A DIFFERENT DEVELOPMENTAL PATTERN OF THE SEABIRD TICK *AMBLYOMMA LOCULOSUM* WHEN LIZARDS ARE PRESENT

BY J. A. RAMOS[1], J. BOWLER[2], L. DAVIS[2], S. VENIS[2], J. QUINN[2] & C. MIDDLETON[2]

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AMBLYOMMA LOCULOSUM
TICK LIFE-CYCLE
TICK-SEABIRD RELATIONSHIPS
TICK INFESTATION

SUMMARY: The developmental pattern and life cycle of the tick *Amblyomma loculosum* infesting seabirds and lizards on Aride Island, Seychelles are described. The activity of *A. loculosum* (from June to September) was coincident with the breeding season of ground-nesting seabirds, particularly *Sterna fuscata*. Nymphs fed on incubating adults in June, adults mostly on young chicks (July) and larvae on skinks (*Mabuya sechellensis*) and large chicks (September/ October). The distribution of adult ticks fitted an aggregated distribution. Duration of the life cycle is typically one year, and most ticks may survive nymphal diapause. Chicks are hosts for more than a tick stage in a season. If alternative hosts to seabirds are absent, the tick developmental pattern is different: adult ticks feed on incubating birds, larvae on young chicks and nymphs on large chicks. Skinks are presumably more reliable hosts for larvae than chicks (which suffer frequent mass mortalities) but are of minor importance for nymphs and adult ticks.

AMBLYOMMA LOCULOSUM
CYCLE DE VIE
OISEAUX MARINS
INTERRELATIONS
TAUX D' INFESTATION

RÉSUMÉ : Le développement et le cycle de vie de *Amblyomma locusum,* parasite d'oiseaux marins et de lézards sur Aride Island (Seychelles) sont décrits. L'activité de *A. locusum* (juin-septembre) coïncide avec la période de nidification de *Sterna fuscata*. Les nymphes se nourrissent sur les adultes pendant la couvaison, les adultes sur les jeunes et les larves sur *Mabuya sechellensis* et les poussins âgés. (septembre-octobre). Les tiques adultes ont une répartition en agrégats. La longueur du cycle de vie est d'une année et la majorité des nymphes survivent à la diapause nymphale. Les poussins constituent un hôte pour plusieurs stades de la tique pendant la saison. Si l'hôte de substitution est absent, le développement est différent, les adultes se nourrissent sur les oiseaux couvant et respectivement les larves et les nymphes sur les jeunes et les poussins plus âgés. Les reptiles sont des hôtes plus ordinaires pour les larves que les poussins (qui sont soumis à une forte mortalité) mais d'importance mineure pour les nymphes et les adultes.

1. Institute of Marine Research (IMAR), Departamento de Zoologia, Universidade de Coimbra, 3004-517 Coimbra, Portugal Email: jramos@ci.uc.pt
2. Aride Island Nature Reserve, C/o post office, Grand Anse, Praslin, Seychelles.

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Tick-seabird relationships have received considerable attention recently because ticks are important to the biology of seabirds, and as vectors of pathogens (CONVERSE *et al.*, 1976; FEARE 1976a; DUFFY 1983; NUTTALL, 1984; NUTTALL *et al.*, 1984; BOULINIER & DANCHIN, 1996; BARTON *et al.*, 1996). However, the distribution, abundance, and life cycle of ticks in most seabirds communities and other potential hosts are poorly known.

Here we describe the developmental pattern and life cycle of the Ixodid tick *Amblyomma loculosum* Neumann, 1907 on Aride Island (4°10'S, 55°40'E), Seychelles. *A. loculosum* is a common ectoparasite of seabirds in the Indian and Pacific Oceans, but humans, reptiles and goats may also be hosts (HOOGSTRAL *et al.*, 1976). On Aride, most seabird species breed seasonally but some breed all year round (MAUL, 1998; Bowler & HUNTER, 1999). There is also a large population of Seychelles Skinks (*Mabuya sechellensis* Duméril & Bibron, 1839) and Wright Skinks (*Mabuya wrightii* Boulenger, 1887). The latter skink species was reported to be a host for female *A. loculosum* by HOOGSTRAL *et al.* (1976).

