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DO SKIN POCKETS OF LIZARDS REDUCE THE DELETERIOUS EFFECTS OF ECTOPARASITES? AN EXPERIMENTAL STUDY WITH *PSAMMODROMUS ALGIRUS*

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ABSTRACT: Many species of lizards have skin invaginations that contain ectoparasites. These structures could concentrate ectoparasites and reduce their harmful effects, but experimental evidence supporting this hypothesis is largely lacking. We report here the first experimental test of this hypothesis which we conducted with the lacertid lizard *Psammodromus algirus*, a species that has a nuchal pocket on each side of the neck and is a regular intermediate host of the tick *Ixodes ricinus*. We manipulated circulating testosterone levels of males to increase tick infestation and blocked pockets to prevent tick attachment. When ticks had free access to pockets, ticks were attached mainly in pockets when tick load was low, but they were present in similar proportions in ears, pockets, and axillae in heavily parasited males. When tick pockets were blocked, infestation rates were comparable to those of unblocked lizards, but ticks were concentrated on the ears and in the axillae. The experimental group, with blocked pockets, was seen over a shorter period and in a smaller patch of habitat. This suggests that survival and home range were reduced. These data indicate that concentration of ticks in pockets may be beneficial for *P. algirus* and support the functional value of these structures.

Key words: Ectoparasites; Lizards; Pockets; *Psammodromus algirus*

NUMEROUS species of lizards have skin pockets that frequently contain mites or ticks. Arnold (1986) observed thickening of epidermis and dense concentrations of lymphoid cells within the skin of these lizard pockets, suggesting that pockets have evolved in these species to concentrate ectoparasites and minimize their harmful effects. Bauer et al. (1990) examined the morphology and contents of pockets in gekkonid lizards (*Rhacodactylus*) and found no supporting evidence of the damage limitation hypothesis. These authors indicated that the net damage caused by ectoparasites should not be any less in pockets than elsewhere on the body, and they suggested that phylogenetic or structural constraints may be responsible for the presence of integumentary pockets. Thus, the function(s) of pockets, if any, remains controversial and unresolved (Arnold, 1993; Bauer et al., 1993).

We propose that the presence of ectoparasites in some regions of the skin may cause interference with some functions related to fitness, and that the presence of pockets in other areas of the body would concentrate ectoparasites in places where this interference is reduced. The number and position of pockets vary among lizard species; for instance, pockets may occur on sides of the neck, axillae, and sides of the tail base in phrynosomatid, lacertid, iguanid, chamaeleontid, gekkonid, and scincid families. This indicates that the structures have evolved independently several times (Arnold, 1986). The lacertid lizard *Psammodromus algirus* has one nuchal pocket on each side of the neck. We observed that during the mating season, adult males of *P. algirus* were frequently infested with ticks (larvae and nymphs of *Ixodes ricinus*) whereas juveniles and females had fewer ectoparasites. Most of the ticks were located in the nuchal pockets, with a minority occurring close to the tympanum and in the axillae, where they may find protection against potential damage when the lizard brushes against vegetation and better attachment conditions. We suggest that ticks attached to the ear region may damage the skin around the tympanum and disrupt hearing and that ticks attached around the axillae may impede locomotion. If nuchal pockets attract ticks that would otherwise attach to the ears or axillae, one would predict that lizards with pockets would have higher hearing performance for predator detection, greater escape ability among other benefits, and thus improved survival.

It is possible that any effects of pockets on lizard fitness would be difficult to detect under conditions of low ectoparasite load. It has been previously shown that males of *Psammodromus algirus* supplemented with testosterone during the mating season were more susceptible to ectoparasitic infestation (Salvador et al., 1996). Consequently, in this study, we implanted males of this species with testosterone to obtain elevated testosterone levels (Marler and Moore, 1991). Also, we blocked nuchal pockets with glue to prevent tick access to them. According to our hypothesis, we predicted that (1) tick numbers will increase in ears and axillae of males with blocked-pockets and (2) males with blocked-pockets will show a restricted movement pattern and a higher mortality.

METHODS

We conducted our study with the lizard *Psammodromus algirus* at a site in a deciduous oak-forest (*Quercus pyrenaica*) near Navacerrada (40°44′ N, 4°00′ W), Madrid province, Spain during the breeding season of 1996. From 1–15 March, we established a 3-ha grid with markers every 10 m, within which we captured adult individuals (both males and females) by noosing between 18 March and 3 April, shortly after lizards emerged from hibernation. All individuals were weighed, their snout–vent length (SVL) measured, and marked by toe-clipping and with two or three color spots for individual recognition. There were no ticks (*Ixodes ricinus*) on males at first capture. Females and small males (SVL < 75 mm), not involved in our experimental manipulation, were immediately released at the capture site. Only males with SVL > 75 mm were selected for the experiment, because testosterone supplementation in subordinate, small male lizards does not increase ectoparasite load (Salvador et al., 1997).

