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Influences of parasites and thermoregulation on grouping tendencies in marine iguanas

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I determined whether grouping behavior influences parasite load and body temperature of Galápagos marine iguanas, reptiles that rest gregariously. Mobile (or predatory) *Ornithodoros* ticks (4.7 mm average body length) approached at a ground speed of 65 cm/min and parasitized sleeping marine iguanas for 3.7 h per night, drawing about 0.1 ml blood. Contagiously transmitted *Amblyomma* ticks hang on to iguana hosts for days or weeks. Marine iguanas sleeping alone had 2.0 mobile ticks per night, while individuals sleeping in groups had 0.1 to 1.1 mobile ticks per night. Single iguanas decreased their mobile parasite load to 0.2 ticks per night by sleeping on bushes. Experimental nightly translocation of iguanas to areas without other sleeping iguanas significantly increased their mobile parasite burden above levels encountered by naturally single individuals ($n = 4.6$ ticks per night). Creating an experimental group of two animals reduced infestation with mobile ticks by 59% compared to levels on single animals. Over the course of weeks, mobile ectoparasite loads at grouping sites increased to levels found at single sites, at which point marine iguanas changed sleeping sites. Grouping had no effect on the prevalence of contagious ticks. Furthermore, grouping did not help to conserve body temperature in Genovesa iguanas, as measured by radiotelemetry. I conclude that marine iguanas group during daytime at microhabitats favored for thermoregulation (predation is absent in this population). Thermoregulation was not of prime importance for nightly aggregations, which instead served to reduce mobile ectoparasite load. As a minimum cost of infestation, I estimate that individuals sleeping alone would have a 5.4% lower annual energy budget due to tissue removal, not including potential internal infections. *Key words:* body temperature, ectoparasites, grouping, iguanas, host–parasite interactions. *[Behav Ecol 10:22–29 (1999)]*

Marine iguanas are peculiar among reptiles for their gregariousness, which may result in enormous aggregations and even ''piles'' of individuals (Darwin, 1883). Two hypotheses have been put forward to explain their active gregariousness: (1) grouping at night has the thermoregulatory benefits of ''cuddling'' (Boersma, 1982) and (2) grouping into territories serves to avoid harassment during the breeding season (Wikelski and Bäurle, 1996; Wikelski et al., 1996). Here I evaluate another factor that potentially influences grouping: parasite load (Côté and Poulin, 1995).

In most animal groups, individuals trade off the benefits of grouping against its costs (e.g., Hamilton, 1971; Magurran, 1990; Strassmann, 1992; Wittenberger and Hunt, 1984). Two of the most important benefits in groups are increases in vigilance and numeric dilution. Both factors reduce the chances that individual group members will suffer fitness losses due to predation (for a review, see Krebs and Davies, 1993). However, large groups are more conspicuous and may therefore attract more predators (e.g., for primates see Noe and Bshary, 1997). This logic can be extended to ''micropredators,'' the ubiquitous parasites of animals. Parasite prevalence often constitutes a cost of living in groups (e.g., Côté and Poulin, 1995; Kunz, 1976; Mooring and Hart, 1992; but see Arnold and Lichtenstein, 1993). The mechanism behind this cost is that parasite transmission from one individual to the next is facilitated when animals are in closer contact, as are grouped individuals compared to single individuals. In a meta-analysis, Côté and Poulin (1995) confirmed the expected positive correlation between host group size and both prevalence and intensity of contagious parasites. There was no effect of host group mobility on the strength or direction of these relationships. However, this positive correlation between group size and infestation prevalence only held for contagious, or nonmobile (sensu Côté and Poulin, 1995), parasites. Mobile, or predatory, parasites, on the other hand, usually infected grouping individuals in smaller numbers than they did single individuals (Côté and Poulin, 1995).

Here I determined the effect of grouping in marine iguanas on the prevalence of two types of parasites, one sedentary (permanently attached to hosts) and contagious (*sensu* Côté and Poulin, 1995), the other mobile and predatory, parasitizing hosts only during the night (see below for details). I used obvious and highly abundant ectoparasites of marine iguanas, the ticks *Amblyomma* spp. (sedentary) and *Ornithodoros* spp. (mobile; see Gadsen and Guerra, 1991; Keirans et al., 1973, 1980; Kohls et al., 1969). My aim was to quantify the prevalence of parasites for individuals sleeping in groups versus those that sleep singly. I also experimentally manipulated this situation to avoid possible effects of interindividual differences in parasite avoidance or resistance. To assess the costs of the parasite burden, I provided an analysis of the energetic costs suffered by parasitized individuals. As an alternative explanation for nightly groupings in marine iguanas, I considered thermoregulatory ''cuddling'' for warmth. Boersma (1982) suggested that marine iguanas on Fernandina island in the Galápagos archipelago group and establish body contact to conserve heat during the night.

