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GROWTH OF BROWN PELICAN NESTLINGS EXPOSED TO SUBLETHAL LEVELS OF SOFT TICK INFESTATION

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Abstract. Ectoparasites are a common component of seabird colonies and are generally considered to have a negative impact on their hosts. Nest parasites such as the soft tick *Carios capensis* may pose a distinct threat to altricial nestlings confined to the nest and unable to escape infestation. To assess the potential effects of ticks on growth, we measured linear growth rates of Brown Pelican (*Pelecanus occidentalis*) nestlings during early development in relation to *C. capensis* infestation at insecticide treated and untreated nests at two colonies in South Carolina during the 2004 and 2005 breeding seasons. Tick infestation levels differed between colonies but not between years. We found a positive relationship between tick infestation and both growth rates and hatching success at the more infested colony. We did not find a consistent relationship between insecticide treatment and growth rates, although chicks from nests treated with insecticide had fewer ticks compared to chicks from untreated nests. Our study suggests that the cohabitation of ectoparasites and seabirds within colonies may result in behavioral or physiological adaptations of adults or nestlings that inhibit the expected negative effect of ectoparasites on nestling growth at sublethal levels of infestation.

Key words: Brown Pelican, Carios capensis*, ectoparasite, growth rate,* Pelecanus occidentalis*, seabird, soft ticks.*

Crecimiento de Pichones de *Pelecanus occidentalis* Expuestos a Niveles Subletales de Infestaciones de Garrapatas

Resumen. Los ectoparásitos son un componente común de las colonias de aves marinas y generalmente se considera que tienen un impacto negativo sobre sus hospederos. Los parásitos de nido como la garrapata *Carios capensis* pueden resultar una amenaza particular para los pichones nidícolas confinados al nido e incapaces de escapar de la infestación. Para evaluar los efectos potenciales de las garrapatas sobre el crecimiento, medimos las tasas lineales de crecimiento de los pichones de *Pelecanus occidentales* durante el desarrollo temprano con relación a la infestación de *C. capensis* en nidos tratados y no tratados con insecticida, en dos colonias en Carolina del Sur durante las estaciones reproductivas del 2004 y 2005. Los niveles de infestación de garrapatas difirieron entre las colonias pero no entre los años. Encontramos una relación positiva entre la infestación de garrapatas tanto con las tasas de crecimiento como con el éxito de eclosión en la colonia más infestada. No encontramos una relación consistente entre el tratamiento con insecticida y las tasas de crecimiento, aunque los pichones de los nidos tratados con insecticida tuvieron menos garrapatas que los pichones de los nidos no tratados. Nuestro estudio sugiere que la convivencia de los ectoparásitos con las aves marinas en las colonias puede causar adaptaciones de comportamiento o fisiológicas de los adultos o de los pichones que inhiben el efecto negativo esperado de los ectoparásitos sobre el crecimiento de los pichones a niveles subletales de infestación.

INTRODUCTION

Most seabirds exhibit strong fidelity to breeding sites, have relatively lengthy chick-rearing periods, and breed in dense colonies (Coulson 2002, Schreiber and Burger 2002). Such life history traits make seabirds favorable hosts of ectoparasites (Duffy 1983, Ramos et al. 2001), which are often considered a cost of colonial breeding. High densities of ectoparasites at colonies may lead to nest or colony desertion and mortality of adults or chicks (Duffy 1983, Proctor and Owens 2000, Ramos et al. 2001). The level and effect of ectoparasite infestation may not always be this extreme; however, even at sublethal levels, ectoparasites may serve to reduce the condition of affected adults and chicks. For example, ticks that infest nestlings may deplete resources crucial for normal postnatal development, resulting in reduced growth rates and altered fledging periods (Chapman and George 1991, Morbey 1996, Ramos et al. 2001). In infested colonies, therefore, ectoparasites may play a

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key role in determining reproductive success through various means, especially during brood rearing when the cost of infestation can be greatest for nestlings (Lehmann 1993).

Numerous ectoparasites are associated with seabird species. Body ectoparasites (e.g., hard ticks, feather lice) reside primarily on their hosts, while nest ectoparasites (e.g., soft ticks, fleas) occur more frequently in the nest substrate than on the host. Much of the previous research exploring the relationship between ectoparasites and seabirds has focused on body ectoparasites. However, nest ectoparasites may pose just as great a threat, especially to altricial nestlings that are confined to the nest during an extensive period of development and hence unable to escape repeated exposure. The soft tick *Carios capensis* (formerly *Ornithodoros capensis*) is a nest ectoparasite that has a wide distribution and is associated almost exclusively with seabirds (Duffy 1983, Hoogstraal 1985). During the breeding season, *C. capensis* takes refuge in nesting material, where it has access to multiple hosts (i.e., incubating birds and nestlings) that are necessary to support its development. Larvae of this soft tick may attach to their hosts for several days at a time, whereas nymphal instars and adults rapidly engorge in less than an hour (Hoogstraal 1985). When breeding birds are not present, *C. capensis* burrow in nest material and surrounding substrate, where they can overwinter and survive long periods without feeding (Hoogstraal 1985). Populations can thereby be sustained year-round, and *C. capensis* can become common and long-term residents at colony sites. To avoid constant ectoparasite pressure, seabirds may emigrate from heavily infested colonies to less infested ones when multiple sites are available (Boulinier and Danchin 1996). In contrast, when colony sites are limited, as is the case along much of the Atlantic coast of the U.S., the option to relocate and evade escalating tick densities is no longer available. The effect this may have on seabird populations is unclear.

