# OVIPOSITION BY TWO AUSTRALIAN SPECIES OF REPTILE TICK

BY NEIL B. CHILTON *† and C. MICHAEL BULL *

AMBLYOMMA LIMBATUM APONOMMA HYDROSAURI OVIPOSITION

ABSTRACT : A comparison was made of the number and viability of eggs laid by females of two reptile tick species, *Amblyomma limbatum* and *Aponomma hydrosauri* on each day of the ovipositional cycle. The ovipositional curves of both species followed a similar pattern, with the number of eggs laid increasing sharply during the first few days but then gradually declining. The peak of the oviposition period of *Amb. limbatum* females was however two days earlier than that of *Ap. hydrosauri* females. *Amb. limbatum* females also laid significantly more eggs than *Ap. hydrosauri* of an equivalent body weight and their eggs were significantly lighter in weight. These differences may reflect adaptations to the different conditions experienced by each species throughout most of their range.

AMBLYOMMA LIMBATUM APONOMMA HYDROSAURI OVIPOSITION

RÉSUMÉ : Une comparaison du nombre des œufs pondus, de la modalité de l'oviposition et de la viabilité des œufs entre les femelles des espèces de tiques *Amblyomma limbatum* et *Aponomma hydrosauri*, qui se trouvent chez les reptiles, a montré que la modalité de l'oviposition était la même, avec beaucoup d'œufs pondus pendant les premiers jours après le gorgement et moins d'œufs pondus pendant les jours suivants. Le maximum d'oviposition chez *Amb. limbatum* était accompli deux jours avant *Ap. hydrosauri.* Les femelles d' *Ap. hydrosauri* ont pondu moins d'œufs que les femelles d' *Amb. limbatum* et les œufs étaient moins lourds. Ces différences correspondent probablement aux conditions de l'environnement pour les deux espèces de tiques, qui ont une répartition geographique separée.

Within Australia there are approximately 52 species of ixodid tick yet little is known of the general biology (e.g. distributional limits, life cycle development, ecology, behaviour, physiology) of most species (ROBERTS, 1970). The most notable exceptions are the reptile ticks *Amblyomma limbatum* and *Aponomma hydrosauri*, where detailed studies have been made of their mating behaviour (ANDREWS & BULL, 1980, 1981a, 1981b ; ANDREWS, 1982 ; CHILTON & ANDREWS, 1988), attachment sites to hosts (ANDREWS & PETNEY, 1983 ; ANDREWS, PETNEY & BULL, 1982 ; BULL, SHARRAD & BURZACOTT, 1989 ; CHILTON, BULL & ANDREWS, 1992a, 1992b), off-host survival (BULL & SMYTH, 1973 ; BULL, CHILTON & SHARRAD, 1988) and microhabitat choice (PETNEY & ANDREWS, 1983 ; KLOMP & BULL, 1987). Despite these extensive studies, there are few comparative data on reproductive parameters, which are needed to assess population dynamics and species interactions in these species. The present study compares the number, weight and viability of eggs laid by females of the two species on each day of the ovipositional cycle.

## MATERIALS AND METHODS

Stocks of the sleepy lizard host (*Tiliqua rugosa*) and of the two tick species were collected from the Mount Mary area in South Australia. Unfed adult

* School of Biological Sciences, Flinders University of South Australia, GPO Box 2100, Adelaide, South Australia 5001, Australia.
† Present Address : Department of Veterinary Science, University of Melbourne, Parkville, Victoria 3052, Australia.
*Acarologia*, t. XXXIV, fasc. 2, 1993.

