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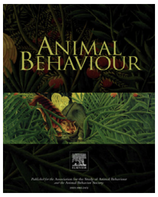

# The functions of male–male aggression in a female-dominated mammalian society

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In most mammals, male–male contests over access to resources select for males to be larger, more aggressive and better armed than females. However, the functional significance of male–male aggression has been little studied in sex-role-reversed species, such as spotted hyaenas, *Crocuta crocuta*. This species has highly aggressive, socially dominant females, to which male access cannot be directly improved by fighting. Here, we first demonstrated that males nevertheless display intrasexual aggression at rates similar to rates of intrasexual aggression displayed by adult females. We then tested three hypotheses suggesting functions of this aggression among males. Males aggressed significantly less in the presence of an adult female than when adult females were absent, suggesting that they do not use aggression to prevent other males from remaining in close proximity to females. New immigrants received significantly more aggression from other immigrants than did established immigrants, but new and established immigrants were treated equally by adult natal males. These results supported a hypothesis suggesting that male–male aggression functions to restrict clan membership, although the data indicated that immigrants, not adult natal males, engage in aggression for this reason. Finally, a hypothesis suggesting that this behaviour functions to provide access to food was supported by data showing that male–male aggression occurred significantly more frequently, and at higher intensities, in the presence than the absence of food. In contrast to male–male contests in most mammals, those in spotted hyaenas appear to increase a male's access to females only indirectly, which is presumably due to the sex-role-reversed nature of social dominance in spotted hyaenas.

Although aggression can impose substantial costs on both aggressors and recipients (Aureli, 1997; Briffa & Elwood, 2004; Castro, Ros, & Becker, 2006; Charpentier & Drea, 2013; Clutton-Brock, Albon, Gibson, & Guinness, 1979; Huntingford & Turner, 1987; MacCormick et al., 2012; Schino, Rosati, Geminiani, & Aureli, 2007), intraspecific aggression is nevertheless widespread in animals, especially among males (Andersson, 1994). Male–male aggression generally occurs during competition over access to resources, particularly mates (Andersson, 1994; Darwin, 1871; Le Boeuf, 1974). Agonistic interactions may determine male dominance status (Alberts, Watts, & Altmann, 2003; Haley, Deutsch, & Le Boeuf, 1994; Packer, 1979b; Pelletier & Festa-Bianchet, 2006), which can have significant fitness implications. For example, females sometimes use displays of male–male aggression to evaluate male quality and aid in mate choice (Cox & Le Boeuf, 1977; Hunt, Breuker, Sadowski, & Moore, 2009; Pizzari, 2001; Wong & Candolin, 2005). Although male dominance rank is not correlated with reproductive success in all species (Ellis, 1995), higher-ranking winners of male fights often have the best access to females and frequently also enjoy the greatest reproductive success (Alberts et al., 2003; Cowlishaw & Dunbar, 1991; Haley et al., 1994; Natoli, Schmid, Say, & Pontier, 2007; Packer, 1979b). However, male–male aggression may also occur over resources only indirectly related to mate access (Richard, 1992; West-Eberhard, 1979, 1983), including food (Baker, Dietz, & Kleiman, 1993; Janson, 1985; Richard, 1992), group membership (Pereira & Weiss, 1991; Richard, 1992), territory (Emlen & Wrege, 2004; Stamps & Krishnan, 1997) and nesting materials (Takahashi, Kohda, & Yanagisawa, 2001).

In most mammals, male–male contests over access to these resources select for males that are larger, more aggressive and better armed than females (Andersson, 1994; Darwin, 1871; Short &

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Balaban, 1994). These sex differences typically allow males to attain social dominance over females and outcompete females for shared resources (Cowlishaw & Dunbar, 1991; Haley et al., 1994; Packer, 1979b). In contrast, a small group of ‘role-reversed’ mammalian species exists in which females consistently show social dominance over males (for review, see Holekamp & Engh, 2009); this group includes bonobos, *Pan paniscus* (Paoli, Palagi, & Borgognini Tarli, 2006), multiple species of mole-rats (Bennett & Faulkes, 2000), lemurs (Drea, 2007; Jolly, 1966), and spotted hyaenas, *Crocuta crocuta* (Frank, 1986b; Kruuk, 1972; Smale, Frank, & Holekamp, 1993). Males of these species may be the same size or smaller than females, and may also lack the strongly dimorphic weaponry that is typically selected for by intense male–male combat (Andersson, 1994; Haley et al., 1994; Mitani, Gros Louis, & Richards, 1996; Surbeck, Deschner, Schubert, Weltring, & Hohmann, 2012). Males in role-reversed species often engage in intrasexual aggression (Berglund, 2005; Cavigelli & Pereira, 2000; Charpentier & Drea, 2013; Drea, 2007; Jolly, 1966; Kappeler, 1990, 1996; Lawler, Richard, & Riley, 2005; Pereira & Kappeler, 1997; Richard, 1992; Sauther, 1991), and in many cases this aggression seems to be over direct access to oestrous females (e.g., Cavigelli & Pereira, 2000; Drea, 2007; Gould & Ziegler, 2007; Jolly, 1966). However, other circumstances, including female dominance, can preclude males from converting physical victories over other males into mating opportunities with oestrous females (Drea, 2005; Pereira & Weiss, 1991; Richard, 1992); in these cases the functions of male–male aggression may be less clear. Our goal here was therefore to explore the functions of intrasexual male aggression in a female-dominated species, the spotted hyaena.

