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SPATIAL SEPARATION OF INTRASPECIFIC ATTACHMENT SITES OF *AMBLYOMMA SYLVATICUM* ON ANGULATE TORTOISES *CHERSINA ANGULATA*

A. Pearcy[1] and J. Beyer[2]

[1]Animal Plant and Environmental Sciences, University of Witwatersrand, Johannesburg, Private bag 3, Wits, 2030, South Africa; e-mail: ashley.pearcy@gmail.com
[2]Department of Biology, 215 Cox Science Center, 1301 Memorial Dr, University of Miami, Coral Gables, Florida, 33124 USA; e-mail: jennabeyer9@gmail.com

ABSTRACT: Host-parasite relationships are partly determined by the inter- and intraspecific competition of the present parasiste community. Preference in attachment site has evolved to counter both interspecifc and conspecific competition along with threat of dislodgement and reproductive success in ectoparasites. 3929 ticks (*Amblyomma sylvaticum*) were collected in West Coast National Park, South Africa from 24 Angulate tortoises (*Chersina angulata*). *Amblyomma sylvaticum* uses spatial segregation in attachment site preference to allow for simultaneous success of all life stages. The high density of *A. sylvaticum* and its preferred host *C. angulata* create an environment where the parasite population's potential for growth and distribution is unparalleled by other tick species in that location as seen through the lack of other tick species and *A. sylvaticum* presence on other host species.

KEY WORDS: intraspecific competition, attachment site, Amblyomma, ticks, parasite

INTRODUCTION

Parasite communities are governed by the same laws of competition that influence larger species. Intra- and interspecific competition drive niche division through morphological and physiological differences. In parasite communities, this often leads to host-specificity, which can lead to increased chances of reproductive success and reduced interspecific competition (Rohde 1979). As ectoparasites, ticks have other factors which drive competition for attachment site. Chilton et al. (1992) suggests three explanations for the segregation in attachment site of ticks: niche segregation from interspecific interactions, maximizing of feeding and breeding success, and protection from physical disturbance. However, within a single species, different life stages will feed on different hosts or different locations within a single host to avoid intraspecific competition (Fielden and Rechav 1994).

Amblyomma is a common Ioxid tick genus found throughout the African continent, with 22 African species being redescribed in 2003 by Voltzit and Kierans. Ticks are primarily known for their potential as disease vectors and this has been a foremost reason behind conducting ecological or behavioural studies in southern Africa. While this has led to studies of economically important species, such as *Amblyomma hebraeum* due to its preference for large, iconic African mammals, others have remained understudied.

Prominent in the Cape region, *Amblyomma sylvaticum* is the second most frequently found reptile tick in South Africa behind *Amblyomma marmoreum* (Horak et al. 2006), but is far less studied. *A. sylvaticum* primarily attaches to the Angulate tortoise *Chersina angulata*. Such host preference leads to greater intraspecific competition because it limits potential attachment sites to the number of preferred hosts within range, whereas as a wider host option could lead to higher potential for attachment site and detectability. Ticks can reduce intraspecific competition on a single host by attaching to different sites depending on the life stage and sex of the tick (Fielden and Rechav 1994). This study, therefore, looks at the attachment site preference of *A. sylvaticum* on Angulate tortoises.

METHODS

Study species

Amblyomma sylvaticum is strictly South African and is predominantly present in the cape provinces with only a single record found in the centre of the North Cape province (Horak et al. 2006). All stages of *Amblyomma sylvaticum* infest Angulate tortoises *Chersina angulata* by preference (Horak et al. 2006). While lacking repetitive seasonal data, the implications of *A. sylvaticum* life stages are: larvae occur May-November, nymphs August-January, and adults August-February (Horak et al. 2006).

Experimental protocol

Twenty-four Angulate tortoises were collected over a five-day field period in October 27-31 2012 at Duinepos, West Coast National Park (GPS acquired location: S33°11.700′, E18°08.283′). All tortoises collected were parasitized. All ticks were removed and attachment site was recorded (shell, forelimb pits, hind limb pits, head and neck region, and tail/anus). If tortoises had over 50 larvae

Table.
Other host species of *Amblyomma sylvaticum* collected, including the life stage and tick count per host species.

