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The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation

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According to current evolutionary theory, advertising traits that honestly indicate an organism's genetic quality might be costly to produce or maintain, though the kind of costs involved in this process are controversial. Recently the immunocompetence hypothesis has proposed that testosterone (T) stimulates the expression of male sexually selected traits while decreasing immunocompetence. Even though some recent studies have shown an effect of T on ectoparasite load, the dual effect of the hormone has not been addressed in free-living populations. Here we report results of an experiment in a free-living population of the lizard *Psammodromus algirus* during the mating season. Males implanted with T had larger patches of breeding color and behaved more aggressively than control males. In T-implanted males, the increase in number of ticks during the mating season was significantly higher than in control males and this negatively affected several hematological parameters. T-males suffered significantly higher mortality than control males during the experiment. The results from the manipulation of T are consistent with the dual effect of this hormone. *Key words:* parasites, *Psammodromus algirus,* secondary sexual characters, testosterone. *[Behav Ecol 7:145–150 (1996)]*

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Advertising traits that honestly indicate quality might be costly to produce or maintain (Grafen, 1990a, b; Kodric-Brown and Brown, 1984; Zahavi, 1975, 1987). There is much controversy about the kind of costs involved in this process, though in recent years disease induced by parasites has acquired a paramount importance in sexual selection debates (Hamilton and Zuk, 1982). The evolution of advertising traits may be the result of a physiological trade-off between the benefits of increased reproductive success afforded by exaggerating signals and the cost of disease induced by parasites (Folstad and Karter, 1992). This mechanistic model is based on the assumption that testosterone stimulates the expression of male sexually selected traits while decreasing immunocompetence. Most evidence, however, has come from laboratory studies in which the postulated dual effects of the hormone were not addressed simultaneously. Several recent studies have shown an effect of testosterone on ectoparasite load (Saino and Møller, 1994; Saino et al., 1995; Weatherhead et al., 1993), but none of them focused on the simultaneous effect of the hormone on secondary sexual traits and parasite load as proposed by the Folstad and Karter (1992) hypothesis. Hence, as far as we know, this hypothesis remains untested for free-living populations.

Males of the lacertid lizard *Psammodromus algirus* have an orange nuptial coloration on the throat and sides of the head that appears in spring and disappears during summer, once the mating season has concluded. The extent of breeding coloration shows marked individual variation (Díaz, 1993; A. Salvador, personal observations). Several lines of evidence strongly suggest that plasma androgen levels are responsible for such variation in this species. First, orange breeding coloration is not expressed in adult females. Second, large territorial adult males show extensive breeding coloration, whereas small adult males, which usually are subordinates, have a breeding coloration consisting of an orange spot on the mouth commissures that is only fully exposed when the mouth is open (Salvador et al., 1995). Third, the extent of nuptial coloration in a Spanish population was positively correlated with plasma testosterone levels among males captured at the beginning of the breeding season (Díaz et al., 1994). Fourth, in an earlier study we observed that by implanting males with testosterone in summer, we induced them to resume the breeding coloration lost several weeks before (unpublished data). Also, data on other lizards shows that the development of traits that function as sexual signals is dependent on plasma androgen levels (Cooper et al., 1987; Pratt et al., 1994; but see Olsson, 1994a).

It is not known whether the orange head coloration of *P. algirus* is used as a status signal in intrasexual competition or whether it represents a trait on which females base their mate choice. There is strong evidence in other lizards that conspicuous coloration developed during the breeding season is used as a badge of status in male-male competition (Cooper and Vitt, 1993; Olsson, 1994a; Zucker, 1994). However, after a few studies in which mate choice has been addressed, it seems that ornaments are not the target of female preferences (see Cooper and Vitt, 1993).

During previous studies conducted on the same *P. algirus* population (Salvador et al., 1995), we realized that during the mating season adult males frequently had a number of ticks on the ears, sides of the head, and axillae, while juveniles and females had fewer ectoparasites. These observations are congruent with a role of sex hormones in the prevalence of ectoparasites. However, other factors such as the greater mobility and larger home ranges of males (Bauwens et al., 1983) during the mating season may explain the observed differences between sexes in parasite load.