ticks were derived from nymphs which had engorged, detached and moulted in the laboratory. Sleepy lizards were each infested with 5-7 females and 5-7 males of a single tick species, and were maintained in laboratory cages in a *12 :12* photoperiod, with heat lamps on during the light phase. Under these conditions, mating and engorgement of female ticks take an average 38 days (for *Amb. limbatum*) or 41 days (for *Ap. hydrosauri*) (CHILTON & ANDREWS, 1988 ; CHILTON & BULL, 1991). Fully engorged females that detached from hosts were collected from metal trays beneath the host cages and weighed. They were kept in separate, ventilated, 6 cm diameter petri dishes at 22°C and 85 % R.H., in a *12 :12* photoperiod. Eggs were laid by 18 *Amb. limbatum* females (engorged weight 356-733 mg), and 14 *Ap. hydrosauri* females (376-775 mg). The eggs laid by each female were removed daily at 10.00 hours, weighed (to 0.1 mg), and placed in separate ventilated vials (5 cm × 1 cm). They were maintained in the same conditions as the ovipositing females. Hatching took place several weeks after oviposition. At this stage, the number of eggs laid by each female on each day, and the number that successfully hatched, were counted. Correlation analyses were used to determine if the mean egg weight, the minimum hatching time or the proportion of eggs that hatched, were related to the day of the oviposition period on which eggs were laid. For each female on each day, average egg weight was calculated from total weight of eggs laid that day divided by the number of eggs. Then, for each species, a mean daily egg weight was calculated from all females. The reproductive performance of females was determined using the Conversion Efficiency Index (CEI = weight eggs/weight of engorged female at the time of detachment ; DRUMMOND & WHETSTONE, 1970), and the reproductive fitness index (RFI = no. of eggs that successfully hatched/weight of engorged female at the time of detachment ; CHILTON, 1992).

## RESULTS

The mean number of eggs laid each day by females of each species is shown in Fig. 1. Females laid for up to 41 (for *Ap. hydrosauri*) or 49 (for *Amb. limbatum*) days. Mean oviposition by *Amb. limbatum* females peaked on the 5th day of egg laying and between days 2-9 averaged 178.7 (s.e. = ± 4.0) per day. Oviposition subsequently declined steadily. Mean oviposition by *Ap. hydrosauri* females peaked on the 7th day of egg laying and between days 3-11 averaged 89.6 (± 3.5) per day. Again, oviposition declined steadily after this. Although the mean engorged weight of the 18 *Amb. limbatum* females was significantly lighter than that of the 14 *Ap. hydrosauri* females, they laid significantly more eggs (table 1).

Fig. 2 shows the mean weights of eggs laid by *Amb. limbatum* and *Ap. hydrosauri* females on each day of the ovipositional period. Mean egg weight increased markedly over the first four days for each species. For *Amb. limbatum*, mean egg weight increased to day 13, then declined, while the mean egg weight for *Ap. hydrosauri* females tended to remain the same over the remaining days of the ovipositional cycle until the last recorded day. *Amb. limbatum* eggs were significantly lighter than *Ap. hydrosauri* eggs (table 1). The CEI and RFI were both significantly larger in *Amb. limbatum*, indicat-

TABLE 1 : The mean number and weight of eggs laid by *Amb. limbatum* and *Ap. hydrosauri* females maintained at 22°C and 80-85% R.H. F values show the results of one-way ANOVAs comparing means between species. U values show the results of Mann Whitney U tests comparing species.

| Species | No. | Mean (± s.e.) engorged weight (mg) | Mean (± s.e.) no. of eggs laid/female | Mean (± s.e.) egg weight (mg) | Mean (± s.e.) CEI | Mean (± s.e.) RFI |
|---|---|---|---|---|---|---|
| *Amb. limbatum* | 18 | 489.6 (22.5) | 2763.3 (150.8) | 0.11 (0.09) | 0.589 (0.016) | 4.70 (0.27) |
| *Ap. hydrosauri* | 14 | 599.3 (27.7) | 1517.9 (132.4) | 0.20 (0.18) | 0.486 (0.033) | 1.99 (0.28) |
| | | $F_{1,30}$ = 9.66 ** | $F_{1,30}$ = 36.10 ** | $F_{1,30}$ = 736.90 ** | U = 65.0 * | U = 11.0 *** |

