

Male sexual behavior does not require elevated testosterone in a lizard (*Coleonyx elegans*, Eublepharidae)

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ABSTRACT

Male sexual behavior depends on gonadal androgens in species of all major vertebrate lineages, including reptiles. However, male sexual behavior includes distinct appetitive and consummatory phases, typically denoted as courtship and mounting, with potentially different hormonal control. Different proximate controls of courtship versus mounting could enable disconnected evolutionary losses and gains of various aspects of male sexual behavior. Male courtship display, which is activated by testosterone (T) in many species, is an ancestral trait in the lizard family Eublepharidae. However, *Coleonyx elegans* (Yucatan Banded Gecko) lost the courtship display, while retaining a highly simplified male sexual behavior that involves only mounting for copulation. We performed surgical manipulations (castration with and without T replacement in adult males; implantation of adult females with exogenous T) to investigate hormonal mechanisms involved in this evolutionary novelty. Our results indicate that the expression of simplified sexual behavior in *C. elegans* does not require elevated circulating levels of T, a finding that is previously unreported in lizards. In females, however, exogenous T induced male-like mounting. Thus, the mounting phase of sexual behavior is not activated by T in the traditional sense of this term but probably requires post-natal, maturational organization (if not periodic reorganization) by androgens. We conclude that the simplification of male sexual behavior and its independence from elevated levels of circulating androgens in *C. elegans* evolved via 1) evolutionary loss of the androgen-activated courtship display and 2) retention of the mounting phase, which has a longer “functional memory” for the effects of androgenic steroids.

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Introduction

Circulating gonadal steroids or their metabolites mediate the expression of sex-specific traits, including male sexual behavior, in all classes of vertebrates (reviewed in Adkins-Regan, 2005). However, temporal relations between gonadal steroids and sexual behavior are highly variable among species. Early investigators dichotomized this temporal variability in terms of the organizational/activational paradigm with regard to ontogeny (Phoenix et al., 1959; Goy, 1966) and in terms of associated versus dissociated reproductive patterns with regard to seasonal cycles (Crews, 1984). In the ensuing years, it has become abundantly clear that these dichotomies are more accurately described as poles on continuums rather than discrete categories into which all species fit neatly (Woolley et al., 2004; Arnold, 2009; Schulz et al., 2009).

A further complication arises from the fact that male sexual behavior is composed of separate phases. Classical ethologists made a

distinction between appetitive and consummatory phases of behavior (Lorenz, 1950; Tinbergen, 1951; Beach, 1956). The appetitive phase of male sexual behavior involves searching for and approaching a potential mate, as well as most courtship behaviors that serve to attract and stimulate the female into a sexually receptive condition. The consummatory phase involves physical contact between the sexes, culminating in copulation and the transfer of gametes. In current literature, the classical terminology is rarely used, and the phases of sexual behavior are more commonly described simply as courtship and copulatory behavior.

Studies on the physiological control of male sexual behavior sometimes fail to distinguish between phases and implicitly combine courtship and copulatory behaviors (reviewed in Woolley et al., 2004 for reptiles). As a result, such studies may conclude that all components in the sequence of male mating behavior are driven by a common regulatory factor without actually having demonstrated this. Specifically, observed reductions in sexual behavior following castration and restoration by androgen replacement in adult males of most avian and non-avian reptiles studied thus far have led to the generality that sexual behavior is activated by gonadal androgens (reviewed in Ball and Balthazart, 2004; Woolley et al., 2004), but it is

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unclear whether this conclusion applies equally to both courtship and copulatory behaviors. Separate phases of a complex behavioral repertoire can have different proximate controls, but once set into motion, the first phase may trigger the second (e.g., Balthazart et al., 1998; Balthazart and Ball, 2007; Adkins-Regan, 2009). In point of fact, androgens may activate courtship behavior, and successful courtship may sequentially trigger mounting and copulation as in a fixed action pattern.

Alternatively, androgens may activate courtship and copulation through separate but correlated mechanism. To date, most species of reptiles that have been studied follow an associated breeding pattern, in which gametogenesis and elevated levels of circulating androgens occur in association with sexual behavior during the mating season (Woolley et al., 2004). In these species, experimental manipulations have demonstrated that elevated T is required for the expression of both aggressive and sexual behaviors in males (e.g., *Sceloporus jarovii*, Yarrow's Spiny Lizard: Moore, 1987; reviewed in Woolley et al., 2004), an example of behavioral hormonal pleiotropy (see McGlothlin and Ketterson, 2008). Likewise, the coordinated activation of courtship and copulatory behaviors could be a pleiotropic effect of T. Hormonal pleiotropy, whereby one hormone controls the expression of multiple traits, is a simple and effective mechanism ensuring the coordination of features that comprise a functional phenotype (Finch and Rose, 1995). Pleiotropic activation of all components of male sexual behavior by gonadal androgens could evolve as an adaptation to past selection for the coordinated expression of behavioral traits at the appropriate ontogenetic stage or season.

