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Compatibility drives female preference and reproductive success in the monogamous California mouse (*Peromyscus californicus*) more strongly than male testosterone measures

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ABSTRACT

Female assessment of male attractiveness and how preferred qualities impact reproductive success is central to the study of mate choice. Male attractiveness may depend on traits beneficial to the reproductive success (RS) of any female, termed 'universal quality', and/or on behavioral and biological interactions between potential mates that reflect 'compatibility'. The steroid hormone testosterone (T) often underlies male attractiveness in rodents and is associated with enhanced paternal care in the monogamous and biparental California mouse (*Peromyscus californicus*). We hypothesized that (1) T-characteristics are universally attractive to female California mice and that (2) if reproductive success is higher for females mated with preferred males, then females mated with males preferred by other females will also have higher reproductive success. Alternatively, we speculated that pair compatibility, based on emergent pair qualities, is important for a species with coordinated offspring care. We assessed individual T-characteristics in three ways: (1) T-response to GnRH challenges (2) baseline T-level and (3) T-response to a female. Testosterone-response did not predict female preference, but females spent more time investigating males with higher baseline T (accounting for only 9.6% of the variation in investigation time). None of the T-measures was associated with RS. Females paired with males they preferred produced litters more quickly and had higher RS than females paired with their non-preferred males. Naïve females who did not undergo preference tests had equivalent RS regardless of whether their mate was preferred or non-preferred by another female. These data suggest that higher male T elicits investigation, but female preference in the California mouse is more strongly linked with compatibility because individual preference was a better predictor of RS than any T measure.

Introduction

Mate choice is one of the most pivotal processes in biology, as these decisions can influence which genes are passed to future generations to ultimately shape the physiology and behavior of a species. Strategies for mate choice vary greatly among individuals, species and life history stages, typically reflecting a desire to maximize benefits to oneself or one's offspring while limiting the negative outcomes associated with a poor choice (Trivers, 1972). Although active mate choice is unlikely to revolve around any single factor (Wagner, 1998), there are some distinctions that can be made regarding what drives female preference for certain males. Female preference for certain males could indicate that these males have traits beneficial to the reproductive success (RS) of any female who chooses them, which we will term 'universal quality' (Andersson, 1982, 1994; von Schantz et al., 1989). Alternatively, female preferences could depend on the level of 'compatibility' between the male and female, reflecting the quality of behavioral or biological interactions between specific individuals that in turn determine pair RS (Ryan and Altmann, 2001). These two models of male attractiveness are not mutually exclusive and may be weighted differently depending on a number of factors including species social organization and availability of mates.

The breeding system of a species is one factor that may underscore the importance of active mate choice. The monogamous and biparental California mouse, *Peromyscus californicus*, is a genetically monogamous species in which individuals typically have only one mate in a lifetime (Ribble, 1991, 1992). In addition, offspring survival relies on the presence and care of both the mother and father (Gubernick and Teferi, 2000). Taken together, these data suggest that whether a California mouse successfully produces offspring is significantly dependent on the one-time choice of a mate.

Testosterone (T) is one biological factor that has been shown to support universal attractiveness of male odors in rodents (Ferkin et al., 1992; Taylor et al., 1982), and may be of particular significance for mate choice in the California mouse given that it is associated with critical male social behaviors in this species; recently, we reported

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that male T-response to courtship interactions predicts future paternal behavior, specifically in the amount of pup huddling and grooming performed when the female is temporarily absent (Gleason and Marler, 2010). Moreover, these findings are consistent with a general promotion of paternal behavior by T in the California mouse (Trainor and Marler, 2001, 2002). Indeed, examples of female preference for males who signal their paternal competence are found in other taxa (Forsgren, 1997; Lindström et al., 2006; Ostlund and Ahnesjo, 1998), although this relationship has yet to be shown in mammals. Our goal was to test whether male quality is primarily associated with ability to express high levels of T, specifically in a monogamous mammal. Given the importance of paternal care and its dependence on T in the California mouse (Trainor and Marler, 2001, 2002), in the present study we tested the hypothesis that female California mice prefer males who mount higher T-responses to courtship interactions, or have higher baseline T. In showing mating preferences for higher-T males, female California mice may be able to secure higher levels of paternal behavior, which would be universally beneficial to the RS of any female who chooses them.

Alternatively, mate preference in female California mice could reflect a focus on compatibility between mates, in which case mate preference and/or RS would be more closely associated with individual preference rather than a consistent male trait such as T-response. Few studies have considered how male qualities are differentially weighted when there are multiple factors to which a female can attend; that is, we accounted for the possibility that females would show mate preferences, but not for T-characteristics. Thus, we also tested the alternative hypothesis that female preference and male attractiveness are based on pair quality derived from compatibility, not universal quality.

