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ACTIVITY PATTERNS AND EFFECT OF TICKS ON GROWTH AND SURVIVAL OF TROPICAL ROSEATE TERN NESTLINGS

JAIME A. RAMOS,[1,3] JOHN BOWLER,[2] LAURA DAVIS,[2] SARAH VENIS,[2] JOHN QUINN,[2] AND CAROLE MIDDLETON[2]

[1]*Institute of Marine Research (IMAR), Departamento de Zoologia, Universidade de Coimbra, 3004-517 Coimbra, Portugal;*

[2]*Aride Island Nature Reserve, c/o Post Office, Grand Anse, Praslin, Seychelles*

ABSTRACT.—Patterns of abundance of the seabird tick *Amblyomma loculosum* and their effects on Roseate Tern (*Sterna dougallii*) nestling growth, fledging age, and survival are described on Aride Island, Seychelles, in 1997–1999. Female ticks attached to nestlings from 4 to 14 days (to engorge) whereas male ticks attached for 1–3 days. The linear growth rate of birds carrying female ticks (0.24 g/day) was significantly different from that of nonparasitized nestlings of the same age and similar (or even lower) hatching weight (4.07 g/day). Parasitized nestlings that fledged did so 5.2 days later than nonparasitized nestlings of similar age. Only 37.5% of the nestlings infested with female ticks fledged compared with 83.3% of the noninfested nestlings. During the successful 1998 breeding season, around 100 nestlings died from tick infestation (24.3% of the nestling deaths). Ticks appeared to accelerate nestling mortality during periods of food shortage. Despite an annual difference of two weeks in the timing of breeding of the Roseate Terns between 1997 and 1998, adult ticks parasitized nestlings in July, with an infestation peak occurring between 8–12 July in both years. However, in 1997, nestlings were parasitized at a younger age, suggesting that ticks (nymph stage) must attach to Roseate Tern adults as soon as they make a nest scrape (usually in May). Ironically, the frequent breeding failures of the Roseate Terns will result in lower infestation levels in subsequent years, which will benefit the birds. *Received 1 March 2000, accepted 20 January 2001.*

PARASITES ARE one of the main costs of coloniality (Alexander 1974). Seabirds nest at high densities, are long-lived, and show high interannual fidelity to their breeding sites (Furness and Monaghan 1987, Aebischer and Coulson 1990), and therefore represent a large potential host population for parasites with limited mobility. High densities of ticks in seabird colonies have been related to desertion of nests and nestlings, delayed development or mortality of nestlings due to blood loss and the transmission of diseases (Feare 1976, Duffy 1983, Harris 1984, Nuttal et al. 1984, McKilligan 1996, Morbey 1996). The activity periods of ticks and their effects on the breeding success of seabirds have received some attention recently (Duffy 1983, Nuttal et al. 1984, Morbey 1996, Barton et al. 1996) but most studies have concentrated on high-latitude seabird colonies, and few studies analyzed the relationship among reduced growth or increased mortality and ticks.

This study examines the effect of an infestation by the hard tick *Amblyomma loculosum* on the growth and survival of Roseate Tern (*Sterna dougallii*) nestlings on Aride Island, Seychelles. The Roseate Tern is a globally threatened seabird species and Aride Island has one of the largest Roseate Tern colonies in the world. Their breeding success is highly variable and characterized by frequent complete breeding failures (Ramos 2001). Those failures are mainly due to food shortages (Ramos 2000), but in the study colony infestation by *A. loculosum* has been considered, without supporting evidence, to be a contributory factor for many years (Warman 1979, Maul 1998).

Two tick species occur on Aride, the Ixodid (*A. loculosum*) and the Argasid (*Ornithodoros capensis*) (Hoogstraal and Feare 1984). Nymphs of *O. capensis* were observed in soil samples but virtually no ticks were detected on birds. Low infestations by *O. capensis* occur on Aride but heavy infestations, such as those described by Feare (1976) on Bird Island, have not been recorded on Aride (Maul 1998 and references within) nor on other islands of the Seychelles

[3] E-mail: jramos@ci.uc.pt

since the 1970s (Feare and Gill 1997); therefore the effect of the soft tick on the Aride seabirds should be small. The main aim of this study is to quantify the effect of the currently dominant tick, *A. loculosum,* on the breeding success of Roseate Terns. Special attention is paid to female ticks because they take several days to engorge and should have a greater effect on nestlings than males.