Like other Ixodids *A. loculosum* has three developmental stages: larva, nymph and adult. Its life cycle takes 5 months to complete in the laboratory without diapause (HOOGSTRAL *et al.*, 1976), and one or two years in a colony of Sooty Terns (*Sterna fuscata* Linnaeus, 1766) in the Seychelles (FEARE & GILL, 1997). The activity period of seabird ticks coincides with the breeding season of their hosts (STEELE *et al.*, 1990; FEARE & GILL, 1997), but most studies have concentrated on high latitude seabird colonies where alternative hosts to seabirds are generally absent. On Bird Island (about 80 Km north of Aride Island), Seychelles, the life cycle of *A. loculosum* appeared closely synchronised with that of the Sooty Tern: adult ticks were numerous during the incubation of the birds in June, larvae were abundant when young chicks were present in July, and nymphs were found when older chicks were present in September (FEARE & GILL, 1997). Virtually no other hosts were available on the Sooty Tern colony on Bird Island. FEARE & GILL (1997) suggested that when hosts are present all year round all stages of *A. loculosum* might occur simultaneously.

We surveyed the distribution and abundance of different stages of *A. loculosum* on seasonally and aseasonally ground-nesting seabird species, and reptiles in order to describe the life cycle of *A. loculosum* in a multi-host situation and assess the importance of lizards in the developmental pattern of this tick species. We concentrated tick sampling during the breeding season of the ground-nesting seabird species because previous observations (BETTS 1998, RAMOS et al. 2001) suggested that ticks were active during this period. At the same time we sampled opportunistically seabird species breeding on trees, boulders and burrows in order to assess how important would be these species as hosts, when compared with ground-nesting species.

METHODS

Aride Island, with 72 ha, is a Royal Society for Nature Conservation nature reserve, dominated by *Pisonia grandis* trees. The island supports large populations of seabird species and skinks (TABLE 1). We concentrated tick sampling on the most likely hosts: the three ground-nesting seabird species (two seasonally: Sooty Tern and Roseate Tern, (*Sterna dougallii* Montagu, 1813) and one aseasonally: White-tailed Tropicbird (*Phaethon lepturus* Daudin, 1802) and one skink species, the Seychelles Skink (TABLE 1). Seabird species nesting on trees (Fairy Tern *Gygis alba* Sparrman, 1786; Lesser Noddy *Anous tenuirostris* Temminck, 1823), rocks (Brown Noddy *Anous stolidus* Linnaeus, 1758) and burrows (Wedged-tailed Shearwater *Puffinus pacificus* Gmelin, 1789, AUDUBON's Shearwater *Puffinus lherminieri* Lesson, 1839) were examined opportunistically when most adults were breeding (May-August) to assess if they are hosts to the ticks.

The most abundant ground-nesting seabird species, the Sooty Tern, was caught during six periods of 4-6 days each from 18 June-22 July 1999 and examined for ticks. White-tailed Tropicbirds were caught weekly from March to July 1999. Skinks were caught in June-July, September and November (TABLE 1). Roseate Tern chicks were caught daily in June-July. Roseate Tern adults were not caught, in order to avoid disturbance of this threatened species, but

