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Testosterone supplementation in subordinate, small male lizards: consequences for aggressiveness, color development, and parasite load

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According to the immunocompetence hypothesis, testosterone stimulates the expression of male sexually selected traits while decreasing immunocompetence. This proposed trade-off was studied by experimental supplementation of testosterone to small, subordinate, dull-colored male lizards, *Psammodromus algirus*. Experimental males showed a tendency to overlap their home range with fewer small males than did control males and tended to be more aggressive. However, control males were observed more frequently attending females than experimental males. The area of patches of breeding coloration, the number of ticks, and the frequency of recoveries of testosterone-supplemented and control males did not differ significantly. The results suggest that small adult males with high levels of testosterone behave more aggressively, which may be advantageous to securing a breeding territory in the next season. However, the hormone did not apparently affect ornamentation or parasite load. We argue that, whatever the mechanisms involved, blocking effects of testosterone may be adaptive because being cryptic facilitates a sneaking strategy, and low ectoparasite load may improve survival. *Key words:* breeding ornaments, parasites, *Psammodromus algirus*, social status, testosterone. *[Behav Ecol 8:135–139 (1997)]*

In some species of vertebrates, the expression of ornamental traits in males may depend on an individual's condition and age (Andersson, 1994; Johnstone, 1995). The development of such traits is also mediated by testosterone; males with high levels of circulating testosterone have the most elaborately developed secondary sexual traits (Ligon et al., 1990; Rand, 1990, 1992). Testosterone, however, exerts a simultaneous and detrimental effect on the immune system (Folstad and Karter, 1992) and on growth (Crews et al., 1985; Thomson et al., 1993) and increases aggressiveness, which in turn increases energy expenditure and lowers life expectancy (Marler and Moore, 1988, 1989, 1991). Thus, there is a trade-off between production of elaborate ornaments that are useful during courtship and other body condition, including the ability to resist pathogen infection. Only those individuals able to cope with the negative consequences of elevated testosterone would be able to exhibit the most elaborate ornaments.

Males of some species of lizards vary in their color among individuals in a population. These color morphs may be associated with different reproductive behaviors. Differing social status has been associated with color differences in males of the iguanid *Urosaurus ornatus* (Thomson and Moore, 1991, 1992) and *Sceloporus undulatus* (Morrison et al., 1995) and in the agamids *Agama agama* (Madsen and Loman, 1987) and *Amphibolurus maculosus* (Mitchell, 1973). In the lacertid lizard, *Psammodromus algirus*, there are two color classes of reproductive males. During the breeding season, the larger males exhibit an orange color on the sides of the head and throat that varies among individuals. The smaller males have only a small orange spot at each side of the mouth, which shows little variation among individuals. Large males hold exclusive territories that include the home ranges of several females. Small males pursue a submissive association with large males, moving around the larger male's territory and attempting to mate with unguarded females (Salvador et al., 1995, 1996).

The role of testosterone on the origin of this color variation in lizards is poorly known. Some authors report that testosterone is important in color enhancement, but not in the change of one color morph to another (Cooper et al., 1987; Rand, 1990, 1992; Salvador et al., 1996; Thomson and Moore, 1992). Moore and Thomson (1990) and Moore (1991) state that sex hormones have permanent actions during early development, which organize target tissues regulating expression of secondary sexual traits, and have temporary actions during adulthood when these tissues are activated. However, the role of hormones in mediating the expression of ornamental traits remains unknown.

In a previous study, we showed that experimental supplementation of testosterone in large male *P. algirus* induced an increase in the area of orange color associated with breeding and also induced an increase in aggressiveness. The experimental males simultaneously suffered a higher ectoparasite load, which negatively altered several blood parameters (Salvador et al., 1996). Here we explore the idea that smaller lizards are best served by growing rapidly, so they hold back on production of testosterone, but still try to sneak some matings. When they become larger, body growth is less important, so they produce more testosterone and defend females from the smaller males. Thus each lizard goes through both morphs and reproductive behaviors.

METHODS

The terrestrial lizard *Psammodromus algirus* is common in Mediterranean forests of the Iberian peninsula (Böhme, 1981). Our study was conducted at a site in a deciduous oak forest (*Quercus pyrenaica*) near Navacerrada (40°44′ N, 4°00′

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W), central Spain, during April–May 1994 and 1995 (the reproductive season of the lizards).

