs by engorged ticks under natural conditions (Dipeolu 1984).

Engorged *A. variegatum* were detached from cattle during slaughter at the Ibadan abattoir. In order to eliminate the effect of type of host blood, all ticks used on each occasion were obtained from only one head of cattle shortly before slaughter. The ticks were taken immediately to the laboratory; each one was weighed, coded and categorized into weight group and placed in a universal bottle. The bottles were taken to the shady site of a grazing field where they were kept and used for various experiments. This shady site has been described (Dipeolu 1983a) and it has been shown that ticks kept in the shade perform better in terms of number of eggs laid during oviposition, survival of immature stages and duration of life cycle (Dipeolu 1983a, b, 1984).

The first experiment was devoted to ascertaining the various oviposition patterns of engorged *A. variegatum* that may exist under the field condition. Eggs laid daily by ticks of different weight groups were collected at 08:00 hours daily and counted under a dissecting microscope, counting being facilitated by the addition of drops of xylene (Dipeolu and Ogunji 1980). This was done until oviposition by each tick ceased although such ticks were not discarded until 7 days after the last day of oviposition. Ten ticks were used for each weight group. In the second experiment, ticks of various weight groups were weighed daily, the day of arrival in the shady site being regarded as day 0. Weighing was conducted at 08:00 hours daily just as the oviposited eggs were being removed. The eggs were subsequently counted and recorded. Weighing of any experimental tick was terminated only after it has yielded approximately the same weight for seven consecutive days; such tick was regarded as dead. The "convertible blood mass" was obtained by subtracting the weight of tick on the last day of oviposition from its weight on day 0. The "oviposition efficiency" of a tick on any day was calculated from the formula:

$$\frac{\text{number of eggs laid on a day}}{\text{total number of eggs laid during oviposition}}$$

The "mass conversion rate" was calculated from the formula:

$$\frac{\text{weight loss of ticks per day}}{\text{total weight loss through oviposition}}$$

The "mass conversion efficiency" of a tick on a particular day was obtained from the formula:

$$\frac{\text{weight loss of tick on a day}}{\text{number of eggs oviposited on the day}}$$

Twenty ticks were used for each weight group.

In the third experiment, eggs laid every three days by ovipositing ticks of various weight groups (10 ticks per each weight group) were weighed and counted. This was undertaken throughout the oviposition period of each tick. The approximate weight of one egg in each egg-batch was obtained through the division of the weight of egg batch with the number of eggs in the batch. In the fourth experiment, eggs laid every three days by engorged ticks of various weight groups (10 ticks per each weight group) were weighed daily from the day of oviposition until the day of hatching started. The average weight of each developing egg in a batch was estimated as in the third experiment although

the number of eggs in the batch was obtained by counting the hatched larvae and the unhatched eggs. The aim was to determine the fluctuations of weight of developing eggs during embryonic development. As fifth experiment, the sequentially laid eggs of each ovipositing tick were pooled ever 3 days and the eclosion period as well as the hatching pattern of each pooled egg-batch recorded. Larvae were separated from unhatched eggs as described by Dipeolu (1982a).

The sixth experiment was devoted to the effect of flooding the eggs and engorged ticks with water and was conducted in phases. In the first phase, water was added to each engorged tick; contained in a universal bottle in the shade such that the ticks was submerged for periods ranging from 1 to 10 days. Control ticks which were not immersed in water were set up. The preoviposition and oviposition periods of the experimental ticks, the eclosion period of the eggs laid and the proportion of the eggs which hatched were recorded. In the second phase, eggs laid by ticks of various weight groups (10 ticks per each weight group) were put in universal bottles, kept in the shade and water was added such that the bottle was filled to the brim. The eggs were thus flooded with water for periods ranging from 1 to 7 days. Batches of eggs which were not flooded with water served as control. The eclosion period and the proportion of each egg-batch which hatched were recorded.

RESULTS

Though the experiments were undertaken during the peak and end of rains of 1983 to 1985, the results of each of the three years showed similarities. Fig. 1 shows the two types of oviposition patterns exhibited by engorged *A. variegatum* under natural conditions. Type 1 was observed in about 83% of experimental ticks and was characterized by an initial low oviposition and attainment of peak oviposition after a few days. Type 2 was observed in a few ticks (17%) and was characterized by early attainment of peak oviposition usually with the first sets of eggs.