Hosts :	Breeding season	Population size (adults)	Nesting habitat	Periods of tick sampling and methods
Sooty Tern	May-November.	720,000	Ground	Adults and chicks: during six periods of 4-6 days each from 18 June-22 July 1999.
Roseate Tern	May-August	2698	Ground	Adults: observed daily from a permanent hide in June-July 1998; the % of these with signs of tick infestation (see text) were noted. Chicks: caught daily in June-July 1997 and 1998.
White-tailed Tropic bird	All months of the year	2,550	Ground	Adults and chicks: From March-June 1999
AUDUBON's Shearwater	All months of the year	114,000	Burrow	Adults and chicks in burrows: July 1999; Fledglings: opportunistically in November 1998.
Wedge-tailed Shearwater	All months of the year	39,000	Burrow	Adults in burrows: July 1999
Lesser Noddy	March-September	220,000	Tree	Adults and chicks: June-July 1997 Chicks: June-July 2001
Fairy Tern	All months of the year	8,500	Tree	Chicks: opportunistically May-August 1997
Seychelles Skink	May-August	153,072	Ground	15-17 September 1998, November 1998, June-July 1999 and 14-15 September 1999.
Wright Skink	May-August	46,656	Ground	15-17 September 1998, June-July 1999

TABLE 1: Timing of breeding season, population size, nesting habitat (from MAUL, 1998; BOWLER & HUNTER, 1999, 2001) and sampling periods for *Amblyomma loculosum* on likely seabird and skink host species on Aride Island.

those with signs of tick infestation (standing on one foot only, sometimes being possible to observe engorged females) were observed and noted from a permanent hide (RAMOS 2001).

Skinks were captured within and on the periphery of the Roseate and Sooty Tern colonies during and after the terns breeding season: (1) during the peak of nymph and adult tick infestation, June to July 1999, to assess how important are skinks as hosts when compared to seabirds. 2) 30 to 60 days after (September 1999), to record larvae parasites on skinks. (3) In mid-November (of 1998), to see whether larvae had moulted into nymphs. Skinks were also captured within areas >100 m from the Roseate and Sooty Tern colonies to act as control for each of the previous sampling periods, therefore investigating whether skinks are important hosts per se for each tick stage. Wright Skinks were not examined for larvae in 1999 because they were less abundant and hosted few larvae in1998 (see results).

Larvae of two tick species infested skinks: *Amblyomma loculosum* (Ixodidae, dorso-ventrally compressed) and *Ornithodoros* sp (Argasidae, globular in appearance, identified by the Natural History Museum, London through courtesy of Prof. Chris FEARE). Larvae of both species were not identified in 1998, but those attached to Seychelles Skinks were distinguished in 1999 with a hand lens. Larvae of *A. loculosum* are very small (average length 0.62 mm, HOOGSTRAL *et al.*, 1976) and no attempt was made to count them on chicks. Larvae and nymphs readily quest on humans, and this was used to check their presence or absence in the colonies.

Nymphs and adult ticks were found through skin palpation and visual search, especially the feet, legs, head, neck and underwings; these being the most common sites of attachment for *A. loculosum*. Nymphs and adults were counted separately per location of attachment (around eye, around bill and on head, feet, leg and others parts of the body). Adult ticks were also sexed. Contrary to other ixodids such as *Ixodes uriae* (BARTON *et al.* 1996), adult male *A. loculosum* are frequently found on hosts (FEARE & GILL, 1997, RAMOS *et al.* 2001).

On-host tick data for each sampling period are presented as: a) prevalence of infested birds, that is the % of individuals parasitised by one or more ticks, and b) the number of ticks per bird. Tick prevalence on daily caught Roseate Tern chicks was expressed as a running mean pooled over 3-day periods.

Differences in the timing of activity and abundance of each tick stage, between adult and juvenile seabird

hosts, were examined using KRUSKAL-WALLIS test. Variance to mean ratios and GREEN's Index (G = (variance/mean) — 1/n-1) were carried out to investigate the dispersion of nymphs and adult ticks among hosts. GREEN's Index can be used to compare samples varying in the total number of individuals, their sample means and the number of sample units (hosts) in the sample (LUDWIG & REYNOLDS, 1988). Comparison of skink infestation inside and outside colony areas was analysed using Chi-square and G-test values computed from contingency tables, and the Fisher-exact test.