The life cycle of *A. loculosum* on Aride is typically one year, and is fairly synchronized with the breeding season of the most abundant, synchronous, and successful ground-nesting seabird species, the Sooty Tern (*Sterna fuscata*). Nymphs feed on adults in June, adult ticks on young nestlings in July, and larvae on older nestlings and skinks (Seychelles skink, *Mabuya sechellensis* and Wright skink, *Mabuya wrightii*) in September (Davis 1998, Ramos 1999). Most Roseate Terns breed in a colony ~40 m away from the nearest Sooty Tern colony (Ramos 1998a) and, in addition to a highly variable breeding success, show strong annual variations in timing of breeding (Ramos 2000). This situation is important to describe patterns of tick activity in relation to variations in hosts' reproductive cycles.

This study is part of a wider program on the breeding ecology of Roseate Terns on Aride Island and aims to: (1) quantify the effects of ticks on nestling growth, fledging age and survival, (2) establish feeding times of adult ticks from ringed nestlings in the field, and (3) investigate the activity periods of ticks in relation to birds' breeding success and breeding cycle.

METHODS

General methods.—Roseate Tern breeding ecology was studied on Aride Island, Seychelles, from June to August, 1997–1999. Roseate Terns nest at high densities (0.63–1.23 nests/m^2) under a canopy of *Pisonia* trees and select nest sites close to boulders or logs (Ramos 1998a).

Roseate Terns were studied in a main colony (1,000–1,300 pairs) and in three discrete groups, with 8–12 pairs (small colonies) in the vicinity of the main colony. A low-disturbance method and a moderate-disturbance method were used to study nests (Ramos 1998a, in press). The low-disturbance method entailed mapping, from a permanent hide, all nests in a defined study plot of about 180–200 m^2, and monitoring the fate of eggs and nestlings daily. We refer to that as the *hide area.* The moderate-disturbance method consisted of establishing two study quadrats with corner posts and string. Nests in those quadrats and in the small colonies were marked, and nestlings were banded at hatching and weighed. We refer to that as the *study quadrats.* Thereafter, nestlings were searched for daily and weighed (throughout the period of nestling development, June–July) whenever encountered to the nearest 0.1, 0.2, or 0.5 g using Pesola balances. Fledged nestlings were considered as those that were not losing weight when last weighed at more than 5 days, and were not found dying in the area around the quadrats and subcolonies (Nisbet et al. 1990).

The body of every Roseate Tern nestling caught during daily visits to study quadrats was examined for ticks, especially the feet, legs, and underwing; the most common sites of attachment of *A. loculosum* (Feare and Gill 1997). Adult ticks were counted and, in 1998 and 1999, were also sexed (differences between sexes described by Hoogstraal et al. 1976).

Effects of ticks on nestling growth and survival.—Linear growth rate was compared between nestlings with and without female ticks because those attach for long periods and may be a considerable burden to nestlings. When ticks fall off, infested nestlings are still easy to recognize because female ticks leave a scar that lasts for several days. Ticks also leave some nestlings with apparently stiff joints in the legs, forcing them to use the carpal joint for support when walking. Linear growth rate was defined as the slope of a regression line to mass data during the quasilinear growth period (3–14 days, Nisbet et al. 1995). Linear growth rate was calculated for nestlings (with at least four data points) carrying female ticks; each one of those nestlings was given a pairwise comparison with a nestling of the same age and similar (or even lower hatching weight), in order to control for the effects of hatching mass and nestling age on growth.

Feeding times of adult ticks.—Feeding times of adult ticks were established from banded nestlings. That was defined as the number of days between the first morning that the tick was first observed on a banded nestling, and the morning following the last observation. Those nestlings were captured prior to tick attachment and on every morning from the day when ticks were first detected until they dropped off. It is assumed that adult ticks attach and fall off during the night or early morning (Feare and Gill 1997).