Significance levels : *** = $P < 0.001$, ** = $P < 0.01$ ; * = $P < 0.05$

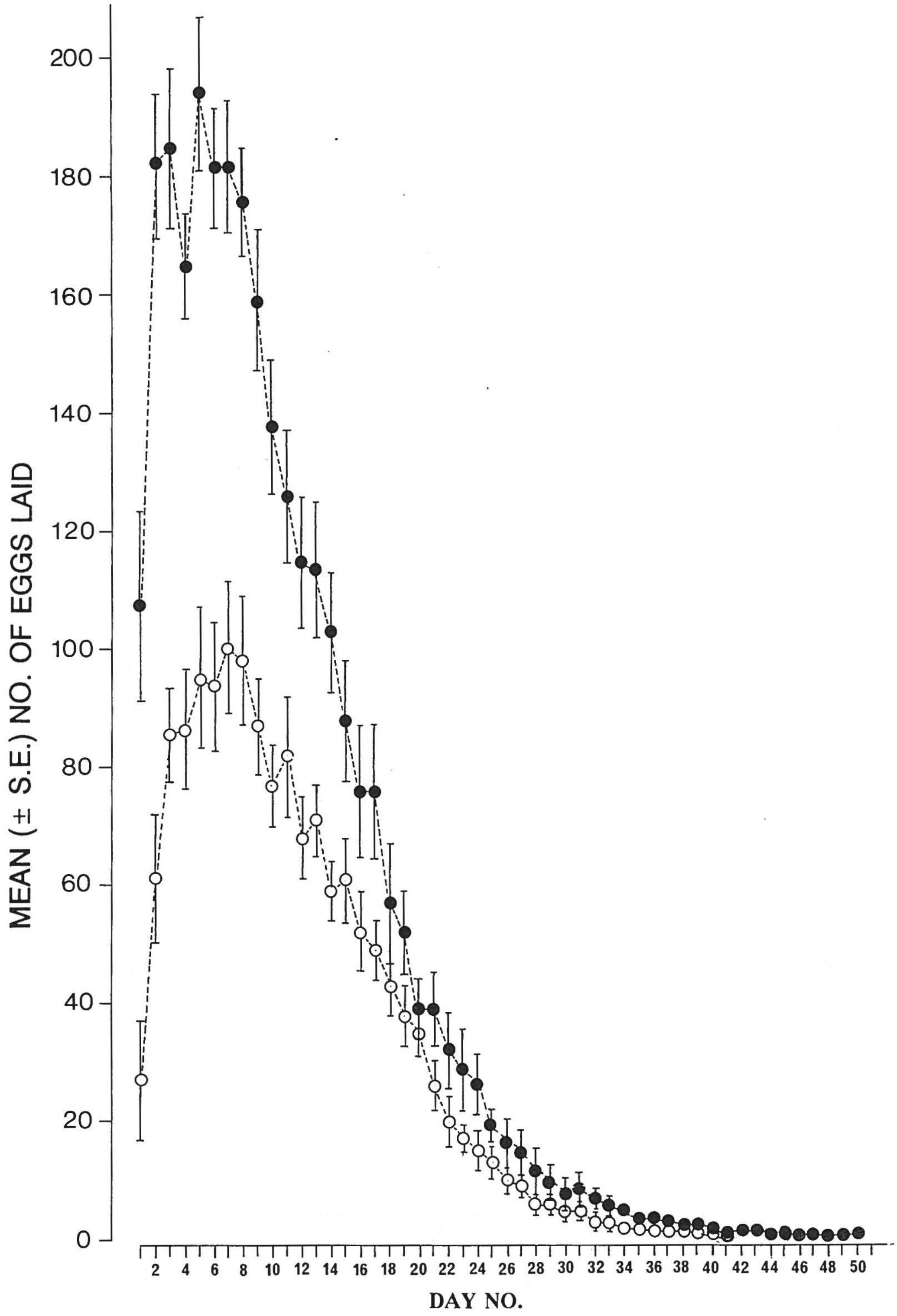


FIG. 1 : The mean (± s.e.) number of eggs laid by *Amb. limbatum* (solid circles) and *Ap. hydrosauri* females (open circles) on each day of the ovipositional cycle.

