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# LABORATORY INVESTIGATIONS ON THE LIFE-CYCLE OF THE KAROO PARALYSIS TICK (*IXODES RUBICUNDUS* NEUMANN, 1904)

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ABSTRACT

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Detailed data on the rearing of three groups of *Ixodes rubicundus* ticks at different temperature and humidity levels are presented in a series of tables and figures. The differences between the life-spans are seen to be dependent mainly upon the temperature. The average duration of 405 days at relatively high temperatures is extended to 1115 days at lower temperatures. The reason for the mortality rate of approximately 96% of the immature stages in all groups during the prefeeding, feeding and premoulting periods is obscure.

## INTRODUCTION

The first records on the incidence of ovine tick paralysis in South Africa appeared in letters from two farmers published in the Agricultural Journal of the Cape of Good Hope (1890). Ralph (1890) from Fort Beaufort (Eastern Cape Province) and L.C.K. (1890) from Rivierzondereind (Western Cape Province) stated that severe losses occurred among their lambs and that recovery followed within 48 hours after the removal of ticks from affected animals. Hellier (1892) recorded the occurrence of this disease in lambs and kids in the Karoo. Mally (1904) and Lounsbury (1905) incorrectly identified the vector as *Ixodes pilosus* Koch, 1844. Neumann (1904) described *Ixodes rubicundus* as a new species and as a vector of a disease which was subsequently recognized as tick paralysis. During the course of a survey on the distribution of both these *Ixodes* spp., Theiler (1949) established that *I. rubicundus* is widely distributed but that *I. pilosus* is absent in the extensive enzootic tick paralysis regions of the Karoo. This observation justified the conclusion that *I. rubicundus* is the vector. Whether or not this species is the only vector in the Karoo still needs to be determined. Theiler (1950) and Stampa (1959) established the presence of *Rhipicephalus evertsi evertsi* Neumann, 1897 in the tick paralysis enzootic zones of the eastern Karoo. Some strains of this species have been recognized as transmitters in the Eastern Cape Province (Lounsbury, 1900; Neitz & Walters, 1971).

Surveys in the Karoo have shown that the hosts of adult *I. rubicundus* female ticks are chiefly domestic ruminants. Several species of antelopes, wild carnivores and hares have also been found to be infested. Immature stages have been collected from elephant shrews, *Elephantulus capensis karoensis* Roberts by Stampa (1959) and *E. rupestris* A. Smith by Theiler (1962) and from hares, *Pronolagus crassicaudatus* I. Geoffroy by Theiler (1962), *P. rupestris saundersiae* Hewitt and *Lepus saxatilis albaniensis* Roberts by Stampa (1959).

Successful feeding of immature stages on wild hosts has been recorded by Stampa & du Toit (1958). They found that larvae attach themselves anywhere on the body of elephant shrews except on the tail and ears, whereas on the hare the medial surface of the limbs and ventral region of the abdomen are the feeding sites of choice. Nymphae readily feed to repletion on elephant shrews. Larvae also feed satisfactorily on the backs of small rodents (species not mentioned). Their attempt to feed larvae on the ears of rabbits failed while nymphae generally detached from this host before reaching full engorgement.

Investigations by Stampa & du Toit (1958) and Stampa (1959) have contributed greadly towards the clarification of the biology and ecology of *I. rubicundus*. The tick population counts on sheep, shrews and hares as well as those made directly from pastures by flagging and dragging for ticks occurring on the vegetation have established the environmental conditions favourable for the maintenance of ticks and their natural hosts, the presence of either toxic or non-toxic tick strains in several regions of the extensive *I. rubicundus*-infested areas of the Karoo and the seasonal incidence and activity of immature and mature ticks.

Tick activity commences during the latter half of February and persists until the middle of November after which it rapidly declines to a level of relative inactivity during December, January and the first half of February. The active period for the imagines extends from the middle of February to the middle of November with the peak activity during April and May; larvae are active from March to the middle of August and reach the peak of activity in April and May; nymphae are active from July to November with the peak activity in September and October.

Investigations by De Vries & Davey [cited by Stampa & du Toit (1958)] have shown that eggs survive well under average local conditions but are unable to tolerate dry heat. No larval hatching was obtained at relative humidities lower than 70%. They also found that hatching was somewhat retarded at 70 to 80% RH, whereas all eggs hatched within a relatively short period at 80 to 100% RH.

Stampa & du Toit (1958) established that larvae readily hatched when kept at about 100% RH and at temperatures between 18 to 21 °C, whereas at 15 °C (lower limit) and 25 °C (upper limit) the hatching period was considerably extended. According to them engorged nymphae survived almost anywhere and were less affected by adverse environmental conditions than were the unfed nymphae and either the unfed or fully engorged larvae. Their records on the activity of adult ticks over a period of approximately 10 months in their natural habitat show that they survive well under the different climatic conditions of summer, winter and autumn.

Studies on the life-cycle of *I. rubicundus* have been undertaken by Stampa & du Toit (1958) and Stampa (1959). Their findings are listed in Table 1. Incomplete

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as these developmental records are they were nevertheless found useful, when considered in conjunction with the established activity periods in the field, as a basis for planning breeding methods under laboratory conditions.