Activity patterns of ticks in relation to Roseate Tern breeding cycle and breeding success.—The activity patterns of ticks during the Roseate Tern breeding season were established with two methods: (a) handling Roseate Tern nestlings from hatching to fledging (2 to 35 nestlings were handled daily, median = 12); and, (b) observing from the hide area adults (1998–1999) and nestlings (1997–1999) with signs of tick infestation. Birds with signs of tick infestation are easily recognized because they stand on one foot only and, when walking, may have to use the carpal joint

for support (Feare and Gill 1997, Ramos 1998a). During the incubation period, legs and feet of 16 to 33 (median = 32) adults (off-duty birds standing by the nest) were observed daily with binoculars between 9–10 h for signs of tick infestation. Similarly, during the nestling rearing period, 20–55 adults (median = 50) and 20–70 nestlings were observed daily. Engorged female ticks (about 13–17 mm long) are easily observed with binoculars; males (about 4.7 mm long) are more difficult to see, and nymphs (about 1/3 the size of males) are unlikely to be seen (Hoogstraal et al. 1976, J. Ramos pers. obs., C. Feare pers. comm.). Therefore, it is not possible to differentiate between tick stages using method (b). It was impossible to ascertain whether nonbanded nestlings that appeared in the study quadrats (i.e. presumably from adjacent areas) and caught on consecutive days were the same individuals. Therefore, all Roseate Tern nestlings caught on the study quadrats, including recaptures of banded nestlings, were considered in estimating tick prevalence, that is, the proportion of nestlings infested with at least one tick. Tick prevalence using both methods (a) and (b) were expressed as a three-day running mean of the prevalence of tick infestation.

The on-host activity periods of ticks during the 1999 breeding season could not be followed after early July because Roseate Terns deserted their clutches (see below). To assess the effect of that host absence on tick abundance, we took 300 cm^3 scoop samples of soil and debris from 38 nests of both Roseate Terns and Sooty Terns. All samples were taken from nests with eggs: recently abandoned Roseate Tern nests (~90% of the Roseate Terns abandoned their clutches between 1–10 July) and incubating Sooty Terns. Soil samples were sorted by hand, and nymphs (engorged or molting) and adult ticks were counted. Unfed nymphs would be too small for accurate counts, but none of those were seen in the soil samples. Similarly we compared the abundance of larval ticks on Seychelles skinks (larvae of both tick species, *A. loculosum* and *O. capensis*, infest skinks but they are very small and were not distinguished) between a successful year for the Roseate Tern (1998) and a failure year (1999), in order to assess the effect of the absence of adult tick hosts (the Roseate Tern adults and nestlings) on the abundance of tick larvae. Between 15–24 September of 1998 and 1999, Seychelles skinks were captured by hand in the area of the Roseate Tern colony, marked with a paint spot, and examined for the number of tick larvae.

Analyses.—Statistical tests followed Zar (1986). Chi-square tests were used to compare differences in (1) Roseate Tern breeding success and timing of breeding between years, (2) fledging success between infested and noninfested nestlings, (3) the number of soil samples with ticks between Roseate and Sooty tern, areas and (4) annual differences in the number of Seychelles skinks infested with larvae. For timing of breeding we compared the number of eggs in each year that hatched before and after the overall median hatching date for 1997–1999 (median test). Influence of nestling age on tick infestation was evaluated using chi-square, testing the null hypothesis that the number of infested nestlings of each five-day age class was similar. A *t*-test and Mann-Whitney *U*-test were used to compare, respectively, growth rates and fledging age between parasitized and nonparasitized nestlings with female ticks.

Results

Effects of ticks on nestling growth, fledging age and survival.—Male ticks attached for 2.4 days on average (range 1–3 days, SD = 0.89, $n = 5$), whereas female ticks attached for 8.16 days on average (range 4–14 days, SD = 3.97, $n = 6$). Engorging female ticks seemed to be considerable burden to the nestling: nestlings were reluctant to stand on the infested foot and some feet and legs were permanently deformed with large scars. The linear growth rate of birds carrying female ticks in 1998 was significantly lower (0.24 g/day, SD = 1.11) than the linear growth rate of uninfested birds of the same age and similar (or even lower) hatching weight (4.07 g/day, SD = 2.59; $t = 3.32$, df = 10, $P < 0.01$).