From 14 to 20 March, we established a 2-ha grid with markers every 10 m. Within these markers, we captured adult individuals (both males and females) by noosing between 21 and 30 of March, 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. The number of ticks (*Ixodes ricinus*) present on each individual was also recorded (ticks were left in situ). Larval and nymphal stages of *Ixodes ricinus* are often found in several species of European lizards (Bauwens et al., 1983; Salvador et al., 1996). The detrimental effects of ticks on its hosts are known (Aeschlimann, 1991; Dunlap and Mathies, 1993; Wikel, 1996). Females and large males, not involved in our experimental manipulation, were immediately released at the capture site. Only small males (i.e., those between 70 and 79 mm SVL) were selected for a testosterone implant experiment. Minimal SVL at sexual maturity is 65 mm for males (Mellado and Martínez, 1974). Four males captured at the end of March 1994 had a SVL of 70–77 mm (mean ± SE = 73.2 ± 1.4 mm), and 80–85 mm (mean ± SE = 82.0 ± 1.2 mm) when recaptured at the end of March 1995. These limited recaptures between the two study years suggest that small males are at least 1 year younger than the large males (SVL = 80–85 mm) previously studied (Salvador et al., 1996).

Small males were viewed during April at a distance of 7–12 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, courtship, 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. We described attending behavior as when a male stayed close to a female (<20 cm), and we considered it an indication of courtship activity. Copulation was rarely observed during this study. However, in a previous study conducted in an open enclosure, we observed that both large and small males copulated after having remained close to a female for some time (Salvador A and Martín J, unpublished data). We noted the location in the plot of each small 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 home range areas of control (C) males and testosterone-implanted (T) males. Between 3 and 26 May, we surveyed the study plot daily to recapture the focal males. Each time a focal male was not encountered, an additional search was conducted to assure 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 and measure breeding coloration area. The number of days between first capture and recapture of C males (mean ± SE = 39.1 ± 3.4 days) and T males (41.3 ± 2.5 days) did not differ significantly (Mann-Whitney test, two tailed, $U = 60.5$, $p = .42$). 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). To examine the relationship between the size (area) of the orange spot and SVL, we only measured the right side of the head of each male.

Small males were captured between 21 and 30 March, and every individual was alternately assigned to a control ($n = 19$) or an experimental group ($n = 18$). Snout-vent length of T males (mean ± SE = 74.0 ± 0.5 mm) and C males (mean ± SE = 73.6 ± 0.5 mm) did not differ significantly (Mann-Whitney test, two tailed, $U = 158.0$, $p = .68$). Both C and T males received a subcutaneous implant of a 9-mm long silastic tube (Dow Corning; 1.95 mm outer diam; 1.47 mm inner diam). Each end was plugged with a wooden cap and sealed with silastic adhesive. Males were cold-anaesthetized and implanted through a small dorsal incision which was closed with a suture. C males received an empty implant; the implant of T males contained 3 mm of packed crystalline testosterone-propionate (Sigma chemicals). We released males within a radius of about 5 m from the capture site 1–4 h after capture. Implants contained a small amount of testosterone when lizards were recaptured.

Table 1

Movement variables and increase in mass (means ± SE) of control and testosterone-implanted males

Treatment	*N*	Minutes of observation	Movement (No. of moves/min)	Distance (m/min)	Increase in mass (%)
Control males	10	40 ± 9	0.85 ± 0.06	0.97 ± 0.1	0.27
Testosterone-implanted males	10	58 ± 10	0.69 ± 0.09	0.84 ± 0.1	0.21
Mann-Whitney *U* test *p* (two tailed)			.26	.38	

We used parametric statistics only for variables that, according to the Lilliefors test, were normally distributed. We used one-tailed tests when the hypothesis tested clearly established the direction of the results. Explicitly, T males should develop more extensive breeding coloration, should be more aggressive, and should be more susceptible to ectoparasite infestation than C males.

RESULTS

Movements and home range

Behavioral field observations of T males and C males during April showed that there were no significant effects of treatment on movement rates and distances moved (Table 1). The mean increase of mass per day of C males and T males did not differ significantly (Table 1). Home range size of C males and T males did not differ significantly (Table 2). Also, the number of female and large-male home ranges overlapped by C males and T males did not differ significantly (Table 2). However, the number of small- male home ranges overlapped by T males showed a nonsignificant tendency to be lower than among C males (Table 2). Home range overlap was low between neighboring small males. In eight pairs of C versus T males, mean overlap was 9.4%; in two pairs of C males, overlap was zero, and in one pair of T males overlap was also zero. We observed large males chasing C males ($n = 3$), but no observations were made of large males chasing T males (Fisher's Exact Test, $p = .210$). One T male was seen chasing two small males, but no C male was observed chasing other small males. Also, one C male and one T male were observed while being chased by other small males. The number of observed C males ($n = 5$) attending females was significantly higher than the number of T males ($n = 0$) (Fisher's Exact Test, $p = .032$). Two C males and no T male attempted unsuccessful forced copulation.