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It has been reported that ticks may create severe alterations of blood composition in their lizard hosts (Dunlap and Mathies, 1993), which may lower physiological and behavioral performance (Schall et al., 1982). In the present study we first focus on the effects that ticks had on several hematological parameters as a prerequisite to demonstrate that an eventual elevation of the tick load due to testosterone represents a cost to the hosts. We also report the results of an experimental test of the Folstad and Karter (1992) hypothesis in a free-living population of *P. algirus*. According with this hypothesis we predict that 1) testosterone-implanted male lizards (T-males) will exhibit more nuptial coloration and will behave more aggressively than control males (C-males), and 2) T-males will be more susceptible to parasitization by ticks than C-males.

METHODS

Species and study site

Psammodromus algirus is a ground-dwelling lizard, common in Mediterranean forests of the Iberian peninsula (Díaz and Carrascal, 1991). The minimum snout–vent length of adults is 65 mm for males and 62 mm for females (Mellado and Martínez, 1974). During an ongoing study of this lizard, we conducted a field experiment in a deciduous oak forest (*Quercus pyrenaica*) near Navacerrada (40°44′ N, 4°00′ W), in central Spain, during the 1994 mating season (April to May). Shrubs, grasses, and rocks predominated at the study site. For a more detailed description of cover see Salvador et al. (1995). The lack of leaves on oak trees and bushes during most of the spring allowed high visibility of individuals during focal observations and censuses.

General methods

From 14 to 20 March we established a 1.5 ha plot, with markers on a grid every 10 m, within which we captured by noosing as many adult individuals (both males and females) as possible between 21 and 29 March, shortly after lizards emerged from hibernation. All individuals were weighed, snout–vent length (SVL) and tail length measured, and marked by toe-clipping and with two or three color spots for recognition. The number of ticks present on each individual was also recorded (ticks were left in situ). Females and small males, not involved in our experimental manipulation, were immediately released in the capture site. Only large males (i.e., those between 80 and 85 mm SVL) were selected for a testosterone implant experiment (see below).

Each large male was viewed during April at a distance of 7 to 12 m using binoculars. The experimental treatment of each male was unknown to observers during field observations. We noted on a tape recorder the number of male movements, distances moved, and agonistic interactions with other males. We defined a chase as when a male pursued another male at high speed and displaced him from the site. The low number of observed courtship behaviors did not allow comparison between treatments. Copulation behavior was rarely observed. We noted the location in the plot of each large male once every 2 days (15 censuses). Home range area was measured using the convex polygon method (Rose, 1982). We made an effort to identify all the individuals observed within the territories of focal males. Between 3 and 26 May we surveyed the study plot daily in order to recapture the focal males. Each time a focal male was not encountered an additional search was conducted to ensure that his disappearance was due to mortality, not to lack of visible activity or dispersion.

As many individuals as possible were recaptured in May to count ticks, measure breeding coloration area, and take blood samples. The number of days between first capture and recapture of C-males (mean ± SE = 49.0 ± 2.6 days) and T-males (47.4 ± 3.3 days) did not differ significantly (ANOVA, $F_{1,19} = 0.15$, $p = 0.70$). To measure the surface of the orange breeding coloration we used a camera lucida fitted to a Wild M5A dissecting scope. We placed the head in both lateral and ventral positions and drew the profile of orange areas. A drawing tablet was used to digitize and compute the total orange surface for each male. Finally, the values obtained were standardized to vary between 0 (minimal coloration) and 1 (maximal coloration).

Experimental procedures

Large males were captured between 21 and 29 March and every second individual was assigned to a control (C-males, $n = 14$) and an experimental group (T-males, $n = 15$). Snout–vent length of T-males (mean ± SE = 82.8 ± 0.5 mm) and C-males (81.8 ± 0.5) did not differ significantly ($F_{1,27} = 1.9$ $p = 0.179$). Both C- and T-males 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 a wooden cap and sealed with silastic adhesive. Males were cold anesthetized and implanted through a small dorsal incision that was closed with a suture. C-males received an empty implant, while the implant of T-males contained 5 mm of packed crystalline testosterone propionate (Sigma Chemicals). Between 1 and 4 h after being captured, males were released within a radius of about 5 m from the capture site. Implants contained a small amount of testosterone when lizards were recaptured. To measure blood parameters at recapture, blood was collected with heparinized syringes in the laboratory. Aliquots of blood were diluted (200 and 50 times for red and white cells, respectively) in hematological pipettes with Natt and Herrick's (1952) solution. Red and white blood cells were counted using 96 small squares for red cells and all the large squares for white cells of a cell counting Thoma chamber. Hematocrit (percent packed cell volume) was determined by centrifugation at 10,000 rpm for 12 min. Hemoglobin (g/100 ml) was assayed according to the colorimetric method of Drabkin (1945) using hemoglobin standard from Sigma Chemicals (USA).

