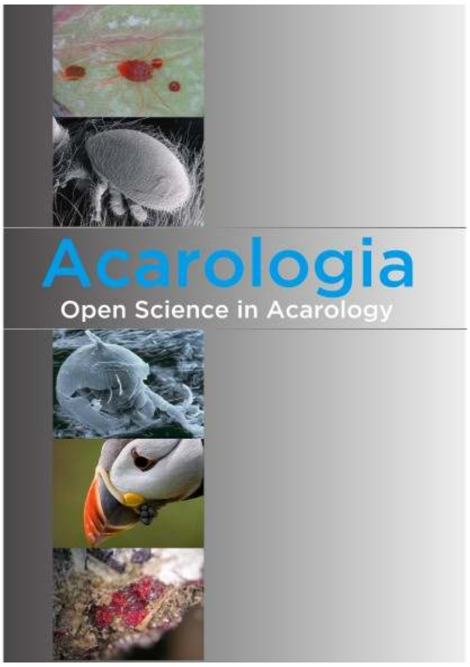

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OVIPOSITION OF *BOOPHILUS MICROPLUS* (CANESTRINI) (ACARIDA : IXODIDAE)
I. INFLUENCE OF TICK SIZE ON EGG PRODUCTION

BY

GORDON F. BENNETT [1]

RÉSUMÉ

La production d'œufs par les femelles de *Boophilus microplus* (Canestrini) de tailles différentes est linéaire. Les petites femelles ont une production inférieure à celles dont le poids est optimal (de 160 à 300 mg.) La durée de la période d'oviposition varie avec la température et présente un pic au début du cycle. Les œufs pondus au début et à la fin de la période d'oviposition (représentant 10 % du total) sont plus longs à éclore et ne sont pas aussi viables que les autres. La longueur et la largeur des œufs ne varie pas sensiblement au cours de la période de ponte, mais leur poids diminue vers la fin du cycle.

ABSTRACT

Egg production by *Boophilus microplus* (Canestrini) of different sizes has been shown to be linear; small ticks were found to be less efficient in producing eggs than ticks in the optimal weight range of 160 to 300 mg. The duration of the oviposition period varied with temperature, the peak occurring early in the cycle. Eggs laid at the beginning and end of oviposition (representing 10 % of the total) required a longer period until eclosion and were not as viable as eggs laid during the peak. Length and breadth of the eggs did not vary markedly throughout oviposition but the weight decreased towards the end of the cycle.

INTRODUCTION

The free-living portion of the life cycle of the cattle tick, *Boophilus microplus*, is acted upon by a number of unavoidable climatic factors. The effect of some of these factors has been reported by a number of workers (LEGG, 1930; WILKINSON and WILSON, 1959; HARLEY, 1966; McCULLOCH and LEWIS, 1968) and summarized by WILKINSON (1970). With the exception of HITCHCOCK'S (1955) and KITAOKA and YAJIMA'S (1958) publications, few detailed studies have been made of the oviposition of *B. microplus* under controlled laboratory conditions. Such studies provide basic information essential to the interpretation of field experiments.

It is generally conceded that large *B. microplus* lay more eggs than do small individuals. KITAOKA and YAJIMA (1958), working with *B. caudatus* (= *B. microplus*), demonstrated a linear relationship between the weight of the engorged female and the number of eggs laid. However,

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since the Japanese and Queensland populations of *B. microplus* are undoubtedly genetically isolated, Kitaoka and Yajima's work was repeated, using Queensland material.

On the basis of the studies of HITCHCOCK (1955) and KITAOKA and YAJIMA (1958), it could be concluded that all ticks, regardless of size, followed a similar pattern of both pattern and efficiency of oviposition when held at the same temperature. However, preliminary observations suggested that small ticks followed a different pattern and this aspect was further investigated. In addition, data on the dimensions, weight, prehatch period and viability of the eggs laid on each day of the oviposition cycle are presented. HITCHCOCK (1955) indicated two peaks of egg-laying and Tatchell (pers. comm.) concurred. These studies, using groups rather than individual ticks, did not support these findings, and the matter was studied in greater depth.