Our experimental design was based on the combination of testosterone supplementation and blocking of nuchal pockets. We assigned males with SVL > 75 mm to one of four groups according to their order of capture. The first male captured (EE-male) received a subcutaneous implant of a 9-mm long silastic tube (Dow Corning: 1.95 mm outer diameter, 1.47 mm inner diameter). Each end was plugged with silicone adhesive. The male was cold-anaesthetized and implanted through a small dorsal incision which was closed with a suture. The implant contained 5 mm of packed crystalline testosterone-propionate (Sigma Chemicals). Also, nuchal pockets were closed with glue (Superglue). The second male captured (EC-male) received the same testosterone implants as EE-male. Nuchal pockets remained open and they received the same amount of glue as EE-male on scales located between the pocket and the ear opening to control for the glue effect. The third male captured (CE-male) received empty implants following the same procedure as in EE and EC-males, and their nuchal pockets were closed with Superglue. The fourth male captured (CC-male) received empty implants following the same procedure as in EE, EC, and CE-males and their nuchal pockets remained open. Also, to control for the glue effect as in EC-males, these males received the same amount of glue on scales located between the pocket and the ear opening. Each subsequently cap-

TABLE 1.—Number of ticks ($\bar{x}$ ± SE) in testosterone-supplemented, blocked-pockets males (EE-males), testosterone-supplemented, control-pockets males (EC-males), empty implants, blocked pockets males (CE-males), and empty implants, control-pockets males (CC-males), when recaptured during late breeding season (May).

	EE-males	EC-males	CE-males	CC-males
Ears	7.1 ± 1.0	6.4 ± 1.6	5.0 ± 1.1	3.2 ± 0.5
Pockets	0	5.3 ± 1.1	0	4.9 ± 0.4
Axillae	5.4 ± 0.5	3.2 ± 0.8	3.8 ± 0.9	3.1 ± 0.5
Total	12.7 ± 1.1	14.2 ± 3.0	9.6 ± 0.9	11.3 ± 1.0
n	9	9	8	15

tured male was assigned sequentially to the four groups. There was no significant difference between treatments in SVL (blocking-pockets treatment, $F_{1,40} = 0.47$, $P = 0.49$; testosterone treatment, $F_{1,40} = 0.03$, $P = 0.87$) or in mass (blocking-pockets treatment, $F_{1,33} = 0.007$, $P = 0.93$; testosterone treatment, $F_{1,33} = 0.05$, $P = 0.82$). Experimental males were released during the same capture day at the capture site. To assess if glue was effective in blocking the access of ticks to pockets, we randomly captured 10 EE and CE-males during middle April and found no ticks in the pockets. Also, EE and CE-males recaptured in May had their pockets blocked by the glue, and no ticks were found inside. To test whether the glue treatment had some effect on the number of ticks in CC-males, we captured in the plot eight additional males during May. The number of ticks in their ears, pockets, and axillae did not differ significantly from CC-males ($P > 0.45$ in all cases). The SVL and mass did not differ between these groups. In consequence, we pooled both groups for analyses of tick location.

We monitored male behavior during April at a distance of 7–12 m using binoculars. All males were observed during the morning (0800–1200 h) over the same days. The experimental treatment of each male was unknown to the observers. We noted during periods of continuous recording ($\bar{x} \pm SE = 115 \pm 8$ min/male), the number of male movements and distances moved. We determined the minimum number of sightings that estimate home range size (Rose, 1982). Approximately 12 sightings describe 100% of the home range of males in this population (A. Salvador and J. P. Veiga, unpublished data). We noted the location in the plot of every experimental male during 15 censuses made in April on different days (15 points per male). Home range area was measured using the convex polygon method (Rose, 1982). During 1–15 May, we surveyed daily the study plot in order to recapture the experimental males. We made an additional effort in these days to locate males not detected in late April. We assumed that their disappearance was due to mortality, not to lack of visible activity or dispersal. Recaptured males were weighed and the number and position of ticks (ears, pockets, or axillae) on each individual was noted.