Statistical procedures

We used the SPSS statistical package. We utilized parametric statistics only for variables that, according to the Lilliefors test, were normally distributed. Homocedasticity of within-group variances in ANOVA analyses was checked by means of the Levene test. We used one-tailed tests when the hypothesis tested clearly established the direction of the results. Explicitly, T-individuals should develop more extensive breeding coloration, should be more aggressive, and should be more susceptible to ectoparasite infestation than C-males. Also we expect that heightened levels of parasite load have a negative effect on blood parameters.

RESULTS

Home range and movements

Behavioral field observations of 12 T-males (mean ± SE = 97 ± 11 min) and 12 C-males (118 ± 11 min) during April showed that there were no significant effects of treatment on male movement rates, distances moved, and home range size (Table 1). The number of chases per hour of T-males was, however, significantly higher than those of C-males (Table 1). The number of female ranges overlapped by C-males and T-

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Table 1

Space use and behavior variables (means ± SE) of C-males (control) and T-males (testosterone implanted)

Treatment	N	Movement (No. mov./min)	Distance (m/min)	Home range (m^2)	No. of chases/h	No. of female ranges overlapped
C-males	12	0.30 ± 0.05	0.59 ± 0.12	330 ± 41	0.22 ± 0.14	1.83 ± 0.4
T-males	12	0.40 ± 0.06	0.76 ± 0.10	302 ± 50	0.67 ± 0.20	1.58 ± 0.2

MANOVA of movement, distance, and home range: $F_{3,20} = 0.53$, $p = .664$. Mann-Whitney *U* test (one-tailed), no. of chases/h, $p = .03$; no. of female ranges overlapped, $p = .44$.

males did not differ significantly (Table 1). The home ranges of 28.5% of females were overlapped by two large males and 14.2% by three large males, suggesting competition for shared females.

Effect of T implants: nuptial coloration, tick load, and mortality

Breeding coloration at first capture was absent or nearly so. When males were recaptured during May, the surface occupied by orange breeding coloration was larger in T-males than in C-males (Figure 1). Males carried larval and nymphal stages of *Ixodes ricinus* in nuchal pockets, ears, and axillae during both capture months (March and May). The initial number of ticks did not differ significantly between C-males and T-males. However, the final number of ticks tended to differ between treatments, and the increase in the number of ticks between both periods was significantly higher in T-males than in C-males (Figure 2). During the experiment we noted the disappearance of 40% of T-males but only 7.1% of C-males (Fisher's Exact test, one-tailed, $p = .049$).

Relationship between tick load, blood parameters, and performance

A multivariate ANOVA showed a significant effect of tick increase on blood parameters. Univariate tests, however, indicated that only the hemoglobin and hematocrit values were significantly affected. The relative number of white blood cells tended to be lower in T-males (Table 2). There were, however, no significant effects of testosterone treatment. Also the lack of interaction between tick increase and testosterone treatment indicates that the effect of ticks on blood parameters did not depend on treatment (Table 2 and Figure 3). Similar results were obtained using the final number of ticks instead of tick number increase. The increase of ticks induced by testosterone had no significant effect on performance variables (home range, number of overlapped females, and mobility) (ANCOVA, $p > .3$ in all cases).

DISCUSSION

Our results showing experimental elevation of testosterone increases both parasite load and favors the expression of a secondary sexual trait are consistent with the postulated dual effect of this hormone, namely, that testosterone stimulates the development of traits targeted in sexual selection while simultaneously depressing the immune system (Folstad and Karter, 1992). It might be argued that, because we did not measure testosterone plasma levels during the experiment, we cannot reject the possibility that what we recorded was the effects of pharmacological doses of the hormone on the experimental lizards. Though we cannot completely reject this contention, several lines of evidence suggest this was not the case. First, we did not observe any abnormality in the behavior of the experimental individuals during the monitoring sessions. Mobility related variables and home range were not affected by the treatment, and experimental individuals were even more aggressive than controls, which would not be expected if the levels of testosterone had toxic effects (see Marler and Moore, 1988). Second, previous studies in lizards implanted with doses of testosterone only slightly smaller than