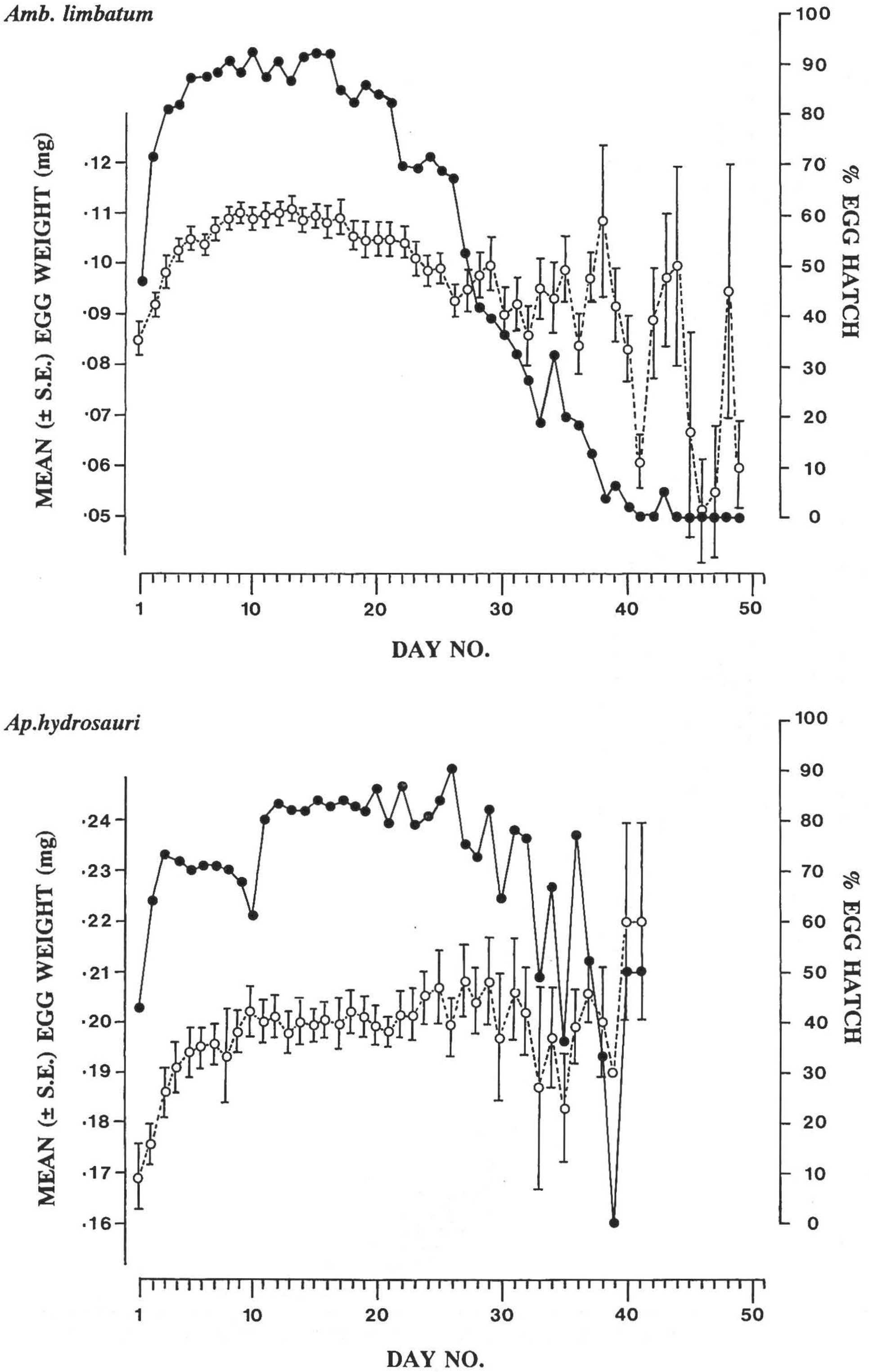


FIG. 2 : Mean weight of eggs (open circles) and viability of eggs (solid circles) laid by *Amb. limbatum* and *Ap. hydrosauri* females on each day of the ovipositional cycle.