Table 2

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

Treatment	*N*	Home range (m²)	No. of large male home ranges overlapped	No. of small male home ranges overlapped	No. of female home ranges overlapped
Control males	8	328 ± 36	2.1 ± 0.3	2.0 ± 0.5	2.1 ± 0.3
Testosterone-implanted males	9	296 ± 40	1.5 ± 0.3	0.8 ± 0.3	2.1 ± 0.4
Mann-Whitney *U* test *p* (one tailed)		.39	.13	.06	.46

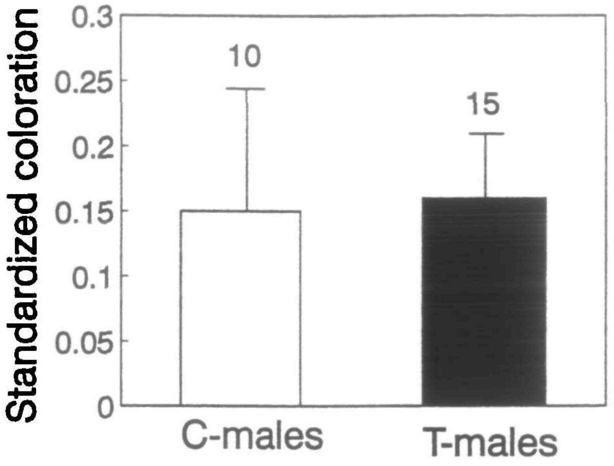

Figure 1
Orange breeding coloration area (mean ± SE) in males implanted with testosterone (T males) and males with empty implants (C males). Values were standardized to vary between 0 (minimal coloration) and 1 (maximal coloration). Numbers above bars indicate sample sizes. (Mann-Whitney *U* test, one tailed, $p = .38$.)

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

Breeding coloration at first capture was little or absent. Nine (SVL = 71–77 mm) of 10 C males recaptured in May had a small orange spot on each mouth comissure, and the remaining one (SVL = 75 mm) had orange bands on temporal regions of the head. Eleven (SVL = 70–78 mm) of 15 T males recaptured in May had the orange spot on the mouth comissures, and the other four (SVL = 73–75 mm) developed orange bands on temporal areas. The frequencies of individuals with orange bands on temporal areas in C males and T males did not differ significantly (Fisher's Exact test, one tailed, $p = .31$). When males were recaptured during May, the surface occupied by orange breeding coloration in C males and T males did not differ significantly (Figure 1). In those males that only presented coloration at each side of the mouth, spot area (0.81 ± 0.08 mm²) did not vary significantly with SVL when controlling for treatment effects (ANCOVA, $F_{3,25} = 0.25$, $p = .62$).

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. Similarly, the final number of ticks did not differ significantly between treatments (Figure 2).

We recorded the disappearance of 1 of 12 C males and 1 of 12 T males during the 1995 breeding season.

DISCUSSION

The results of this study indicate that an increased level of circulating testosterone in small adult males has consequences on behavior, but not on coloration or ectoparasite load. The lack of consequences of varying testosterone levels on breeding colouration contrasts with the results recorded for large males (Salvador et al., 1996), even though the experimental procedures were similar in both studies. In some vertebrates the secondary sex characteristics can be induced by sex steroids at any time from birth onward (Finch and Rose, 1995), but it appears that the effect of testosterone is age dependent in *P. algirus*. It is possible that small males develop the structures responsible for pigment production (xanthophores and iridophores; Morrison et al., 1995) only in the mouth comissures, where all the individuals had colouration. Also, testosterone seems to be involved in pteridine biosynthesis (Morrison et al., 1995; Rand, 1990), so small males may lack some precursors and/or biochemical cofactors required in the production of pigments responsible for the production of nuptial coloration (Brown, 1985). A third explanation may be that small males have not yet developed specific receptor isoforms in target tissues neccessary for hormone function (Finch and Rose, 1995; Grossman and Roselle, 1986). This last argument may also explain the apparent lack of effect of testosterone on the immune system, as evidenced by the similar ectoparasite load on T males and C males at the conclusion of the experiment (cf. Salvador et al., 1996). There are numerous possible molecular mechanisms that can fine tune hormone responses at different target tissues and life-history stages (Ketterson and Nolan, 1992).