MATERIALS AND METHODS

Ticks of the acaracide-susceptible Yeerongpilly reference strain (Y strain) were used throughout as the basis of this study. The ticks were obtained each morning from a variety of susceptible and resistant British and Zebu breeds of cattle. The majority of the ticks engorged and dropped from the host in the early hours of the morning (WHARTON and UTECH, 1968), probably 6-8 hours before use in an experiment. All ticks were used individually or in groups of 50 or more and were selected from ticks in the weight range of 175-250 mg. Specific techniques are cited, where appropriate, in text.

RESULTS AND DISCUSSION

A. General Pattern of Oviposition

(i) *Pattern at 85°F.*

In this study, essentially the same approach as that used by KITAOKA and YAJIMA (1958) was employed, but the weight of eggs, rather than the number, was the basis of comparison. The weight of eggs laid per day was expressed as the accumulated percentage of the total weight of eggs produced. In this study, three groups of 50 ticks were held at 85°F. and as the results for the three groups were closely similar, the data was pooled and the curves (Fig. 1) obtained. From this oviposition curve it can be seen that the majority of eggs are laid during the early portion of the cycle, peak egg-laying occurring on the fourth and fifth day following engorgement. The accumulated percentage curve shows that 50 % of the eggs were laid by day 5 and 95 % by day 10 ; oviposition was completed by day 16.

The results of HITCHCOCK (1955) indicated that some ticks have two peaks of egg-laying ; Tatchell (pers. comm.) concurs. KITAOKA and YAJIMA (1958) indicate two peaks of oxygen consumption and Cherry (pers. comm.) found two periods of increased wax deposition on the cuticle of ovipositing ticks. In the face of this evidence, the results (Fig. 1) appear anomalous. Possibly, by using groups of 50 or more ticks, the performance of the individual was masked.

This possibility was further studied by weighing the eggs laid each day by 57 individual ticks, held at 80°F., the same temperature that HITCHCOCK (1955) reported two peaks of oviposition. The results of this study (Table I) indicated that only 10 individuals (18 %) of the group showed two or more peaks of oviposition. The other individuals laid eggs in a pattern similar to that illustrated (Fig. 1). On the basis of these results there is no indication that a two-peak oviposition cycle is of normal occurrence for *B. microplus*, but it can happen in some individuals.