ing that *Amb. limbatum* females were able to convert a greater proportion of their initial engorged body weight into egg production and into viable progeny than *Ap. hydrosauri* females of an equivalent body weight.

The viability of eggs is also shown in Fig. 2. For both species, only 40-50 % of the first day eggs subsequently hatched, but survival then rapidly rose and remained high to day 24. After day 24, egg viability declined markedly for *Amb. limbatum*, and to a lesser extent for *Ap. hydrosauri*. There were significant correlations between the proportion of eggs that hatched and the mean weights on that day of *Amb. limbatum* eggs ($r_s = 0.2288$, $p < 0.001$) and *Ap. hydrosauri* eggs ($r_s = 0.2354$, $p < 0.001$). For both species, on days when eggs were heavier, hatching success was higher.

## Discussion

The shape of the oviposition curves of *Amb. limbatum* and *Ap. hydrosauri* females conform to those reported for females of other ixodid ticks (Sweatman, 1967 ; Sonenshine & Tigner, 1969 ; Drummond *et al.*, 1969 ; Drummond & Whetstone, 1970 ; Drummond *et al.*, 1971a, 1971b ; Bennett, 1974a, 1974b ; Drummond & Whetstone, 1975 ; Iwuala & Okpala, 1977a, 1977b ; Davey *et al.*, 1980a, 1980b ; Ouhelli *et al.*, 1982). There were differences between the two reptile tick species in the quantity and quality of eggs laid by females on different days of the ovipositional cycle. For *Amb. limbatum*, eggs laid on the first few days and towards the end of the ovipositional cycle were lighter in weight and had a lower hatching success than eggs laid in the middle portion of the ovipositional cycle. Later eggs may have reduced viability because females may not have enough nutrients left to convert into the production of viable eggs. Alternatively, females may be unable to produce enough wax to protect later eggs from desiccation. For *Ap. hydrosauri*, eggs laid on the first few days of the cycle were lighter in weight and had low hatching success. Unlike *Amb. limbatum*, eggs laid by *Ap. hydrosauri* females at the end of the cycle did not decline in weight and there was no marked decline in hatching success. *Ap. hydrosauri* laid fewer eggs than *Amb. limbatum*.

We have suggested previously that interspecific differences in the reproductive parameters of these species may represent adaptations to the different environmental conditions each species experiences throughout the majority of its range (Chilton & Bull, 1991). In South Australia, the two tick species have allopatric distributions that abut (Bull *et al.*, 1981). *Amb. limbatum* occupies the warmer semi-arid areas of the state, while *Ap. hydrosauri* is found in more cooler, temperate areas (Smyth, 1973). *Amb. limbatum* females are on average lighter after feeding on hosts than *Ap. hydrosauri* females, yet they produce more eggs, possibly a response to maximize the number of progeny reaching the adult stage (Chilton & Bull, 1991). In the context of r- and k-selection (McArthur & Wilson, 1967), *Ap. hydrosauri* could be considered more of a k-strategist because the females are larger in size and produce fewer but larger eggs than *Amb. limbatum*, an adaptation for a more stable environment. *Amb. limbatum* produce more eggs over a longer period. However, this elongated period of oviposition is of relatively little significance because of the declining viability of those later *Amb. limbatum* eggs, at least in the conditions of this experiment. Despite this, the greater RFI value of *Amb. limbatum* females indicates that they produce 2-3 times more viable progeny than *Ap. hydrosauri*.