Natural history of the host

Marine iguanas are ubiquitous along the rocky shores of the Galápagos Islands and can occur in densities as high as 8000 individuals per km coastline (Laurie, 1989; but see Cayot et al., 1994). There are three types of aggregations that may be formed: (1) after foraging in intertidal areas, marine iguanas

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may temporarily congregate along the coast at sites suited for thermoregulation (Buttemer and Dawson, 1993; Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994). I did not investigate this behavior here; (2) toward the late afternoon, individuals may congregate at sites relatively close to the coast. This mode of aggregation is especially prevalent in the larger individuals of a population, which often position themselves somewhat symmetrically like the spokes of a wheel (Boersma 1982). In these aggregations, individuals may also pile on top of each other, and may or may not stay throughout the night; (3) toward dusk, most individuals retreat from the coast to rest either in crevices, caves, below bushes, or in lava cracks. Individuals may also pile up in these nightly aggregations.

Predation pressure is largely absent for marine iguanas above hatchling size. The only exception are nesting females, which fall prey to the Galápagos hawk (Laurie and Brown, 1990). This, however, happens only during daytime, during specific times of the year, and at areas usually far off the coastal sleeping sites (Wikelski M, personal observation). Furthermore, hawks are absent on Genovesa island and thus predation can be excluded as a selective force influencing grouping during my study.

Marine iguana parasites

Marine iguanas suffer ectoparasitism from at least three groups of ticks. The most prominent ticks are the black, round *Amblyomma darwini* and *Amblyomma williamsii* (Bequaert, 1932; Hirst and Hirst, 1910; Schatz, 1991). Darwin's ground finches (*Geospizae* spp.) are known to remove those ticks occasionally, although marine iguanas lack a pushup body posture which aids cleaning birds in removing ticks (but see Galápagos land iguanas and Galápagos land tortoises; Carpenter 1966). Nymphs of *Amblyomma* species reside in skin folds along the neck of marine iguanas. Adult *Amblyomma* ticks are mainly found on ventral parts of marine iguanas, especially at the soft tissues of the cloaca, where they hang on for several days to weeks. It is unknown what determines infestation duration. From what little is known about the ecology of these ticks, they are presumably contagiously transferred between individual hosts (Schatz, 1991, personal communication).

The second, less conspicuous group of parasites consists of *Ornithodoros darwini* and *O. galapagensis* ticks, which only infest marine iguanas at night or when the iguanas are in crevices. *Ornithodoros* spp. fill with blood in a few hours. Both species are Galápagos endemic and were first described about 30 years ago (Kohls et al., 1969). They occur on at least eight Galápagos islands (Gadsen and Guerra, 1991; Keirans et al., 1980). *O. galapagensis* outnumbers *O. darwini* by far and is mainly associated with marine iguanas. The only other *Ornithodoros* species in Galápagos is *O.* near *denmarki,* a parasite of marine birds. Of the approximately 100 species in the genus *Ornithodoros,* only 4 are host specific to reptiles; 56% parasitize cave-dwelling bats, 20% infest birds nesting in rocks and caves, and another 20% infest mammals. Although nearly 90% of *Ornithodoros* species are restricted to the Western Hemisphere, some species are truly cosmopolitan on marine birds, swifts, and swiftlets (Keirans et al., 1980). It is unclear how important marine iguanas are as mating-encounter sites for ectoparasites (Yuval, 1994).

A third group of marine iguana parasites, which I do not consider here, are three species of *Vatacarus* ticks living in the nasal fossae (Schatz, 1991). In this study I concentrate on the northeastern-most population of marine iguanas on Genovesa Island, which has the smallest adult body sizes of all marine iguana populations (Rassmann et al., 1997; Wikelski and Trillmich, 1997; Wikelski et al., 1997). Nevertheless, all of the above-mentioned parasites, especially *Ornithodoros* spp., have also been found in other island populations of marine iguanas (Keirans et al., 1980; Wikelski M, unpublished data).

Marine iguanas have no malarial infections (Wikelski M, unpublished data), and there is no information on other bloodborne diseases or parasites. There were no coccidial infections in 128 marine iguanas from different islands (Couch et al., 1996).

MATERIALS AND METHODS

I studied marine iguanas at the ''Salvaje de Corazon'' site on Genovesa Island (89°59′ W, 0°19′ N) from 1 November 1992 until 3 March 1993. This period experienced a long-term El Niño, during which environmental conditions were unusually hot and moist (Wikelski and Trillmich, 1997).

Body temperatures of marine iguanas were measured either by inserting a fast-acting thermoprobe deep into the cloaca of individuals or by radiotelemetry (see Wikelski and Trillmich, 1994, for details). I implanted 20 animals with radio thermistors, which transmitted body temperatures for 14–90 days. Operative environmental temperatures were measured radiotelemetrically by monitoring temperature inside a black copper ball (15 cm diam; see Bakken, 1992; Wikelski et al., 1996). To evaluate temperature differences between sites, I recorded temperature within two copper balls simultaneously. To compare operative temperatures inside and outside of beach piles, I mounted each copper ball on a 4-m long bamboo pole and put one into the presumed center of the pile, while the other was placed approximately 1.5 m away. Animals did not react to this treatment if it was performed extremely slowly and carefully.