Host spp.	Common name	Tick life stage	Count
Aparallactus capensis	Centipede eater snake	larvae	20
Dasypeltis scabra	Egg eater snake	larvae	8
Pseudaspis cana	Mole snake	adult male	3
		adult female	2
		nymph	5
		larvae	26
Pedioplanis lineoocellata	Spotted sand lizard	larvae	2

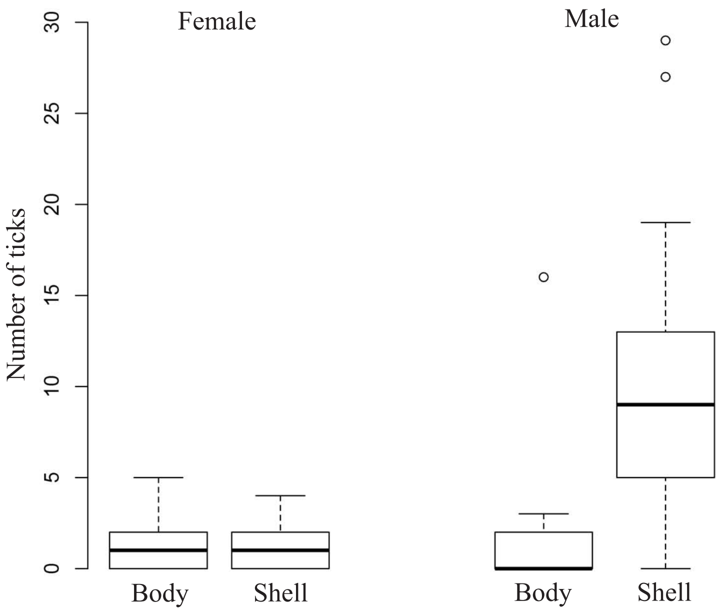

Fig. Female ticks show no preference for shell or body, while male ticks prefer to attach to the shell.

per an attachment site, only 50 of the larvae were counted. Though Angulate tortoises were the target host species, ticks were also removed from other reptile species encountered during the collection period. The ticks were stored in 70% ethanol solution for later identification. Only *A. sylvaticum* were found on the reptiles collected.

Data analysis

Comparisons of tick attachment site preferences at different life stages were done using Chi Square tests (Excel 2008). To compare the effects of multiple parameters, a mixed-effect logistic model was produced in R (2013) to analyse the impact of sex and attachment site in adult ticks with the random factor being individual tortoises.

RESULTS

3929 ticks were removed from 24 Angulate tortoises. Of these, 63 were adult females, 289 were adult males, 3200 were larvae and 377 were nymphs.

Each life stage has a preference for attachment site. Adults prefer the shell to the soft body parts (X^2=145.10, df=1, p<0.0001), while nymphs ((X^2=369.04, df=1, p<0.0001) and larvae (N=3200, all on soft tissue) prefer soft tissue.

All tick life stages considered, more ticks attach to the fore parts of the tortoise than to the hind (X^2=824.58, df=1, p<0.0001). However, adult ticks have no preference (X^2=2.68, df=1, p=0.10).

When only adult ticks are assessed, males prefer the shell while females show no preference (Fig.).

Other hosts

While the Angulate tortoise is the preferred host of *A. sylvaticum*, we found the tick in different life stages on other hosts (Table).

DISCUSSION

All life stages were found in high number on Angulate tortoises and were present on other species. Each life stage appears to have a preferred attachment site, allowing for all life stages to be simultaneously successful on a host by reducing intraspecific competition. This may indicate a spatial rather than temporal segregation, which is seen in other *Amblyomma* species (Fielden and Rechav 1994). Spatial separation can allow for the increase in the presence of all life stages more frequently. The lack of other tick species, previously found in the area and on the Angulate tortoise, may be driven by temporal differences. However, an overwhelming dominance of a single species, especially capable of spatial separation, can offset the balance of the parasite community and, in turn, the fitness and recovery of the host. Further studies in different parts of the year should be conducted to understand the life cycle of *A. sylvaticum* and its demography in comparison to other tick and host species populations.

