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Third-party intervention behaviour during fallow deer fights: the role of dominance, age, fighting and body size

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Third-party interventions of dyadic contests are often explained by appealing to high-level cognitive processes such as coalition formation between group members. However, alternative accounts that do not appeal to sophisticated cognitive processes have been proposed. We tested predictions from two such models using the fallow deer, *Dama dama*, as the model taxon: (1) a random target model that argues that intervention is directed randomly towards a target and (2) a specific target model that assumes that targeting is directed at contestants that have low resource-holding potential. Contrary to predictions of the specific target model, we found no evidence that targeting following third-party intervention increased as the resource-holding potential of the target declined. Both models argue that intervention serves to prevent individuals from gaining a winner effect and advancing up the hierarchy. Being targeted did not result in a decline in dominance rank, although targeting was associated with investment in dominance-related fighting tactics. Fight intervention was associated with an increase in rank early in the rut and accounted for increased mating success. Therefore, interveners benefited beyond simply preventing rivals from advancing in the hierarchy. In theoretical terms, a random target as opposed to a specific target model explains intervention behaviour in the fallow deer.

A range of factors such as body and weapon size, body mass, physiological state, age, gender and contest experience have been identified as central to affecting the strategic decisions made by competing animals (Riechert 1998; Arnott & Elwood 2009). All things being equal, because larger individuals potentially have a greater ability to inflict injury on opponents, body size has been identified as probably the most important factor influencing contest outcome (Archer 1987; Riechert 1998; Arnott & Elwood 2009). However, in certain situations the experience of winning or losing a fight can either increase or decrease the probability of success in subsequent encounters, a phenomenon referred to as the winner–loser effect (Hsu & Wolf 1999). Although the precise mechanism by which the winner–loser effect operates remains open to debate, one area in which its importance has been illustrated is in regulating the stability of dominance hierarchies (Dugatkin 1997; Beacham 2003; Dugatkin & Earley 2004), an issue of considerable importance in many studies of animal behaviour (e.g. Drews 1993; de Vries & Appleby 2000; Gammell et al. 2003; Bang et al. 2010).

Studies of the relationship between the winner–loser effect and its effect on the development of dominance hierarchies have focused primarily on dyadic interactions (e.g. Dugatkin & Earley 2004). However, a class of models have been developed that specify the circumstances under which triadic interactions, third-party interventions, might be important for understanding this effect (e.g. Dugatkin 1998a, b). During a triadic interaction, an ongoing contest between two group members is interrupted before it reaches a conclusion by the physical intervention of a third group member. These simple models differ substantially from other, more Machiavellian approaches that describe intervention behaviour in terms of specific knowledge concerning the social relations that exist between group members (e.g. Seyfarth & Cheney 1984; Engh et al. 2005; Smith et al. 2010). Rather than appeal to social intelligence as a driver of intervention behaviour, these winner–loser

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effect models reason that when low-ranking individuals achieve a victory they also experience a winner effect, and consequently become a threat to individuals of higher rank (Dugatkin 1998a, b). The knock-on effect of such a rise in dominance status potentially includes displacement to lower rank on one level and a greater concentration of pressure for ownership of limited and/or non-divisible resources such as territories and mates on another. In this sense, these models are theoretically analogous to more general models of contest behaviour in which strategic decisions serve to maximize access to scarce resources (see Mesterton-Gibbons & Sherrat 2007; Arnott & Elwood 2009; Briffa & Elwood 2009).

Despite being commonly reported in vertebrate species, the role of the winner and loser effect in driving intervention behaviour is largely unknown. However, a study conducted on fallow deer, *Dama dama*, has shown some support for a winner effect in regulating intervention behaviour (Jennings et al. 2009). These findings were interpreted as showing support for a model in which intervention behaviour is random with regard to target selection and acts simply to prevent either contestant from achieving a winner effect (Dugatkin 1998a). Nevertheless, these results could be compatible with a second model of intervention behaviour that argues that intervention serves to ensure that a loser effect is imposed on an opponent; critically this latter model assumes that selection of the target is not random (specific target model: Dugatkin 1998b). This assumption is based on the reasoning that the benefits that accrue to a weaker opponent should it win will be substantially greater than those that accrue to a stronger opponent should it win. As noted above, individuals that are bigger or possess larger weapons have been shown to be more likely to defeat smaller opponents (see Table 1 in Arnott & Elwood 2009); therefore, under this model interveners should selectively target the opponent with the lower resource-holding potential (RHP: Parker 1974; see also Johnstone & Dugatkin 2000).