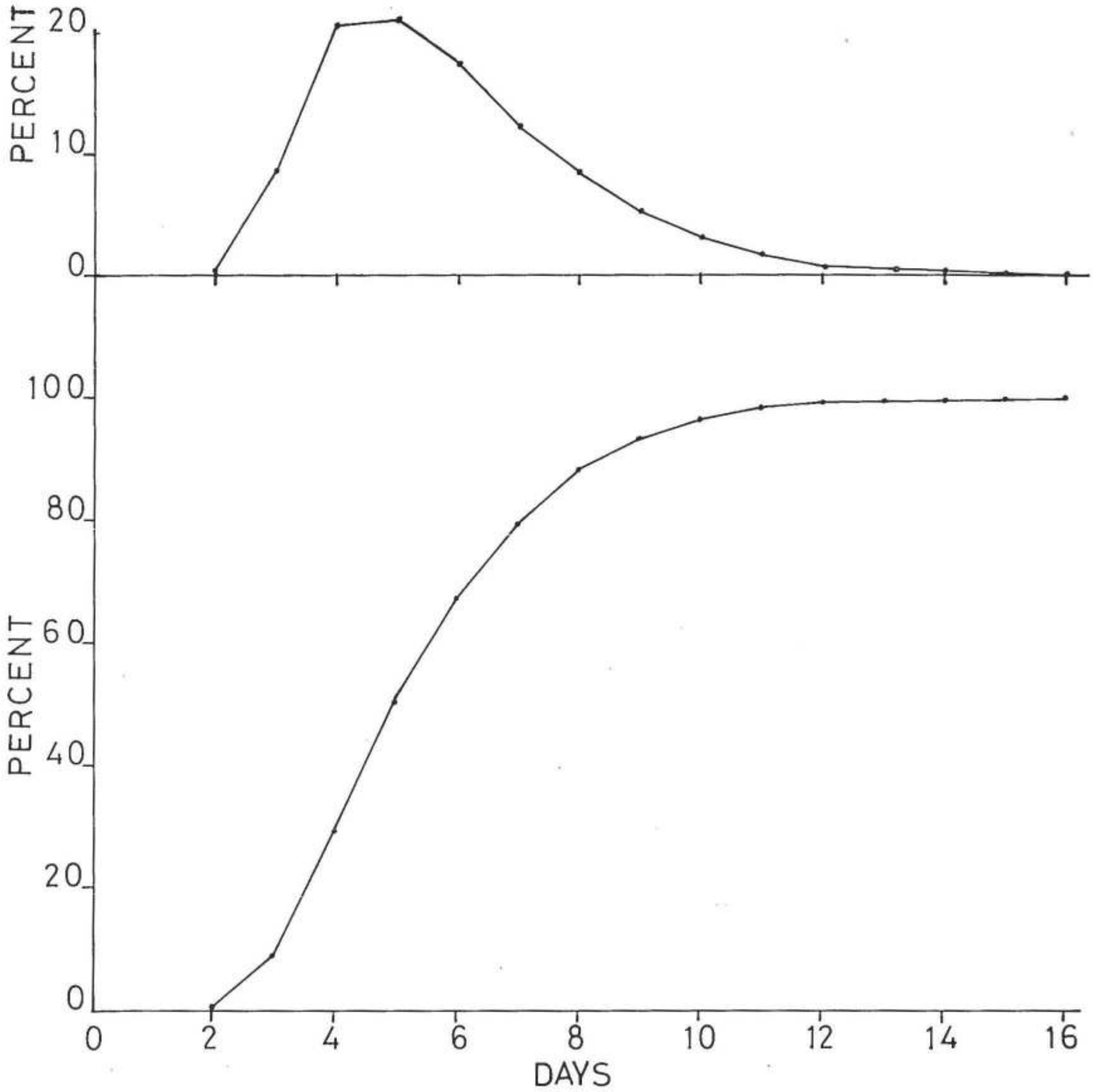

FIG. 1. — Oviposition and accumulated percentage oviposition curves for 150 ticks held at 85°F. in darkness.

TABLE I. — Number of peaks of oviposition by ticks of various weights maintained at 80°F.

No. of Peaks Shown	1 Peak	2 Peaks	3 Peaks
Number	47	9	1
% of total	82 %	16 %	2 %
Av. day of peak(s)	5 ½	5.9	5, 8, 10

