



## Suffering third-party intervention during fighting is associated with reduced mating success in the fallow deer

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Numerous studies have shown that dyadic fights are regularly disrupted by the intervention of third-party group members. Empirical and theoretical attention with respect to these interventions have focused predominantly on the fitness advantages that accrue to the intervening individual; conversely, little attention has been given to studying the fitness implications of suffering from third-party intervention behaviour. Therefore, we investigated this issue by examining the relationship between variation in individual mating success and suffering third-party interventions during a fallow deer, *Dama dama*, rut. Mating success was analysed using a 'hurdle' model against three explanatory variables: daily variation in suffering an intervention, dominance rank and fight rate. The lower, logistic level of the model indicated a negative interaction between variation in suffering an intervention and fight rate in relation to whether a mating was achieved or not. Further investigation of this interaction showed that the proportion of matings achieved by males declined as interventions suffered increased regardless of whether males had a high (five or more fights per day) investment in fighting. There was no meaningful effect observed in the upper level of the model. We also investigated whether there was evidence for a temporal association between suffering interventions and mating success: two models investigated interventions suffered on a previous day and the cumulative sum of interventions suffered over 2 days in relation to mating success. Neither model showed a meaningful association at the lower or upper level indicating that the effects of intervention behaviour are temporally limited in this population. Our results underline the complex nature of the relationships at play during third-party interventions in relation to mating success. We suggest that there is a need for greater empirical investigation and wider theoretical scrutiny with respect to suffering intervention.

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The study of animal contest behaviour in relation to outcome and fight dynamics has tended to focus on the importance of resource value and fighting ability (resource-holding potential, RHP; Parker, 1974). Such considerations have led to the development of a number of influential models that focus on the decision processes used by combatants during fights (e.g. Payne, 1998; Taylor & Elwood, 2003). A key aspect of these models is that they specifically address aggression at the dyadic level. However, there is accumulating evidence that contest behaviour can involve more complex forms of aggressive interaction. Specifically, a number of studies conducted on (semi-) captive (e.g. African wild dog, *Lycaon pictus*; de Villiers, Richardson, & van Jaarsveld, 2003; raven, *Corvus*

*corax*; Fraser & Bugnyar, 2012; gelada, *Theropithecus gelada*; Pallante, Stanyon, & Palagi, 2016; Grant and Chapman zebra, *Equus quagga boehmi* and *E. q. antiquorum*; Schilder, 1990) and field populations (e.g. fallow deer, *Dama dama*; Jennings, Carlin, & Gammell, 2009; baboon, *Papio cynocephalus*; Silk, Alberts, & Altmann, 2004; rhesus macaque, *Macaca mulatta*; Widdig et al., 2006) have shown that third-party individuals frequently intervene and disrupt ongoing contests.

Theoretical explanations underpinning the study of intervention behaviour have been largely driven by the extensive body of work conducted on primate species (Bissonnette et al., 2015; Smith et al., 2010). Such accounts typically emphasize that intervention behaviour serves to underpin the formation of coalitions; thus, individuals are expected to be able to track shifting dominance relationships (e.g. Chapais, 1995) or to remember past relationships (i.e. who helped whom previously, e.g. Gavrillets, Duenez-Guzman,

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& Vose, 2008). Alternative accounts hold that individuals might simply disrupt dyadic fights to prevent successful rivals from advancing in the hierarchy via a winner effect (Dugatkin, 1998). Therefore, rather than coalition formation, intervention acts to maintain the social status quo by insulating high-ranking individuals from challenges by lower ranking adversaries (Jennings et al., 2009). Yet, regardless of whether one appeals to a coalitionary or noncoalitionary account of third-party behaviour, the majority of these theories tend to argue that interventions serve to improve fitness by helping the intervener secure access to valuable resources.

Nevertheless, determining whether intervention confers fitness benefits has proven to be difficult. For example, benefits might accrue directly (e.g. an increase in rank: Jennings, Carlin, Hayden, & Gammell, 2011) or indirectly (e.g. kin support: Engh, Siebert, Greenberg, & Holekamp, 2005). However, despite numerous studies, the relationship between reproductive opportunities and triadic behaviour is not clear cut. Consequently, few studies have shown that third-party intervention behaviour benefits individuals with respect to mating success (but see Gilby et al., 2013; Jennings et al., 2011). One possibility is that the lack of evidence supporting such a relationship might be due to the temporal relationship between intervention behaviour and the fitness outcome (Harcourt & de Waal, 1992). From a coalitionary perspective for example, it is possible that the degree of (in)stability in the nascent relationship between individuals introduces a temporal lag between intervention acts and the accrual of any actual benefits. Although we are not aware of any studies that focus specifically on the temporal relationships between intervention behaviour and mating success, coalitionary behaviour (which includes third-party behaviour) tends to peak just prior to the most likely day of conception in the baboon (Bercovitch, 1988). In terms of improvement in rank the evidence is somewhat mixed; for example, temporal lag appeared to be minimal with respect to male rank advancement in chimpanzees, *Pan troglodytes* (e.g. de Waal, 1982; 1984), whereas in bonnet macaques, *Macaca radiata*, there was little evidence that intervention was associated with an increase in rank over time (e.g. Silk, 1993). Given that there has been relatively little investigation of this question, one objective of this study was to gain a more comprehensive understanding of the temporal association between intervention behaviour and mating success.