The effect of piling on body temperature was directly evaluated by measuring body temperature changes over a 4h period from 1730 h to 1930 h to 2130 h. I only used data on body temperature change when two conditions were met: (1) two animals with implanted thermotransmitters had joined the same pile location (within a radius of 50 cm) before 1730 h and (2) one of those animals touched other animals in the pile with at least half of its body, while the other animal was not touching other animals (except with its foot or its tail). Thus, one animal was piling, the other one not, but both experienced a similar microclimate. Seven such instances for different combinations of implanted individuals could be recorded.

I conducted observations on the prevalence of both *Ornithodoros* and *Amblyomma* spp. after sunset. I combined the two sets of congeners, *Ornithodoros darwinii* and *O. galapagensis,* as well as *Amblyomma darwinii* and *A. williamsii,* respectively, into two ecological species groups. This seems justified by the fact that hybridization between congeneric tick species may occur (Guglielmone and Mangold, 1993) and by the respective morphological and ecological similarities of each congeneric pair (see Verdammen-Grandjean, 1966). Nothing is currently known about the ecology of either Galápagos tick genus, but in a closely related Peruvian seabird tick (*O. amblus*), females lay about 450 eggs, and the life cycle is completed in 63 to 401 days. Adult *O. amblus* also only feed for short periods (15–55 min.; Clifford et al., 1980; Khalil and Hoogstraal, 1981). Unfed adults of other closely related species can survive for many years (Anastos, 1957).

Marine iguanas went to sleeping places before sunset and moved little at night, except for occasional leg and tail movements in what appeared to be active sleep phases (Wikelski M, unpublished data; for behavioral data on sleep phases in lizards, see Ayalaguerrero and Huitronresendiz, 1991). Therefore, I assumed that the observed sleeping aggregations were stable throughout the night. Iguanas were not active at night; thus nightly groupings were presumably not primarily influenced by mating decisions (see Wikelski et al., 1996). I considered individuals as grouped if four or more individuals were resting within half a body length of each other. A "pile" of iguanas is defined as individuals touching the body of another animal with at least one third of their own body.

To conduct observations and parasite counts, groups of sleeping iguanas were approached by a single observer who either used moonlight or the darkened light of a flashlight for vision. The total number of group members was counted. In several cases individuals sleeping in groups were touching each other. As a conservative (tick-centered) estimate of "apparent" group size, I used only the approximate surface area of an individual to determine the number of individuals per group (e.g., if half the individual was covered by another animal, I counted it as 0.5 individual only; final group numbers were rounded to the nearest integer number). This measure accounted for the reduced surface area suitable as attachment site for ectoparasites. In only a few cases were individuals entirely covered by one or two other individuals. In these cases, I did not count the covered animals as group members, since covered animals were not found to be infested by *Ornithodoros* ectoparasites in control counts. However, covered individuals were parasitized by *Amblyomma* ticks. This apparent group size is a conservative measure of infestation rate compared to including covered individuals; the latter would make the differences between group and single individuals even more pronounced. I used the same measure of apparent group size for *Amblyomma* and *Ornithodoros* ticks. Infestation rate is defined as the total number of ticks found in a group divided by the number of group members. On 23 January 1993, all iguanas sleeping in 10 groups throughout the study area were counted and their *Ornithodoros* and *Amblyomma* parasite burden investigated after midnight. This count provided an independent determination of group size on infestation rate. I refer to the "start" of a new group if I found a group of sleeping iguanas at a site where I had not seen iguanas sleeping during the preceding week. The "break up" of a group was defined when fewer than four iguanas were found sleeping at a site that was occupied by a sleeping group during the preceding 3 weeks.

I found *Ornithodoros*. spp. preferentially located on the dorsal parts of animals, although I initially searched all parts of individuals carefully for the occurrence of ticks. The preferred infestation sites appeared to be the tail vein and the dorsal spine vein, where about 90% of ticks were located. The remainder were distributed at femoral veins and the flanks of animals. Only *Ornithodoros* ticks > 2 mm carapace length were found to infest iguanas at night.

In contrast, *Amblyomma* spp. were distributed almost exclusively on the ventral part of the body of hosts, except for the nymphs, which infest the host around its skin folds at the neck. I only included *Amblyomma* individuals > 2 mm body length in the counts. I did not want to disturb nightly groupings, thus I could not check for *Amblyomma* ticks in the same groups in which I counted *Ornithodoros* ticks (because of the ventral attachments sites of *Amblyomma* spp.). Therefore, I used adjacent groups of similar size to count *Amblyomma* ticks during the same nights. Marine iguanas at my study site were not awakened or otherwise disturbed by these observations.

