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Testosterone, Endurance, and Darwinian Fitness: Natural and Sexual Selection on the Physiological Bases of Alternative Male Behaviors in Side-Blotched Lizards

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The mechanistic bases of natural and sexual selection on physiological and behavioral traits were examined in male morphs of three colors of the side-blotched lizard, *Uta stansburiana.* Orange-throated males are aggressive and defend large territories with many females. Blue-throated males defend smaller territories with fewer females; however, blue-throated males assiduously mate guard females on their territory. Yellow-throated males do not defend a territory, but patrol a large home range. They obtain secretive copulations from females on the territories of dominant males. Males with bright orange throats had higher levels of plasma testosterone (T), endurance, activity, and home range size and concomitantly gained greater control over female home ranges than blue- or yellow-throated males. Experimentally elevating plasma T in yellow- and blue-throated males increased their endurance, activity, home range size, and control over female territories to levels that were seen in unmanipulated orange-throated males that had naturally high plasma T. However, the enhanced performance of orange-throated males is not without costs. Orange-throated males had low survival compared to the other morphs. Finally, some yellow-throated males transformed to a partial blue morphology late in the season and the endurance of these transforming yellow-throated males increased from early to late in the season. In addition, yellow-throated males that transformed to blue also had significantly higher plasma T late in the season compared to the plasma T earlier in the season. T appears to play an important role in the physiological changes that all three color morphs undergo during the process of maturation. In some yellow males, T plays an additional role in plastic changes in behavior and physiology late in the reproductive season. We discuss natural and sexual selection on physiological and behavioral traits that leads to the evolution of steroid regulation in the context of alternative male strategies.

Key Words: **testosterone; territorial behavior; ESS; alternative male strategies; endurance.**

The presence of aggressive territory holding males versus “satellite” or “sneaker” males is a widespread reproductive strategy found in a variety of vertebrates, including birds (Lank *et al.*, 1995), lizards (Sinervo and Lively, 1996), and fish (Gross, 1984; Cardwell and Liley, 1991; Gross, 1991; Brantley *et al.*, 1993). Behavioral morphs have been linked to the effects of gonadal steroids such as testosterone (T) or perhaps the regulation of gonadal steroids via gonadotropin or gonadotropin releasing hormone (Bass, 1996; Kindler *et al.*, 1989; Brantley *et al.*, 1993). Studies of the role of steroids on alternative male strategies often focus on the organizing effect that gonadal steroids such as T have on juvenile phases of the life history (e.g., Hews *et al.*, 1994; Bass, 1996). For example, Hews *et al.* (1994) found that experimentally elevated plasma T in hatch-

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ling lizards caused them to develop into aggressive territorial morphs at a higher frequency.

While the organizational effects of steroids are critical for the neurodevelopment of alternative male behaviors, steroids have activational effects that are manifest at maturity when males initiate reproduction. Later acting activational effects trigger changes in behavior and physiology in adults. Dramatic changes in behavior often leave the individual exposed to the efficient effects of natural and sexual selection. Selection on activitional events is under "direct selection" in that the survival or reproduction of males is temporally associated with changes during maturation. In contrast, direct selection on earlier acting organizational effects is less likely as differentiation is not yet complete. However, the direct selection on activational events can lead to indirect selection on organizational effects if activational and organizational effects are governed by the same sets of genes. Thus, direct selection on activational events and indirect selection on organizational events may primarily take place during maturation when activational events are manifest. Understanding the interplay between natural selection and steroid regulation is critical to understanding microevolutionary changes in steroid regulation that might have led to larger macroevolutionary patterns found among extant classes of vertebrates.

The activational effects of gonadal steroids include changes in levels of aggression (Moore, 1986, 1988) and changes of morphology and physiology, such as muscle development necessary for sexual behavior (Regnier and Herrara, 1993). In this paper, we investigate later acting activational effects arising from variation in levels of plasma T of maturing lizards that lead to enhanced endurance, territorial behavior, and control of female home range. Experimental analysis of performance and fitness is facilitated by a comparative analysis that focuses on three color morphs of side-blotched lizards, *Uta stansburiana,* that differ in dominance, physiological capacity, and circulating levels of T. Male side-blotched lizards develop into one of three discrete throat color morphs (orange, blue, and yellow throats). Throat color only becomes differentiated in March, when lizards begin maturing at an age of 6 to 8 months (Sinervo and Lively, 1996). Throat color has a genetic basis (Sinervo *et al.*, 2000). Orange-throated males are considered ultradominant and actively defend a very large territory. They are very aggressive and vigorously attack other territory holding males that venture onto their territory. Blue-throated males are likewise territory holders, but they are less aggressive and tend to defend smaller territories. Yellow-throated males do not defend a territory and they will often mimic female behavior when they are confronted by territory holding males. Throat color and dorsal color patterning of yellow-throated males is also superficially similar to the phenotype of females. Yellow-throated males are furtive and do not perch on conspicuous rocks like the territorial orange- and blue-throated males.

Although links between T, behavior, and aggression have been established (Crews, 1974; Fox, 1983; Moore, 1986; DeNardo and Licht, 1993; DeNardo and Sinervo, 1994), these patterns are largely derived from "manipulative experiments" performed in the laboratory or in the wild. In addition, T has also been shown to have multiple effects on performance of males, but the majority of data are likewise based on manipulative laboratory studies (Fennell and Scanes, 1992; Young *et al.*, 1993; Rand and Herrera, 1993; Regnier and Herrara, 1993; Van Breda *et al.*, 1993; Staron *et al.*, 1994). The physiological and selective significance of "natural variation" in plasma T is rarely documented in nature, and it is rarer still for manipulative experiments to be directly compared to natural variation. We complement comparative analysis of differences in hormones, physiology, and behavior among the three alternative male morphs with experimental manipulations of T in laboratory and field experiments. "Phenotypic engineering" (Ketterson and Nolan, 1992, sensu "allometric engineering," Sinervo and Huey, 1990) is useful for testing cause and effect relations between hormones and their manifold behavioral and physiological effects. Moreover, natural differences in plasma T and physiology observed among morphs can be used as a metric against which we can compare effects of experimentally induced variation to ensure that pharmacological effects of hormones do not affect our conclusions (Sinervo and Svensson, 1998; Sinervo, 1998).

We correlated endurance as measured on a laboratory treadmill, a stringent measure of whole-organism physiological capacity (Bennett, 1978; Sinervo and Huey, 1990; Garland and Losos, 1994), with hormones and territorial behaviors of males. High endurance and high levels of aggression may be necessary to maintain a large territory and defend a large aggregation of females. The high endurance and aggression of orange-throated males compared to blue-throated males could be parsimoniously brought about by elevated plasma T, given demonstrated effects of T on muscle physiology (e.g., Saborido *et al.*, 1991). In keeping with their more modest territory size, blue-throated males presumably have lower performance than orange-throated males, but higher performance