Nestlings infested with female ticks had a significantly lower success than those that were not infested ($\chi^2 = 18.7$, df = 1, $P < 0.05$). For example, the 24 nestlings with ticks had only a 37.5% fledging success rate, whereas the 96 nestlings without ticks had an 83.3% fledging success rate. Because hatching success in 1998 was ~80%, that means 1,012 eggs hatched in the main colony ($0.8 \times 1{,}265$). A maximum of ~20% (202) of the nestlings were infested with female ticks, and from those only 37.5% fledged (76 nestlings). If the 202 nestlings had no ticks, 168 were likely to fledge (0.833×202), meaning that approximately 92 ($168 - 76$) nestlings died due to ticks. This represents 24.3% ($92/1{,}012 - 633$) of the nestling deaths. The nestlings that were parasitized and fledged did so 5.2 days later than nestlings of similar age that were not parasitized (nestlings with ticks = 29.2 days, nestlings without ticks = 34.4 days, Mann-Whitney U-test, $U = 9$, $P < 0.05$).

In 1997, there was an acute food shortage and virtually all nestlings died of starvation (Ramos 1998b). No ticks were found on the 11 nestlings of three isolated small colonies, and

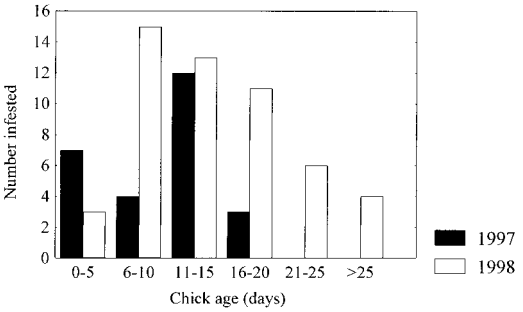

FIG. 1. Number of infested Roseate Tern nestlings in relation to age for 1997 (n = 26) and 1998 (n = 53).

the proportion of nestlings with ticks in the hide area (40%, n = 97) was, therefore, significantly higher than that in the small colonies (χ^2 = 9.18, df = 1, $P < 0.001$).

Nestling age and tick infestation.—The probability of a nestling being infested varied significantly with its age for both 1997 (χ^2 = 12.15, df = 3, $P < 0.01$) and 1998 (χ^2 = 13.73, df = 5, $P < 0.05$; Fig. 1). There were, however, important differences between those two years because, in 1997, a greater proportion of nestlings were parasitized at an earlier age (Fig. 1). In 1998, the observed frequency of very young (0–5 days) and very old (>21 days) nestlings with ticks was less than expected (3:8.8 and 4:8.8), whereas for nestlings of intermediate age, it was higher than expected (11–15:8.8).

Tick activity patterns in relation to Roseate Tern timing of breeding and breeding success.—Timing of breeding and breeding success varied enormously between the three study years (Table 1). Hatching date was significantly different between 1997, 1998, and 1999 (median test: grand median = 26 June, χ^2 = 84.04, df = 2, $P < 0.001$). In 1998, hatching success was ~80% and fledging success ~55%. Virtually no nestlings fledged in either 1997 or 1999 but, in 1997, 60% of the eggs hatched and most nestlings died after 10–15 days, whereas, in 1999, only 4% of the eggs hatched and all nestlings were abandoned within 2–4 days. Both hatching (χ^2 = 172.1, df = 2) and fledging success (1997 and 1999 combined so expected frequencies exceed 5; χ^2 = 81.8, df = 1, both $P < 0.001$) varied significantly between years (Table 1).

The seasonal activity patterns of ticks are shown in Figure 2. Adults with signs of tick infestation were first detected in early June (i.e. soon after the peak of egg laying) but the ticks themselves were not observed. However, in five sites where adult Roseate Terns showed signs of tick infestation in early June, adults and nestlings were again infested with adult female ticks ~30 days later. That suggests infestation in early June may have been by nymphs, despite the fact that, for Sooty Terns, nymphs attach preferentially around the bill (Ramos 1999). That is corroborated by Figure 2 showing that the peaks of tick infestation on adults in June and July of 1998 were about one month apart, during which no adults were observed with signs of tick infestation. Nymphs molting into adults were obtained in the soil samples in early July of 1999.