The pattern of spatial use, with T male home ranges scarcely overlapping the home ranges of C males, suggests that experimental males tended to be more intolerant of other small

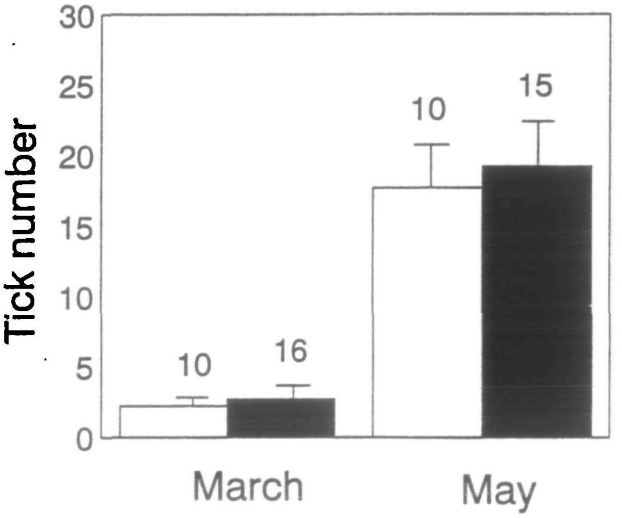

Figure 2
Number of ticks (mean ± SE) in control (C) males (open boxes) and testosterone-implanted (T) males (filled boxes) when captured during early breeding season (March) and recaptured during late breeding season (May). Numbers above bars indicate sample sizes. (Mann-Whitney *U* test, one tailed, March: $p = .42$; May: $p = .44$.)

adult males than C males. This is congruent with an increase in aggressiveness induced by testosterone (Marler and Moore, 1988, 1989, 1991; Marler et al., 1995; Salvador et al., 1996) and with the fact that androgens play an important role in territorial acquisition in lizards (Fox, 1983; Tokarz, 1995a). Observations of chases seem to corroborate that T males behaved more aggressively than C males. However, T males were observed attending females less frequently than C males. A possible explanation is that in small males, there is a trade-off between the time spent patrolling the home range and the search and courtship of females. We did not register a similar result for large males (Salvador et al., 1996), possibly because the showy colorations of large males might attract females and reduce the need for active search of mates. Nevertheless, the evidence supporting this point is scarce (Cooper and Vitt, 1993; Olsson and Madsen, 1995; Tokarz, 1995b).

Our experiment was designed to investigate the consequences on ornaments and parasite loads of variable circulating testosterone levels, assuming the existence of obligate connections between sexual hormones, ornamental traits, and immune system (Folstad and Karter, 1992). According to Andersson (1994), the sole manipulation of sex traits is problematic because it usually does not reflect all the changes in development and other costs that would result from corresponding natural changes in the expression of the trait. However, it is possible to imagine a mutant that, by eliminating any one of these connections, could succeed as a cheater (Wedekind and Folstad, 1994). A male of *P. algirus* that increases the expression of its ornaments without varying the susceptibility to parasites may acquire a profitable position, for example, by avoiding costly escalated interactions to establish dominance relationships (Rohwer, 1975, 1982). Large males fit well with this pattern because they often occupy elevated places on rocks, where they exhibit their nuptial coloration. Also, the frequency of aggressive encounters among large males is relatively low (Salvador et al., 1995, 1996). Small males of *P. algirus* may use a sneaking strategy, trying to be cryptic to large males, which usually win over small males (Olsson, 1992; Salvador et al., 1995), or even mimicking females. Hence, an increase of the coloration area possibly facilitates dominance on individuals of similar size, but could also promote escalated contests with larger males showing a similar color development (Olsson, 1994). In fact, small adult males only show a small color spot on the mouth comissures, which is fully exposed only when the individual opens his mouth. The lack of a relationship between size of this spot and snout-vent length suggests that this trait does not indicates size or condition in small males. For a human observer, it is often difficult to distinguish between small males and females, so the orange spot may serve to facilitate the identification of their bearer's sex during intra-/and intersexual interactions.

Our T males were apparently more interested in territorial assessment than in courting females. It is possible that the low reproductive success of a small male could be compensated by benefits derived from the obtaining of a larger or better territory the next year, once he becomes larger. In this way, it could be profitable to maximize body growth because body size is the main determinant of the hierarchical relationship between individuals of the same sex (Cooper and Vitt, 1987; Olsson, 1992, Tokarz, 1985). Small males (both controls and experimentals) exhibited higher mobility than large males (Salvador et al., 1995, 1996), which could increase their encounter rates with potential prey and may explain the relatively high increase in mass registered in individuals of this size class (see also Anderson and Karasov, 1988, Anderson and Vitt, 1990).

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