RESULTS

Very few ticks were found on seabird species nesting on trees, rocks and burrows. No ticks were recorded from 30 Lesser Noddy adults and five Fairy Tern chicks sampled in 1997. From 60 Lesser Noddy chicks sampled in June 2001 one chick was infested with a nymph, and one chick had both a male and a female tick (these chicks were on branches 1.5 m above the ground and close to a Sooty Tern area). MAUL (1998) does not report parasited animals during previous work on Brown Noddy (546 adults and 200 chicks were ringed between late April and mid-September 1995-1997), but in June 2001 we observed a Brown Noddy adult (breeding close to a Sooty Tern area) carrying an engorged female tick. From 10 Wedged-tailed Shearwater adults, 10 AUDUBON's Shearwater chicks and 12 adults captured in burrows from June to August 1999, only one nymph was recorded on one AUDUBON's Shearwater adult nesting within a Sooty Tern area.

Most ticks were found on ground-nesting seabirds: Sooty Tern, Roseate Tern and White-tailed Tropicbird. There were marked differences in the activity patterns of nymphs and adult ticks infesting ground-nesting seabird hosts, but each stage had a peak of infestation at around the same time for each seabird host (FIG. 1). Nymph ticks presented unimodal patterns of activity with peak infestation in mid-June, when Sooty and Roseate Terns were incubating, followed by a unimodal patterns of adult tick activity with peak infestation in mid-July, when Sooty and Roseate Terns had young chicks. Roseate Tern adults with engorged female ticks attached on the feet were also observed from a permanent hide in July of 1997 and 1998. Over 80% of the nymphs on Sooty Tern adults were found around the bill, whereas over 80% of the adult ticks were found on the feet.

From the end of August to mid-September large numbers of larvae were present in the Sooty Tern and Roseate Tern colonies in 1995, 1996 (BETTS, 1998; MAUL, 1998) and 1998. Larvae quickly appeared on the feet and legs of humans and were found on Seychelles Skinks captured in the Roseate Tern colony (FIG. 1). Vast numbers of larvae were also present on the 2 October 1999.

Nymphs were also observed on AUDUBON's Shearwater juveniles wandering on the island in July 1999 [four chicks captured, respectively with: (1) two engorged nymphs, (2) three engorged females, (3) three females and one male, and (4) 48 nymphs, one male and one engorged female], and on juvenile Sooty Terns, Lesser Noddies, and Wedge-tailed Shearwaters standing on the ground away from nest-sites in mid November 1998. These observations show that *A. loculosum* was strongly associated with seabird species nesting on the ground in large, dense and persistent colonies (especially Sooty Terns) or nest-sites, but are not prevented from infesting other species if they happen to be on the substrate used by the ticks.

Significant differences in the timing of activity between the six sampling periods of June-July 1999 were found for nymphs and adult ticks on Sooty Tern adults (Kruskal-Wallis H (5, n = 612) = 38.51 and 18.73, $P < 0.001$ and $P < 0.01$, FIG. 1). No significant differences in the timing of activity were detected for nymphs on Sooty Tern chicks (H (3, n = 507) = 3.69, ns) but that of adult ticks approached significance (H (3, n = 507) = 6.91, $P = 0.075$, FIG. 1). In July, when both Sooty Tern adults and chicks were present, a mean (± SD) of 0.11 ± 0.43 nymphs/bird occurred in adults whereas only 0.026 ± 0.26 nymphs/bird were found on chicks; this nymph infestation differed between Sooty Tern adults and chicks (H (1, n = 772) = 19.36, $P < 0.001$). In contrast, 0.18 ± 0.71 adult ticks/bird were found on Sooty tern adults, whereas 0.99 ± 2.42 adult ticks/bird occurred on Sooty Tern chicks (H (1, n = 772) = 34.66. $P < 0.001$).