## Acknowledgements

This research was funded by grants from the Flinders University Research Budget, and the Australian Research Council. Dr R. Andrews discussed ideas and commented on the paper, while Dr. I. Beveridge assisted us in the translation of the abstract.

## References

Andrews (R. H.), 1982. — Mating behaviour and reproductive isolation of three species of reptile tick. — Anim. Behav., **30** : 514-524.

ANDREWS (R. H.) and BULL (C. M.), 1980. — Mating behaviour in the Australian reptile tick, *Aponomma hydrosauri*. — Anim. Behav., **28** : 1280-1286.

ANDREWS (R. H.) and PETNEY (T. N.), 1981. — Competition for sites of attachment to hosts in three parapatric species of reptile tick. — Oecologia (Berlin), **51** : 227-232.

ANDREWS (R. H.), PETNEY (T. N.) and BULL (C. M.), 1982. — Niche changes between parasite populations : An example from ticks on reptiles. — Oecologia (Berlin), **55** : 77-80.

BENNETT (G. F.), 1974a. — Oviposition of *Boophilus microplus* (Canestrini). I. Influence of tick size on egg production. — Acarologia, **16** : 52-61.

BENNETT (G. F.), 1974b. — Oviposition of *Boophilus microplus* (Canestrini) (Acarina : Ixodidae). II. Influence of temperature, humidity and light. — Acarologia, **16** : 250-257.

BULL (C. M.), BURZACOTT (D.) and SHARRAD (R. D.), 1989. — No competition for resources between two tick species at their parapatric boundary. — Oecologia (Berlin), **79** : 558-562.

BULL (C. M.), CHILTON (N. B.) and SHARRAD (R. D.), 1988. — Risk of predation for two reptile tick species. — Expt. Appl. Acarol., **5** : 93-99.

BULL (C. M.), SHARRAD (R. D.) and PETNEY (T. N.), 1981. — Parapatric boundaries between Australian reptile ticks. — Proc. Ecol. Soc. Aust., **11** : 95-107.

BULL (C. M.) and Smyth (M.), 1973. — The distribution of three species of reptile ticks, *Aponomma hydrosauri* (Denny), *Amblyomma albolimbatum* Neumann, and *Amb. limbatum* Neumann. II. Water balance of nymphs and adults in relation to distribution. — Aust. J. Zool., **21** : 103-110.

CHILTON (N. B.), 1992. — An index to assess the reproductive fitness of female ticks. — Int. J. Parasitol., **22** : 109-110.

CHILTON (N. B.) and ANDREWS (R. H.), 1988. — Mating behaviour and parapatry in two species of Australian reptile ticks. — Oecologia (Berlin), **75** : 146-152.

CHILTON (N. B.) and BULL (C. M.), 1991. — A comparison of the reproductive parameters of females of two reptile tick species. — Int. J. Parasitol., **21** : 907-911.

CHILTON (N. B.), BULL (C. M.) and ANDREWS (R. H.), 1992a. — Niche segregation in reptile ticks : Attachment sites and reproductive success of females. — Oecologia (Berlin), **90** : 255-259.

CHILTON (N. B.), BULL (C. M.) and ANDREWS (R. H.), 1992b. — Differences in attachment site of the Australian reptile tick *Amblyomma limbatum* (Acari : Ixodidae) on two host species. — Int. J. Parasitol., **22** : 783-787.

DAVEY (R. B.), GARZA, Jr. (J.), THOMPSON (G. D.) and DRUMMOND (R. O.), 1980a. — Ovipositional biology of the southern cattle tick, *Boophilus microplus* (Acari : Ixodidae), in the laboratory. — J. Med. Ent., **17** : 117-121.

DAVEY (R. B.), GARZA, JR. (J.), THOMPSON (G. D.) and DRUMMOND (R. O.), 1980b. — Ovipositional biology of the cattle tick, *Boophilus annulatus* (Acari : Ixodidae), in the laboratory. — J. Med. Ent., **17** : 287-289.