TABLE 1 The life-cycle of *I. rubicundus* according to (a) Stampa & du Toit (1958), and (b) Stampa (1959)

| Developmental phases | Period in days |
|---|---|
| Pre-oviposition | 34–35 (a) |
| Oviposition | 42 (2000 eggs) (a) |
| Larval hatching | Not determined |
| Larval prefeeding | „ |
| Larval engorgement | „ |
| Larval premoulting | 73–149 (a) |
| Nymphal prefeeding | Not determined |
| Nymphal engorgement | „ |
| Nymphal premoulting | 180 (a) |
| Adult males survival | 3–24 in nature (b) |
| Adult females survival | 7–71 in nature (b) |
| Adult females engorgement | 4–7 (a), 3–13 (b) |
| Total life-cycle | 730 (a) |

In this paper are recorded the results of investigations on the breeding of *I. rubicundus* over a period of 10 years. During this period attempts were made to determine suitable temperature and relative humidity levels at which the tick could complete its life-cycle under laboratory conditions.

## MATERIALS AND METHODS

1. *Origin of the ticks*

Eleven batches of engorged *I. rubicundus* adult females were kindly supplied by the Senior State Veterinarians of Middelburg (C.P.), Grahamstown (C.P.), Heidelberg (Tvl.) and Pietermaritzburg (Ntl.). The localities and the tick paralysis-affected animals from which the ticks were obtained are listed in Table 2.

2. *Tick-breeding*

(*a*) *Standardized procedures at Onderstepoort*

Methods employed for rearing three-host ixodid ticks are to place a single engorged female, up to 60 engorged larvae and not more than 15 engorged nymphae respectively into small glass tubes (20 mm by 10 mm) plugged with cotton wool. Up to four such tubes, harbouring the same stage, are accommodated in a test tube (170 mm by 20 mm) which is also plugged with cotton wool. The test tubes are held in wire baskets in the acaridarium where the temperature (25 to 26°C) and the relative humidity (85 to 90%) are automatically regulated. Ticks are examined daily until metamorphosis occurs. The dates of receipt, oviposition, hatching, infestation, detachment and moulting and the identification number of the host are recorded in the tick register.

All stages are fed on the ears of adult rabbits and various domestic animals. Ear-bags provided with a wide flange at the open end and capable of holding one to four small tubes containing ticks are secured around the base of the ear by means of heated, molten Unna's paste. When the paste has solidified, ticks are released by removing the plugs from the tubes. On the following day an incision is made into the ear-bag for the removal of the tubes and cotton wool. The incision is sewn up and reopened on subsequent days for the collection of detached ticks into a test tube by means of a suitable glass funnel. The ticks are sorted out into tubes and are then retained in the acaridarium for further observation.

Maintenance of ticks in the acaridarium has proved to be satisfactory for breeding most species commonly found on domestic animals.

(*b*) *Modified procedures for rearing* I. rubicundus

The behaviour of ticks during the four seasons in the Karoo, as described by Stampa & du Toit (1958), makes it apparent that the climate to which *I. rubicundus* is exposed is subject to wide variations. During winter the temperatures are lower than 15°C at night and during the spring and summer days higher than 25°C. The relative humidity, dependent upon dew and rainfall, also shows significant variations during the four seasons.

Our first attempts to rear *I. rubicundus* in the acaridarium under the standardized procedures failed. The engorged adult females laid eggs but these died within a period of 2 months. It thus became apparent that climatic conditions resembling those in the Karoo would have to be created for successful tick-breeding.

Systematic investigations were started in 1961 and terminated in 1970. During this period 27 batches were reared. These included 11 batches from the field and their progeny of 16 batches. They were divided into Groups A, B and C, each of which was maintained under an artificially created climate as specified below.

Group A

This group was represented by a single batch of eight engorged females which were maintained daily for 17 hours in the acaridarium (25 to 26°C, 85 to 90% RH) and for the remaining 7 hours in the adjoining laboratory (18 to 22°C, 40 to 60% RH) for 80 days and subsequently for 247 days at 22 to 32°C and 40 to 60% RH, excluding the weekends. Daily observations lasted throughout the life-cycle of 327 days.

Group B

This group was represented by 15 batches of 62 engorged females which were kept daily for 17 hours in the acaridarium and for 7 hours (weekends excluded) in a refrigerator (15 to 18°C, 55 to 60% RH). The observation periods lasted throughout the duration of the life-cycles, which varied from 331 to 782 days.

Group C

This group was represented by 11 batches of 53 engorged females which were permanently maintained in a refrigerator (15 to 18°C, 55 to 60% RH). The observation periods lasted throughout the life-cycles, which varied from 860 to 1285 days.

The duration of the life-cycles given above for ticks of Groups A, B and C are examples of the actual periods as recorded in the tick register and hence differ from the calculated minimum, maximum and average periods recorded in the tables and figures.

3. *Tick hosts*

As shrews and hares were not available weaned rabbits, approximately 60 days old, were used for feeding all the stages. To determine whether adult ticks would cause tick paralysis they were also fed on sheep, goats and dogs.

## RESULTS

Details of the tick-breeding results of Groups A, B and C, which were maintained under different temperature and humidity levels, are listed in Tables 2 to 6. A summary of these results is presented schematically for each group in Fig. 1, 2 and 3.