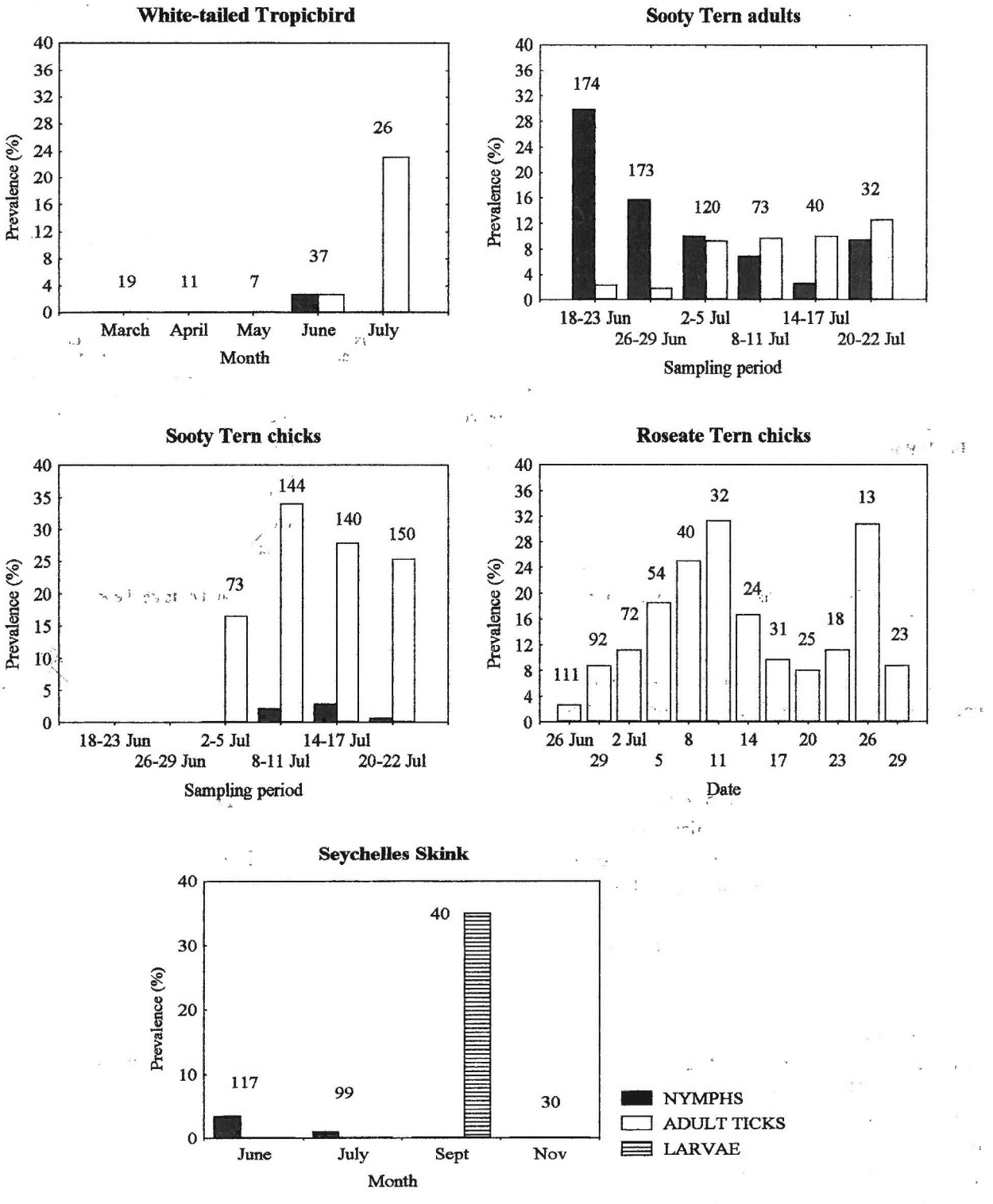

FIG. 1: Prevalence of the three developmental tick stages (nymphs, adult ticks and larvae) on hosts. Numbers above bars indicate sample size. White-tailed Tropicbirds and Sooty Terns were sampled in 1999, Roseate Terns in 1997 and 1998 and Seychelles Skinks in 1998 and 1999.