Our goal was to investigate the effect of *C. capensis* on seabird nestling condition along the coast of South Carolina. We studied Brown Pelicans (*Pelecanus occidentalis*) at two colonies in the state during the 2004 and 2005 breeding seasons. Pelicans have been experiencing a population decline of undetermined cause within the state since the late 1980s (Jodice et al. 2007). *C. capensis* can reach very high densities in pelican colonies (King et al. 1977, Norcross and Bolen 2002) and have been implicated in periodic desertions of colonies in South Carolina and, along with other soft tick species, throughout the Brown Pelican breeding range (King et al. 1977, Duffy 1983, Wilkinson et al. 1994). Pelican colonies in South Carolina have been treated with insecticides for the past several years in an effort to control tick populations, and a recent study in North Carolina found reduced numbers of *C. capensis* in nests treated with an insecticide compared to control nests (Norcross and Bolen 2002). Although infestation levels were not manipulated in our study, nests were subjected to an experimental treatment whereby study nests were either treated with insecticide during incubation or left untreated.

Our primary objective was to assess the relationship between growth rates of nestlings and *C. capensis* infestation levels, insecticide treatment, colony, hatching order, brood size, and year. Examination of tick infestation in relation to variation in growth rates rather than merely survival allows for an assessment of potential sublethal effects of parasitism on nestling condition (Gebhardt-Henrich and Richner 1998). In the process of meeting our primary objective, we also sought to 1) compare tick infestation levels of nests treated with insecticide and those left untreated and 2) examine reproductive parameters including clutch size, hatching success, and survival of nestlings during early development in relation to tick infestation level and nest treatment. Hereafter, any mention of ticks refers to *C. capensis* unless stated otherwise.

METHODS

STUDY SITE AND SPECIES

Brown Pelican colonies at Marsh Island (32°59′N, 79°32′W) and Crab Bank (32°46′N, 79°53′W), both located within Charleston County, South Carolina, served as study sites for this research. Marsh Island is a 19 ha island that lies approximately 4.6 km off the coast of Awendaw, South Carolina in Cape Romain National Wildlife Refuge. Crab Bank is a 9 ha sand-spit island located within Charleston Harbor. Crab Bank lies approximately 40 km south of Marsh Island. Marsh Island has supported a pelican colony since the 1940s, while Crab Bank was colonized by pelicans only in 1994 (Jodice et al. 2007). Both study colonies are infested with *C. capensis*, which was first identified in South Carolina in 1987 (Keirans et al. 1992), when ticks were found in deserted pelican nests at the Marsh Island and Bird Key Stono colonies. It is not known if *C. capensis* occurred in pelican colonies in the state prior to this. It does appear, however, that ticks may have contributed to reduced reproductive success of Brown Pelicans at colonies in South Carolina by causing nest desertion (Keirans et al. 1992, Wilkinson et al. 1994), especially in years of severe infestation.

Brown Pelicans generally nest on the ground at both colonies. It is typical for a breeding pair to produce a single three-egg clutch per season. Nestlings hatch asynchronously, with the first-hatched nestling usually benefiting from a size advantage and dominant position over its siblings (Pinson and Drummond 1993, Shields 2002). Nestlings are altricial and spend at least the first three weeks of development confined to the nest. Thereafter, chicks are mobile and may move short distances from the nest or form crèches, small groups comprised of neighboring chicks and siblings. Nestlings rely on parental provisioning at or near the nest during the entire developmental period of approximately 11 weeks (Shields 2002).

For several years prior to initiation of this study, pelican colonies in South Carolina were treated annually with a single application of insecticide in an effort to control levels of ticks. In 2004 and 2005, as in previous years, the treated nests were hand-sprayed with approximately 175 ml of a 0.5% dilution of Rabon® 50 WP insecticide (Boehringer Ingelheim Vetmedica, Inc., St. Joseph, MO) during the third week in May, corresponding with peak incubation of pelicans. In 2005, nontoxic red food coloring was added to the insecticide so treated nests could be easily detected. For the purposes of this study, we delineated six study plots within each colony prior to treatment. Plots represented the range of occupied ground nesting habitat and tended to reflect natural clusters of nests. Within each plot, we randomly selected eight study nests: four were treated with insecticide, and four were not treated. All other pelican nests in the colony were treated.