Walking speeds of each 10 *Ornithodoros* and *Amblyomma* ticks were measured in empty (presumably hungry) ticks in the shade of a tent. Ticks were set on a 2-cm wide runway consisting of a calibrated driftwood board of 30 cm length with side walls of 3 cm height. The ticks were stimulated with a pen held behind them (simulating a bird's beak) to run at least 20 cm. The time taken for this exercise was measured with a wrist watch.

To determine the amount of blood extracted from the host, 11 *Ornithodoros* ticks were collected after they naturally left their respective host, and 11 *Amblyomma* ticks were actively removed from their hosts when they appeared full of blood. Their full body volume was measured to the nearest 0.01 ml by submersion in water. Thereafter, ticks were killed and gut contents measured.

Experimental manipulations

I carefully picked up 10 nonparasitized individuals from nonfocal groups between 2000 h and 2200 h, covering the iguanas' eyes with one hand and the head with the other hand. When done extremely carefully, other group members were not affected by the removal of a conspecific. Thereafter, animals were translocated to different places in the study site. I placed animals on the ground and again held my hand above their head for approximately 5–10 s until the animals stopped moving and continued to rest or sleep. To create eight experimental groups of two, this procedure was repeated twice, and a second animal of similar body size was placed within one body length distance of the first experimental individual. After an initial test trial period, all translocated animals except one remained sleeping throughout the night at the new place. One iguana woke up and left and was therefore discarded from the analysis. The *Ornithodoros* infestation of experimental animals was checked every half hour throughout the night until 0400 h, when *Amblyomma* ticks were also counted. The maximum number of ticks was found between midnight and 0200 h and usually did not show any changes between these two sampling points. Only the maximum number of ticks per animal and night was used for the analysis. During these experiments I also determined the attachment duration to the nearest half hour by marking the first and last appearance of an individual tick on a host.

Statistical analysis

I analyzed data using SPSS (1991) for Windows; means ± SD are given unless otherwise noted. Error estimates in regression equations are given as means ± SE. Two-tailed tests were used and the α level was set at 5%. Data from natural and experimental situations were compared using ANOVA.

RESULTS

Parasites and infestation rates

Both *Amblyomma* and *Ornithodoros* ticks moved relatively fast over a plain surface (Table 1; total body lengths of measured individuals about 4 mm, ambient temperature about 33°C; Mann-Whitney *U* test, $N_{1,2} = 11$, $p > .05$). On average, adult *Ornithodoros* ticks were about 40% larger and had about 50% larger gut volumes compared to *Amblyomma* ticks (for both cases: Mann-Whitney *U* test, $N_{1,2} = 11$, $p < .001$). While *Ornithodoros* spp. attached only at night for several hours, *Amblyomma* spp. infested hosts for days (Table 1). *Ornithodoros* ticks attached to hosts between 1900 h and 2300 h, and the last ticks left their hosts at 0430 h.

Mean group size of all marine iguana groups sampled on 23 January 1993 was 29.7 ± 27.4 individuals ($n = 10$ groups). The infestation rates per individual were initially low but increased over time when animals were using the same sleeping location. When animals appeared at a new sleeping site, the infestation rates were initially moderate and declined as more and more animals joined the sleeping aggregation. However, after about 3 weeks, infestation rates increased again. This observation was qualitatively repeated twice (Figure 1).

Ornithodoros infestation rates were influenced by group size, but *Amblyomma* infestation rates were not. *Ornithodoros* infestation rates were lowest in individuals sleeping in groups

Table 1
Characteristics of ticks parasitizing Galápagos marine iguanas on Genovesa Island

	Ornithodoros darwinii, Ornithodoros galapagensis	*Amblyomma darwinii, Amblyomma williamsii*
Attachment sites	Dorsal body parts, tail, legs	Belly, around cloaca
Attachment duration	3.7 ± 1 h (9)	>Several days
Attachment time per day	1600 h–0430 h	continuous
Total body length (mm)	6.5 ± 2.0 (11)	3.7 ± 2.2 (11)
Blood volume extracted (ml)	0.114 ± 0.02 (11)	0.05 ± 0.01 (11)
Walking speed (cm/min)	65 ± 21 (10)	51 ± 14 (10)

Only individuals larger than 2 mm total body length were included in the measurements. Data represent mean ± SD (*n*).

or singly in bushes (Figure 2). There was a significantly higher prevalence of ticks when individuals were sleeping alone on rocks than when they slept in groups or in bushes. The prevalence of *Ornithodoros* ticks in single experimental individuals was significantly higher than in any other treatment group (ANOVA, $F_{5,57} = 12.8$, $p < .001$; followed by post-hoc least-significant difference tests; see Figure 2 for differences between groups). However, there was no significant difference in *Amblyomma* tick infestation rate between any of the treatment groups (ANOVA, ns).