	Nymphs on Sooty Tern adults (18-23 June)	Adult ticks on Sooty Tern chicks (8-12 July)	Adult ticks on Roseate Tern chicks (7-13 July)	Larvae on Seychelles Skink (14-15 September 1999)
Number of hosts	174	144	85	40
Prevalence	29.9%	34.0%	27.1%	35%
Mean no. of ticks per host	0.51	1.28	0.38	0.53
Variance	1.01	8.46	0.55	0.67
Variance/mean ratio	1.98	6.61	1.45	1.26
GREEN's index of dispersion	0.019	0.117	0.015	

TABLE 2: Abundance, prevalence and degree of clumping (variance/mean ratios and GREEN's index of dispersion) of nymphs, adult ticks and larvae at the time of peak infestation.

	Nymphs (June-July 1999)		Larvae (14-15/09/1999)
	No. of Seychelles Skinks (% infested)	No. of Wright Skinks (% infested)	No. of Seychelles Skinks (% infested)
Inside Roseate Tern colony	89 (0.0)	21 (0.0)	40 (35%)
Outside Roseate Tern colony	84 (0.0)	31 (0.0)	20 (25%)
Inside Sooty Tern colony	117 (3.4)	25 (4.0)	
Outside Sooty Tern colony	76 (0.0)	28 (0.0)	
Statistic	$G = 3.81$ ns	Fisher exact = 0.47	$\chi^2 = 0.19$ ns

TABLE 3: *A. loculosum* nymphal and larval infestation in Seychelles Skinks and Wright Skinks, inside and outside the Roseate and Sooty Tern colonies.

The mean density of parasites was smaller than the variance, suggesting an aggregated distribution (TABLE 2). The Green's index of dispersion ranged between 0.015 and 0.117 (TABLE 2), suggesting that ticks presented a low degree of clumping. The immature stages seemed opportunistic because nymphs and larvae were active on several substrate (soil, boulders and ferns), which should maximise their chances of finding a host.

In September 1998, when the larvae of both *A. loculosum* and *Ornithodoros* sp were not separated, 92% (n = 48) of the Seychelles Skinks captured in the Roseate Tern colony were infested, whereas only 33% (n = 12) of the Wright Skinks had larvae. Seychelles Skinks were revealed as important hosts for larvae, marginal hosts for nymphs and of no importance for adult ticks (FIG.1, TABLE 2 and 3). The prevalence of larvae on Seychelles Skinks did not differ significantly between the Roseate Tern colony and areas outside the colony (TABLE 3). The number of skinks with nymphs was lower outside than inside the Sooty Tern areas (TABLE 3), suggesting that nymphal populations outside the seabird colonies were marginal.

DISCUSSION

On Aride Island, *A. loculosum* was active mostly from May to mid-October, and largely inactive from November to April. The activity period is concomitant with the breeding season of ground-nesting seabird species. The feeding activity of nymphs, adult ticks and larvae in June, July and September, respectively, suggests that the life cycle of *A. loculosum* is matched to the breeding cycle of the most abundant and synchronous ground-breeding species, the Sooty Tern. Although ticks may parasitise tree and burrow-nesting seabirds the results of this study suggests that these species have a small role as hosts. Reptiles were important hosts for tick larvae and marginal hosts for nymphs and may play an active roll in tick dispersal. The strong peak of nymph activity in June and the fact that nymphs firstly appeared on the legs of