Many species of ticks tend to attach to the hind part of the tortoises, as this is where the tortoise hormones are released. *A. sylvaticum*'s preference for the front may have to do with the environment in which the two species live and the feeding strategy utilized by *A. sylvaticum*. The habitat is predominantly sand with low scrubby bush. The ticks may attach to the anterior regions of the tortoise as the tortoise moves through the scrub or sand because that is the first area encountered. Also, many reptile-specific ticks employ an ambush feeding strategy as they have a limited detection range (Belan and Bull 1991) and would attach to the first area of the host contacted. Unlike other *Amblyomma* species (Fielden and Rechav 1994), however, *A. sylvaticum* ticks remain in these positions rather than moving to the posterior region. Anterior preference may be due to the high density of the ticks (Andrews and Petney 1981). Limited detection may not be an issue in this region as Angulate tortoises are very common in the area (pers. obs.). Though Angulate tortoises, the preferred host, are common, the finding of *A. sylvaticum* on different host species in all life stages, shows its adaptability in claiming a host, and the presence of multiple hosts also suggests the potential for a high distribution of *A. sylvaticum*.

The immature life stages of *A. sylvaticum* were found almost exclusively in the soft skin of the tortoises. Ticks prefer to attach in areas of the host that allow for efficient feeding with the least chance of being dislodged (Andrews and Petney 1981). Immature ticks have shorter feeding apparatus and may also have less effective anticoagulants, which would make soft skin and areas of high vascularity, such as the neck and pockets around the legs, more preferable for attachment (Ernst and Ernst 1977). These pockets also give the ticks the protection of the shell, reducing the chances of being dislodged. Adult ticks are able to produce histolytic secretions that can dissolve the shell and create pits for attachment (Ernst and Ernst 1977). The longer feeding apparatus would allow the adults to hold strongly to a more exposed feeding site.

Efficient feeding and protection from dislodgement, however, are not the only considerations for adult ticks. Andrews et al. (1982) found that on sleepy lizards (*Tiliqua rugosus*) in Australia adult male ticks chose attachment sites based on the likelihood of detecting female pheromones. This could also be an important factor in choosing attachment sites for *A. sylvaticum* males on Angulate tortoises. The shell is more open than the soft tissue pockets behind the legs and on the neck. A male attached in one of these pockets would likely not receive pheromones from a female attached at a different part of the tortoise due to the increased interference of the leg and shell. Attaching to the shell may decrease the amount of interference immediately around the male and increase the chances of the male detecting the pheromones of a female attached at different locations on the tortoise.

With spatial segregation of life stages, *A. sylvaticum* has adapted a successful life history strategy within the Cape region and possibly, this ecology has made it one of the more prevalent species in South Africa. The attachment site preferences found in *A. sylvaticum* give the species an advantage over other ectoparasites in the region, which rely on temporal differences in the appearance of different life stages. Since all life stages can be present simultaneously, a larger population of *A. sylvaticum* potentially can survive. *A. sylvaticum* was the only species found on the animals sampled within the study site, despite known presence of other tick species within the region (Horak et al. 2006). The Angluate tortoise is one of the more common species in the region, which may be adding to the population growth potential of *A. sylvaticum*. The area has very few tick predators and therefore the population may continue to grow until carrying capacity is reached or surpassed. The possibility of dominance may present a potential hazard to other ectoparasite species. Since *A. sylvaticum* has the ability to attach to hosts other than their preferred host species, they may be forced to attach more frequently to these other species if the population increases, potentially out competing other ectoparasites.

Intraspecific spatial segregation allows for a parasite population to expand more quickly than other species, which are temporally segregated in their life stages. This gives an evolutionary adaptation, which should be further explored in common parasite populations, especially those with a commonly occurring preferred hosts. The lack of complete host-specificity could also allow for further distribution and density of the parasite population. The combination of these characteristics creates a parasite, which could dominate parasite communities and more quickly reduce fitness of host populations, under suitable environmental conditions. This trait suite should be identified in other tick species, which may have more economic importance, in order to highlight studies on countering this successful life history strategy.

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