To analyze the influence of grouping on infestation rate, I determined the slope of the regression of the total number of parasites against the apparent number of individuals in a group (Figure 3). A slope of 1 would indicate that the average number of parasites per host is constant, while a slope below 1 would indicate a decrease of infestation rate with group size. The total number of *Ornithodoros* ticks increased with group size by a factor of 0.27 [linear regression: total *Ornithodoros* ticks in group = 7.8 (±4.1) + 0.27 (±0.10)× individuals in group; $F_{1,10} = 6.7$, $p = .03$, $R^2 = .46$]. Therefore, individuals in larger groups had lower *Ornithodoros* infestation rates per individual than individuals in smaller groups. Infestation by *Amblyomma* ticks, on the other hand, did not change with group size, as indicated by a regression slope of close to 1.0 [linear regression: total *Amblyomma* ticks in group = 6.7 (±7.1) + 0.86 (±0.18)× individuals in group; $F_{1,10} = 23$, $p = .001$, $R^2 = .74$; other regression models did not fit better than a linear one]. To investigate whether parameters other than average number of ticks per iguana may relate to group formation, I determined the variance in number of parasites per

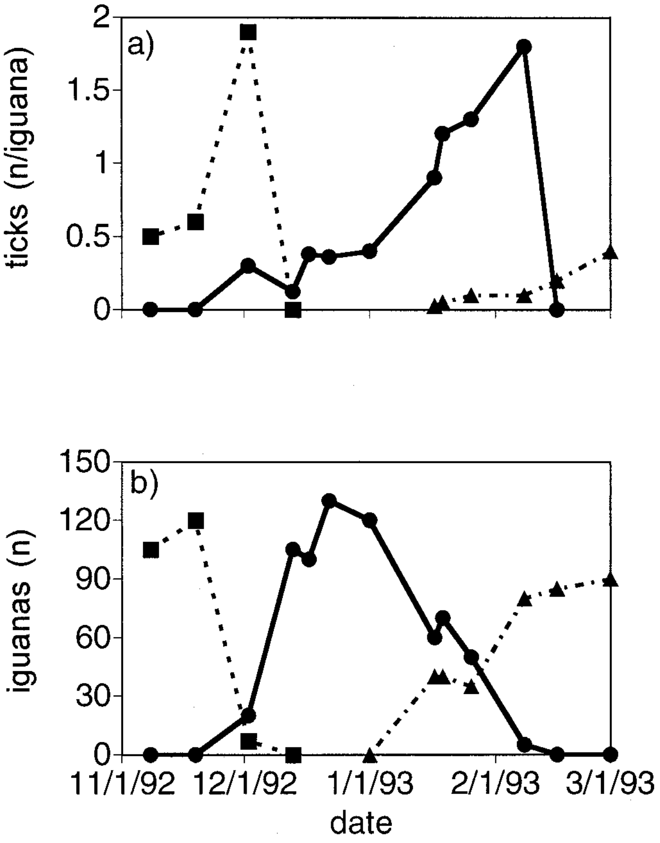

Figure 1
Time courses of (a) the number of *Ornithodoros* ticks per iguana and (b) the corresponding group size of marine iguanas at nightly sleeping sites. Different symbols and lines represent different group locations. Note that the number of parasites per iguana was initially low in each group and then increased over time until iguanas suddenly abandoned a formerly popular nighttime retreat (i.e., not more than three iguanas slept at those former sites).

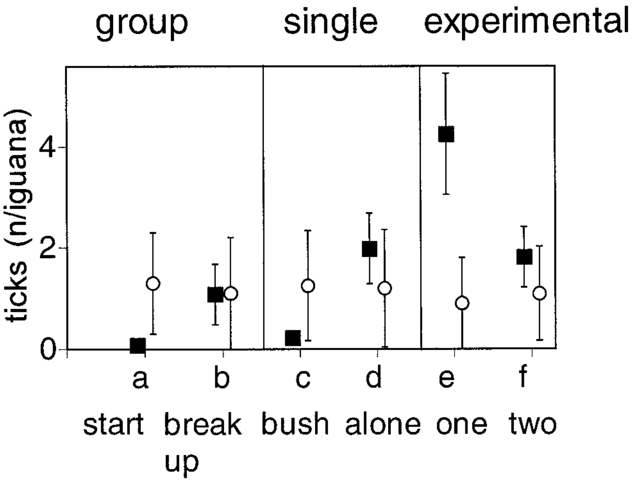

Figure 2
A comparison of the number of *Ornithodoros* ticks (filled squares) and *Amblyomma* ticks (open circles) per individual iguana when sleeping in groups ("start" = within the first week of group formation; "break up" within the last 3 weeks of group formation), singly (on a bush or on the ground), or in experimental groups (of one or two individuals). The data show means ± SD. Sample sizes were, from left to right, 10, 10, 10, 10, 9, and 8 for each pair of data, respectively. There were no differences in the *Amblyomma* infestation rates between treatment groups. There were significant differences in *Ornithodoros* infestation rates between *e* and all other group means, as well as between *a* and *d, a* and *f, c* and *d,* and *c* and *f* (determined by least-significant difference tests after ANOVA, see text).