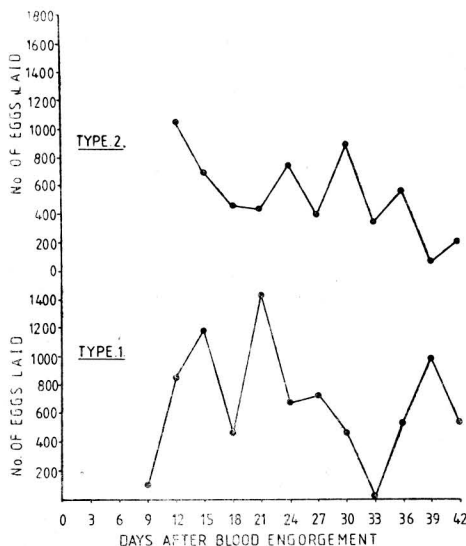


Fig. 1. Oviposition patterns exhibited by engorged *A. variegatum* under natural conditions.

Table 1 shows the relationship between the weight of engorged ticks (actual mass), the approximate weight lost during oviposition (convertible blood mass) and the number of eggs laid. At low engorgement weights of 0.5 to 1.99 g, the total number of eggs laid and the number of eggs per milligram of engorged blood increased while the quantity of blood utilized for oviposition of one egg decreased with increasing

Table 1. Relationships of actual mass, convertible blood mass and oviposition of *A. variegatum* under natural conditions

Weight group (g)	* Actual mass (g)	Convertible blood mass	Percent of actual mass	No. of eggs laid	Average No. of eggs/mg. of blood (mg)	Average quantity of blood per egg (mg)
0.5—0.99	0.64	0.27	42.72	294	1.07	0.94
	0.66	0.06	9.36	119	1.92	0.52
1—1.49	1.28	0.94	73.44	2,647	2.82	0.29
	1.28	0.88	68.94	3,033	3.42	0.26
1.5—1.99	1.65	1.16	70.21	4,056	3.49	0.29
	1.77	1.33	75.29	5,105	3.82	0.26
	1.94	1.37	70.82	5,322	3.87	0.26
	1.94	1.46	75.19	6,101	4.18	0.24
	1.98	1.52	76.92	6,011	3.95	0.25
		2.02	1.49	73.76	5,794	3.89
2—2.49	2.03	1.44	71.18	5,844	4.04	0.25
	2.11	1.43	67.82	6,974	4.86	0.21
	2.24	1.67	74.55	6,524	3.91	0.26
	2.45	1.71	69.80	7,046	4.12	0.24
	2.27	1.82	80.14	7,919	4.35	0.23
		2.55	1.89	74.47	6,158	3.24
2.5—2.99	2.68	1.96	73.08	7,465	3.80	0.26
	2.75	2.07	75.18	9,030	4.36	0.23
	2.79	2.13	76.59	8,397	3.92	0.29
	3.07	2.22	72.31	8,215	3.7	0.27
3—3.49	3.07	2.07	67.39	8,297	4.00	0.25
	3.04	2.14	70.40	8,528	3.99	0.52
	3.14	2.12	67.39	8,260	3.90	0.26
	3.32	2.35	70.31	7,932	3.40	0.29
		3.72	0.46	12.57	579	1.24
4	4.18	0.58	13.89	304	0.52	1.91

* Individual ticks whose data are presented were selected by random sampling from among experimental ticks. Number of ticks in each group is to the numbers detached from cattle

weight. At high engorgement weights of 2 g and above, there was variation among individual ticks in the total number of eggs produced and this was more pronounced among individual ticks within a weight group. Individual ticks with high oviposition were characterized by relatively higher number of eggs produced from 1 mg of blood and relatively lower quantity of blood utilized for the production of 1 egg.

Ticks heavier than 3.4 g oviposited small numbers of eggs. It was observed that about 20% and 5% of ticks heavier than 3.49 g and 4.0 g, respectively, laid eggs; in the less heavier ticks, all engorged ones normally oviposited.

