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 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 transform- ing 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.© 2000 Academic Press

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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-
Throat color has a genetic basis (Sinervo at an age of 6 to 8 months (Sinervo and Lively, 1996). Differentiated in March, when lizards begin maturing blue, and yellow throats). Throat color only becomes one of three discrete throat color morphs (orange, levels of T. Male side-blotched lizards develop into side-blotched lizards, native analysis that focuses on three color morphs of performance and fitness is facilitated by a 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...
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