



## Beyond aggression: Androgen-receptor blockade modulates social interaction in wild meerkats



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### ABSTRACT

In male vertebrates, androgens are inextricably linked to reproduction, social dominance, and aggression, often at the cost of paternal investment or prosociality. Testosterone is invoked to explain rank-related reproductive differences, but its role within a status class, particularly among subordinates, is underappreciated. Recent evidence, especially for monogamous and cooperatively breeding species, suggests broader androgenic mediation of adult social interaction. We explored the actions of androgens in subordinate, male members of a cooperatively breeding species, the meerkat (*Suricata suricatta*). Although male meerkats show no rank-related testosterone differences, subordinate helpers rarely reproduce. We blocked androgen receptors, in the field, by treating subordinate males with the antiandrogen, flutamide. We monitored androgen concentrations (via baseline serum and time-sequential fecal sampling) and recorded behavior within their groups (via focal observation). Relative to controls, flutamide-treated animals initiated less and received more high-intensity aggression (biting, threatening, feeding competition), engaged in more prosocial behavior (social sniffing, grooming, huddling), and less frequently initiated play or assumed a 'dominant' role during play, revealing significant androgenic effects across a broad range of social behavior. By contrast, guarding or vigilance and measures of olfactory and vocal communication in subordinate males appeared unaffected by flutamide treatment. Thus, androgens in male meerkat helpers are aligned with the traditional trade-off between promoting reproductive and aggressive behavior at a cost to affiliation. Our findings, based on rare endocrine manipulation in wild mammals, show a more pervasive role for androgens in adult social behavior than is often recognized, with possible relevance for understanding tradeoffs in cooperative systems.

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### Introduction

Cooperative breeding, by which dominant individuals monopolize a group's breeding efforts, is rare among vertebrates, although several theories can be invoked to explain why subordinate helpers might delay their own reproduction to care for the offspring of others (Arnold and Owens, 1998; Lukas and Clutton-Brock, 2012). The mechanisms involved in ensuring differential reproduction can differ rather dramatically across species: In some, helpers are hormonally

suppressed, such that they are physiologically unable to reproduce (Arnold and Dittami, 1997; Bales et al., 2006; Schoech et al., 1991), whereas in others, helpers are behaviorally suppressed, but retain the physiological capacity to reproduce (Bennett et al., 1993; Creel et al., 1992; Khan et al., 2001; Oliveira et al., 2003). Among the latter, the role of reproductive hormones, such as testosterone (T), which might not vary substantially between breeders and helpers, remains poorly understood. Within social species, reproductive hormones often regulate (or are regulated by) the within-group interactions that are necessary to maintain stable relationships (Albers et al., 2002; Monaghan and Glickman, 1992). In males, androgen function is best understood in the context of mediating reproductive and aggressive behavior — activities that often come at the cost of paternal investment (Hegner and Wingfield, 1987; Ketterson and Nolan, 1994). Androgen function is

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also invoked to explain rank-related differences in courtship and competition (Wingfield et al., 1987). Nevertheless, there is recent evidence to suggest an even broader role for T in mediating adult social interaction, particularly in monogamous or cooperatively breeding species (Eisenegger et al., 2011; Gleason and Marler, 2010; Storey et al., 2006; van der Meij et al., 2012; Wang and De Vries, 1993). Here, using a wild population of the cooperatively breeding meerkat (*Suricata suricatta*), we investigated these issues by blocking the androgen-receptor system of adult, subordinate males.

Meerkats are social mongooses that live in relatively stable clans or structured groups, typically comprising a dominant breeding pair and various subordinate relatives or offspring of both sexes that contribute to pup rearing (Clutton-Brock et al., 2001). Among males, breeders and helpers express similar concentrations of T and luteinizing hormone (LH), and show comparable LH spikes in response to a GnRH challenge (Carlson et al., 2004; O'Riain et al., 2000). Thus, although the dominant male monopolizes most of a group's breeding (Griffin et al., 2003), subordinate males are not reproductively suppressed (Carlson et al., 2004). They may gain some breeding success, as well as experience raised T concentrations, during extraterritorial prospecting forays (Spong et al., 2008; Young et al., 2005, 2007). T does not correlate with aggression or dominance between male social classes (Carlson et al., 2004) and there is no evidence to date that T relates to rates of pup provisioning (Carlson et al., 2006a). Yet, because behavioral endocrinologists tend to focus on understanding dominance or the differences between social classes, little is known about the role of T in regulating subordinate male interaction in this or other species (although see: Virgin and Sapolsky, 1997). Given that dominant and subordinate animals may respond differently to the same T treatment (Fuxjager et al., 2015) or that T-associated variation in behavioral 'style' may exist within the same class (Virgin and Sapolsky, 1997), it is increasingly relevant to understand how the different social classes respond to endocrine challenges.

Meerkats are an appropriate model in which to test the proposition that androgens may regulate social behavior beyond aggression: Firstly, subordinates are far more numerous than are dominant animals and necessarily account for a large proportion of social interaction; secondly, these helper males rarely reproduce, but curiously maintain androgen concentrations commensurate with those of dominant males; thirdly, access to an exceptional wild population allows us to consider social and ecological relevance, while overcoming logistical challenges that typically preclude field neuroendocrine studies (see Fusani et al., 2005).