Fig. 2 shows the relationship between oviposition efficiency and mass conversion rate. Although their increases and decreases coincided except in ticks heavier than 3.49 g, their peaks did not coincide except in ticks of low engorgement weights of 1—1.49 g. There was also no difference between the mass conversion rates of ovipositing and non-ovipositing ticks whose engorgement weights were higher than 3.49 g. Their mass conversion rates were often characterized by the absence of a peak for about 24 days post detachment (p.d) apart from the early peak of day 3. In addition, death was noticed in such ticks at about 55—60 days p.d. compared with the

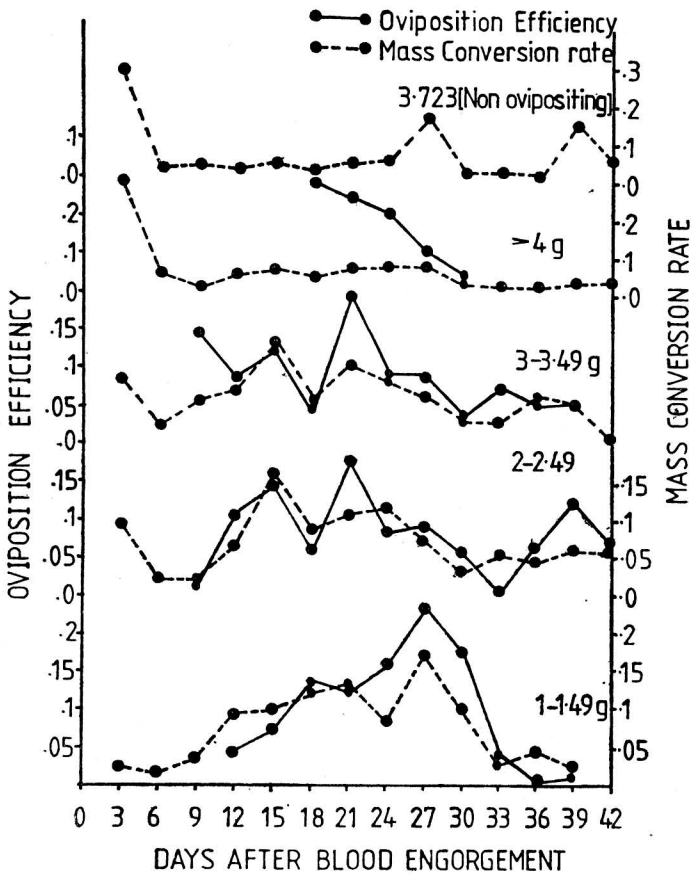


Fig. 2. Relationship between oviposition efficiency and mass conversion rate for engorged *A. variegatum*.

43—48 days of the less heavier ticks. Fig. 3 shows the daily mass conversion efficiency of three weight groups of *A. variegatum* until cessation of oviposition. After the initial peak at the onset of oviposition, the mass conversion efficiency of each weight group fluctuated until the end of oviposition when the second peak was reached. Fig. 4 shows the relationship between the number of eggs laid daily by an engorged *A. variegatum* and the approximate weight of one egg. Eggs were heavier when few eggs were laid than when numerous eggs were oviposited. The heaviest eggs were usually those laid towards the last days of oviposition. These observations were similar for ticks of all weight groups.

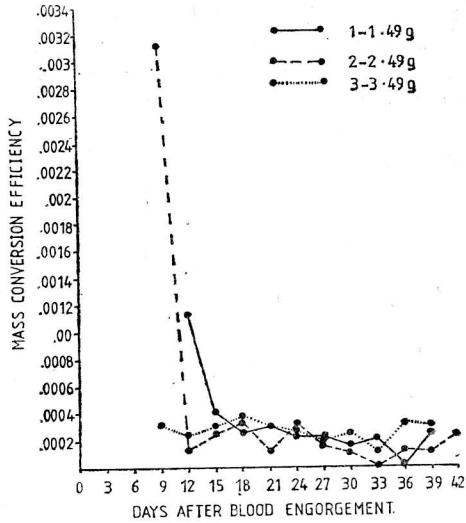


Fig. 3. Fluctuations of mass conversion efficiency during oviposition of *A. variegatum*.