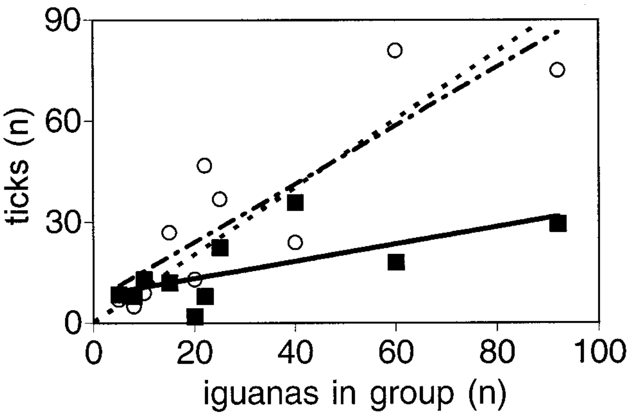

Figure 3
The total number of *Ornithodoros* ticks (filled squares) and *Amblyomma* ticks (open circles) for 10 groups of marine iguanas as counted on 17 December 1992. The lines represent linear regressions with a slope of 0.28 (for *Ornithodoros* ticks, straight line), a slope of 0.86 (for *Amblyomma* ticks, dashed and dotted line), and a slope of 1.0 (dotted line, line of equality). Note that although the number of *Amblyomma* ticks increases symmetrically with group size, the relative number of *Ornithodoros* ticks becomes lower in larger groups.

iguana in relation to group size. The variance in *Ornithodoros* infestation declined with group size [a logarithmic model fitted significantly better than a linear one: logarithmic regression: $y = 1.57\ (\pm 0.35) - 0.33\ (\pm 0.11)\ \ln(x)$; $F_{1,8} = 8.6$, $p = .01$, $R^2 = .51$). In contrast, there was no change in variance in *Amblyomma* infestation with group size [linear regression: $y = 0.47\ (\pm 0.18) + 0.0\ (\pm 0.0)\ x$, $F_{1,8} = 0$, $p = .95$, $R^2 = 0$).

Body temperature and nightly grouping
To determine whether grouping affected nighttime body temperature, I considered, as two alternatives, whether the grouping site per se affected body temperature and whether "cuddling" (Boersma, 1982) affected body temperature. These measurements were conducted after the reproductive season, in February and March 1993.

Site effects
First, I determined whether marine iguanas sleeping alone in crevices or cracks (usually 20–50 m off the coast) could achieve similar nighttime body temperatures to individuals sleeping in beach piles (usually found very close to the coast, as described by Boersma, 1982). This tests for the effect of sleeping site selection on nightly body temperature. I found that individuals of all body sizes achieved considerably higher body temperatures in crevices compared to beach piles (mean differences in body temperature between crevice and beach individuals: 0.72 ± 0.64°C; Wilcoxon test, df = 15 individual pairs of similar body sizes measured during 15 nights at 2000 h, $Z = -3.1$, $p = .002$). This effect was corroborated by measuring standard operative temperature at those places at about 2000 h. Operative temperature was always higher around crevices than at beach piling sites (28.8° ± 3.1°C versus 27.7° ± 2.5°C, same setup as above: Wilcoxon test, df = 15, $Z = -3.2$, $p = .001$). Furthermore, there was always a higher standard operative temperature inside as compared to 1.5 m outside of the pile location (mean difference in temperature was 1.61° ± 0.65°C, Wilcoxon test, df = 8 pile locations on 8 days, $Z = -2.5$, $p = .01$).

"Cuddling" effects
If piling conserves body temperatures in iguanas, I expected to find higher body temperatures in piled than in single individuals at the same site after the same sleeping duration. In a repeated-measures ANOVA I determined whether there were differences in the body temperatures at three different times (1730 h, 1930, 2130 h) between piling versus nonpiling individuals while correcting for their respective body masses (330–720 g) as a covariate. I did not find any significant difference in body temperature change over time between piling and nonpiling marine iguanas (repeated-measures ANOVA with mass and day of measurement as covariates, $F_{2,14} = 0.01$, $p = .96$; for mass, $p = .18$, for date, $p = .46$; higher level interactions were not significant).

DISCUSSION

Observational and experimental data showed that grouping of the host reduced the infestation rate by mobile, but not by contagious, ectoparasites. Because the numbers of mobile parasites increased at sleeping locations over time, hosts shifted their sleeping locations and thus ensured a low infestation rate. Singly-sleeping iguanas encountered lowest infestation rates at places that were hard for the investigated parasites to access, on bushes. Sleeping in groups did not influence body temperature of Genovesa Island marine iguanas.