With relatively few exceptions, typically involving avian species (e.g., Apfelbeck et al., 2013; Hegner and Wingfield, 1987; Schwabl and Kriner, 1991), hormones or their actions are rarely experimentally manipulated in the field (see Fusani et al., 2005), particularly to explore their relationship to the broad social repertoire. Instead, androgen-manipulation studies in laboratory animals, particularly rodents and birds, aim to improve our mechanistic understanding of isolated traits (either e.g., reproduction: Södersten et al., 1975; aggression: Searcy and Wingfield, 1980; play: Meaney et al., 1983; scent marking: Fuxjager et al., 2015; or song: Grisham et al., 2007). This historical focus can occur at the expense of gaining comparative, ecological, and evolutionary understanding of hormone action: detecting tradeoffs and constraints, for instance, requires an integrated approach (Wingfield et al., 2008).

To test the role of androgens in subordinate, male meerkats, we administered the nonsteroidal antiandrogen, flutamide, that competitively blocks the binding of androgenic hormones (primarily T) to androgen receptors (Hellman et al., 1977; Peets et al., 1974). Androgens often relate to the initiation of aggression (e.g. Virgin and Sapolsky, 1997) or the outcome of aggressive encounters (e.g. Rose et al., 1972), and androgen-mediated cues can also influence susceptibility to aggressive attacks (Monaghan and Glickman, 1992). Consistent with studies in various species showing that flutamide administration leads to reduced adult aggression (Sperry et al., 2010; Taylor et al., 1984; Vleck and

Dobrott, 1993), we expected flutamide-treated meerkats to initiate less, but receive more, aggression than their control counterparts.

Beyond the relationship to overt aggression, androgens also may be linked to other more subtly competitive or even prosocial interaction in animals. Rough-and-tumble play, for instance, which can facilitate the establishment of dominance relations among the males of certain species (Panksepp, 1981; Pellegrini, 1995), is often sexually differentiated, with males playing more vigorously than females (Boulton, 1996; Goy and Phoenix, 1971; Meaney et al., 1985). The expression of mammalian social play is masculinized through early androgen exposure (Goy and Phoenix, 1971; Olioff and Stewart, 1978; Wallen, 2005) and can be feminized through reduced prenatal exposure to androgens (Meaney and Stewart, 1981; Meaney et al., 1983). Typically, postnatal androgens do not mediate social play (Meaney et al., 1985), as neither the frequency nor vigor of play are influenced by administration of T to juvenile females (Joslyn, 1973) or by castration of juvenile males (Beatty et al., 1981; Goy, 1970; Pedersen et al., 1990). Nevertheless, few researchers have addressed the potential link between activation of androgens and adult social play, largely because playful behavior tends to decrease dramatically in adulthood. Meerkats, however, continue to play as adults (Sharpe, 2005), so we might expect flutamide-treated meerkats to play less vigorously (e.g. initiate less rough-and-tumble play) than those experiencing normal androgen action.

With regard to the role of androgens in more purely prosocial, affiliative, or even cooperative behavior, the nature of the correlations can vary considerably. Paternal care (including huddling and grooming), for instance, is generally thought to be inhibited by T (Hegner and Wingfield, 1987; Ketterson et al., 1992), but can increase with androgens in the males of various species (Desjardins et al., 2008; Gleason and Marler, 2010; Neff and Knapp, 2009; Rodgers et al., 2006; Storey et al., 2000; Trainor and Marler, 2001; Wang and De Vries, 1993). Moreover, depending on prenatal androgen exposure (Millet and Dewitte, 2006; van Honk et al., 2012), T in men can increase affiliative behavior (van der Meij et al., 2012), reduce deceit (Wibral et al., 2012), promote reciprocity (Boksem et al., 2013) and increase cooperation (Huoviala and Rantala, 2013). Meerkats show a range of prosocial behavior (including grooming, social sniffing, and huddling) and cooperative behavior (including babysitting and provisioning pups, as well as vigilance and guarding against predators; Clutton-Brock et al., 1999, 2000, 2001). If androgens in meerkats implicate the traditional tradeoff between aggression and affiliation, we might expect rates of prosocial interaction to increase with flutamide treatment. If androgens in meerkats function to increase cooperation, to the benefit of the entire group, we might expect flutamide treatment to reduce pup care or antipredator activities.

Lastly, androgens also may be involved in aspects of olfactory and vocal communication (Dryden and Conaway, 1967; Ulibarri and Yahr, 1988; Wingfield et al., 1987). In this regard, scent marking is often linked to territorial defense (Hediger, 1949; Johnson, 1973) and reproductive advertisement (Brown and Macdonald, 1985; Drea, 2015; Eisenberg and Kleiman, 1972) with dominant individuals generally marking more than subordinates (Johnson, 1973; Ralls, 1971). Scent marking increases following early exposure to androgens and decreases if such exposure is inhibited (Epple, 1981; Turner, 1975; Ulibarri and Yahr, 1988). Postnatal T similarly mediates the frequency of scent marking (Johnston, 1981) and can also influence the chemical composition of odorants (Novotny et al., 1984). Castration causes retardation or atrophy of scent glands, with accompanying effects on odorant production (Dryden and Conaway, 1967; Epple, 1981), whereas hormone replacement restores these attributes (Dryden and Conaway, 1967). Within adult male meerkats, there is no strong evidence of rank-related differences in scent marking at latrines (Jordan, 2007), although we suspect that they might emerge in other contexts. Despite equivalence in circulating T between male classes, anal gland secretions appear to be more pronounced in dominant males than in subordinate males (see Fig. 1 in Leclaire et al., 2014) and preliminary analyses of these

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