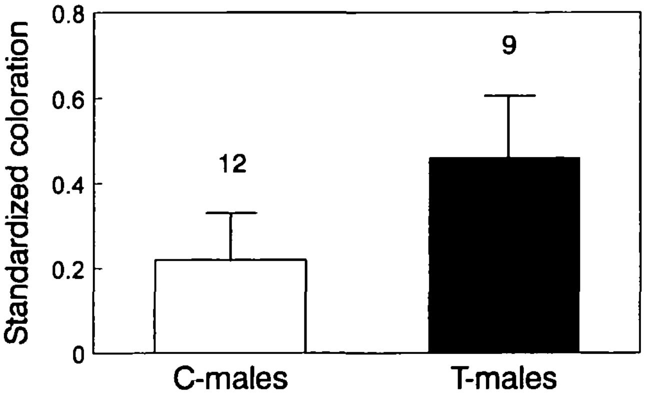

Figure 1
Orange breeding coloration area (mean ± SE) in males implanted with testosterone (T-males) and males with empty implants (C-males). Values were standardized to vary between 0 (minimal coloration) and 1 (maximal coloration). Numbers above bars indicate sample sizes. Mann Whitney *U* test, one-tailed, $p = .035$.

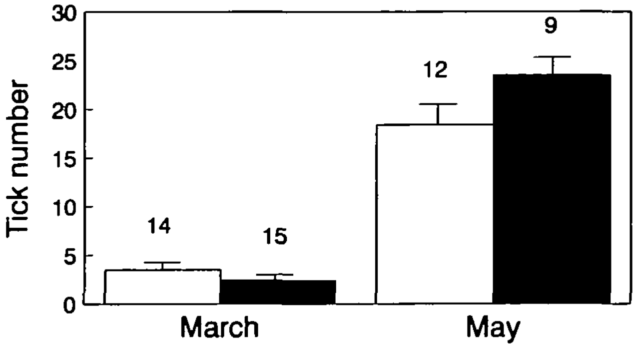

Figure 2
Number of ticks (mean ± SE) in C-males (white boxes) and T-males (black boxes) when captured during early breeding season (March) and recaptured during late breeding season (May). Numbers above bars indicate sample sizes. March: ANOVA, $F_{1,27} = 3.31$, $p = .080$; May: ANOVA, $F_{1,19} = 2.98$, one-tailed, $p = .05$; increase in number of ticks between March and May: ANOVA, $F_{1,19} = 5.24$, one-tailed, $p = .017$).

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Table 2

Blood variables (means ± SE) of C-males (control) and T-males (testosterone implanted)

Treatment	Red blood cells (10^6 cells/mm^3)	White blood cells (10^3 cells/mm^3)	Hematocrit (%)	Hemoglobin (g/100 ml)
C-males	1.75 ± 0.1	25.6 ± 3.0	32.7 ± 2.0	8.5 ± 0.5
N	12	12	12	12
T-males	1.73 ± 0.1	17.8 ± 1.6	33.5 ± 1.5	7.9 ± 0.6
N	9	9	7	8

MANOVA, tick increase effect: $F_{4,13} = 4.22$, $p = .023$ (ANOVA, red blood cells, $F_{1,16} = 0.05$, p (one-tailed) = .41; white blood cells, $F_{1\,16} = 1.56$, p (one-tailed) = .11; hematocrit, $F = 3.09$, p (one-tailed) = .049; hemoglobin, $F = 5.51$, p (one-tailed) = .016).

MANOVA, testosterone treatment effect: $F_{4,13} = 0.26$, $p = .899$.

MANOVA, tick increase × testosterone treatment: $F_{4,13} = 0.45$, $p = .767$.

those used in this study showed that the increase of plasma testosterone levels in experimental individuals paralleled the normal increase that precedes the breeding season, and apparently did not cause pharmacological effects (Marler and Moore, 1988, 1991).