Infested nestlings carried between 1–4 adult ticks, mostly on one foot only; 73% carried only one tick. No nymphs were detected on nestlings. Nestling infestation levels in 1998 were similar using both methods: nestling handling and observation of nestlings with signs of tick infestation (r_s = 0.88, $P < 0.001$; Fig. 2).

Nestling infestation rates varied during the season, with a peak of birds infested on 9–12 July both in 1997 and 1998, despite the yearly differences in breeding phenology (Table 1). The second peak of infestation on 28–30 July

TABLE 1. Breeding dates for Roseate Terns in 1997–1999. The number of nests (and eggs) followed in the study quadrats were 149 (152), 141 (175), and 127 (136), respectively. Median hatching is based on 97, 130, and 11 eggs, respectively. Productivity refers to the number of fledged nestlings per breeding pair.

	1997	1998	1999
First egg seen	1 June	17–20 May	14 June
Peak of laying	8 June	31 May	20 June
First young seen	22 June	9 June	7 July
Median hatching	30 June	21 June	8 July
First fledge date	20–25 July	7 July	None
Peak of fledging	none	15–25 July	None
Hatching success (%)	59.9	76.6	3.7
Productivity	0.01	0.53–0.63	0

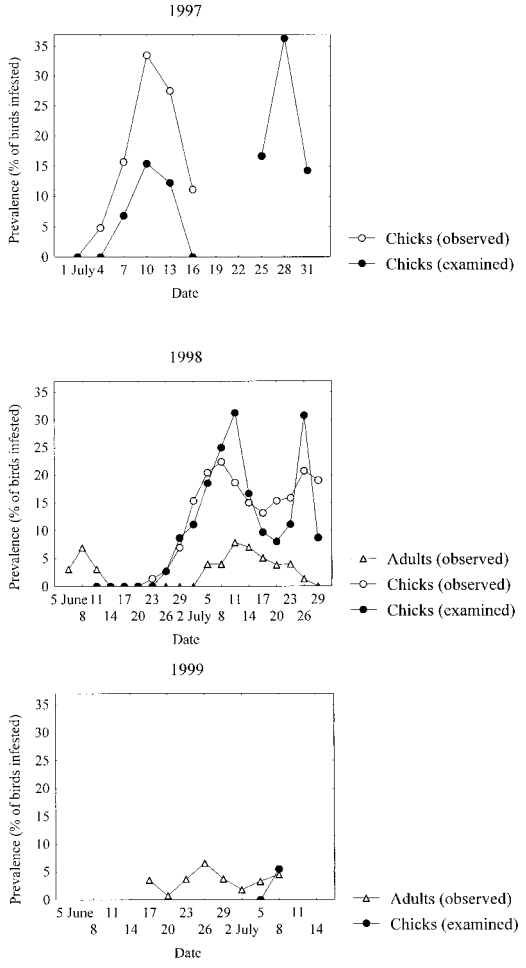

FIG. 2. Temporal changes in the prevalence of *Amblyomma loculosum* on Roseate Tern adults and nestlings. Figure presents tick prevalence estimated from the hide (using birds with signs of tick infestation, e.g. those standing on one foot) and obtained examining nestlings in study quadrats. Prevalence is expressed as a three-day running mean of the prevalence of tick infestation.

1997 and 26–29 July 1998 is explained by the fact that by then only a few weak nestlings remained in the colony. In 1997, most nestlings had died and in 1998 most had fledged, which may have lead to a concentration of the parasites on the remaining nestlings. In 1999, Roseate Tern adults showed signs of tick infestation since 17 June (Fig. 2) but there were virtually no nestlings present in July to be parasitized; from a total of 18 weak nestlings, with 0–5 days of age, present on the whole colony on the 10 of July, only one was infested with one unfed female tick (Fig. 2).

TABLE 2. Comparison of prevalence and abundance of nymphs and adult ticks on 38 soil samples taken at Roseate and Sooty tern nests in 1999.