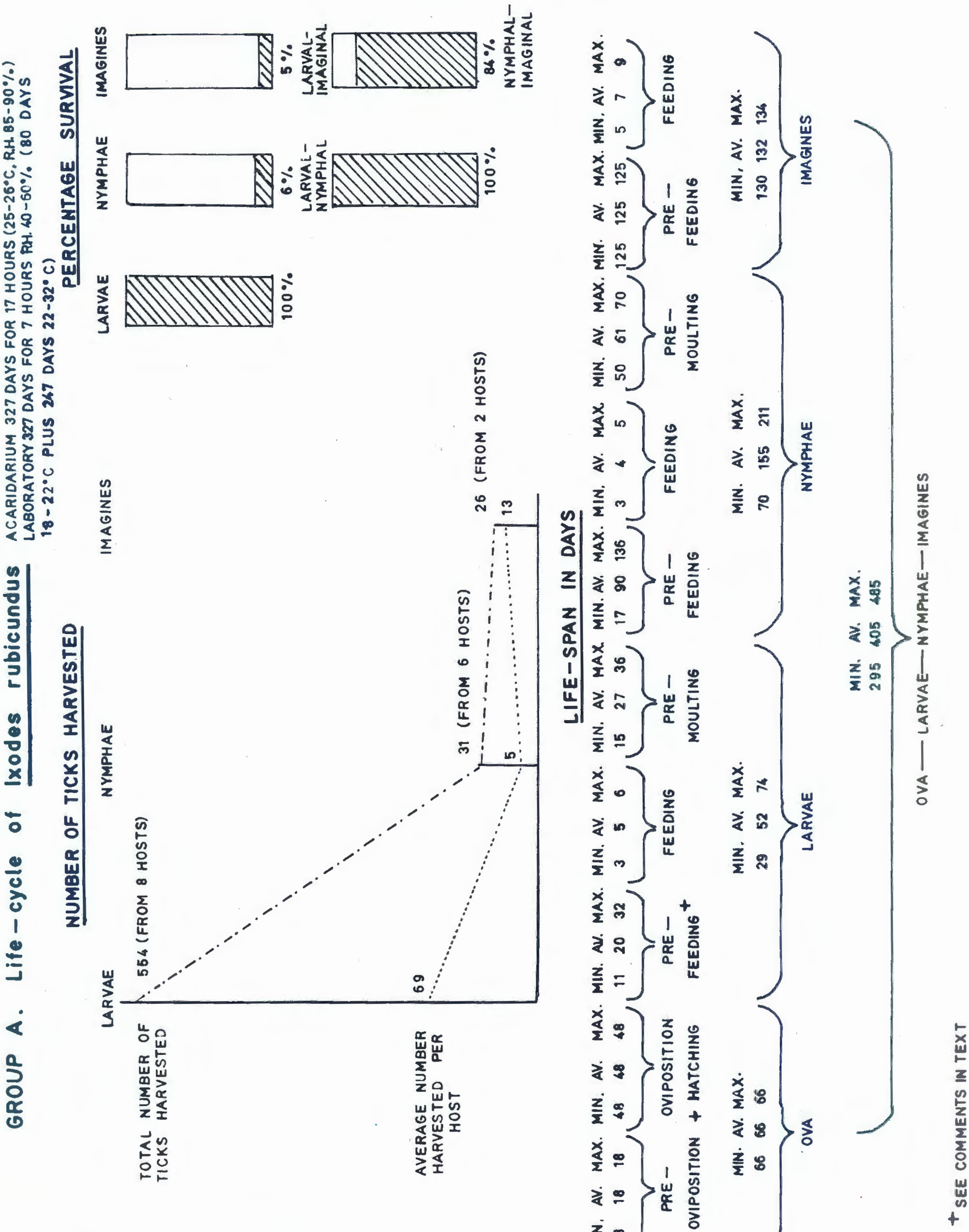


FIG. 1 Group A. Life-cycle of *Ixodes rubicundus*

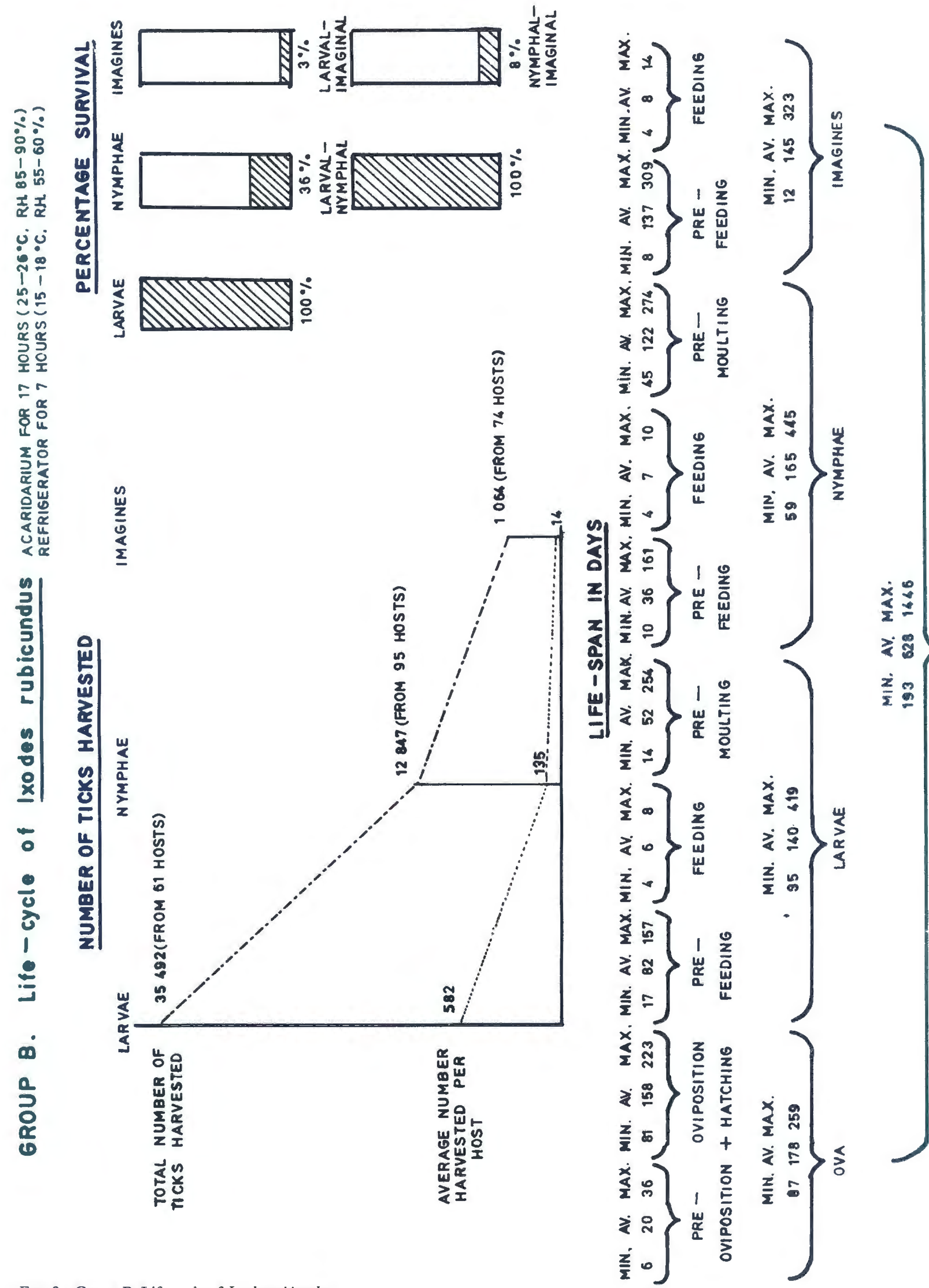


FIG. 2 Group B. Life-cycle of *Ixodes rubicundus*

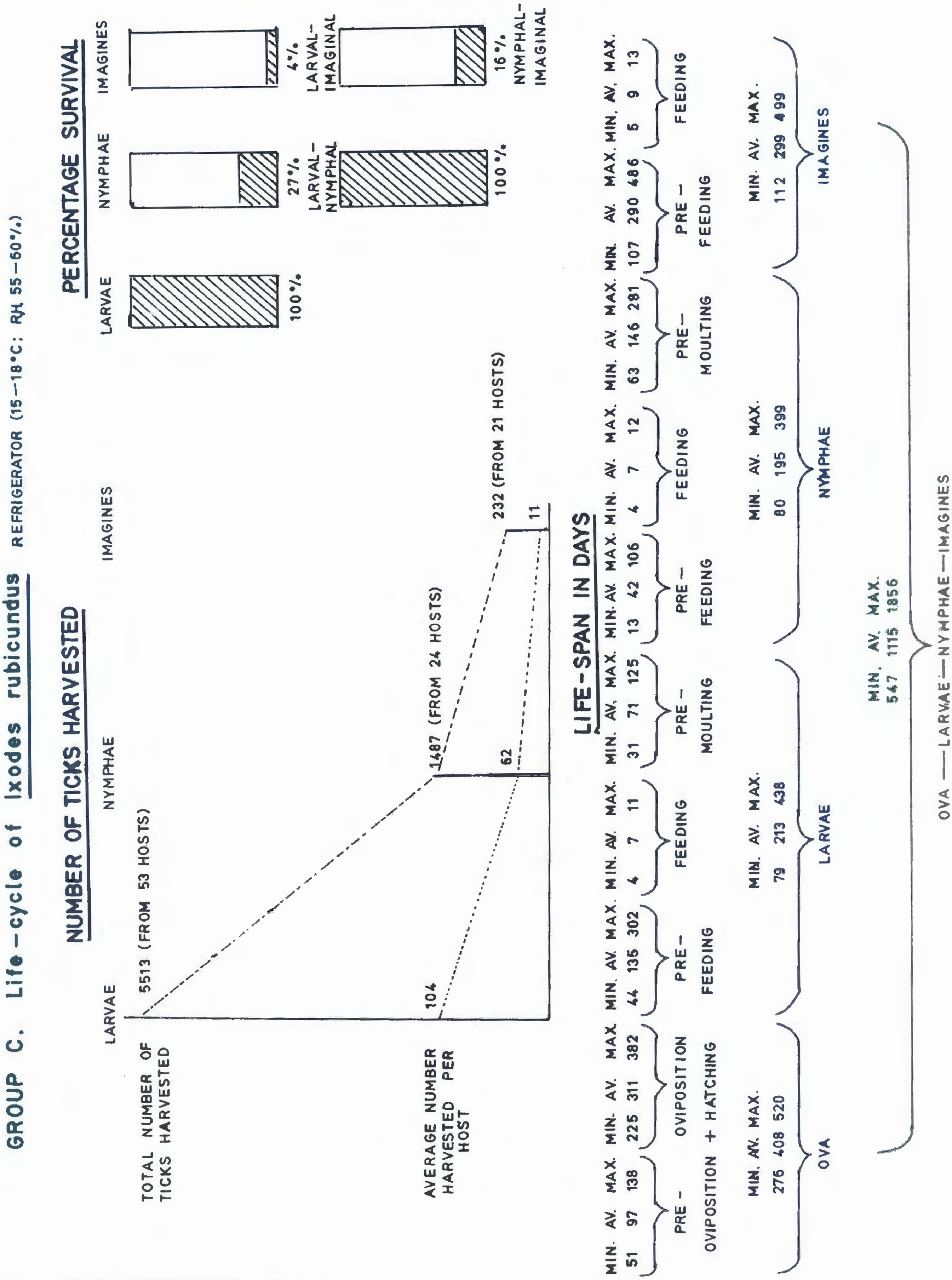


FIG. 3 Group C. Life-cycle of *Ixodes rubicundus*

TABLE 2 *Observations on the life cycle of* I. rubicundus

| Origin of *I. rubicundus* engorged adult females from paralysed animals | | Rearing of ticks for one or more generations (Gen) on rabbits (R), sheep (S), goats (G) or dogs (D). Duration of the pre-oviposition (Pre-ov), oviposition plus hatching (Ovip + Hatch), prefeeding (Pref), feeding (Feed) and pre-moulting (Prem) periods is given in days. Total number of ticks harvested from each host group is listed. | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Farm District Province | Animals affected | Batch No | Date | Group and Gen | Oval phases | | Larval phases | | | | | Nymphal Phases | | | | | Imaginal phases | | | |
| | | | | | Pre-ov | Ovip + Hatch | Pref | Hosts | Feed | No | Prem | Pref | Hosts | Feed | No | Prem | Pref | Hosts | Feed | No |
| The Chestnuts . . .<br>Lions River . . . .<br>Natal . . . . . . . | Cattle<br>6 died<br>(8 ticks) | 2579 | 12.6.61 | A, F1 | 18 | 48 | 11–32 | 8R | 3–6 | 554 | 15–36 | 17–136 | 6R | 3–5 | 31 | 50–70 | 125 | 2S | 5–9 | 13 (13) |
| ? . . . . . . . | Merino | 2709 | 11.10.62 | B, F1 | 16 | 104 | 50 | 5R | 4–6 | 2098 | 20 | 20–22 | 12R | 4–7 | 1485 | 49–65 | 80–140 | 7S | 6–11 | 22 (22) |
| Middelburg . . . . | Sheep | 2829 | 9.10.63 | B, F2 | 18 | 94 | 41–82 | 2R | 4–7 | 3505 | 22–29 | 38–66 | 6R | 5–8 | 987 | 80–159 | 90–221 | 3S, 1R | 6–11 | 32 (32) |
| Cape Province . . . | (5 ticks) | 2834 | 21.10.63 | B, F2 | 17 | 118 | 34–98 | 2R | 5–7 | 775 | 32–42 | 38–161 | 2R | 4–8 | 447 | 119–160 | 120 | 2S | 6–7 | 48 (48) |
| | | 2835 | 21.10.63 | B, F2 | 21 | 135 | 17–81 | 6R | 4–7 | 3100 | 20–42 | 10–38 | 12R | 4–8 | 1580 | 45–161 | 42–160 | 8S | 8–14 | 39 (39) |