In the present study, we addressed predictions derived from the random and specific target models by comparing individual investment in fighting and RHP in relation to how frequently fallow deer males were targeted by a third-party male during fights. Under the specific target model interveners were expected to target individuals with low RHP, as it is assumed they will gain disproportionately relative to a larger rival should they be victorious (Dugatkin 1998b). Individuals that have lower RHP correlates relative to their competitor, therefore, should receive higher levels of targeting than individuals with higher body weight or neck girth (Table 1). The random target model makes no such assumption. We sought to test the generality of the specific target model with respect to individual investment in fighting. Theoretical models and empirical studies of contest behaviour suggest that individuals with low RHP are less able to invest in fighting (e.g. Enquist & Leimar 1983; Mesterton-Gibbons et al. 1996; reviewed in Arnott & Elwood 2009). Therefore, in line with predictions concerning individual RHP, we predicted that individuals that received high levels of targeting should also invest less in fighting. Because both models share the broad assumption that intervention prevents opponents from advancing up the hierarchy, we expected that targeted individuals would experience no increase in rank. Furthermore, because the intervener is considered to be acting to protect its dominance rank and since most interventions occur during the breeding season, we also investigated whether intervention behaviour influences mating success.

Table 1
Factors predicted to affect targeting of individuals following third-party intervention under the random and specific target models

Model	RHP	Contest behaviour		Dominance rank
		Costly actions*	Dominance related	
Random target	Not considered	No	Yes	Prevent increase
Specific target	Target low RHP	Yes	Yes	Prevent increase

* Costly actions are defined as those behavioural actions used during escalated contests that result in a decline in body condition, e.g. jump clashing and vocalizations (see Jennings et al. 2010).

METHODS

Study Site and Population

We recorded the behaviour of a herd of free-ranging European fallow deer at Phoenix Park, Dublin, Ireland, over two consecutive rutting seasons. Fawns are tagged in each ear with unique colour/numbered tags shortly after birth during June and July each year. Identification of mature males in the population is facilitated by a combination of coat colour, antler conformation and identity tag. Over both years of the study there were a similar number of females (1996: $N = 394$; 1997: $N = 349$) and of immature males (ages 1–3 years: 1996: $N = 100$ males; 1997: $N = 126$ males) in the population. In 1996 and 1997 there were 72 mature males (4 years or older) and 62 males, respectively, included in the present study; further details are provided below.

Data Collection

From late August to the end of October we monitored and recorded mature males' agonistic interactions using an all-event sampling protocol. Rutting male fallow deer interact aggressively with multiple rivals as either the initiator or receiver of aggression (Jennings et al. 2006). Therefore, individual males can potentially take on any of several different roles with regard to intervention behaviour over the course of the rut: intervener, target or nontarget. Therefore, we calculated the number of fights each individual male had overall, how many it intervened in, how many fights it was in that suffered an intervention and correspondingly how many times it was a target following intervention. This yielded two variables of interest concerning intervention behaviour: the number of fights in which each mature male intervened and the number of times these males were targeted following intervention. Matings were recorded in the herd during the annual rut, which falls between the middle and end of October in each year (Moore et al. 1995); when a mating sequence was recorded we also noted the identity of the male and the female, the time and location. For the purpose of the present study, mating success was defined as the number of matings each male was recorded as achieving in a particular year.

Fights involving males were recorded opportunistically on videotape over two successive breeding seasons and analysed using the Observer version 3.0 (Noldus Information Technology, Wageningen, The Netherlands). Three measures of fighting behaviour were analysed in relation to intervention behaviour: number of backward pushes, jump clashes and groan rate. Following the description of Alvarez (1993), backward pushes involved one male forcing his opponent backwards while their antlers were locked during a bout of fighting; jump clashes involved one male initiating antler contact with his opponent by jumping towards his opponent while rapidly lowering his antlers; groaning is a stereotyped atonal vocalization of males during the rut. Jump clashing and groan rate are related to a decline in RHP-related phenotypic characters (body weight and neck girth: Jennings et al. 2010) and, therefore, are directly relevant to the first prediction as it relates to investment in fighting and targeting. If the specific target model were supported, we expected a negative relationship between the rate of jump clashing and/or groan rate and being targeted following