Numbers of ticks were normally distributed but variances were heterogeneous. Differences in number of ticks among ears, pockets, and axillae were evaluated by Kruskal-Wallis tests. Home range and movement variables were normally distributed and variances were homogeneous. We used two-way ANOVAs to test the effects of blocking-pockets and testosterone treatments on these variables; SVL was included as a covariate, because both the tick load and the mobility varied with body size (Salvador et al., 1996, 1997).

RESULTS

The total number of ticks carried by focal males when they were recaptured did not vary significantly with the glue treatment ($H = 0.09$, $P = 0.76$), but there was a slight tendency for increase in number attached as a result of the testosterone treatment ($H = 1.93$, $P = 0.16$) (Table 1). The total number of ticks attached in both axillae and ears was significantly higher in

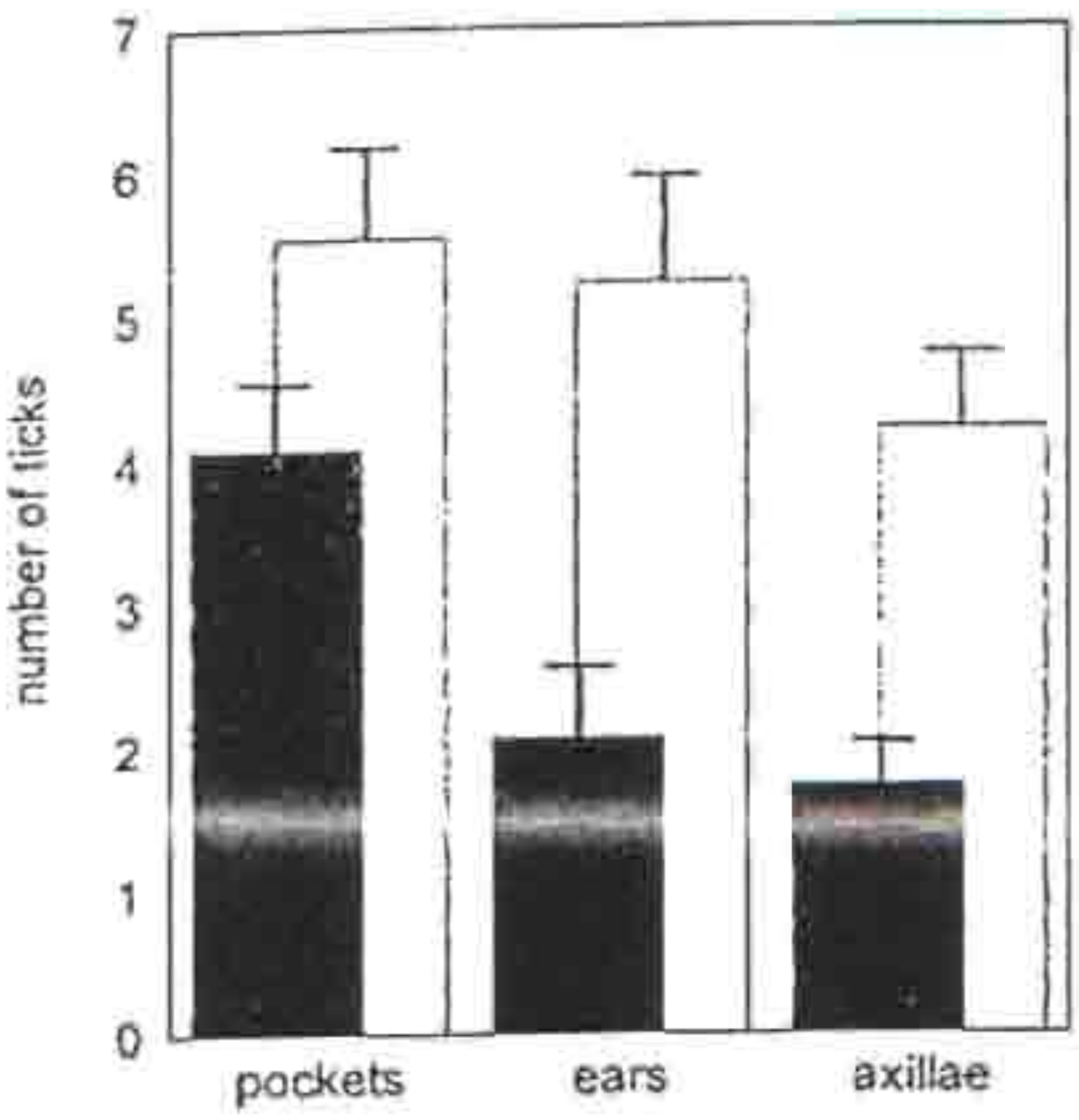

FIG. 1.—Number of ticks ($\bar{x}$ and SE) in relation to position. Black boxes = males with low numbers of ticks (4–12); grey boxes = males with high numbers of ticks (13–23).

males with blocked pockets ($H = 6.82$, $P = 0.009$) and males implanted with testosterone ($H = 6.82$, $P = 0.009$).