| | | 2845 | 2.12.63 | B, F2 | 16 | 99 | 66 | 2R | 4–6 | 2195 | 24 | 10–21 | 7R | 4–8 | 1125 | 63–131 | 25–199 | 5S | 6–9 | 17 (17) |
| | | 3026 | 28.5.65 | C, F3 | 51 | 355 | 65 | 2R | 5–7 | 359 | 125 | 37 | 1R | 5–7 | 1–6 | 125 | 310 | 2R | 9 | 3 (3) |
| | | 3051 | 19.4.65 | C, F3 | 129 | 297 | 114–120 | 7R | 6–7 | 115 | 51–85 | 79 | 1R | 5–12 | 60 | 232 | 107 | 2R | 7–13 | 9 (9) |
| Elandsfontein . . .<br>Heidelberg . . . .<br>Transvaal . . . . . | Boer Goat<br>(4 ticks) | 2770 | 22. 4.63 | B, F1 | 19 | 170 | 50 | 4R | 7–10 | 527 | 38–39 | 21 | 2R | 6–8 | 91 | 50–51 | 67 | 2G | 7–9 | 5 (5) |
| Waterkloof . . . .<br>Somerset East . . . | Merino<br>Sheep | 2808 | 4.6.63 | B, F1 | 36 | 202 | 21–34 | 4R | 4–7 | 1804 | 22–25 | 13–22 | 8R | 5–7 | 845 | 67–274 | 21–266 | 3S, 1D<br>1R | 6–11 | 25 (25) |
| Cape Province . . . | (4 ticks) | 2967 | 16.9.64 | B, F2 | 26 | 161 | 150 | 2R | 7–8 | 189 | 110 | 24 | 1R | 5–7 | 48 | 142 | 132 | 1R | 4–9 | 4 (4) |
| | | 3028 | 7.5.65 | C, F2 | 61 | 382 | 110–201 | 3R | 5–7 | 190 | 51–66 | 41 | 1R | 5–6 | 43 | 281 | 232 | 1S | 8–11 | 2 (2) |
| Wolwekloof . . . .<br>Middelburg . . . .<br>Cape Province . . . | Goat<br>(2 ticks) | 2822 | 20.5.63 | B, F1 | 19 | 174 | 122 | 2R | 5–8 | 840 | 23–28 | 14–29 | 4R | 6–10 | 215 | 125–172 | 209–238 | 3S | 7–10 | 13 (13) |
| Rietpoort . . . . . | Merino | 2824 | 1.6.63 | B, F1 | 18 | 214 | 28–62 | 6R | 4–7 | 3328 | 21–29 | 31–45 | 13R | 4–7 | 1633 | 63–224 | 8–253 | 4S, 1G | 4–8 | 73 (73) |
| Cradock . . . . . | Sheep | 3029 | 5.5.65 | C, F2 | 63 | 287 | 120–267 | 11R | 5–6 | 2380 | 31–95 | 13–100 | 6R | 6–9 | 365 | 63–154 | 273–411 | 2S, 1R | 6–13 | 28 (28) |
| Cape Province . . . | (6 ticks) | 3046 | 4.5.65 | C, F2 | 71 | 307 | 148–253 | 6R | 5–8 | 480 | 51–77 | 43 | 3R | 5–8 | 145 | 115–276 | 145–306 | 2R | 6–9 | 12 (12) |