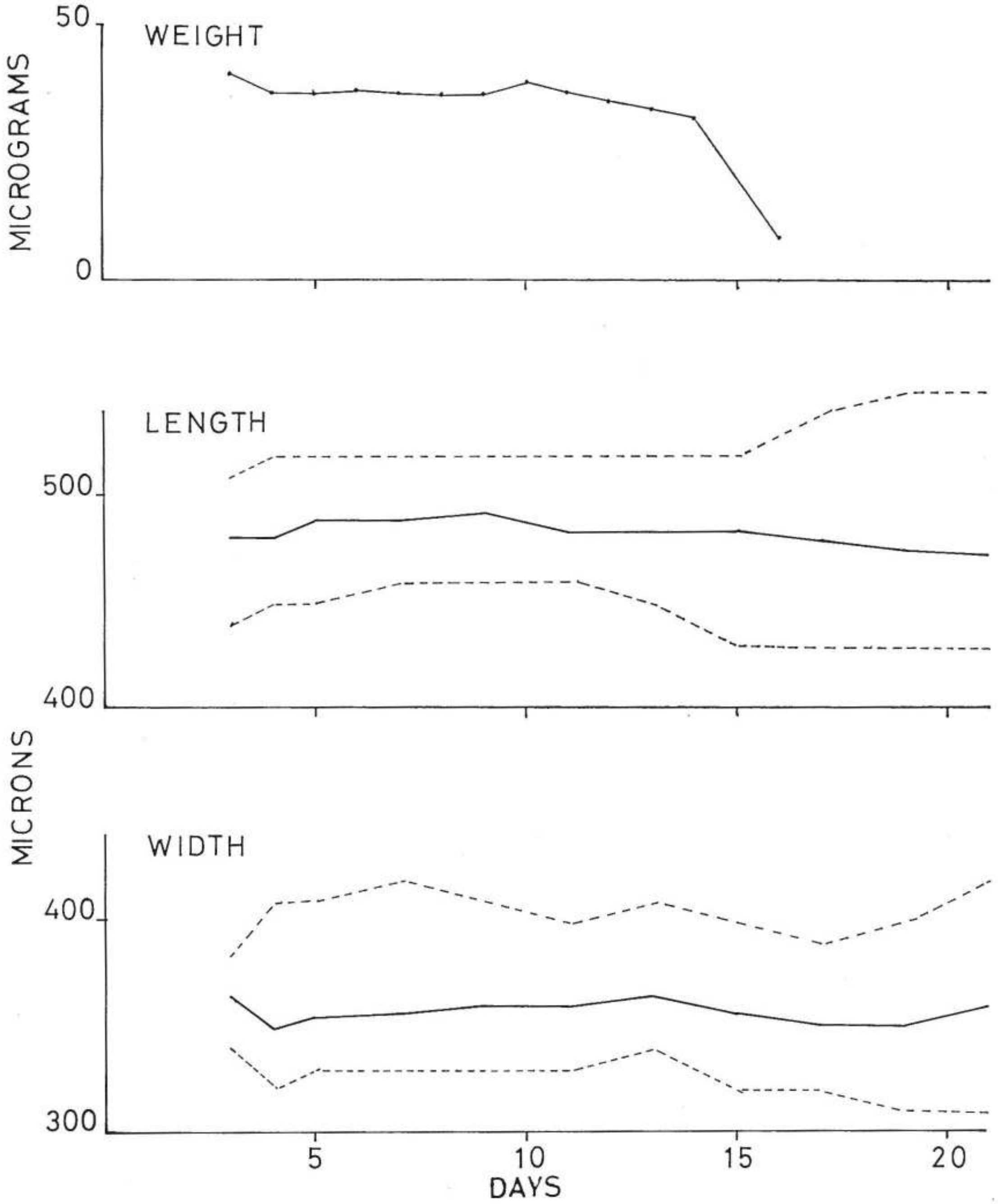

FIG. 2. — Weight, length and width of eggs during oviposition cycle.

(ii) *Size and weight of eggs throughout oviposition.*

KITAOKA and YAJIMA (1958) indicated that the average weight of the egg increases slightly as oviposition proceeds but gave no indication of any changes in length or breadth although illustrating changes in length, breadth and weight of eggs of *Haemophysalis ias*. These studies were repeated on the Queensland strain of *B. microplus* (Fig. 2), held at both constant and diel temperatures of 75°F. (diel temperature = 12 hours at 67.5°F., 12 hours at 82.5°F. to average 75°F.) and a relative humidity of 80-85 %. The data (based on individual measurements of 60 eggs per day) were pooled and the mean range illustrated (Fig. 2). The weight of the eggs laid throughout the course of the oviposition cycle were studied on ticks maintained at a constant 80 ± 1°F. and at a relative humidity of 80-85 %.

The results (Fig. 2) indicated that there was little change in the mean length (484 microns) or width (356 microns) of the eggs throughout the oviposition cycle. The range, however, did tend to increase towards the end of the cycle. A mean weight of 45 micrograms per egg was also relatively constant during the first half of the cycle but egg weight decreases as egg-laying terminates.

(iii) *Prehatch period and viability of eggs laid throughout cycle.*

Samples of the eggs produced each day by ticks under constant and diel temperatures of 75°F. were compared for (a) duration of prehatch period and (b) viability. The experiment was replicated three times and as the prehatch periods did not vary by more than one day for any given day of the cycle, the results of the three replicates were pooled (Table II). Under the above conditions, the prehatch period for eggs laid each day of the first 17 days of the cycle were similar, averaging 29 days from laying to eclosion ; the pre-hatch period increased for eggs laid near the end of the cycle. Under diel conditions, the pattern was similar to the preceding but averaged 30.5 days over the same 17 days. Again, eggs laid near the end of the cycle required a longer pre-hatch period.