While a general finding shows that dominance rank is positively associated with mating success in many species (Dewsbury, 1982; Ellis, 1995), the evidence that the relationship between third-party behaviour and fitness is influenced by dominance rank is more limited (e.g. de Waal, 1984), albeit theoretically expected (e.g. Chapais, 1995; Dugatkin, 1998; van Schaik, Pandit, & Vogel, 2006). Whether the same relationships hold for recipients of third-party intervention behaviour has received little attention. While it has been reported that the costs to individuals of suffering an intervention can be severe in terms of consortship with females (e.g. Noë, 1992), we are unaware of any detailed studies that have investigated the relationship between suffering third-party intervention, dominance and fitness. We might speculate that depending on the way in which dominance interacts with intervention behaviour, a negative (lower ranks depose higher ranks: revolutionary) or positive (higher ranks defeat lower ranks: conservative) interaction between suffering an intervention and dominance should hold in relation to fitness. Nevertheless, theory is generally silent on the matter; therefore, one possibility investigated in this study was whether suffering intervention is associated with fitness via an interaction with dominance rank.

However, if we ignore the bulk of theoretical and empirical work on third-party behaviour, perhaps the most parsimonious explanation is that irrespective of rank, a direct negative impact of

suffering intervention on mating success is expected. Specifically, the intervener behaves opportunistically in disrupting ongoing fights (Jennings et al., 2009, 2011); therefore, rather than interacting with dominance, suffering an intervention should be directly associated with reduced mating success. An alternative possibility is that intervention behaviour forms part of the general aggressive repertoire of males as they compete for mating opportunities (Jennings, Boys, & Gammell, 2017). Therefore, suffering from intervention might well interact with other aspects of competitive behaviour such as fighting (see de Waal & Harcourt, 1992 for a discussion of facial and vocal signals aligned with triadic behaviour); therefore, in relation to fitness, an interaction between fighting and suffering from intervention might be expected.

Male fallow deer display a heightened tendency to fight with conspecifics during the annual rutting season (e.g. Apollonio, Festa-Bianchet, Mari, Mattioli, & Sarno, 1992; Clutton-Brock, Green, Hiraiwa-Hasegawa, & Albon, 1988; Moore, Kelly, Cahill, & Hayden, 1995), and approximately 10% of fights are disrupted by the intervention of third-party males (Jennings et al., 2009). Studies have focused almost exclusively on intervention behaviour in relation to the intervener rather than the recipient of the intervention; these have shown that intervention is associated with increased mating success (Jennings et al., 2011), and is most likely to be committed by high-ranking males (Jennings et al., 2009). Furthermore, the tendency for individuals to engage in interventions varies based on aggression experienced, rather than resource access. Therefore, the number of different opponents fought and whether the individual itself suffered from fight interventions on a given day, rather than the number of mating opportunities available, are important correlates of intervention behaviour (Jennings et al., 2017). Taken together, these findings indicate that it is males at the upper end of the hierarchy (Jennings, Gammell, Carlin, & Hayden, 2006), that is, those most likely to mate, that are most likely to disrupt each other's fights. The question we asked here is why, and to what end? Given the lack of empirical studies on this question, and in the absence of theoretical direction, we sought to investigate a number of possibilities in relation to the impact of suffering third-party behaviour on fitness.

We sought to determine whether there was evidence for any detrimental effect of suffering an intervention on mating success by examining whether any association between suffering intervention and mating success was direct or via an interaction with dominance and fighting, two variables that correlate with mating success (Clutton-Brock, Albon, Gibson, & Guinness, 1979; Moore et al., 1995). Given that numbers of oestrous females represent a variable resource over the course of the rut, we also investigated the temporal relationship between variation in suffering from intervention and any potential fitness gain (e.g. Bercovitch, 1988; Silk, 1993; de Waal, 1984). Therefore, we investigated whether any association between suffering an intervention and mating success was temporally proximate (evident on the same day) or delayed (evident on the following day).

## METHODS

### *Study Population*

Aggressive behaviour in a herd of free-ranging fallow deer resident in Phoenix Park, Ireland (53°22'N, 6°21'W) was recorded from late August/early September and throughout the annual rut in the latter half of October during two successive years (1996/1997). The park encloses 709 ha; most of the area of the park (80% approximately) is open grassland with the remaining area consisting of mixed woodland. The management plan for the deer involves tagging fawns shortly after birth (annually between June and

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