To examine if ticks prefer to attach in pockets, ears, or axillae, we grouped control males for the glue treatment into poorly parasitised (number of ticks below the median 4–12) and heavily parasitised males (number above the median 13–23). The number of ticks in pockets differed between both groups ($H = 5.99$, $P = 0.01$)(Fig. 1). The differences in the number of ticks in ears and axillae were clearly higher (ears: $H = 8.80$, $P = 0.003$; axillae: $H = 8.22$, $P = 0.004$). Also in males with low parasite loads, the numbers of ticks varied significantly among pockets, ears and axillae ($H = 12.95$, $P = 0.001$). However, in heavily parasited males, we did not detect significant differences among locations ($H = 2.37$, $P = 0.30$)(Fig. 1). These results showed that when the number of ticks in the host was small, they tended to be attached in pockets. However, as pockets have a limited capacity to shelter ticks, ticks also attached in other locations when their number per host was high.

Males with blocked pockets tended to have smaller home ranges than control males ($F_{1,26} = 2.8$, $P = 0.10$). However testosterone implanted males had a similar home range to controls ($F_{1,26} = 0.49$, $P = 0.49$)(Table 2). Similarly, males with blocked pockets made fewer movements per time and moved shorter distances than males with free pockets ($F_{1,27} = 7.02$, $P = 0.01$ and $F_{1,27} = 6.15$, $P = 0.02$, respectively). Testosterone supplementation, however, did not affect movement rates ($F_{1,27} = 1.57$, $P = 0.22$), but there was a tendency to reduce the distances moved ($F_{1,27} = 3.66$, $P = 0.068$).

A log-linear analysis of the trifactorial table for the blocking-pockets treatment, the testosterone treatment, and survival showed that during the interval of the study more males with blocked pockets disappeared than males with free pockets (log-linear analysis: blocking-pockets × survival, $G = 4.69$, df = 1, $P = 0.027$)(Table 3). We did not, however, observe more disappearances among testosterone supplemented males than among testosterone controls (log-linear analysis: testosterone supplementation × survival, $G = 0.36$, df = 1, $P = 0.55$). The interaction between the three factors was not significant (log-linear analysis: testosterone supplementation × blocking-pockets × survival, $G = 1.19$, df = 1, $P = 0.27$).

TABLE 2.—Movement variables ($\bar{x}$ ± SE) of testosterone-supplemented, blocked-pockets males (EE-males), testosterone-supplemented, control-pockets males (EC-males), empty implants, blocked pockets males (CE-males), and empty implants, control-pockets males (CC-males).

Treatment	n	Home range (m^2)	Movement (no. moves/min)	Distance (m/min)
EE-males	6	167.8 ± 70.1	0.24 ± 0.06	0.30 ± 0.08
EC-males	9	318.1 ± 66.9	0.50 ± 0.07	0.58 ± 0.07
CE-males	7	264.1 ± 65.4	0.45 ± 0.11	0.46 ± 0.08
CC-males	6	328.2 ± 61.7	0.69 ± 0.15	0.65 ± 0.12

TABLE 3.—Number of survivors and non-survivors in testosterone-supplemented, blocked-pockets males (EE-males), testosterone-supplemented, control-pockets males (EC-males), empty implants, blocked-pockets males (CE-males), and empty implants, control-pockets males (CC-males) at late breeding season (May).

	EE-males	EC-males	CE-males	CC-males
Survivors	6	9	5	7
Non-survivors	3	0	3	1
n	9	9	8	8

DISCUSSION

The manipulation of the capacity of the skin pockets to shelter ticks showed that males with blocked pockets did not differ in their ectoparasite load from control males with free pockets. Thus, a first conclusion is that the possession of pockets does not increase the susceptibility of the host to infestation by ticks. On the contrary, males with open pockets had fewer ticks on ears and axillae, where they might have caused damage (Goldberg and Bursey, 1991). In fact, males with blocked pockets significantly altered their mobility pattern, with less frequent and shorter movements than males with open pockets. This shift of behavior may be compared to that shown by individuals with experimentally amputated tails which move less than intact animals in the same population (Salvador et al., 1995). In both cases, reduced movement could be interpreted as a conservative strategy adopted by individuals that are more vulnerable to predators. It may be argued that individuals with the external auditory meatus partially or totally plugged with ticks is likely to have reduced hearing acuity and, as a result, impaired ability to detect approaching predators. Also, the presence of ticks in the axillae may make movement of the forelegs difficult, especially during rapid running.