The viability of the eggs showed more variation than the pre-hatch period ; eggs laid under both constant and diel conditions showed a similar pattern. Eggs laid on the first day of the cycle had low viability but eggs laid from the 2nd through the 12th day had a hatch rate of 75-100 %. Viability then decreased sharply and only 0-10 % of the eggs laid near the end of the cycle hatched ; however, this low viability involved only 10-12 % of the total eggs laid.

B. Effect of initial tick weight on oviposition

(i) *Pattern of oviposition of ticks of different initial weight.*

The engorged female tick is essentially a sac filled with nutrient (blood) and the necessary organs and metabolic pathways to convert the nutrient to eggs. At the end of the egg-laying cycle there is little left of the tick except the exo-skeleton, residual reproductive tissues, and the by-products of metabolism. The differential in weight between the initial weight and the residual weight of the tick is thus close to the weight of the nutrient available for conversion to eggs. Two expressions of the efficiency of this conversion are used throughout this study.

(a) *Egg production index* (Apparent conversion index). This measure is obtained by the formula

$$\frac{\text{Weight of eggs}}{\text{Initial weight of engorged tick}} \times 100 = \text{egg production index.}$$

TABLE II. — Viability and pre-hatch period of eggs laid throughout the oviposition cycle by ticks held under constant and 12 hour diel cycle of temperatures averaging 75°F.

Day of oviposition cycle	Constant		Diurnal	
	Prehatch period days	Percent hatched	Prehatch period days	Percent hatched
2	30.5	33	—	—
3	30	55	33	57
4	29.5	78	32.5	78
5	29.5	89	32	92
6	28	89	32	91
7	29	86	31	85
8	28	83	30.5	65
9	28.5	79	31	66
10	28.5	79	30	81
11	28.5	79	30	75
12	28.5	67	30	69
13	28.5	45	30	53
14	29	34	30	39
15	29	33	30	37
16	29.5	17	31	28
17	29.5	1	32	20
18	31	2	34	6
19	34	6	36	15
20	—	0	38	7
21	33	4	38	11
22	35	2	40	2
23	36	3	39	2
24	—	0	—	0

This was a useful means of obtaining the expected weight of eggs from a known weight of engorged females.

(b) *Nutrient index* (Real conversion index). This measure of egg production is obtained by the formula

$$\frac{\text{Weight of eggs}}{\text{Initial weight of engorged tick} - \text{residual weight of tick}} \times 100 = \text{nutrient index.}$$

This formula was a definition of the way in which blood ingested was converted into eggs as measured by weight. Thus the egg production index and nutrient index of the ticks (Fig. 1) were 62 % and 86 % respectively. The latter figure indicates a high efficiency in that only 14 % of the total nutrient available was expended in converting the remainder to eggs.

Preliminary observations suggested that ticks of different weights did not oviposit similarly at the same temperature. This aspect was further studied by comparing the pattern of oviposition of four groups of ticks (Table III) of different weights with that illustrated in Fig. 1. Three differences were noted between the performances of the groups : (a) the smallest females laid all their eggs in a shorter time span than the others ; (b) groups I, II and V had low egg production indices ; (c) groups I and II had low nutrient indices and group V had a lower efficiency of conversion than groups III and IV. From these results it was concluded that ticks in the weight range of 180-225 mg. were of optimal size and that small ticks, particularly those 50 mg. or less, were inefficient. The largest number of eggs laid per day (day 4) was the same for each group, suggesting that the rate of oviposition was the same for all groups. The small ticks, having less nutrients to convert to eggs, completed oviposition in the shortest time.

TABLE III. — Pattern of oviposition of five groups of ticks of different weights. Group IV are those illustrated in Figure 1.