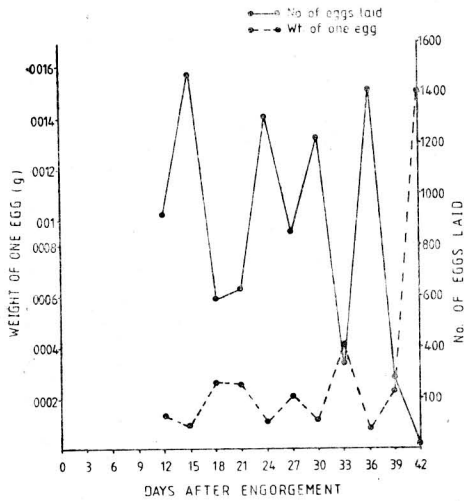


Fig. 4. Relationship between number of eggs laid daily by *A. variegatum* and approximate weight of one egg.

Table 2. Increase in weight of eggs of *A. variegatum* during phases of embryonic development

Phase of development (Dipeolu 1982b)	** Average increase in weight of an egg (mg)
1	No increase
2a	0.001 7 ± 0.000 016
2b and 2c	0.009 4 ± 0.000 024
3—7	0.007 5 ± 0.000 013

* Weight of individual eggs ranged from 0.15—1.4 mg with an average of $0.17 \pm 0.000 13$ mg.

** A total of 78,950 developing eggs weighed

Table 2 shows that eggs of *A. variegatum* increased in weight slightly during embryonic development. This increase in weight was highest in the phases 2b and 2c characterized by the appearance of a distinct plate at the anterior pole and assumption of crescent or canoe shape by the egg (Dipeolu 1982b).

Table 3 shows the relationship between the sequence of oviposition and the eclosion period of the oviposited eggs. Two types of relationships were observed in all the weight groups. The first type, which was predominant and found in 70—75% of all engorged ticks, was characterized by the later ovipositions having shorter eclosion periods than the earlier ovipositions. Decrease in eclosion period to below 50 days was observed with the eggs oviposited from the 30th day p.d. onwards. This group was also characterized by a late beginning of oviposition which did not start until after the 9th day p.d. The second type which was in fewer instances (25 to 30 % of engorged ticks) was characterized by the earlier ovipositions having the shorter eclosion period than the later ovipositions. This type was also characterized by an early onset of oviposition which started as early as 7 days p.d. The eclosion pattern of both types was similar (Table 4) with eclosion lasting 4—6 days and peak reached around the 2nd or 3rd day.

When adult engorged *A. variegatum* were submerged in water for periods ranging from 1 to 7 days, their preoviposition, oviposition and eclosion periods were unaffected. Although Table 5 represents the results for ticks immersed in water for 7 days, those of ticks immersed for periods ranging from 1 to 6 days were similar. When ticks which weighed over 2.49 g were immersed in water for longer than 7 days the water became dark red signifying the escape of the engorged blood through the cuticle into the water. Such ticks died without ovipositing any eggs when released from the water. Similar observations were made on ticks which weighed less than 2.49 g only after they have been submerged for a minimum of 9 days. As shown in Table 6, eggs immersed in water for periods ranging from 1 to 7 days hatched in about the same number of days as the control eggs and their viability in terms of percent-hatch was not affected. The results of eggs immersed in water were similar for any of the days 1 to 7; hence, only the results of immersion for 7 days are given as Table 6. It was however observed that egg masses were never fully submerged in water; usually only about one-quarter of each egg mass would submerge. Furthermore, flooding with water in the universal bottles was found to cause gradual slitting of some eggs from the egg mass. Such eggs usually sank to the bottom of water but they were observed to hatch at approximately the same time as the other eggs in the egg mass.

Table 3. Relationship between sequence of oviposition and eclosion period of eggs of *A. variegatum*