| Waterkloof . . . . | Merino | 2825 | 10.7.63 | B, F1 | 6 | 198 | 28–69 | 3R | 4–8 | 1764 | 28–42 | 38 | 4R | 5–8 | 600 | 190–223 | 57–185 | 2S, 1R | 4–7 | 31 (31) |
| Somerset East . . .<br>Cape Province . . . | Sheep<br>(3 ticks) | 3047 | 18.4.65 | C, F2 | 113 | 326 | 114–302 | 3R | 5–8 | 298 | 51–65 | 35 | 2R | 5–8 | 97 | 82–96 | 310–468 | 2S | 7–11 | 8 (8) |
| Bosfontein . . . .<br>Somerset East . . . | Merino &<br>Dorper<br>Sheep | 2826 | 24.4.63 | B, F1 | 22 | 193 | 131 | 3R | 4–7 | 881 | 14–26 | 14–22 | 2R | 4–6 | 563 | 53–234 | 73–304 | 1S, 1D,<br>1R | 6–11 | 23 (23) |
| Cape Province . . . | (3 ticks) | 3048 | 5.5.65 | C, F2 | 63 | 344 | 120 | 2R | 5 | 228 | 65 | 29 | 1R | 8 | 135 | 126 | 148 | 1R | 8 | 1 (1) |
| Bosfontein . . . .<br>Somerset East . . .<br>Cape Province . . . | Merino &<br>Dorper<br>Sheep<br>(3 ticks) | 2830 | 24.4.63 | B, F1 | 12 | 203 | 107 | 3R | 4–7 | 243 | 20–22 | 20 | 1R | 6 | 51 | 56 | 133 | 1S | 10 | 2 (2) |
| Waterkloof . . . . | Merino | 2833 | 4.7.63 | B, F1 | 21 | 223 | 34 | 5R | 5 | 3427 | 254 | 18–38 | 8R | 5–8 | 1721 | 64–244 | 22–249 | 7S, 1D | 5–9 | 143 (143) |
| Somerset East . . . | Sheep | 3027 | 18.4.65 | C, F2 | 122 | 301 | 44 | 2R | 6 | 124 | 125 | 37 | 1R | 5 | 60 | 125 | 148 | 1S | 7 | 1 (1) |
| Cape Province . . . | (5 ticks) | 3050 | 18.4.65 | C, F2 | 138 | 325 | 80–128 | 6R | 5–8 | 674 | 65–77 | 35–106 | 3R | 5–8 | 270 | 111–214 | 306–486 | 2R | 7–12 | 19 (19) |
| ? . . . . . . . | Merino | 2912 | 4. 5.63 | B, F1 | 32 | 81 | 157 | 12R | 4–6 | 10816 | 40–58 | 38–150 | 13R | 5–8 | 1456 | 108–244 | 29–309 | 17R | 6–12 | 55 (55) |
| Middelburg . . . . | Sheep | 3086 | 1. 6.66 | C, F2 | 135 | 288 | 76–160 | 10R | 4–11 | 456 | 57–88 | 27–50 | 3R | 5–8 | 113 | 84–112 | 204–471 | 1S, 1R | 9 | 13 (13) |
| Cape Province . . . | (12 ticks) | 3211 | 25. 9.68 | C, F3 | 83 | 225 | 78 | 1R | 4–7 | 109 | 49 | 45 | 2R | 8 | 73 | 146 | 163 | 1S | 9 | 1 (1) |