To assess whether female preference is associated with male T characteristics, we first used gonadotropin releasing hormone (GnRH) challenges in combination with blood sampling to determine whether male T-measures or response characteristics are consistent within individual males. We then conducted preference tests in which we allowed female California mice to choose between males with high or low T-responses to GnRH challenges, and compared RS of breeding pairs comprised of a female paired with a high or low T-response male. In addition, we collected blood samples from males 1 day prior to and 1-h after preference testing to compare T-response to GnRH challenge with T-response to a female. To test the alternative hypothesis that mate choice is driven by compatibility, meaning that preferences are based on emergent pair qualities that cannot be predicted from either individual alone, we measured the relative impacts of preference and T on RS. We compared the RS of pairs formed after preference testing in the following four categories: 1) females that underwent preference tests and were paired with their preferred (P) males, 2) females that underwent preference tests and were paired with their non-preferred (NP) males, 3) naïve females that did not experience a preference test and were paired with a P male (preferred by another female in preference tests) and 4) naïve females that did not experience a preference test and were paired with a NP male (male that was not preferred by another female in preference tests). By comparing these four groups, we were able to simultaneously investigate the impact of both male T-characteristics (a putative universal benefit) and preference (which may or may not be T-based) on RS in the California mouse. We expected that if preferences are based on an assessment of either biological or behavioral compatibility between the male and female, then the strongest predictor of pair RS would be whether females are paired with males that *they* preferred during preference tests.

Methods

Animals

Forty-six male California mice between 5 and 6 months old were chosen at random from our breeding colony. Twelve of the 46 animals initially served as saline controls, and then again as subjects for GnRH challenges after a two-week rest period. Animals were housed in standard laboratory cages (48.3-cm-long × 26.7-cm-wide × 15.6-cm-high) with one or two same-sex cage mates during GnRH challenges and prior to preference testing, and later as breeding pairs. Purina 5015 mouse chow and drinking water were provided ad libitum. The testing room was maintained at 25°C on a 14:10 light/dark cycle with all behavioral observations occurring under dim red light. Animals were cared for in accordance with the *National Institutes of Health Guide for the Care and Use of Laboratory Animals*, and all procedures were approved by the University of Wisconsin-Madison IACUC. For clarification, a timeline of study events can be found in Chart 1.

GnRH challenges

Exogenously administered GnRH triggers the hypothalamic–pituitary gonadal (HPG) axis, causing an endogenous cascade of endocrine signals that ultimately results in T secretion from the testes. At low doses, the change in T is correlated with the amount of GnRH administered. At the high doses used during a GnRH challenge, however, it is possible to measure the maximum response that a male is capable of producing (Lacombe et al., 1991). By administering a standardized, high dose of GnRH to each animal, resultant plasma T-levels reflect individual differences in the ability to rapidly produce T (Jawor et al., 2006). GnRH challenges were conducted in two rounds, one in October of 2009 ($n = 26$ animals) and the second in January of 2010 ($n = 24$ animals). Challenges occurred 30 to 60-min after lights-out, under dim red light. Once per week for three consecutive weeks, each male was tested as follows: mice were transported in their home cages from the colony to a laboratory room directly across the hall on a wheeled cart covered to prevent exposure to hallway lighting. Each male was lightly anesthetized using Isoflurane anesthesia and 60μL of blood were drawn from the left eye with a heparinized capillary tube. Capillary tubes were immediately placed in a 5-mL microcentrifuge tube on ice. Light pressure was applied to the eye to ensure that bleeding had stopped, and the mouse was immediately injected with 50.0 ng of i.p. GnRH (Sigma, catalog # L7134) dissolved in 1.0 cm^3 of 0.9% sterile saline; the appropriate GnRH dose and time-course of sampling were both determined in pilot studies and based on doses reported in the literature (Gábor et al., 1998; Jawor et al., 2006; Millesi et al., 2002). The mouse was weighed, returned to his home cage and transported back to the colony to minimize the stress associated with the scent of blood sampling from other animals in the laboratory. 45 min after GnRH injections, animals were returned to the laboratory, lightly anesthetized and another 60μL of

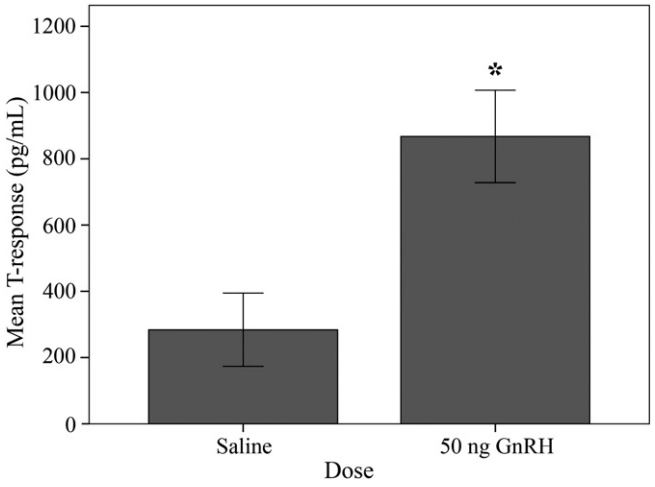

Fig.1. A 50-ng injection of GnRH causes a significant rise in plasma T as compared to saline injection.