Spotted hyaenas are role reversed in that they show moderate female-biased sexual dimorphism in body size (Ralls, 1976; Swanson et al., 2013), monomorphism in weaponry (Van Horn, McElhinny, & Holekamp, 2003) and female social dominance (Frank, 1986b; Kruuk, 1972; Smale et al., 1993). Furthermore, in many different contexts, female hyaenas are considerably more aggressive than their male counterparts. For instance, females are more likely to win postnatal dominance contests than are their male siblings (Golla, Hofer, & East, 1999; Smale et al., 1993; Smale, Holekamp, Weldele, & Frank, 1995), females are seen leading attacks on alien hyaenas during clan wars roughly twice as often as are males (Boydston, Morelli, & Holekamp, 2001), and females engage in intersexual aggression at higher rates and intensities than do males (Frank, Glickman, & Zabel, 1989; Szykman et al., 2003; Van Meter, 2009). In fact, given that winning fights with other males does not improve male mating success, affiliative behaviour directed towards females is the mating tactic adopted by the most successful male hyaenas (East, Burke, Wilhelm, Greig, & Hofer, 2003).

However, despite these role reversals, sexual selection theory predicts that male hyaenas nevertheless should compete among themselves, because females have the limiting reproductive rate (Darwin, 1871; Holekamp, Smale, & Szykman, 1996; Kruuk, 1972; Mitani et al., 1996). Although male hyaenas rarely engage in the life-threatening physical conflicts typical of males in other species (Andersson, 1994; East & Hofer, 2001), they do demonstrate intrasexual aggression (Kruuk, 1972; Van Meter, 2009). Previous research found the rate of male–male aggression to be significantly lower than the rate of female–female aggression (Szykman et al., 2003), but these calculations did not control for the number of potential targets; as social subordinates, adult males typically have far fewer potential targets of aggression than do adult females. When the number of potential targets is taken into account, the difference between the sexes may disappear. Here, we examine this possibility by comparing rates and intensities of intrasexual aggression between adult male and female spotted hyaenas.

The functions of this aggression among male hyaenas remain unclear. As in the societies of many primate species (Alberts et al., 2003; Frank, 1986b), male spotted hyaenas have linear dominance hierarchies that partially predict mating success (East et al., 2003; Engh et al., 2002). However, hyaenas differ markedly from these primates in that male hierarchies are not determined by physical contests, but are instead determined by tenure in the clan (East & Hofer, 2001; Smale, Nunes, & Holekamp, 1997). Male–male aggression therefore does not function in this species to improve a male's social rank. It also cannot directly improve a male's access to oestrous females, because the unique morphology of the female's reproductive tract (Matthews, 1939) gives her complete control over copulation (East et al., 2003; East & Hofer, 1997; East, Hofer, & Wickler, 1993; Frank, 1997; Kruuk, 1972). Because of these social and morphological limitations, male–male aggression has largely been ignored in spotted hyaenas. Here we suggest three non-mutually exclusive functions of male–male aggression in this species, each of which could potentially increase an aggressor's fitness without directly influencing his social rank or his access to oestrous females.

Although male hyaenas cannot directly leverage agonistic contests into copulations (East et al., 2003; East & Hofer, 2001; Kruuk, 1972), they may compete for access to females less directly (e.g. Parga, 2006). Given that male hyaenas attempt to associate with females, and that females often mate with their closest male associates (East & Hofer, 2001; Szykman et al., 2001), male hyaenas might use aggression to prevent other males from forming amicable relationships with females (East et al., 2003; East & Hofer, 2001). In addition, males might use intrasexual aggression to display their fitness to choosy females (Cox & Le Boeuf, 1977; Pizzari, 2001; Procter, Moore, & Miller, 2012). Because both scenarios suggest that female presence should dictate male–male aggression, our first hypothesis generalizes the two and posits that male–male aggression functions to provide the aggressor with enhanced access to females. Under this hypothesis, we predicted that males would aggress more often (or at higher intensities) against other males when at least one adult female was present than when females were absent. Furthermore, in light of previous research demonstrating the effects of female sexual receptivity on male–male aggression (Cavigelli & Pereira, 2000; Gould & Ziegler, 2007; Parga, 2006), we predicted that the presence of an oestrous female would intensify this predicted effect of female presence on male–male aggression.

Male–male aggression might also function to influence clan membership. Aggressive contests among males over territory or group membership are well documented in other species (e.g. French & Snowdon, 1981; Pereira & Weiss, 1991; Richard, 1992; Wingfield & Marler, 1988), and this aggression may occur in place of competing over direct access to oestrous females (Takahashi et al., 2001), particularly in species showing female social dominance (Shibata & Kohda, 2006). In spotted hyaenas, which show male dispersal and female philopatry (Smale et al., 1997; Van Horn et al., 2003), females usually choose resident males that have permanently immigrated into the clan as sires for their cubs (Engh et al., 2002; Höner et al., 2007), rather than males that are not current members of the clan. Thus, it follows that the strength of male–male competition should increase with the number of resident males present in a clan, and the community of adult males in a clan can be viewed as an oligopolistic market in which all resident males have a mutual interest in limiting new entrants. Resident males might therefore use intrasexual aggression to restrict potential immigrants from joining the clan (East & Hofer, 2001). Under the hypothesis that male–male aggression functions to influence clan membership, we predicted that prospective