Ecology of parasitic ticks
Amblyomma spp. and *Ornithodoros* spp. were the most commonly observed groups of macroscopically visible parasites on marine iguanas (Keirans et al., 1980; Kohls et al., 1969). They belong to the 88 known species of 14 families of Galápagos *Acari* (Schatz, 1991).

Although ticks are usually considered "contagious" parasites (sensu Côté and Poulin, 1995), this infestation mode only describes the situation in *Amblyomma* ticks. *Amblyomma darwini* and *A. williamsi* stay firmly attached to the host for at least several days if not weeks. These parasites seem astonishingly unaffected by the hosts' prolonged foraging and diving bouts in the sea (Carpenter, 1966). The fast speed of ground movement (about 50 cm/min.) enables these ticks to switch easily between hosts resting adjacent to each other, making a contagious infestation possible (see also, e.g., Kunz, 1976).

Although *Ornithodoros* ticks achieve similar ground speeds, they seem to have adopted a generally much more mobile, or predatory, way of life. In this study *Ornithodoros* spp. were only observed to ambush marine iguanas at night. The spatial distribution of *Ornithodoros* ticks demonstrated by my experimental study seemed to resemble an equal distribution along the habitat, at least for the habitat suitable as marine iguana nightly resting sites.

A clear distinction between the two types of ticks is the attachment site on the host. *Amblyomma* is confined to the neck skin folds as nymphs and mostly to the ventral body parts as adults, whereas *Ornithodoros* infests mostly the dorsal and tail parts of marine iguanas. It appears that a niche segregation along a host's body is common in ectoparasites, but the reasons for this are generally not well understood (Chilton et al., 1992b).

The most striking difference between the two marine iguana ticks, however, is the duration of attachment on the host. While *Amblyomma* individuals stay attached for at least several days, *Ornithodoros* individuals fill up within hours and thereafter leave to retreats between rocks (for related cases, see Chilton et al., 1992a; Matuschka et al., 1990a,b). However, it is not known if *Amblyomma* ticks slowly draw blood during the entire attachment duration or if the prolonged attachment duration serves other functions. For example, it could be important for reproduction. We currently lack information on the reproductive ecology of both *Amblyomma* and *Ornithodoros* ticks to answer this question.

Host–parasite interactions: why group?

So far, it has been suggested that marine iguanas group either at night for the thermoregulatory benefits (Boersma, 1982) or that grouping during daytime helps to avoid harassment in a reproductive context (Wikelski et al., 1996). During the present study, only nonreproductive groupings were investigated, even though the study also covered the reproductive period (December).

Nonreproductive grouping has so far been attributed solely to the thermoregulatory benefits (Boersma, 1982). However, Boersma could not measure the body temperature of individuals as they joined the pile, nor did she measure the standard operative environmental temperature at the site of piling versus the sites where single iguanas were sleeping. My radiotelemetry data showed no effect of pilling versus single sleeping on the rate of body temperature change; thus there was no benefit of ''cuddling'' in my population. However, marine iguanas on Genovesa have about seven times smaller body masses than the animals investigated by Boersma (1982) on Fernandina. It could therefore be argued that a cuddling effect found in piles of large iguanas might not be detectable in piles of small marine iguanas, due to a different surface-to-volume ratio (e.g., Schmidt-Nielsen, 1984).

A more likely explanation for the formation of beach piles is that iguanas gather at spots that offer a slightly better (i.e., warmer) microclimate during the late afternoon hours, when piles usually develop. This was supported by the measurements of standard operative environmental temperature (after Bakken, 1992), which were always slightly higher at places where iguanas piled. Circumstantial evidence also shows that iguanas often left those beach piles shortly before sunset only to join conspecific groups farther off the coast (Wikelski and Hau, 1995; Wikelski M, personal observation). This supports the view that the direct thermoregulatory benefits at piling sites are only short lived, as they may only exist during the afternoon hours. For sleeping, iguanas may then search for the warmer sites farther inland.

In addition to possible thermoregulatory reasons for grouping, there seemed to be a clear effect of grouping on parasite load, in that individuals in groups were less parasitized by mobile *Ornithodoros* ectoparasites (see Poulin and FitzGerald, 1989). Furthermore, the variance in infestation rates was less in larger groups of iguanas. In contrast, the infestation rate by contagious parasites and its variance appeared unaffected by these behavioral decisions of the hosts. The likely reason for this difference was that contagious, fast-moving parasites could switch hosts at any time whenever hosts rested close to each other. It is unclear if individual behavioral variation in the host (e.g., the high sleeping/resting site fidelity) influences *Amblyomma* infestation pattern.