FIELD PROCEDURES

Study nests at each colony were checked approximately once every four days to monitor clutch size, hatching, and chick growth and survival, and to determine presence and abundance of ticks on nestlings. We visited colonies on alternate days and maximized time between measurements within each section of the colonies whenever possible to decrease disturbance to breeding birds. We also took care to enter nesting areas slowly, avoid colony work during the warmest hours of the day, and keep visits as short as possible. Nest visits ceased when most chicks became mobile, as it was then too disruptive to the colony to capture and handle chicks.

During each nest check, we measured body mass (electronic scale if ≤ 1000 g; 2500 ± 20 g or 5000 ± 50 g spring scale if >1000 g) as well as culmen, tarsus, and wing length (dial calipers ± 1 mm, wing rule ± 1 mm). We also recorded the number and location of ticks on each nestling. Larval and nymphal stages were not distinguished in the field and were therefore grouped together for the total count. Adult ticks were rarely seen on nestlings. The number of ticks counted on nestlings was considered to be representative of the overall tick population within each nest (Duffy and de Duffy 1986). All morphological measurements and tick counts were performed by the same researcher (LMFE) in both years.

At Marsh Island, there was a strong correlation between the total number of ticks counted on parasitized nestlings in 2004 and the number counted on just the neck and pouch ($r = 0.91$, $P < 0.001$). Therefore, in 2005, we counted only ticks on the neck and pouch, and merely noted the presence of ticks elsewhere on the body. Hereafter, the tick count for each nestling refers to the mean number of ticks counted on the neck and pouch during all checks of that individual. Tick counts were categorized into tick loads as follows: no (0 ticks), low (1–10 ticks), moderate (11–50 ticks), and high (>50 ticks), such that the low category contained approximately 50% of all counts of parasitized nestlings, and the moderate and high categories each contained approximately 25% of all counts of parasitized nestlings.

We determined hatching order among chicks in each nest during the first nest check posthatching, based on 1) nest content at the previous check, 2) relative body size among siblings, and 3) hatchling appearance (Schreiber 1976, Shields 2002). Nestlings were marked with nail polish on their culmens and nontoxic permanent marker on their feathers, once developed, in order to distinguish among alpha (first-hatched), beta (second-hatched), or gamma (third-hatched) nestlings. Occasionally, our marks were not visible at the following nest check, and so we assumed the largest nestling was the alpha nestling, and so on. This assumption is consistent with results from Shields (2000), who demonstrated that the size advantage of asynchronously hatching Brown Pelican chicks is typically maintained for at least the first two weeks of development.

Nestling age was assessed in one of two ways. Where possible ($n = 114$, years and colonies combined), we determined hatching date by observing stages of hatching (e.g., pipped or starred eggs; Shields 2000). In the remaining cases ($n = 249$, years and colonies combined), hatching dates were based on siblings' hatch dates or an equation. If sibling hatching dates were known, we assumed that alpha nestlings hatched approximately one and three days prior to beta and gamma siblings, respectively (Ploger 1992, Shields 1998). If a brood consisted of a single nestling or did not contain nestlings of known age, we then estimated age (in days) as ($\text{age} = 14.13^{*}\ln \text{culmen} - 42.85$). This model was based on culmen length measurements ($n = 218$) of nestlings from our known age sample that survived beyond 21 days ($n = 51$; $F_{1,216} = 6522.9$, $P < 0.001$, $R^2 = 0.97$). Estimated chick age was never greater than seven days. To check the accuracy of our age estimation technique, we estimated the hatching dates of the known age sample and found no difference in the resulting hatching dates (two-tailed paired t-test: $t_{113} = 0.9$, $P = 0.35$). Known and estimated age samples were therefore pooled for all subsequent analyses. All research activities were approved and complied with the Clemson University Animal Research Committee.

STATISTICAL ANALYSES

We assessed growth rates using measurements collected during at least the first three weeks of nestling development (longer whenever possible). The culmens of Brown Pelicans grow linearly throughout development after about four days posthatching, while body mass appears to increase linearly from this point until chicks are approximately 50 days old (Schreiber 1976). Our results are consistent with these findings (Fig. 1); therefore, we analyzed growth by determining the linear growth rate, hereafter referred to as growth rate, for each individual. We used a simple linear regression (Nisbet et al. 1995) to fit the slope of age (days) to body mass (g) and, separately, to culmen length (mm). All nestlings with three or more measurements during the linear phase of growth were included