	Nymph		Adult	
	Prevalence (%)	Abundance (No.)	Prevalence (%)	Abundance (No.)
Roseate Tern	7.9	3	5.3	2
Sooty Tern	21.1	12	26.3	17
χ^2	1.7	4.3	4.8	10.3
P	>0.05	<0.05	<0.05	<0.001

The proportion of soil samples with nymphs did not differ significantly between Roseate and Sooty terns (although the total number of nymphs did), but the proportion of soil samples with adult ticks differed significantly between the two species (Table 2). Those results suggest that nymphs and adult ticks are less abundant on Roseate Tern areas than on Sooty Tern areas, despite the higher nesting density of Roseate Terns (0.63–1.23 nests/m^2, Ramos 1998a) when compared with Sooty Terns (0.3 nests/m^2, Feare et al. 1997) on Aride Island. The proportion of Seychelles skinks infested with tick larvae in the 1998 successful year was significantly higher than in the 1999 failure year (93.7% and 52.5%, $n = 48$ and 40, $\chi^2 = 17.66$, df = 1, $P < 0.001$, with Yates correction). Therefore, the absence of Roseate Tern adults and nestlings in July 1999 apparently resulted in a subsequent decrease of larvae in September.

DISCUSSION

In this study, nestling growth, fledging age, and survival seemed to be significantly reduced by only one female tick. Ticks might also contribute to postfledging mortality because a fledgling that had been infested with a female tick was recovered dead on Bird Island (76 km away from Aride). Negative effects on nestling condition have been documented for *I. uriae* infesting nestling Cassin's Auklets (*Ptychoramphus aleuticus*) at Triangle Island, British Columbia. There, only high levels of tick infestation adversely affected nestlings, but the ticks were probably in the nymph stage (Morbey 1996). High densities of argasid ticks have been linked to egg and seabird nestlings de-

sertion (Duffy 1983) and lower survival of Cattle Egrets (*Ardeola ibis,* McKilligan 1996). Ticks could have adverse effects on nestling condition either directly, through blood loss anemia, or indirectly through disease (Feare 1976). Blood loss must be highly detrimental or lethal for young nestlings, especially when infested by female ticks. Some of the infested nestlings also appeared to be more kleptoparasitized by nearby adults than noninfested nestlings. An arbovirus has been isolated from *A. loculosum* engorged females parasitizing Roseate Terns on Aride (Converse et al. 1976). In this study, there was no direct evidence between disease and tick infestation, although two nestlings with swollen skin on neck and legs were found; one was parasitized with *A. loculosum* but no ticks were seen on the second nestling. Ticks have adverse effects on nestling growth and survival, but their importance in the host population dynamics will depend on how the tick population is regulated. In tropical vegetated seabird colonies such as Aride, predatory ants may feed on tick eggs and larvae thereby reducing tick levels (Duffy 1991).

The two nestlings that definitely fledged in 1997 were from an isolated small colony without ticks, suggesting that without the tick infestation more nestlings might have fledged, though probably in poor physical condition due to food shortage. In 1998, periods of relatively rapid nestling growth were curtailed by one week of food shortage, during which nestlings lost weight; five nestlings died during that week and they were all infested with ticks. That suggests that during periods of food shortage, ticks may accelerate nestling mortality.

The possible relationship between food levels, degree of tick infestation, and behavioral attributes (i.e. adult aggression, Ramos 1998b) means that in years where no single factor is dominant, a relationship between those factors may be necessary to explain reproductive success of Roseate Terns on Aride, although food shortage appears to be the main factor in explaining breeding success and breeding strategies of the Roseate Tern (Ramos 2001).