researchers in May (In 1999, nymphs were firstly detected on humans on the 8 of May) suggest that most ticks survive nymphal diapause. The diapause should cease a few weeks before the onset of laying by Sooty Terns. Around one month elapsed between the peaks of feeding activity of nymphs and adults suggesting that nymphs take about a month to moult into adults. Therefore, on Aride, most *A. loculosum* should take one year to complete its life cycle. Some ticks may diapause in the adult stage or even finish their life cycle without diapause because: (1) an engorged female tick was found on a White-tailed tropicbird on 10 October 1999, (2) nymphs and adult ticks were found simultaneously on two White-tailed tropicbird chicks in June 2001, (3) fledglings of several seabird species were found with nymphs in November 1998 (when very few Sooty Terns were present in the colony), and (3) one nymph quested on one of us (J. B.) in December 1999. However, a strategy of ending the life cycle without diapause should not be available for most ticks because few ground-nesting seabirds are present on Aride from October/November until May. White-tailed Tropicbirds, which breed at 264 days interval, are the exception, but the population is small (around 2550 pairs, Bowler & HUNTER 2001). A successful White-tailed Tropicbird takes 110-140 days from egg laying to chick fledging, which could enable the completion of the tick life cycle without diapause.

On Aride, adult ticks feed mostly on young chicks, whereas on Bird Island adult ticks fed on adult birds. Feeding on young chicks has several advantages: a) the development of immunity should be less in young birds, b) during the chick hatching and the chick rearing period host density reaches a peak, c) chicks remain within the colony until fledging whereas adults may spend relatively long time periods feeding in the sea, representing therefore a risk for ectoparasites because ticks will die if they fall or are removed at sea. This point is especially important for tropical seabirds because their fledging periods are much higher than incubation periods (Sooty Terns: 60-70 days: 28 days, Roseate Tern: 30-40 days: 22 days). Besides adult birds may repeatedly raise and shake their feet during the night, thereby reducing the time available for ticks to attach (FEARE, GILL & MASONOBU, 1995). In temperate seabird species fledging periods are much shorter and parasites attaching to chicks may be at risk (BARTON *et al.*, 1996). On the other hand chicks may be disadvantageous as hosts if young chicks die, but several studies on tropical seabirds showed that breeding failure is often characterised by death of half-grown chicks (FEARE, 1976b; MILTON, SMITH & BLABER, 1996; RAMOS, 2001).

On Bird Island, about 76 km from Aride, the life cycle of *A. loculosum* is linked also to the Sooty Tern breeding cycle. The adult ticks feed on incubating birds, larvae on young chicks and nymphs on older chicks (FEARE & GILL, 1997). The main difference between Bird and Aride is that there are virtually no alternative hosts on Bird Island (the Seychelles Skinks are restricted to the interior woodland and part of the beach fringe, away from the Sooty Tern colony, C. FEARE, pers. comm.). The presence of lizards throughout Aride Island should contribute to explain the different developmental pattern from that observed on Bird Island. Skinks may be especially important if Sooty Terns fail at the juvenile stage around September (FEARE, 1976b). On Bird Island the tick population may decline sharply if mass chick mortality occurs in September (FEARE & GILL, 1997). If food conditions are poor, Aride-Roseate Terns may abandon their eggs and desert the colony, thereby decreasing infestation levels in Roseate Tern areas in subsequent years (RAMOS *et al.* 2001). However, on Aride, ticks are unlikely to disappear such as on Bird Island where Sooty Terns are the only hosts (FEARE & GILL 1997).

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REFERENCES

BARTON (T. R.), HARRIS (M. P.), WANLESS (S.) & ELSTON (D. A.), 1996. — The activity periods and life-cycle of the tick *Ixodes uriae* (Acari : Ixodidae) in relation to host breeding strategies. — Parasitology 112: 571-580.

BETTS (M.), 1998. — Aride Island scientific report 1997. — Report to RSNC. Royal Society for Nature Conservation, Lincoln, UK.

BOULINIER (T.) & DANCHIN (E.), 1996. — Population trends in Kittiwake *Rissa tridactyla* colonies in relation to tick infestation. — Ibis 138: 326-334.

BOWLER (J.) & HUNTER (J.), 1999. — Aride Island scientific report 1998. — Report to RSNS. Royal Society for Nature Conservation, Lincoln, UK.