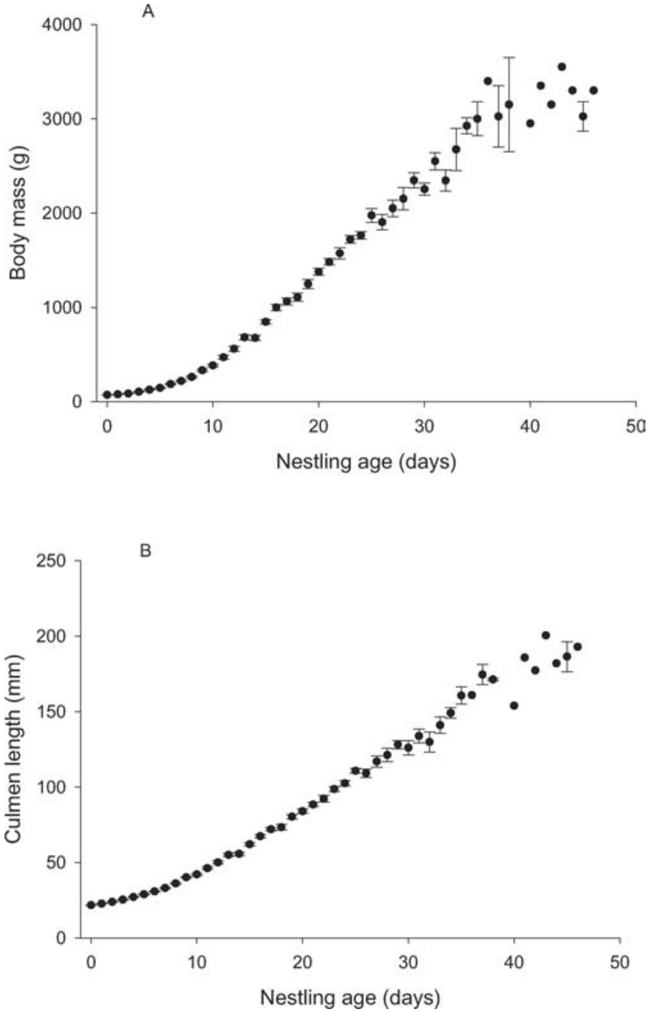

FIGURE 1. Composite growth curve of mean ± SE (A) body mass and (B) culmen length of Brown Pelican nestlings that survived ≥21 days at Marsh Island and Crab Bank, South Carolina in 2004 and 2005.

in growth rate analysis (age range, Marsh Island: 4–45 days; Crab Bank: 4–46 days). Hereafter, this sample is referred to as the growth rate sample. We also included one individual from Marsh Island in 2004 with three growth measurements after two days posthatching and five individuals from Crab Bank in 2005 with two measurements after four days posthatching to provide a representation of insecticide-treated and -untreated individuals within each plot as required by the mixed model design used for these analyses. These exceptions represented 1% and 4% of the growth rate sample at Marsh Island ($n = 112$) and Crab Bank ($n = 113$), respectively.

We used separate mixed models (SAS Version 9.1; SAS Institute, Inc., Cary, North Carolina) to analyze the growth rate of body mass and culmen length. Fixed factors were tick load, hatching order, year, and treatment. Random terms were plot nested within year; nest nested within treatment, plot, and year; and a treatment and plot within year interaction. F and P-values for the variables year, treatment, plot nested within year, and treatment and plot within year interaction were adjusted for the appropriate error terms: plot nested within year; treatment and plot within year interaction; treatment and plot within year interaction; and nest nested within treatment, plot, and year, respectively. The mean sum of squares was used to calculate test statistics as the error term for the remaining variables. Tick infestation levels differed between colonies in both years; therefore, we analyzed each colony separately. Data were tested for equal variance, and no transformations were necessary. Brood size could not be included in the aforementioned models because our growth rate sample did not include representation of all brood sizes (i.e., one, two, and three chicks) in each plot during both years. We therefore ran a separate ANOVA to assess the effects of brood size on growth rates. All growth analyses were performed on the growth rate sample of nestlings as described above ($n = 225$, both colonies combined). Other analyses were conducted on a larger sample of nestlings ($n = 363$) that included the 225 growth rate samples plus an additional 138 nestlings that did not meet the criteria for inclusion in the growth rate sample. Lastly, we measured chick survival to 21 days, which is strongly correlated with fledging success (Shields 1998). The Tukey-Kramer test was used for post hoc pairwise comparisons. Means are presented ± SE. We refer to results as significant when $P \leq 0.05$.

RESULTS

TICK COUNTS AND INSECTICIDE TREATMENT

We monitored 48 nests at Marsh Island and 48 nests at Crab Bank during each year of this study. Ticks were common throughout the Marsh Island colony and were present but less common in the Crab Bank colony. Mean tick counts on all nestlings at Marsh Island were significantly greater than those on nestlings at Crab Bank in both years (2004: $t_{191} = 3.6$, $P < 0.001$; 2005: $t_{168} = 3.5$, $P < 0.001$) but did not differ between years within either colony (Marsh Island: $t_{167} = 1.5$, $P = 0.13$; Crab Bank: $t_{192} = 1.2$, $P = 0.23$; Table 1).