As in other studies, we obtained an inverted U-shaped relationship between nestling age and parasite infestation (Boulinier and Danchin 1996). That has been explained by differential exposure time (which is shorter for very young nestlings), strength of the immune defenses and plumage growth (which may alter the detection of ticks on older nestlings) (Boulinier and Danchin 1996, Duffy and Campos de Duffy 1986), or both. The second hypothesis does not apply because *A. loculosum* attaches mainly on feet and legs. Three points suggest time that adult Roseate Terns settle in the colony to breed is the main factor influencing the age at which Roseate Tern nestlings will be parasitized: (1) a larger proportion of young nestlings was parasitized in 1997, when breeding commenced significantly later than in 1998. That should not be biased by the effects of the 1997 breeding failure because most nestlings weakened and died only between 10–15 days of age. (2) In 1996, the peak of egg laying for Roseate Terns was in mid-May and only older nestlings were parasitized by ticks (Maul 1998). (3) Nymphs are detected biting humans on Aride in early May (J. Ramos pers. obs.) and must attach to Roseate Tern adults as soon as they make a nest scrape.

In 1999, some nymphs attached to Roseate Terns were presumably not returned to the colony, because adult birds abandoned their clutches in early July. Those and other nymphs that were unable to feed should have died, thereby decreasing larval infestation levels on Seychelles skinks in September. Despite the existence of a Sooty Tern sub-colony ~40 m away, the breeding success of Roseate Terns is likely to be the main factor influencing tick levels in the Roseate Tern areas.

Total breeding failures on Aride are common for Roseate Terns (Ramos 2001) but not for Sooty Terns (Bowler and Hunter 1999 and references within), which must contribute to the lower tick levels on Roseate Tern areas. In 1999, 144 Sooty Tern nestlings were examined for ticks and 65% carried more than one tick. Some of those nestlings, infested with up to 18 ticks (Ramos 1999), clearly died by ex-sanguination. Roseate Tern nestling mortality levels due to ticks are likely to be cyclic, following cycles of successful and unsuccessful breeding seasons (because 1984 Roseate Terns failed almost completely in about half of the breeding seasons, Ramos 2000). Ironically, the frequent breeding failures of the Roseate Terns should result in lower infestation levels in subsequent years. Even if Roseate Terns fail for several consecutive years, ticks are unlikely to disappear such as on Bird Island where Sooty Terns are the

only host (Feare and Gill 1997); immature ticks may emigrate from neighboring areas with Sooty Terns or be carried by skinks.

In summary, Roseate Tern breeding success on Aride is unpredictable and is determined mainly by variations in food levels (Ramos 2000, 2001). During a successful breeding season, nestling mortality due to ticks is likely to be additive and may increase in the event of several consecutive successful breeding seasons. Because Roseate Terns are very sensitive to variations in food levels (Shealer 1995, Ramos 2000), a moderate tick infestation may speed up nestling mortality and have detrimental consequences on breeding success if a period of food shortage coincides with the peak of tick infestation.

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Literature Cited

Aebischer, N. J., and J. C. Coulson. 1990. Survival of the Kittiwake in relation to sex, year, breeding experience and position in the colony. Journal of Animal Ecology 59:1063–1071.

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecololgy and Systematics 5:325–383.

Barton, T. R., M. P. Harris, S. Wanless, and D. A. Elston. 1996. The activity periods and life-cycle of the tick *Ixodes uriae* (Acari:Ixodidae) in relation to host breeding strategies. Parasitology 112:571–580.

Boulinier, T., and E. Danchin. 1996. Population trends in Kittiwake *Rissa tridactyla* colonies in relation to tick infestation. Ibis 138:326–334.

Bowler, J., and J. Hunter. 1999. Aride Island Scientific report 1998. Report to the Royal Society for Nature Conservation. Royal Society for Nature Conservation, Lincoln, United Kingdom.

Converse, J. D., H. Hoogstraal, M. I. Moussa, M. N. Kaiser, J. Casals, and C. J. Feare. 1976. Aride virus, a new ungrouped arbovirus infecting *Amblyomma loculosum* ticks from Roseate Terns in the Seychelles. Archives of Virology 50:237–240.

Davis, L. 1998. An investigation of skinks acting as vectors for ticks parasitising Roseate Tern chicks. Report to the Royal Society for Nature Conservation, Royal Society for Nature Conservation. Lincoln, United Kingdom.

Duffy, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. Ecology 64: 110–119.

Duffy, D. C. 1991. Ants, ticks and nesting seabirds: Dynamic interactions? Pages 242–257 *in* Bird–Parasite Interactions: Ecology, Evolution and Behaviour (J. E. Loye and M. Zuk, Eds.). Oxford University Press, Oxford.