	Mean initial weight of groups				
	I 50 mgm.	II 112 mgm.	III 182 mgm.	IV 225 mgm.	V 262 mgm.
Day of 1st eggs laid	2	2	2	2	2
Day 25 % eggs laid	3	3.5	3.5	3.5	3.5
Day 50 % eggs laid	3.7	4.0	4.5	5.0	5.0
Day 75 % eggs laid	4.5	5	5.5	6	6
Day 99 % eggs laid	8	9	10	11	9
Day finished laying	9	11	13	14	14
Peak egg laying	4	4	4	4	4
Apparent conversion	40.7 %	48.9 %	54.2 %	62.0 %	59.9 %
Real conversion	67.1 %	75.5 %	83.8 %	86.0 %	81.5 %
No. ticks involved	45	35	50	150	10

(ii) *Tick size and weight of eggs laid.*

KITAOKA and YAJIMA (1958) demonstrated linearity between the initial weight of the engorged tick and the number of eggs laid. Their experiment was repeated but the basis of comparison was weight, rather than number, of eggs laid. In addition, both the egg production and nutrient indices were calculated. Over 450 ticks, ranging in weight from 11 to 560 mg. were maintained at 85°F. for 17 days. The total egg production of each tick was then plotted against its initial weight. The ticks were then grouped into 20 mg. weight classes, the mean egg weight and standard deviation per class calculated and plotted on the same diagram.

The data were analysed again following removal from the analysis of all ticks which lay outside two standard deviations about the mean. A new mean (Fig. 3) and standard deviations were obtained. Twelve percent of the original sample now lay outside the new mean $\pm$ two standard deviations, 1 % above and 11 % below. The corrected mean (Fig. 3) is virtually linear, thus confirming the work of Kitaoka and Yajima (1958). The smallest tick to oviposit weighed 17 mg. but only one of five ticks weighing less than 20 mg. oviposited ; all ticks over 20 mg. laid eggs.

The mean egg production and nutrient indices, based on the corrected sample, are also illustrated (Fig. 3). It is clear that ticks 100 mg. or less are not as efficient in converting the blood meal to eggs. Ticks in the range 100-370 mg. have a remarkably uniform efficiency of conversion and the standard deviation was small. A single specimen weighing 560 mg. was studied but omitted from the curve (Fig. 3) ; egg production and nutrient indices of 42 % and 72 % were obtained.