Insecticide treatment did not eliminate ticks from pelican chicks at either colony. Tick counts differed between treatments within colonies in 2004 but not 2005. The mean tick count on chicks from untreated nests on Marsh Island in 2004 (10.4 ± 3.0, $n = 50$) was greater compared to chicks from treated nests (1.1 ± 0.8, $n = 45$; $t_{93} = 2.9$, $P = 0.005$). The mean tick count on chicks from untreated nests at Crab Bank in 2004 (0.1 ± 0.1, $n = 50$) followed a similar trend compared to chicks from treated nests (0.01 ± 0.01, $n = 48$; $t_{96} = 1.8$, $P = 0.07$). There was no difference in mean tick count on chicks between treatments at either Marsh Island or Crab Bank in 2005 (Marsh Island: $t_{72} = 1.4$, $P = 0.17$; Crab Bank: $t_{94} = 0.53$, $P = 0.60$). The effect of insecticide treatment in

TABLE 1. Mean and range of average number of ticks (±SE) counted for the full sample of Brown Pelican nestlings as well as for only parasitized chicks measured at Marsh Island and Crab Bank, South Carolina, May–August 2004 and 2005.

	Marsh Island		Crab Bank	
	2004	2005	2004	2005
Number of chicks (number parasitized)	95 (43)	74 (52)	98 (10)	96 (7)
Grand mean tick count:				
All chicks	6.0 ± 1.7	11.9 ± 3.9	0.07 ± 0.03	0.03 ± 0.01
Parasitized chicks	13.3 ± 3.5	16.9 ± 5.4	0.7 ± 0.3	0.4 ± 0.1
Range of mean tick counts for parasitized chicks	0.2–96.8	0.1–233.7	0.2–3.0	0.1–1.0

relation to the presence or absence of ticks on nestlings also varied between colonies. There was a significantly greater proportion of parasitized chicks present in untreated nests than in treated nests at Marsh Island ($\chi^2{}_1 = 11.0$, $P = 0.001$) in both years combined; no such difference occurred at Crab Bank ($\chi_1^2 = 2.5$, $P = 0.11$).

HATCHING SUCCESS AND SURVIVAL

Mean clutch size for both colonies and years combined was $2.7 \pm <0.1$ and did not differ between colonies ($t_{190} = 0.1$, $P = 0.89$). The number of chicks that hatched per nest was significantly greater at Crab Bank (2.13 ± 0.01) than at Marsh Island (1.81 ± 0.01; $t_{190} = 2.3$, $P = 0.02$). Within colonies, there was no difference in clutch size between nest treatments (both $t_{94} \leq 0.4$, both $P \geq 0.69$) or between nests with and without infested nestlings (Marsh Island: $t_{94} = 0.7$, $P = 0.51$; Crab Bank: $t_{21} = 1.2$, $P = 0.25$). The number of chicks hatched per nest did not differ with treatment at either colony (both $t_{94} \leq 1.6$, both $P \geq 0.12$). Significantly more chicks hatched from nests with infested nestlings (2.14 ± 0.01) at Marsh Island compared to nests without infested nestlings (1.37 ± 0.03; $t_{70} = 3.7$, $P < 0.001$), although no such difference was observed at Crab Bank ($t_{20} = 1.2$, $P = 0.26$).

Of the total number of nestlings followed in both years ($n = 169$ at Marsh Island, $n = 194$ at Crab Bank), the fate to 21 days was known for 136 nestlings at Marsh Island and 140 nestlings at Crab Bank. Tick counts did not differ between nestlings that survived to 21 days and those that were found or assumed dead (i.e., not observed beyond 10 days) at either colony (Marsh Island: $t_{134} = 0.3$, $P = 0.79$; Crab Bank: $t_{138} = 1.0$, $P = 0.32$). During nest checks at Marsh Island, we found 16 dead nestlings (tick loads: no = 5, low = 7, moderate = 2, and high = 2). None of the four chicks found dead at Crab Bank had ticks during any previous checks.

GROWTH RATES

Effects of tick load, hatching order, year, plot, treatment, and nest on the rates of increase in body mass and culmen length of Brown Pelican nestlings from Marsh Island and Crab Bank are presented in Table 2. At Marsh Island, both of these rates of increase were significantly related to tick load. The growth rate in terms of body mass for nestlings at Marsh Island with no ticks was significantly lower compared to nestlings with low and high tick loads (both $P \leq 0.04$; Fig. 2A) and tended to be lower compared to nestlings with a moderate tick load ($P = 0.09$). At Marsh Island, the rate of culmen length increase

TABLE 2. Effects of select ecological factors on the linear growth rates of body mass and culmen length of Brown Pelican nestlings at Marsh Island ($n = 112$) and Crab Bank ($n = 113$), South Carolina, in 2004 and 2005. Random variables are: plot nested within year; nest nested within treatment, year, and plot; and a treatment and plot within year interaction. Significant P-values (<0.05) are denoted with asterisks.