Taken together, it appears that marine iguanas group during daytime at places favored for thermoregulation. These may be either relatively cool microhabitats during the heat of the day (e.g., the shade of an observational chair, as seen in the present study) or relatively warm habitats during the late afternoon hours (e.g., places at the beach). It is conceivable that already resting individuals are used as ''thermal indicators'' for suitable areas by passing iguanas. This would explain the attraction of iguanas to model iguanas during the nonreproductive season, which we found during a previous study (Wikelski et al., 1996). The nightly groupings might be influenced both by microhabitat selection and parasite avoidance strategies. Marine iguanas that rested in groups moved to alternative grouping sites when parasite infections surged at ''traditional'' sleeping sites (for similar effects in primates, see Freeland, 1976). This situation parallels the bat fly infections of bats roosting in caves (Kunz, 1976). In all these cases, parasites presumably located persistent piles or groups of hosts.

The pattern of ectoparasitism in marine iguanas confirms a meta-analysis on sociality and parasitism. Côté and Poulin (1995) suggested that parasites have the potential to select for either larger or smaller group sizes, or for solitary individuals, depending on their mode of infestation. In their analysis of 15 host–parasite systems (5 birds, 7 mammals, and 3 fish), the direction of selection pressure on the host depended mostly on the lifestyle of the parasites. Contagious parasites were more prevalent and intense in larger host groups. In contrast, mobile parasites decreased with increasing host group size. My data on marine iguana ectoparasitism demonstrate that only one effect, the decrease in mobile parasites, occurred within this host. My data corroborate the notion that closely related ectoparasites can have different life-history modes and may thus affect host behavior differently (see Poulin, 1994).

The gregariousness during the iguana mating season and a possible temperature/infestation trade-off indicate that there are (seasonally) differing reasons for groupings (cf. Mooring and Hart, 1992; Packer et al., 1990; Underwood, 1982). It is currently unclear whether (ecto-)parasites have any influence on grouping in other iguanids (see, e.g., Burghardt and Rand, 1985).

Does infestation affect iguana fitness?

There is widespread evidence for costs of ectoparasites to hosts (e.g., Duffy, 1983; Richner et al., 1993; see also Hart, 1990). Ticks may transmit blood parasites such as *Rickettsia*-like blood cell inclusions (Schall, 1990). Blood parasites or a combination of ectoparasites and blood parasites reduced the hemoglobin content in lizards, and consequently maximum oxygen consumption dropped by 15%. Running stamina was found to decrease by up to 20%, which would imply a reduced ability to maintain territories (Schall, 1990; Schall et al., 1982; see also Sorci et al., 1996). Tail regeneration was reduced in parasitized *Lacerta* lizards (Opplinger and Clobert, 1997). There were also hormonal alterations in lizard hosts caused by parasites (Dunlap and Schall, 1995). These might increase the host's susceptibility to even larger numbers of ectoparasites (Salvador et al., 1996).

On the other hand, Bull and Burzacott (1993) did not find a fitness effect of tick load on Australian sleepy lizard hosts (these skinks have similar adult body masses as marine iguanas on Genovesa Island, 500–700 g). Nevertheless, there was at least an energetic cost of infestation because an adult tick engorges up to 0.5 ml blood (Chilton and Bull, 1993). Furthermore, parasite effects on fitness were only investigated by correlations, and the authors suggested that only an experimental manipulation would reveal any real effect on individuals (Bull and Burzacott, 1993). Dunlap and Mathies (1993) demonstrated a direct effect of ectoparasites by showing that tick-infested *Sceloporus* lizards had lower hematocrits and possibly much reduced aerobic capacities as compared to noninfected individuals.

In marine iguanas it could not be quantified if infested individuals suffer costs and, for example, mount an immune response to ticks. It is possible that at least *Amblyomma* ticks are largely benign, especially because iguanas show no obvious behaviors to avoid infestation. However, the behavioral changes in marine iguanas related to the infestation by mobile *Ornithodoros* ectoparasites make at least some cost of infestation likely. An immediate cost of ticks, even in the absence of disease transmission, would be the removal of tissue (blood). An iguana that always rests alone would suffer infestation of 723 *Ornithodoros* ticks per year (1.98 ticks × 365 nights), whereas it would only host 219 ticks (0.6 ticks × 365 nights) if it were sleeping in a group every night of the year. Assuming a mean blood removal per *Ornithodoros* tick (0.114 ml) and tissue production (or growth) efficiencies of 75% (Baxter, 1989; Prosser and Brown, 1965), this amounts to an 82.4 ml blood loss, or approximately 549 kJ energy loss per year for a singly-sleeping versus 23.7 ml blood loss or 157 kJ energy loss per year for a group-sleeping individual. This represents 7.5% versus 2.1% of the annual energy budget for a medium-sized Genovesa marine iguana (300 g) of 7300 kJ (20 kJ × 365 days; cf. Drent et al., submitted; Nagy and Shoemaker, 1984; Wikelski et al., 1997). It appears likely that the difference of 5.4% in the annual energy balance between grouping and nongrouping individuals selects for the observed behavioral differences in host grouping behavior.

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