Sequence oviposition (Days)	+ Weight group of ticks				
	1—1.49 g	1.5—1.99 g	2—2.49 g	2.5—2.99 g	3—3.49 g
9 ^a b	— *43	— 45	— 44—47	— —	— —
12 ^a b	54—55 48	55—56 47	54 47—49 (48±0.2)	55 48	54—55 47—48
15 ^a b	55—56 56	53—57 **(54±1.2) 54	54—56 (55±0.9) 50—60 (56±2.1)	54—56 (54±0.9) 52	55—56 54—55
18 ^a b	57 56	54:57 (55±0.8) 55	53—56 (5.4±1.2) 54—56 (55±0.7)	54—57 (55±1.1) 55	53—56 (54±0.8) 54
21 ^a b	55 55	55—56 55—56	54—55 54—55	55 54—55	54—55 54
24 ^a b	54 54	53—54 53—54	53—54 53—56 (54±0.8)	54 54	53 53
27 ^a b	52 53	50—52 (51±0.2) 52	50—52 (51±0.2) 54—55	51—52 53	51 53
30 ^a b	48—49 49	48—49 49	48—49 51	48—49 51	48—49 52
33 ^a b	49 49	49 49	49—50 48—49	49 50	49 51
36 ^a b	48 —	47—48 48	47—48 49	46—48 (47±0.5) 49	47—48 49—50
39 ^a b	47	47—48	46—47 48	44—46 (45±0.7) 48—49	46 49
42 ^a b	47	47—48 48	46—47	44—46 (45±0.7) 48—49	46 49
45 ^a b		43	41—43 (41±0.3)	42	40—42 (41±0.4)

a = 1st type, b = 2nd type, * = eclosion period in days, ** = standard deviation given only when variation of eclosion period exceeded one day, + = observations were made from 20 ticks of each weight group

Table 4. Eclosion pattern in eggs of *Amblyomma variegatum*, which showed different eclosion periods

Type	Length of eclosion (Days)	Average percentage of eggs which hatched on different days					
		Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
1	4—5 *(20,000)	16	29	35	9	7	4
2	4—6 (12,500)	18	32	31	10	5	4

* Figures in brackets indicate the numbers of eggs from which observations were made.

Table 5. Effect of submerging adult engorged *A. variegatum* in water for 7 days

Tick weight group (g)	Preoviposition period (Days)		Oviposition period (Days)		Eclosion period of eggs (Days)		Percent hatch of eggs	
	a	b	a	b	a	b	a	b
* 1—1.49	12	11	30	31	52	94	85	92
1.5—1.99	11	11	32	43	49	51	92	89
2—2.49	9	10	30	33	51	47	95	91
2.5—2.99	11	9	36	31	48	49	96	93
3—3.49	10	9	34	30	49	51	89	91

a = control ticks (not immersed in water), b = experimental ticks

* = 10 ticks observed for each experimental group with a corresponding 10 ticks for control experiment in each weight group

Table 6. Effect of submerging eggs of *A. variegatum* in water for 7 days

Tick weight group (g)	Eclosion period of eggs (Days)		Percent hatch	
	a	b	a	b
* 1—1.49	53	50	89	91
1.5—1.99	51	51	86	89
2—2.49	49	50	92	88
2.49—2.99	32	49	96	91
3—3.49	50	52	92	91

a = control eggs (not immersed in water), b = experimental eggs

* = observations made from eggs laid by 10 ticks in each weight group and 10 ticks for control groups of each weight group

DISCUSSION

Compared with earlier observations (Dipeolu and Ogunji 1980, Dipeolu 1983a, 1984) the number of eggs laid by *A. variegatum* under natural conditions is less than the number laid under laboratory conditions where temperature and relative humidity were regulated. Furthermore, the two types of oviposition pattern recognized in natural conditions were also observed under the laboratory condition although their relative proportion was not studied (Dipeolu and Ogunji 1980). It was customary for previous workers (Drummond et al. 1971, Balashov 1972, Bassal and Hefnawy 1972, Londt 1977, Knight et al. 1978) to relate the number of eggs laid daily to the daily loss in weight of the ovipositing tick. Dipeolu and Ogunji (1980) and Dipeolu (1983c) showed that there is statistical correlation between corresponding daily increases or decreases in number of eggs laid and daily weight losses of ticks. This correlation suggests that the number of eggs laid per day is proportional to the metabolic rate of ovipositing tick and assumes erroneously that metabolic activity of an ovipositing tick is utilized solely for oviposition at the exclusion of other essential functions such as respiration and excretion. It appears that our present method of relating daily oviposition and weight loss to their totals in form of oviposition efficiency and mass conversion rate has corrected this error. Although on some days corresponding increases and decreases in the number of eggs laid and loss of weight of tick occurred, there were no statistical correlations. There were also some days in which increase in metabolic activity resulted in the decrease of number of eggs laid and vice-versa. This is an indication that oviposition efficiency and mass conversion rate relate directly to the measure of metabolic rates of the tick utilized for the process of oviposition without including the rates for other essential physiological functions of the tick.