Observational studies in other lizard species showed that males with more intense nuptial coloration or larger coloration areas had improved ability to gain contests with competitors and might have higher mating success (Olsson, 1994a; Zucker, 1994). In the present experiment the advantage of exaggerating a signaling trait via augmented levels of testosterone is not evident. It has been demonstrated in other lizards that nuptial coloration functions as a status signal that indicates fighting ability to potential competitors (Olsson, 1994a; Zucker, 1994). According to the status signaling hypothesis (Rohwer, 1982), the main advantage conferred by traits that unambiguously indicate the status of the bearers is a reduction of the frequency of risky agonistic interactions with other males competing for valuable resources. In apparent contradiction with this, our experimental males, having more nuptial coloration than controls, were more eager to participate in agonistic interactions with neighbor and subordinate males. Because the home range of a high proportion of females was overlapped by two or three large males, aggressive males might obtain more copulations than less aggressive neighbors. Additionally, aggressiveness might reduce the risks of being cuckolded by territorial and subordinate males (Birkhead and Moller, 1992). Males that developed more nuptial coloration might have been preferred by choosing females. However, there is not conclusive evidence that female lizards use ornamental or other morphological traits as cues to choice mates (see Cooper and Vitt, 1993).

Some lizard studies have reported a positive association between the degree of nuptial pigmentation, presumably mediated by sex hormones (Cooper et al., 1987; Cooper and Greenberg, 1992), and the level of infection with hematozoa (Ressel and Schall, 1989; Schall, 1986). There is no previous evidence in lizards of a correlation between the development of nuptial traits and the ectoparasite load. Such a relationship, however, has been reported for the zebra finch (*Taeniopygia guttata*; Burley et al., 1991). In the sand lizard (*Lacerta agilis*), Olsson (1994b) did not find a significant correlation between the size of an ornamental trait and the number of ticks when controlling for body size. Correlational methods are probably not adequate here because individuals with the highest expression of ornamental traits may have higher resistance to parasites (Hamilton and Zuk, 1982). Our results, however, seem to indicate that an elevation of plasma testosterone concentration renders individuals more susceptible to infestation by ticks and, perhaps, other ecto- and endoparasites. Since variables measuring mobility and home ranges did not show differences between T- and C-males, we conclude that our results evidence a direct effect of testosterone on the immune response.

One of the more important effects of testosterone on the immune system is at the level of cells involved in humoral- and cellular-mediated immunity (Folstad and Karter, 1992). In mammals there is evidence that T-lymphocytes, whose mat-