DRUMMOND (R. O.) and WHETSTONE (T. M.), 1970. — Oviposition of the Gulf Coast tick. — J. Econ. Ent., **63** : 1547-1551.

DRUMMOND (R. O.) and WHETSTONE (T. M.), 1975. — Oviposition of the Cayenne tick, *Amblyomma cajennensae* (F.), in the laboratory. — Ann. Ent. Soc. Am., **68** : 214-216.

DRUMMOND (R. O.) and WHETSTONE (T. M.), 1984. — Effect of the presence of males on engorgement and reproduction of female lone star ticks. — Southwest. Ent., **9** : 145-150.

DRUMMOND (R. O.), WHETSTONE (T. M.), ERNST (S. E.) and GLADNEY (W. J.), 1969. - Biology and colonization of the winter tick in the laboratory. — J. Econ. Ent., **62** : 235-238.

DRUMMOND (R. O.), WHETSTONE (T. M.), ERNST (S. E.) and GLADNEY (W. J.), 1971a. — Oviposition of the American dog tick (Acarina : Ixodidae). — Ann. Ent. Soc. Am., **64** : 1305-1309.

DRUMMOND (R. O.), WHETSTONE (T. M.) and GLADNEY (W. J.), 1971b. — Oviposition of the lone star tick. — Ann. Ent. Soc. Am., **64** : 191- 194.

IWUALA (M. O. E.) and OKPALA (I.), 1977a. — Egg output in the weights and states of engorgement of *Amblyomma variegatum* (Fabr.) and *Boophilus annulatus* (Say) (Ixodoidea : Ixodidae). — Folia Parasit., **24** : 162-172.

IWUALA (M. O. E.) and OKPALA (I.), 1977b. — Studies on oviposition and egg-hatching in *Amblyomma variegatum* (Fabr.) and *Boophilus annulatus* (Say) (Ixodoidea : Ixodidae). — Folia Parasit., **24** : 269-275.

KLOMP (N. I.) and BULL (C. M.), 1987. — Responses to environmental cues by unfed larvae of the Australian reptile ticks *Aponomma hydrosauri* and *Amblyomma limbatum*. — J. Parasitol., **73** : 462-466.

MCARTHUR (R. H.) and WILSON (E. O.), 1967. — The theory of island biogeography. — Princeton University Press, Princeton.

OUHELLI (H.), PANDEY (V. S.) and CHOUKRI (M.), 1982. — The effects of temperature, humidity, photoperiod and weight of the engorged female on oviposition of *Boophilus annulatus* (Say, 1821). — Vet. Parasit., **11** : 231-240.

PETNEY (T. N.) and BULL (C. M.), 1981. — A non-specific aggregation pheromone in two Australian reptile ticks. — Anim. Behav., **29** : 181-185.

PETNEY (T. N.) and BULL (C. M.), 1984. — Microhabitat selection by two reptile ticks at their parapatric boundary. — Aust. J. Zool., **9** : 233-239.

ROBERTS (F. H. S.), 1970. — Australian Ticks. — C.S.I.R.O., Melbourne.

SMYTH (M.), 1973. — The distribution of three species of reptile ticks, *Aponomma hydrosauri* (Denny), *Amblyomma albolimbatum* , Neumann, and *Amb. limbatum*, Neumann 1. Distribution and hosts. — Aust. J. Zool., **21** : 91-101.

SONENSHINE (D. E.) and TIGNER (J. A.), 1969. — Oviposition and hatching in two species of ticks in relation to moisture deficit. — Ann. Ent. Soc. Am., **62** : 628-640.

SWEATMAN (G. K.), 1967. — Physical and biological factors affecting the longevity and oviposition of engorged *Rhipicephalus sanguineus* female ticks. — J. Parasit., **53** : 432-445.

*Paru en Avril 1993.*