The introduction of the entity "convertible blood mass" has led to the recognition of individual capability in the utilization of blood mass for oviposition. Our results showed that the actual mass of the tick is important in determining the range of number of eggs laid. This work also demonstrated the importance of the value of convertible blood mass in that in many ticks belonging to the same weight group, the number of eggs laid tends to increase with the increase in value of the convertible blood mass. As noticed in the results, however, the ability of the tick to utilize the convertible blood mass at its disposal to produce larger or smaller number of eggs resides in the individual tick. This ability, which is also the same as mass conversion rate of the tick, is low per day in ticks with high oviposition efficiency and high per day in ticks of low oviposition efficiency. We are now looking into the possibility of this individual ability being hereditary, in which case results of cross-mating of ticks with high and low oviposition efficiencies shall be of interest in terms of application to tick control. We do not as of now understand why the initial mass conversion efficiency of the intermediate weight groups is very high. Investigation on this aspect is continuing in our laboratory.

The fact that ticks engorged to about 3.5 g laid only a few eggs or failed to lay eggs is an indication that the elastic limit of the cuticle of engorging female *A. variegatum* is around that weight. Dipeolu and Ogunji (1980) have observed that adult females of the tick which engorged up to 4 g either died before ovipositing or after ovipositing a few eggs. Dipeolu (1984) showed that during engorgement of a tick, extension of cuticles takes place anteriorly, posteriorly and laterally and his results indicated that there is an elastic limit for the cuticle of each tick species above which an engorged tick either dies or oviposits only a few eggs. This elastic

limit was shown to be reached for *A. variegatum* when the engorgement weight of 3.5—4 g is reached. Our present work confirmed that observation.

One of the implications of our results is that in experiments dealing with oviposition of ticks and eclosion of their eggs, the sequence of oviposition and the number of eggs in a batch should be considered. These results also showed that the approximate weight of each egg varies depending on the sequence of its oviposition and the number of eggs in the batch. It may therefore be erroneous to ascribe the same number of eggs to the same weight of eggs laid on different days. Work is therefore going on in our laboratory to produce reference data on the average weight of each egg of *A. variegatum* in relation to the sequence of oviposition and weight of the batch.

In previous investigations, Dipeolu (1982a, 1983c) reported that the eclosion period of eggs of later ovipositions of *A. variegatum* was shorter than that of the earlier ones and suggested that intra-uterine development might have taken place in the former. Amoo et al. (1984) made similar observations on the oviposited eggs of *Boophilus decoloratus* and *B. geigy* and suggested that the process of formative embryogenesis in the eggs of early ovipositions is a gradual one whereas that of eggs of the later ovipositions is faster. They attributed the difference in the speed of formative embryogenesis to be one of the causes of their observation of decreased viability of larvae which hatched from eggs of later ovipositions. It is however to be noted that in the present investigations, the eclosion period of the earlier ovipositions of a small group of ticks were found to be shorter than the later ones. It can therefore be reasoned that intra-uterine development is not restricted to later ovipositions only. In the present investigation, ticks oviposited eggs in which the later ovipositions either have shorter or longer eclosion periods than the earlier ovipositions, the former situation being predominant. It appears therefore that the ability to lay any of these two types of eggs is inherent in the individual female tick.

It is apparent from these results that excessive water is not inimical to the viability of engorged adults and eggs of *A. variegatum* if they are not subjected to longer than 7 days. From the practical point of view, it is rare to find a grazing field in any ecological zone of Nigeria which will be water-logged continuously for up to 7 days as a result of a heavy rainfall. This tolerance of *A. variegatum* to high moisture is however in sharp contrast to *B. geigy* and *B. decoloratus* which were found (Amoo 1984) to be sensitive to excessive moisture. In his work in the forest zone of Nigeria, Amoo (1984) showed that engorged females of *B. decoloratus* and *B. geigy* failed to lay eggs after flooding with water for longer than 24 and 72 hours, respectively, while the eggs of both species immersed in water for longer than 48 hours failed to hatch. The tolerance of excessive moisture by adult and eggs of *A. variegatum* for up to 7 days without any adverse effect suggests that this species can survive the prolonged heavy rainfall of the forest and savanna zones of Nigeria and explains why it is more abundant than any other tick in these zones of the country (Dipeolu 1975).

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