	Marsh Island				Crab Bank			
	Body mass		Culmen length		Body mass		Culmen length	
	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P
Tick load	$4.0_{3,45}$	0.01*	$5.5_{3,45}$	0.003*	$0.1_{1,53}$	0.82	$2.0_{1,53}$	0.16
Hatching order	$21.4_{2,45}$	0.01*	$39.5_{2,45}$	<0.001*	$30.2_{2,53}$	<0.001*	$31.1_{2,53}$	<0.001*
Year	$4.0_{1,10}$	0.07	$2.7_{1,10}$	0.13	$0.8_{1,10}$	0.40	$0.3_{1,10}$	0.59
Treatment	$0.7_{1,11}$	0.41	$0.8_{1,11}$	0.39	$1.4_{1,11}$	0.26	$6.5_{1,11}$	0.03*
Plot (Year)	$0.7_{10,11}$	0.73	$0.6_{10,11}$	0.77	$1.3_{10,11}$	0.32	$2.5_{10,11}$	0.07
Nest (Treatment* Year*Plot)	$3.1_{38,45}$	<0.001*	$3.7_{38,45}$	<0.001*	$1.9_{33,53}$	0.02*	$1.7_{33,53}$	0.04*
Treatment*Plot (Year)	$0.9_{11,38}$	0.53	$0.8_{11,38}$	0.64	$0.9_{11,33}$	0.56	$0.4_{11,33}$	0.94
	$R^2 = 0.84$		$R^2 = 0.88$		$R^2 = 0.79$		$R^2 = 0.78$	

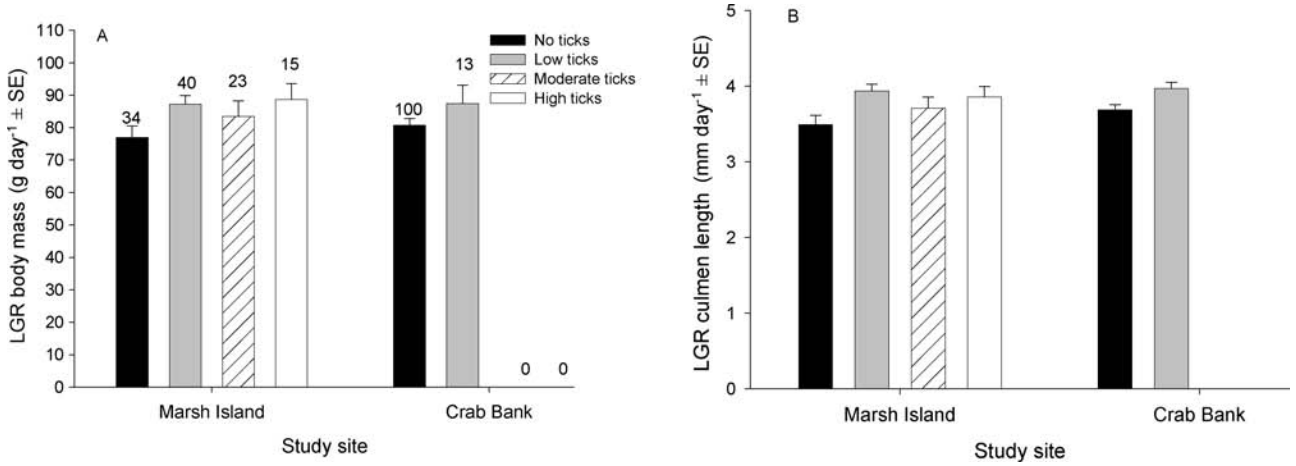

FIGURE 2. Linear growth rate (LGR) of (A) body mass and (B) culmen length of Brown Pelican nestlings at Marsh Island and Crab Bank, South Carolina, in 2004 and 2005, by tick load. No = 0 ticks, low = 1–10 ticks, moderate = 11–50 ticks, and high = >50 ticks. Sample sizes for both graphs presented above bars of (A).

for nestlings with no ticks was significantly lower compared to nestlings with low and moderate tick loads (both $P < 0.04$; Fig. 2B), and tended to be lower compared to nestlings with high tick loads ($P = 0.07$). Growth rates in terms of body mass and culmen length did not differ between low, moderate, or high tick loads at Marsh Island (all $P \geq 0.31$) or among chicks with different tick loads at Crab Bank (Table 2). We also found no significant differences in the rate of increase in body mass or culmen length (both $P \geq 0.15$) of pelican chicks at Crab Bank when tick load was categorized as either present or absent.

The rates of increase in body mass and culmen length differed significantly among all hatching orders at Marsh Island and Crab Bank but did not differ within hatching orders between colonies (Table 2, Fig. 3). Mean tick count was not related to hatching order at either colony (Marsh Island: $F_{2,109} = 1.6$, $P = 0.21$; Crab Bank: $F_{2,110} = 0.8$, $P = 0.47$). Rates of increase in body mass and culmen length did not differ significantly among plots, though the random variable for nest was related to growth rates at both colonies (Table 2). Insecticide treatment was significantly related to only the growth rate in terms of culmen length at Crab Bank in 2005 (Table 2). The rate of increase in body mass or culmen length did not differ between colonies during 2004 (both $t_{112} \leq 1.0$, both $P \geq 0.31$) or during 2005 (both $t_{109} \leq 1.3$, both $P \geq 0.21$).