On an evolutionary scale, pleiotropic effects of hormones lead to correlations among the traits involved and may then constrain further evolutionary changes in the coordinated expression of these traits (Hau, 2007; McGlothlin and Ketterson, 2008). In this model, the evolutionary dissociation of particular phases of male sexual behavior would require a change in the proximate hormonal activation of one or more of the traits. For instance, cessation of the activational effect of androgens on male sexual behavior has been postulated to have been necessary for the evolution of the dissociated breeding pattern present in some snakes, which exhibit uncoupling of elevated gonadal androgens from the expression of male sexual behavior (e.g., *Thamnophis sirtalis parietalis*, Canadian Red-sided Garter Snake: Camazine et al., 1980; Crews, 1984; Crews et al., 1984).

As an alternative explanation to evolutionary change in hormonal activation, ancestral differences in the proximate regulation of male sexual behavior may have been retained in extant species. Differences in proximate control of various behavioral phases would have allowed individual components of sexual behavior to have been independently lost or retained during evolution (see Adkins-Regan, 2009). Male sexual behaviors displayed by the snake, *T.s. parietalis*, may not have been dependent on activational effects of gonadal androgens in the ancestral state. In this species, the seasonal expression of male sexual behavior may only require long-term organization of neural substrates by elevated T before hibernation (Crews, 1984, 1991). In effect, the neural substrate of sexual behavior may have a long "functional memory" for T, which only requires annual re-exposure.

Lineages characterized by evolutionary changes in the repertoire of male sexual behavior (e.g., loss or gain of courtship) are especially suitable to test how such changes are coupled with alterations in hormonal control. The male courtship display typical for most species of the lizard family Eublepharidae, commonly called Eyelid Geckos, involves rapid, audible tail vibrations, so-called high-posture displays, and deposition of secretions from precloacal pores onto the substrate (Gutzke and Crews, 1988; Brillat, 1991; Fig. 1). Phylogenetic analysis indicates that this courtship display was present in the ancestral condition. A few extant species have lost this component, retaining only a highly simplified male sexual behavior that involves biting the female's neck (i.e., body-grip) and mounting for copulation (Kratovichil and Frynta, 2007). Hormonal control of mating behavior

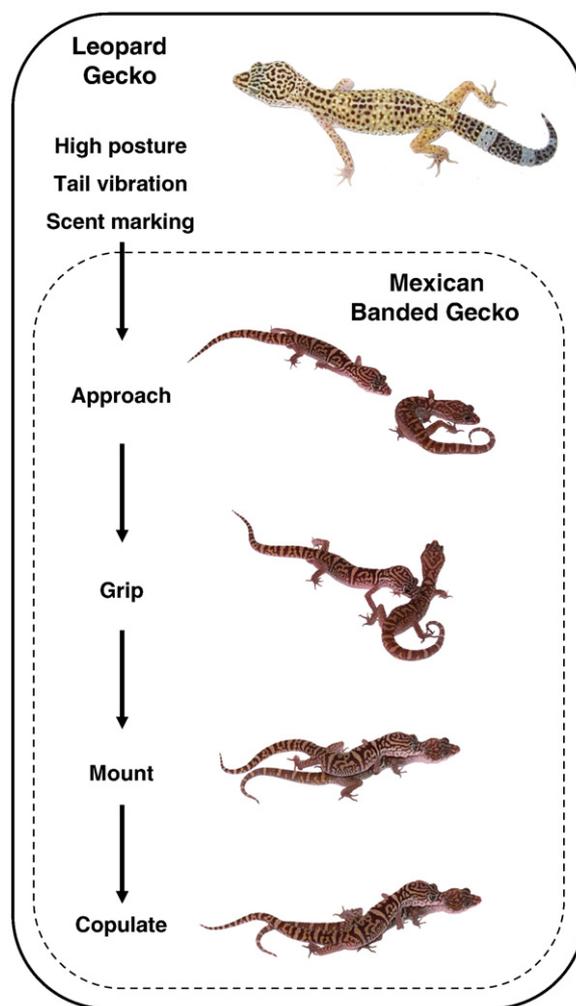


Fig. 1. Typical sequence of male sexual behavior towards a receptive female in *E. macularius* (Leopard Gecko) and *C. elegans* (Yucatan Banded Gecko). In *E. macularius*, male sexual behavior includes courtship displays with the exchange of tactile, visual and olfactory signals.

has been studied in one eublepharid species, *Eublepharis macularius* (Leopard Gecko), which displays the ancestral, complex male repertoire. Surgical castration and hormone replacement in *E. macularius* demonstrated that sexual behavior is dependent on elevated androgen concentrations typical of mature males (Rhen and Crews, 1999; Rhen et al., 2005).

We studied *Coleonyx elegans* (Yucatan Banded Gecko), a eublepharid species in which courtship display has been lost from the repertoire of sexual behavior, to investigate the linkage between T and sexual behavior. This species only displays body-grip and mounting, which are aspects of the consummatory phase (Kratovichil and Frynta, 2007; Fig. 1). In order to gain insight into how underlying physiological mechanisms could allow for the evolutionary loss of courtship display from the complex repertoire of male mating behavior, we investigated (1) the role of T in activating sexual behavior in adult males (via castration, with and without T replacement) and (2) the effects of T-supplementation on behavior in adult females.

Materials and methods

Animals

Animals were treated in accordance with research protocols approved by the Czech Central Commission for Animal Protection

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