TABLE 3 Average and total duration in days of the different developmental phases and total number of immature and mature ticks harvested

| Developmental phases | Group | Pre-oviposition period | | | Oviposition + hatching period | | | Prefeeding period | | | Feeding period | Premoulting period | | | Total period | No. of ticks harvested | | | Average life-span | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Total | B. | Av. | Total | B. | Av. | Total | Sub-B. | Av. | Av. | Total | Sub-B. | Av. | | Total | Sub-B. | Av. | Group | Days |
| Oval | A | 18 | 1 | 18 | 48 | 1 | 48 | — | — | — | — | — | — | — | 66 | — | — | — | | |
| | B | 298 | 15 | 20 | 2369 | 15 | 158 | — | — | — | — | — | — | — | 178 | — | — | — | | |
| | C | 1029 | 11 | 94 | 3448 | 11 | 314 | — | — | — | — | — | — | — | 408 | — | — | — | | |
| Larval | A | — | — | — | — | — | — | 181 | 9 | 20 | 5 | 189 | 7 | 27 | 52 | 554 | 7 | 79 | | |
| | B | — | — | — | — | — | — | 5104 | 62 | 82 | 6 | 3198 | 61 | 52 | 140 | 35492 | 61 | 581 | | |
| | C | — | — | — | — | — | — | 7166 | 53 | 135 | 7 | 3687 | 52 | 71 | 213 | 5513 | 52 | 106 | A<br>B<br>C | 405<br>628<br>1115 |
| Nymphal | A | — | — | — | — | — | — | 538 | 6 | 90 | 4 | 368 | 6 | 61 | 155 | 31 | 6 | 5 | | |
| | B | — | — | — | — | — | — | 3672 | 101 | 36 | 7 | 11875 | 97 | 122 | 165 | 12847 | 97 | 132 | | |
| | C | — | — | — | — | — | — | 1014 | 24 | 42 | 7 | 3499 | 24 | 146 | 195 | 1487 | 24 | 62 | | |
| Imaginal | A | — | — | — | — | — | — | 250 | 2 | 125 | 7 | — | — | — | 132 | 26 | 2 | 13 | | |
| | B | — | — | — | — | — | — | 11125 | 81 | 137 | 8 | — | — | — | 145 | 1064 | 69 | 15 | | |
| | C | — | — | — | — | — | — | 6384 | 22 | 290 | 9 | — | — | — | 299 | 232 | 21 | 11 | | |