There was a significant interactive effect of colony*year on brood size ($F_{1,221} = 9.1$, $P = 0.003$; Table 3). Brood size had no

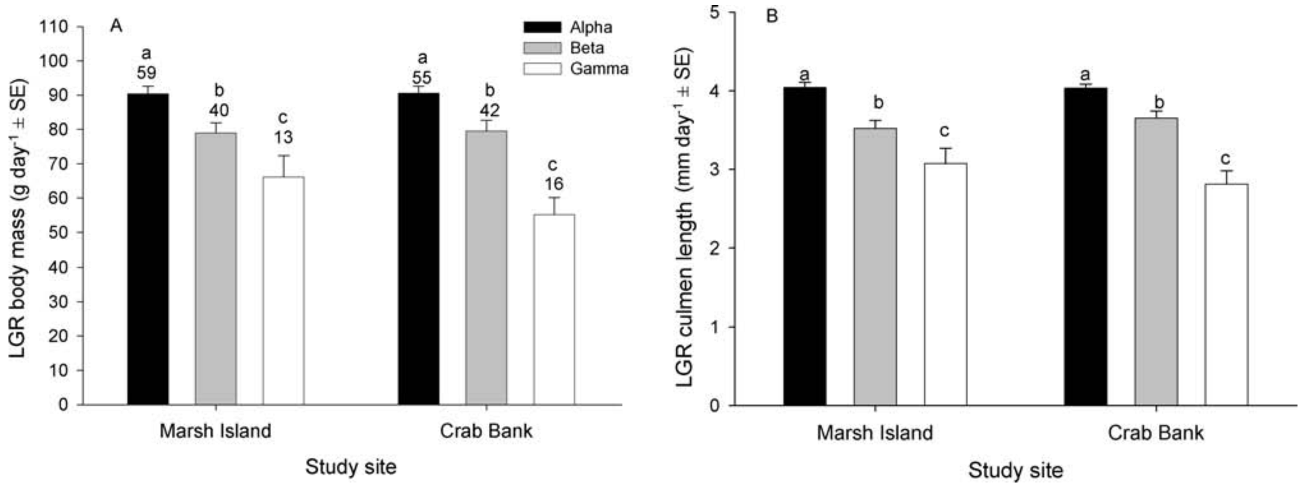

FIGURE 3. Linear growth rate (LGR) of (A) body mass and (B) culmen length of Brown Pelican nestlings at Marsh Island and Crab Bank, South Carolina, in 2004 and 2005 by hatching order (i.e., alpha: first hatched nestlings, beta: second hatched nestlings, and gamma: third hatched nestlings). Sample sizes for both graphs presented above bars of (A). For each growth measure, letters represent groups across which significant differences in growth rates were found based on pairwise comparisons among hatching orders within colonies (Tukey-Kramer: all $P \leq 0.003$) and within hatching orders between colonies (*t*-test: all $P \geq 0.18$).

TABLE 3. Brood sizes for the growth rate sample of Brown Pelican nestlings measured at Marsh Island and Crab Bank, South Carolina in 2004 and 2005.

	Marsh Island		Crab Bank	
Brood size	2004	2005	2004	2005
1	3	10	2	3
2	23	17	23	16
3	38	21	25	44
Mean ± SE	2.5 ± 0.1	2.2 ± 0.1	2.5 ± 0.1	2.6 ± 0.1

effect on the growth rate in terms of body mass at either colony (Marsh Island: $F_{2,109} = 1.2$, $P = 0.29$; Crab Bank: $F_{2,110} = 1.8$, $P = 0.16$) but had a significant effect on the rate of increase in culmen length only at Crab Bank ($F_{2,110} = 4.3$, $P = 0.02$). The rate of culmen length increase for a brood size of three (3.6 ± 0.1) was significantly lower compared to a brood size of one (4.3 ± 0.1; $P \leq 0.05$). A similar trend ($0.05 < P \leq 0.1$) was observed at Marsh Island.

DISCUSSION

Ectoparasites are characteristically harmful to their hosts and typically result in either negative or null effects on chick growth (Rogers et al. 1991, Ramos et al. 2001, Thomas and Shutler 2001). However, during our study, both mass and morphological growth rates of Brown Pelican chicks were not adversely affected by the observed levels of tick infestation during early development. Results from Marsh Island, where ticks were common, instead suggest a positive relationship between tick infestation and growth rates during both years of our study. Unfortunately, the causal mechanisms that may underlie such a relationship remain unclear, as does much of our understanding about chick-tick interactions. Here we explore alternative hypotheses that may explain the results we observed. These include the possibility that 1) our results were affected by missing growth data or unexamined factors such as parental quality, 2) repeated exposure to ticks resulted in physiological or behavioral modifications in chicks that affected their growth, and 3) tick presence caused parents to modify their behavior in such a way as to positively affect chick growth. Each is discussed in turn.