The number of recaptured individuals with blocked pockets was significantly lower than for those with open pockets, a result that can be interpreted as evidence of higher mortality among the former. It is very improbable that this result was due to individuals with blocked pockets tending to disperse out of the study area, because they moved less than individuals with open pockets. Nor was the difference due to our inability to detect or capture them, because the home ranges of missing individuals were intensively searched and, if seen, they would have been recognized by the individual color marks. We argue that predation is the most probable explanation for the absences recorded, although other causes such as hiding or inactivity of males with blocked pockets cannot be entirely discounted. An alternative explanation is that the harmful effect of the ticks was more intense when they were attached outside the pockets. Arnold (1986) suggested, based on a histological study of pockets' integument, that skin pockets may facilitate the deployment of lymphocytes, but there is no robust evidence to support this hypothesis.

It seems that the skin pockets have a function in the population studied, though the benefits of bearing them for a host may depend on its total ectoparasite load. The distribution of ticks inside and outside pockets in control individuals showed, in agreement with the results of the experiment, that ticks tended to locate preferentially within pockets in individuals with a small number of ticks, but they shifted to other places as their number on the host increased. This suggests that the capacity of pockets to accumulate ticks is limited, so that when the ectoparasitic load is high, the benefits derived from the presence of skin pockets may be smaller.

Testosterone treatment increased the total number of ticks in studied males. This result was expected and replicated a previous experiment conducted with the same population (Salvador et al., 1996). However, in the present case, increase in ectoparasitic load did not increase mortality in contrast with the results obtained previously. This difference may be due to the higher ectoparasitic load shown by males in the earlier study ($\bar{x} \pm$ SE, 20.6 ± 1.5, $n = 21$ versus 12.1 ± 0.9, $n = 41$) and, or, to the apparent difference in food availability in both years. Supplementary feeding increased survival of testosterone-implanted individuals of *Sceloporus jarrovi* (Marler and Moore, 1991). In contrast with the tendency to lose mass observed during the earlier study ($\bar{x}$ ± SE, initial mass = 13.57 ± 0.31 g, final mass = 13.30 ± 0.27 g; repeated-measures ANCOVA, $F_{1,18} = 3.78$, $P = 0.068$), during the present study males increased their mass significantly ($\bar{x}$ ± SE, initial mass = 11.16 ± 0.26 g, final mass = 11.54 ± 0.26 g; repeated-measures ANCOVA, $F_{1,23} = 8.42$, $P = 0.008$), which may have reduced the effects of a higher ectoparasitic load.

Integumentary pockets of lizards sometimes seem to have arisen de novo, but in other cases their position suggests that they may be remnants of structures that originally had a different function. In lacertid lizards, there is primitively a backwardly directed fold under the neck which allows the extension of the gular skin during head raising (Arnold, 1973). In *P. algirus*, extension is distributed among several scale rows and the collar is largely lost. However, the sides of the collar have persisted apparently acquiring a new function as a specialized structure that reduces the harmful effects of ectoparasites. Our results indicate that the presence of nuchal pockets is advantageous in the study population, where infestation level is usually high. However, we have not determined if tick presence is as frequent in other populations, or if the possession of pockets is advantageous when ectoparasitic load is lower than in this study. Ticks are often found on *P. algirus* in areas several hundred kilometers distant from our study site, with different climates and vegetation (J. A. Díaz and C. M. Herrera, personal communication; see photographs in Barbadillo, 1987, and Schleich et al., 1996, depicting males with ticks from Jaén province and Morocco, respectively). The presence of ectoparasites throughout the range of the species suggests that the persistence of the collar remnants, which is found in all individuals of *P. algirus*, results from selection for their benefits in control of ectoparasites.

Our results support the hypothesis that pockets may redistribute ticks and yield benefits by preventing attachment in functionally important areas. The conclusions of our study cannot be generalized directly to other species, even to those with pockets in the same position as *P. algirus*. However, pockets are mainly located near legs and ears in most species, suggesting that a possible function of these invaginations is to prevent attachment of ectoparasites at sites where they may impede locomotion and hearing, respectively. A test comparing ectoparasite load between closely related species with and without pockets would provide a powerful insight to discriminate between functional and non-functional explanations for the evolution of skin pockets. Our functional hypothesis predicts that in pairs (or groups) of related species, sharing a common ancestor, those having pockets would be the most susceptible to carry ectoparasites.

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