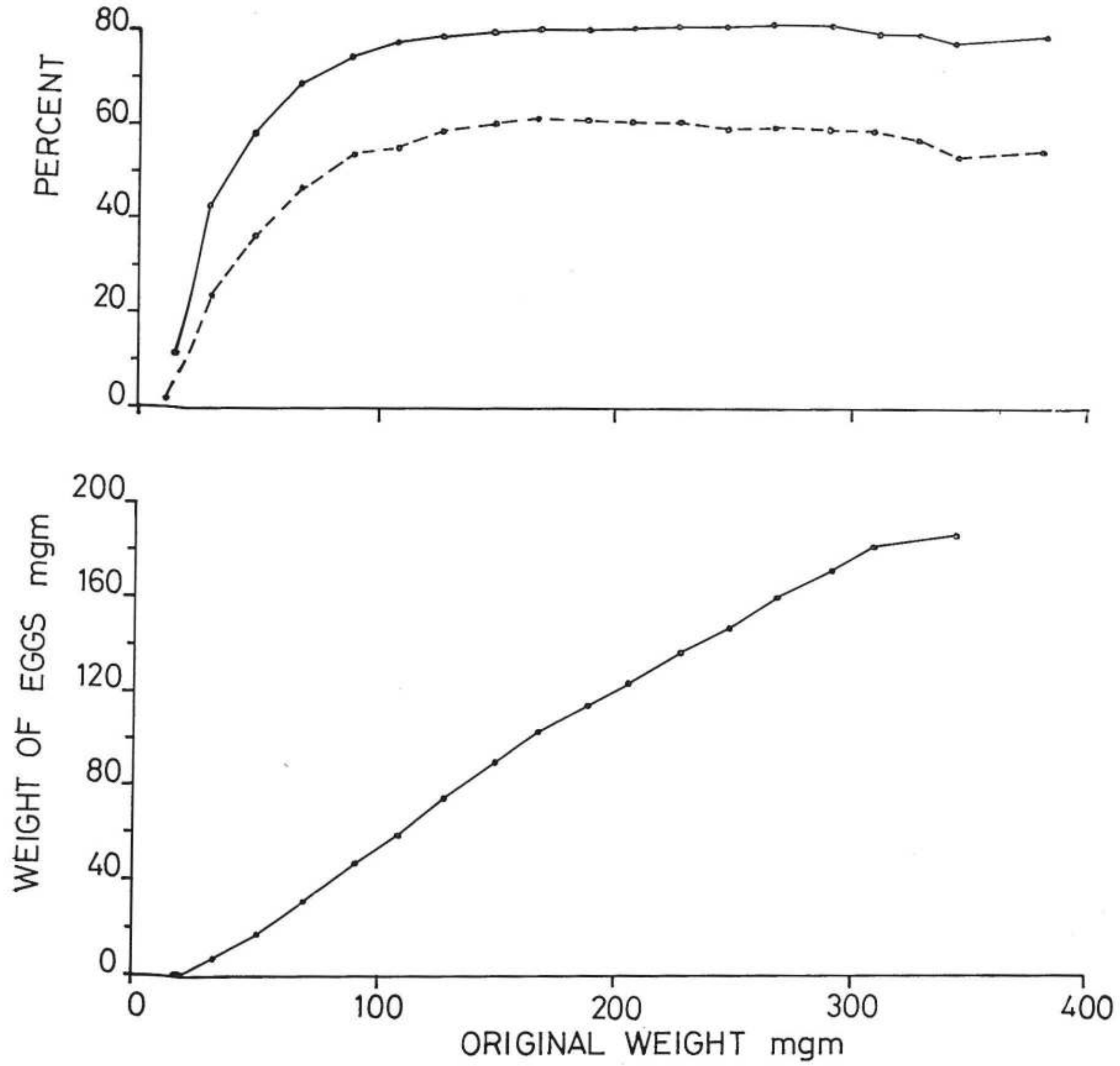

FIG. 3. — Relationship between egg production and initial weight of ticks. Egg production and nutrient indices at top of figure : egg production index — dotted line ; nutrient index — solid line.

The 11 % of the original sample which returned unexpectedly low conversion efficiencies were of considerable interest. This 11 % was evenly distributed over the weight range under study and not confined to a specific weight class. This suggested that the factors responsible for the low productivity were not weight dependent but occurred naturally in about 11 % of the tick population. One possible explanation was that this portion of the tick population had some fault in the blood-concentrating mechanisms. Thus these ticks, although fully engorged, contained a higher proportion of water in the blood meal (and hence a lower nutritional store for egg production) than the rest of the population. If this hypothesis was correct, then a similar sample from the same parental line of ticks, reared on the same hosts, should show a similar proportion of individuals unable to fully concentrate the blood meal.

This hypothesis was tested by randomly selecting some 180 freshly engorged females over the weight range 17-364 mg. Each female was placed in a vial and dried in an oven at 150°F. for six days and then weighed again. The loss of weight (i. e. — moisture) expressed as a percentage of the initial weight, was remarkably uniform (Table IV). Generally, most ticks (89.3 %) lost between 55 and 61 % (mean 59 %) of their initial weight; no tick lost less than 55 % of the initial weight. Significantly, 10.7 % of the sample lost 64 % or more of their initial weight, indicating that these ticks had, initially, a higher water content, and presumably did not concentrate their blood meal as efficiently as the others. This figure compares most favourably with the figure of 11 % of the ticks which laid less than the expected weight of eggs.

The lower conversion values and smaller number of eggs laid by small ticks is also of interest. It has been our experience that engorged ticks from resistant hosts are consistently smaller than those from susceptible animals; Zebu (*Bos indicus*) and Zebu crossbred animals (*Bos tauros* × *Bos indicus*) tend to be resistant to tick infestation and ticks from these animals tend to be small (WILKINSON, 1962; ROBERTS, 1968). Use of such animals, together with *Bos tauros* breeds selected for resistance, would produce fewer ticks which would not have the reproductive potential of the larger ticks produced on susceptible hosts. Thus an additional degree of biological control could be exerted on the *B. microplus* population.

TABLE IV. — Percent loss of weight of engorged *B. microplus* dried at 150°F. for seven days.

Percent Loss Weight	Number of ticks in class		
67 → 75	8		10.7 % (64–75)
66	3		
65	4		
64	5		
61	18		89.3 % (55–61)
60	31		
59	51	54 % (58–59)	
58	50		
57	12		
56	3		
55	2		
0 → 54	0		0 %
Total No.	187		

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