Studies of growth rates in chicks can often be hampered by early mortality of individuals that experience low growth rates. In these cases, slow-growing chicks often do not survive long enough to accumulate sufficient measures for analyses of growth rates, and hence, the low end of the growth spectrum is not represented in the resulting datasets (Nisbet et al. 1998). In this study, it is not likely that exclusion of such nestlings (including eight parasitized nestlings) affected the results because this group was only a small proportion (2%) of our sample. Analyses of growth data also may be hampered by confounding or missing independent variables. In our study, the higher growth rates of infested chicks may have been due to an unexamined parameter such as parental quality. For example, pelicans may repeatedly return to successful nesting locations within a colony and thus be exposed to ticks that have overwintered in the substrate there. We are not aware to what extent this occurs in ground-nesting pelican colonies. In this study, however, the area of Marsh Island where most study plots were located in 2004 experienced damage during winter storms and was not used for nesting in 2005. Regardless, the fact that both mass and morphological growth rates were consistently higher among parasitized nestlings in both years of our study and that hatching success was also greater in tick-infested nests suggests that ectoparasite infestation was in fact a significant factor operating in this system.

If our results are not due to confounding issues as outlined above, then we should seek to identify a mechanism that could underlie the observed positive response in growth rates to tick infestation. Our second hypothesis suggests that consistent exposure to ectoparasites can induce physiological or behavioral modifications in parasitized nestlings that may ultimately enhance growth rates. One mechanism that may be affected by such modifications is the immune response. Hoogstraal (1985) reviewed studies of acquired resistance to soft ticks in birds and suggested that the level of immunity was a result of a complex interaction of host age, tick species, and stage of tick development (see also Nunn et al. 2006). While the effect of ectoparasites on nestling immunity has been explored in other host-parasite systems (Saino et al. 1998, Brinkhof et al. 1999, Tschirren et al. 2007), results have varied, and the subsequent effects on growth rates have not been well examined. It is not clear from these studies how immunity and growth rates of pelican nestlings may respond to *C. capensis* during early development. Saino et al. (1998) found that Barn Swallow (*Hirundo rustica*) chicks infested with ectoparasites showed a positive response in feather growth, an attribute allowing them to depart the infested nest sooner, but also that these chicks had higher concentrations of leukocytes and fledged in poorer body condition. This suggests a physiological trade-off whereby more energy is allocated to growth to hasten nest departure, decrease the level of ectoparasite exposure, and ultimately increase the probability of fledging. During this study, we observed that pelican nestlings from some severely infested nests vacated their nests once they were mobile and relocated to nearby areas that were less infested. The coevolution of parasites and hosts and their defenses is currently an active field of study, and while many of the above mentioned hypotheses have been tested in other host-parasite systems, it is not clear whether results can be generalized to the system studied here.

While the above scenario posits a trade-off between two energy-intensive developmental processes, an alternate solution may be one in which growth rates benefit from an increase in parental provisioning rates to parasitized nestlings. For example, parasitized nestlings may increase begging rates, thus stimulating parents to increase provisioning rates (Christe et al. 1996, but see Thomas and Shutler 2001). Parents also may compensate for resources lost by parasitized chicks via enhanced brood care. However, because there can be a negative relationship between parental effort and adult survival (Deerenberg et al. 1995, Golet et al. 2000), parental effort should increase only when the probability of accruing a benefit also increases. This suggests that parents would compensate for costs of infestation only in manageable situations, such as when nestlings experience sublethal levels of ticks and when food availability is relatively high. Parents could then afford to increase provisioning such that growth rates could be enhanced instead of inhibited. Otherwise, parents would likely abandon their young in order to promote their own survival once tick infestation levels surpassed a manageable threshold or food resources were not available to support nestling demands. This hypothesis is generally consistent with our observations. We observed rare cases of chick mortality that appeared to be due to tick infestation during our study, despite *C. capensis* being a vector of potentially lethal viral and bacterial agents (Reeves et al. 2006). This implies that virulence of *C. capensis* was not high at the levels and conditions we observed. We also observed few abandoned nests, suggesting that the tick infestation threshold was exceeded in rare instances and, for the most part, parents could compensate for infestation levels that were present in the colony. Though insecticide treatment was not consistently related to growth rates in our study, it is possible that annual insecticide treatment of colonies kept tick populations below a threshold that triggers nest abandonment.

The growth rates we measured for both body mass and culmen length are similar to other available data on Brown Pelican growth (Schreiber 1976, Pinson and Drummond 1993). Significant relationships between hatching order and growth rates are common among asynchronously hatching species (Schew and Ricklefs 1998), have been observed previously in Brown Pelicans (Schreiber 1976, Pinson and Drummond 1993, Shields 1998), and were observed in each colony-year in this study. Furthermore, we observed a typical hatching order difference in growth rates of body mass and culmen length, where older siblings outpaced younger siblings (Pinson and Drummond 1993). Effects of brood size were inconsistent, possibly due to the low number of single chick broods in our growth rate sample. We did, however, observe the expected trend in culmen growth rates, where chicks from smaller broods outpaced those from larger broods (Pinson and Drummond 1993). These results demonstrate that, overall, our measures of growth rates were not strongly affected by ectoparasite load or the insecticide treatment employed during this study. Our study suggests that the cohabitation of ectoparasites and seabirds within colonies may result in behavioral or physiological adaptations of adults or nestlings that inhibit the expected negative effect of ectoparasites on nestling growth at sublethal levels of infestation.

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