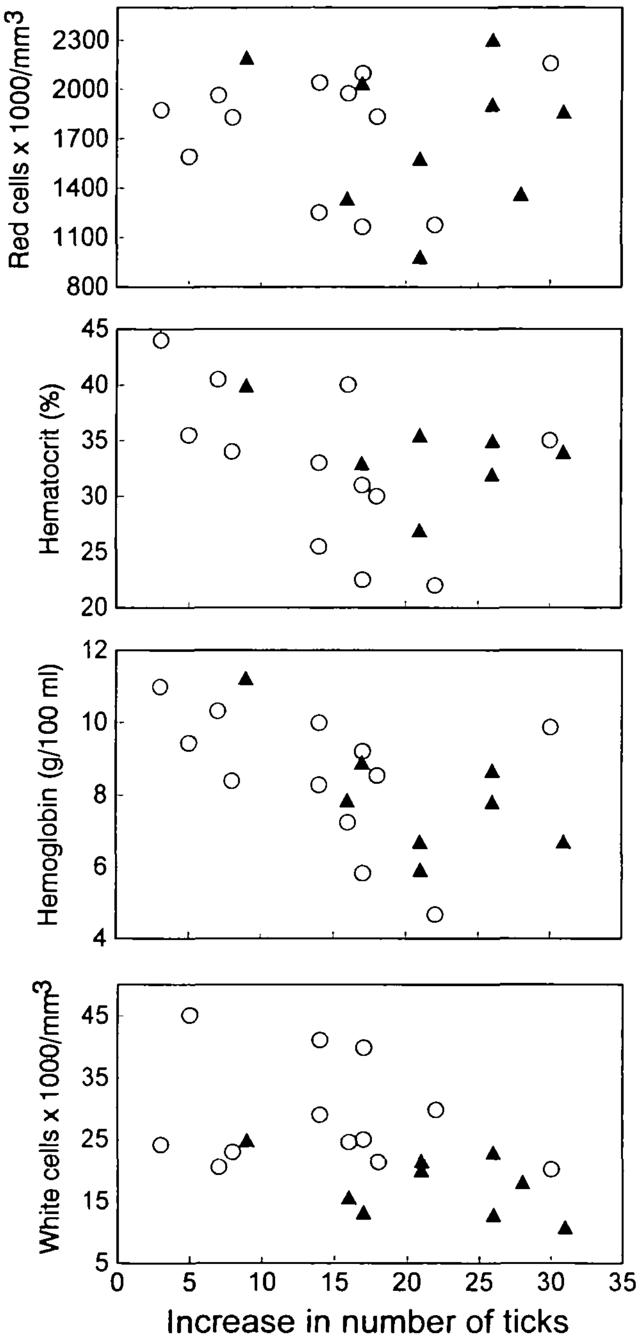

Figure 3

Relationship between tick increase throughout the breeding season and blood parameters in C-males (circles) and T-males (triangles).

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uration is affected by testosterone levels, play an important role in the detection of antigens from ticks (Brossard et al., 1991). In some reptiles there is evidence of response to a second exposure to an antigen with a rapid increase in circulating antibody (Dessauer, 1970), implying that tick fixation may be reduced as an effect of acquired resistance after primary infestation. Male lizards in this study already had some ticks when they were captured initially, but their number increased more in experimental individuals, suggesting that testosterone reduced the ability to produce specific antibodies. However, studies that addressed the precise mechanism that renders individuals with heightened levels of testosterone more susceptible to tick infestation are badly needed.

Irrespective of what causes lizards to be infested with ticks, our results clearly show that increases in tick load negatively affected hematological parameters, especially hemoglobin concentration (see also Dunlap and Mathies, 1993). It has been shown that a strong decrease in hemoglobin concentration may reduce performance in male lizards (Schall et al., 1982). Although the increase in ticks which could be induced by testosterone markedly decreased hemoglobin concentration in our study, we did not detect a parallel significant effect on performance variables (home range, number of overlapped females, and mobility). The effects of ticks on blood, however, might have had delayed consequences, such as losses in size and quality of the territory or even increased mortality. In fact, our results suggest an effect of elevated testosterone levels on the frequency of male disappearance from their territories. This apparently was not due to displacements by territorial neighbors because we did not detect seasonal variations in home range areas during the mating season (Salvador et al., 1995). Also, since lizard dispersion is not usual among adult males with stable territories (Hews, 1993; Salvador A, personal observations), we concluded that disappearances probably reflected mortality. Lower survivorship of T-implanted males may be the cumulative result of the energetic costs of increased territorial aggression (Marler and Moore, 1991) and decreased performance due to lower hemoglobin and hematocrit levels induced by ticks. In the lizard *Sceloporus occidentalis,* Schall et al. (1982) reported a lower physiological and behavioral performance as a consequence of reduced hemoglobin concentration induced by malarial infection. However, the effect of elevated testosterone levels on mortality deserves additional studies.

Lizards could be particularly affected by ticks because of their negative impact on host fitness (Aeschlimann, 1991; Dunlap and Mathies, 1993; Lehmann, 1993; this study). The pocketlike integument structures present in many lizard species (including *P. algirus*) may be adaptations to reduce the harmful effect of ectoparasites (Arnold, 1986). On the other hand, a study on birds showed that, in comparison to endoparasites, ectoparasites were more abundant in hosts with high circulating testosterone levels (Weatherhead et al., 1993). These results suggest that ticks may be especially able to detect weaknesses in the host immune system, and they could be a key group to test evolutionary hypotheses on parasite-host relationships.

In conclusion, our experiment demonstrated that testosterone increased susceptibility to infestation by ticks during the mating season. The negative effects noted in blood parameters as a consequence of higher parasite load might be viewed as a handicap that would explain why high-quality individuals were able to produce more elaborated testosterone-induced traits (Folstad and Karter, 1992; Zahavi, 1975, 1987). Alternatively, lower resistance to ectoparasites might be the adaptive consequence of a resource reallocation (Wedekind, 1992; Wedekind and Folstad, 1994). In our experiment we were unable to resolve whether males with higher T-levels and more developed coloration had higher or lower breeding success than lower T-level males. If, for example, experimental males obtained more fertilizations on shared females than controls due to greater aggressiveness, benefits of increased T-levels in terms of the number of sired offspring might exceed the costs of reduced immunocompetence. This aspect needs to be addressed in experiments that accurately measure reproductive success.

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