Duffy, D. C., and M. J. Campos de Duffy. 1986. Tick parasitism at nesting colonies of Blue-footed Boobies in Peru and Galapagos. Condor 88:242–244.

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

Feare, C. J., and E. L. Gill. 1997. The life cycle of the tick *Amblyomma loculosum* in a Sooty Tern *Sterna fuscata* colony in the Seychelles. Journal of Zoology (London) 241:643–648.

Feare, C. J., E. L. Gill, P. Carty, H. E. Carty, and V. J. Ayrton. 1997. Habitat use by Seychelles Sooty Terns *Sterna fuscata* and implications for colony managment Biological Conservation 81: 69–76.

Furness, R. W., and P. Monaghan. 1987. Seabird Ecology. Blackie, Glasgow, Scotland.

Hoogstraal, H. H., and C. J. Feare. 1984. Ticks and tickborne viruses. Pages 267–280 *in* Biogeography and Ecology of the Seychelles Islands (D. M. Stoddart, Ed.). W. Junk, The Hague, The Netherlands.

Harris, M. P. 1984. The Puffin. T. and A. D. Poyser, Carlton, United Kingdom.

Hoogstraal, H. H., Y. Wassef, J. D. Converse, J. E. Keirans, C. M. Clifford, and C. J. Feare. 1976. *Amblyomma loculosum* (Ixodoidea: Ixodidae) identity, marine bird and human hosts, virus infection, and distribution in the Southern Oceans. Annales of the Entomological Society of America 69:3–14.

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. Ph.D. dissertation, Karl-Franzens University, Graz, Austria.

MCKILLIGAN, N. G. 1996. Field experiments on the effect of ticks on breeding success and chick health of Cattle Egrets. Australian Journal of Ecology 21:442–449.

MORBEY, Y. E. 1996. The abundance and effects of ticks (*Ixodes uriae*) on nestling Cassin's Auklets (*Ptychoramphus aleuticus*) at Triangle Island, British Columbia. Canadian Journal of Zoology 74: 1585–1589.

NISBET, I. C. T., J. BURGER, C. SAFINA, AND M. GOCHFELD. 1990. Estimating fledging success and productivity in Roseate Terns (*Sterna dougallii*). Colonial Waterbirds 13:85–91.

NISBET, I. C. T., J. A. SPENDELOW, AND J. S. HATFIELD. 1995. Variations in growth of Roseate Tern nestlings. Condor 97:335–344.

NUTTALL, P. A., T. C. KELLY, D. CAREY, S. R. MOSS, AND K. A. HARRAP. 1984. Mixed infection with tick-borne viruses in a seabird colony in Eire. Archives of Virology 79:35–44.

RAMOS, J. A. 1998a. Nest-site selection by Roseate Terns breeding on Aride Island, Seychelles. Colonial Waterbirds 21:438–443.

RAMOS, J. A. 1998b. Breeding ecology of Roseate Terns on Aride Island, Seychelles, in 1997. Report to the Royal Society for Nature Conservation, Lincoln, United Kingdom.

RAMOS, J. A. 1999. The 1999 Roseate Tern breeding season on Aride Island. Report to the Royal Society for Nature Conservation, Lincoln, United Kingdom.

RAMOS, J. A. 2000. Characteristics of foraging habitats and chick food provisioning by tropical Roseate Terns. Condor 102:795–803.

RAMOS, J. A. 2001. Seasonal variations in reproductive measures by tropical Roseate Terns: Previously undescribed breeding patterns in a seabird. Ibis 143:83–91.

SHEALER, D. A. 1995. Comparative foraging ecology of Roseate and Sandwich terns in Puerto Rico and its relation to breeding performance. Ph.D. dissertation, Rutgers University, New Brunswick, New Jersey.

WARMAN, S. R. 1979. The Roseate Tern *Sterna dougallii aridensis* on Aride island, Seychelles. Bulletin of the British Ornitologists' Club 99:124–128.

ZAR, J. H. 1996. Biostatistical Analysis, 3rd ed. Prentice Hall, New Jersey.

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