Legend Av. = Average, B. = Batches, Sub B. = Sub-batches

TABLE 4 The possible minimum, maximum and average duration of the life-span in days of *I. rubicundus* based on that of the different developmental phases

| Developmental phases | | Group A Periods | | | Group A Total duration for each phase | | | Group B Periods | | | Group B Total duration for each phase | | | Group C Periods | | | Group C Total duration for each phase | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Min. | Max. | Av. | Min. | Max. | Av. | Min. | Max. | Av. | Min. | Max. | Av. | Min. | Max. | Av. | Min. | Max. | Av. |
| Oval | Pre-oviposition | 18 | 18 | 18 | 66 | 66 | 66 | 6 | 36 | 20 | 87 | 259 | 178 | 51 | 138 | 94 | 276 | 520 | 408 |
| | Oviposition + hatching | 48 | 48 | 48 | | | | 81 | 223 | 158 | | | | 225 | 382 | 314 | | | |
| Larval | Prefeeding | 11 | 32 | 20 | 29 | 74 | 52 | 17 | 157 | 82 | 35 | 419 | 140 | 44 | 302 | 135 | 79 | 438 | 213 |
| | Feeding | 3 | 6 | 5 | | | | 4 | 8 | 6 | | | | 4 | 11 | 7 | | | |
| | Premoulting | 15 | 36 | 27 | | | | 14 | 254 | 52 | | | | 31 | 125 | 71 | | | |
| Nymphal | Prefeeding | 17 | 136 | 90 | 70 | 211 | 155 | 10 | 161 | 36 | 59 | 445 | 165 | 13 | 106 | 42 | 80 | 399 | 195 |
| | Feeding | 3 | 5 | 4 | | | | 4 | 10 | 7 | | | | 4 | 12 | 7 | | | |
| | Premoulting | 50 | 70 | 61 | | | | 45 | 274 | 122 | | | | 63 | 281 | 146 | | | |
| Imaginal | Prefeeding | 125 | 125 | 125 | 130 | 134 | 132 | 8 | 309 | 137 | 12 | 323 | 145 | 107 | 486 | 290 | 112 | 499 | 299 |
| | Feeding | 5 | 9 | 7 | | | | 4 | 14 | 8 | | | | 5 | 13 | 9 | | | |
| Total periods | | 295 | 485 | 405 | 295 | 485 | 405 | 193 | 1446 | 628 | 193 | 1446 | 628 | 547 | 1856 | 1115 | 547 | 1856 | 1115 |
| Total periods excluding prefeeding periods | | | | | | | 170 | | | | | | 373 | | | | | | 648 |

Legend Min. = Minimum, Max. = Maximum, Av. = Average

TABLE 5 The extended duration of the developmental phases of *I. rubicundus* expressed as multiples

| Developmental phases | | Group B as multiples of Group A | | | Group C as multiples of Group B | | | Group C as multiples of Group A | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Sub-phases | Phases | Phases excluding prefeeding | Sub-phases | Phases | Phases excluding prefeeding | Sub-phases | Phases | Phases excluding prefeeding |
| Oval . . . . | Pre-oviposition . . | 1,11 | 2,69 | — | 4,85 | 2,29 | — | 5,38 | 6,18 | — |
| | Oviposition + hatching . . . | 3,29 | | | 1,96 | | | 6,47 | | |
| Larval . . . | Prefeeding . . . | 4,10 | 2,69 | 1,81 | 1,64 | 1,52 | 1,34 | 6,75 | 4,09 | 2,43 |
| | Feeding . . . . | 1,20 | | | 1,16 | | | 1,40 | | |
| | Premoulting . . | 1,92 | | | 1,36 | | | 2,62 | | |
| Nymphal . . | Prefeeding . . . | 0,40 | 1,06 | 1,98 | 1,16 | 1,18 | 1,98 | 0,46 | 1,25 | 2,35 |
| | Feeding . . . . | 1,75 | | | 1,00 | | | 1,75 | | |
| | Premoulding . . | 2,00 | | | 1,19 | | | 2,39 | | |
| Imaginal . . | Prefeeding . . . | 1,09 | 1,09 | 1,14 | 2,11 | 2,06 | 1,12 | 2,32 | 2,26 | 1,28 |
| | Feeding . . . . | 1,14 | | | 1,12 | | | 1,28 | | |
| Total periods . . . . . . | | | 1,55 | | | 1,77 | | | 2,75 | |
| Total periods excluding prefeeding periods . . . . . . . . . | | | | 2,19 | | | 1,73 | | | 3,81 |

TABLE 6 The numerical and percentage stage to stage decreases of ticks

| Group | No. of ticks harvested | | | Numerical decrease | | | Percentage decrease | | |
|---|---|---|---|---|---|---|---|---|---|
| | L | N | I | L to N | N to I | L to I | L to N | N to I | L to I |
| A | 554 | 31 | 26 | 523 | 5 | 528 | 94 | 16 | 95 |
| B | 35 492 | 12 847 | 1 064 | 22 645 | 11 783 | 34 428 | 64 | 92 | 97 |
| C | 5 513 | 1 487 | 232 | 4 026 | 1 255 | 5 281 | 73 | 84 | 96 |

Legend L = Larvae, N = Nymphae, I = Imagines

Observations on the duration of the oval, larval, nymphal and imaginal phases and those made on the number of immature forms are listed in Table 2. The average duration of the four phases and the average numerical tick yield from individual hosts of the three groups are given in Table 3. The possible minimum, maximum and average durations of each phase, used for determining the duration of the life-cycles of ticks of each group, appear in Table 4. The number of times the average duration of each developmental stage, phase or life-cycle of Groups B and C exceeds that of Group A and that of Group C exceeds that of Group B, is given in Table 5. The numerical and the percentage larval to nymphal, nymphal to imaginal and larval to imaginal decreases are recorded in Table 6.