BOWLER (J.) & HUNTER (J.), 2001. — Aride Island scientific report 2000. — Report to RSNS. Royal Society for Nature Conservation, Newark, UK.

CONVERSE (J. D.), HOOGSTRAAL (H.), MOUSSA (M. I.), KAISER (M. N.), CASALS (J.) & FEARE (C. J.), 1976. — Aride virus, a new ungrouped arbovirus infecting *Amblyomma loculosum* ticks from Roseate Terns in the Seychelles. — Arch. Virol. 50: 237-240.

DUFFY (D. C.), 1983. — The ecology of tick parasitism on densely nesting Peruvian seabirds. — Ecology 64: 110-119.

FEARE (C. J.), 1976a. — Desertion and abnormal development in a colony of Sooty Terns infested by virus-infected ticks. — Ibis 118: 112-115.

FEARE (C. J.), 1976b. — The breeding of the Sooty Tern *Sterna fuscata* in the Seychelles and the effects of experimental removal of its eggs. — J. Zool. (Lond.) 179: 317-360.

FEARE (C. J.) & GILL (E. L.), 1997. — The life cycle of the tick *Amblyomma loculosum* in a Sooty Tern *Sterna fuscata* colony in the Seychelles. — J. Zool. (Lond.) 241: 643-648.

FEARE (C. J.), GILL (E. L.) & MASONOBU (F.), 1995. — Behavioural defence by Sooty Terns *Sterna fuscata* against tick infestation ?. — Ibis 137: 116.

HOOGSTRAAL (H.), WASSEF (H. Y.), CONVERSE (J. D.), KEIRANS (J. E.), CLIFFORD (C. M.) & FEARE (C. J.), 1976. — *Amblyomma loculosum* (Ixodoidea: Ixodidae) identity, marine bird and human hosts, virus infection, and distribution in the Southern Oceans. — Ann. Entomol. Soc. Am. 69: 3-14.

LUDWIG (J. A.) & LUDWIG (J. F.), 1988. — Statistical Ecology. — John Wiley & Sons, New York, 337 pp.

MAUL (A. M.), 1998. — Breeding biology and monitoring of three seabird species (Brown Noddy *Anous stolidus*, Lesser Noddy *Anous tenuirostris*, Roseate Tern *Sterna dougallii*) on Aride Island, Seychelles, with special comments on breeding behaviour and biometrics of the Brown Noddy. — PhD. Thesis. Karl-Franzens University, Graz, Austria, 141 pp.

MILTON (D. A.), SMITH (G. C.) & BLABER (S. J. M.), 1996. — Variable success in breeding of the Roseate Tern *Sterna dougallii* on the Northern Great Barrier. — Emu 96: 123-131.

NUTTALL (P. A.), 1984. — Tick-borne viruses in seabird colonies. — Seabird 7: 31-41.

NUTTALL (P. A.), KELLY (T. C.), CAREY (D.), MOSS (S. R.) & HARRAP (K. A.), 1984). — Mixed infection with tick-borne viruses in a seabird colony in Eire. — Arch. Virol. 79: 35-44.

RAMOS (J. A.), 2001. — Seasonal variation in reproductive measures of tropical Roseate terns: previously undescribed breeding patterns in a seabird. — Ibis 143: 83-91.

RAMOS (J. A.), BOWLER (J.), DAVIS (L.), VENIS (S.), QUINN (J.) & MIDDLETON (C.), 2001. — Activity patterns and effect of ticks on growth and survival of tropical Roseate Tern nestlings. — Auk 118. in press.

STEELE (G. M.), DAVIES (C. R.), JONES (L. D.), NUTTALL (P. A.) & RIDEOUT (K.), 1990. — Life history of the seabird tick, *Ixodes* (*Ceratixodes*) *uriae*, at St Abb's Head, Scotland. — Acarologia 31: 125-130.