Details presented in the above tables and figures are self-explanatory so that it will only be necessary to consider the outstanding observations made on (a) the life-cycles and (b) the tick harvests.

(a) *Duration of the life-cycles*

Table 2 shows that ticks of Groups A, B and C, represented by 1 (F1), 15 (10 F1 and 5 F2) and 11 (8 F2 and 3 F3) batches respectively, were able to complete their life-cycles under three different climatic conditions as recorded in Fig. 1 to 3.

An outstanding result is the response of the developmental phases, particularly the oval phase, to the three temperature and humidity levels as shown in Tables 2, 3 and 5. Calculations show that the duration of the oval phases of Group B (178 days) was 2,69 and of Group C (314 days) 6,18 times as long as that of Group A (66 days) while the period of Group C was 2,29 times as long as that of Group B. The extended duration of the larval, nymphal and imaginal phases (excluding the periods of the pre-feeding stages) was less pronounced and showed that the period of Group B (373 days) was 2,19 and of Group C (648 days) 3,81 times as long as that of Group A (170 days) while the period of Group C was 1,73 times as long as that of Group B.

It will be seen from Table 4 that no systematic attempts were made to determine the minimum and maximum duration of the pre-feeding periods of the three stages. Had this been done the differences in the duration of the life-cycles would have been either greater or less. In all instances the lengths of the pre-feeding periods were made to fit in with the laboratory routine and thus do not reflect the minimum hardening or maximum survival for each stage. The results nevertheless show that there is a marked difference between the two extremes. Within these routine laboratory restrictions the prefeeding periods for larvae varied from the extremes of 11 to 302 days, for nymphae 10 to 161 days and for imagines 8 to 486 days, and the average duration of the life-cycles of Groups A, B and C was 405, 628 and 1115 days respectively; that of the total enforced prefeeding periods was 235, 255 and 467 days respectively and occupied a significant portion of the life-spans.

(b) *Tick harvests*

A total of 124 adult females was used for breeding. Egg production and hatching appeared to be within normal limits in the three groups but the mortality rate of larvae during the prefeeding period was estimated to be more than 50%.

The number of immature and mature ticks harvested from each set of hosts (Table 2) and from individual animals (Table 3) in Groups A, B and C varied a great deal. A variable number died during the feeding period and soon after detachment. As many as 2064 engorged larvae and 280 engorged nymphae were recovered from individual rabbits and up to 24 adult females were harvested from a sheep. The average yield per animal of Groups A, B and C was 69, 582 and 104 larvae, 155, 135 and 62 nymphae and 13, 14 and 11 adults respectively.

The numerical and percentage decreases from the larval to nymphal, nymphal to imaginal and larval to imaginal stages are recorded in Tables 3 and 6 and Fig. 1 to 3. The mortality rates were extremely high among the immature stages and the percentage decrease from larvae to imagines in Groups A, B and C were 95, 97 and 96 respectively.

Although a total of 1322 adult females and males became available, none of them caused tick paralysis in any of the infested rabbits, sheep, goats and dogs listed in Table 2.

## Discussion and conclusion

The breeding results of the three tick groups presented in Fig. 1 to 3, show that *I. rubicundus* possesses features which make it possible for this species to complete its life-cycle under different climatic conditions in the laboratory.

Larval hatchings were good even when the eggs were permanently kept at a relative humidity of 50 to 60% which was well below the critical hatchability level of 70% given by De Vries & Davey (cited by Stampa & du Toit, 1958), The reasons for the extremely high mortality rate of larvae and nymphae in all tick batches during the prefeeding, feeding and premoulting stages are obscure.

The duration of the developmental phases is seen to be determined by the temperature at which the 3 groups are maintained. The shortest average duration of 405 days occurs at relatively high temperatures (25 to 26°C and 18 to 32°C) while the longest average period of 1115 days resulted when ticks were constantly held at low temperatures (15 to 18°C).

The different humidity and temperature levels, specified for each of the three groups, were maintained for the duration of the life-cycles. In contrast the climate in the natural habitat of ticks would vary according to the unpredictable combinations of temperature, humidity and solar radiation from one season to another. Although the breeding results do not give a true reflection of the behaviour of ticks under all conditions in nature, they nevertheless reveal some hitherto unrecorded facts about the duration of the four developmental phases which give an explanation for the survival of *I. rubicundus* under adverse conditions. The extended duration of the phases would offer protection to larval embryos and to engorged larvae and nymphae during the premoulting stage until the advent of warmer weather when hatching and moulting would occur under favourable conditions. The ticks in their different stages would then be able to search for hosts in order to continue their development.

## Summary

1. A brief review is given of the first records of tick paralysis and the investigations in the Karoo which led to the identification of *Ixodes rubicundus* as the vector.
2. Published observations on the biology and ecology were used as a guide for creating climatic conditions favourable for rearing *I. rubicundus*.
3. Sixty-day-old rabbits were used to feed immature stages.
4. Attempts to breed ticks for as many as three generations at different temperature and humidity levels were successful.
5. Tables and figures are included to show the duration of the four successive developmental phases and the number of ticks harvested.
6. The duration of the life-cycle is dependent upon the temperature at which ticks are kept.
7. Larvae hatch even when the eggs are maintained permanently at very low temperature and humidity levels.
8. Reasons for the high mortality among the immature stages are obscure.
9. Adult ticks failed to cause tick paralysis.
10. The results of these experiments should serve as a useful guide for developing better breeding methods of this species.

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