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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 two 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.

Key words:

Bayesian model, dominance, fallow deer, fighting rate, mating success, third-party intervention.

Introduction

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, 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 emphasise 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 who previously, e.g. Gavrilets, Duenez-Guzman & Vose, 2008). Alternative accounts hold that individuals might simply disrupt dyadic fights in order 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). Nevertheless, 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.

Nonetheless, 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 Jennings et al., 2011; Gilby et al., 2013). 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 (e.g. de Waal, 1982; 1984), whereas in macaques 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 is 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. Nonetheless, theory is generally silent on the matter; therefore, one possibility investigated here is 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 ten percent of fights are disrupted by the intervention of third-party males (Jennings et al., 2009). To date, studies have focussed 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), i.e. those most likely to mate, that are most likely to disrupt each other's fights. The question we ask 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 oestrus 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; de Waal, 1984; Silk, 1993). 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 hectares; the majority 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 July) with a uniquely coloured and numbered ear tags. Approximately 95% of mature males (4 years or above) retained possession of their ear tags, and we used these in combination with coat colour and differences in antler shape and size to identify individuals. There were 79 individually identifiable males included in this study: 65 males in 1996 and 62 males in 1997, with 48 males present in both years, and 31 present in only one year of the study. We excluded males from the analysis because they joined the rut late, thus, had no ranking for some days, or they died prior to or during the rut.

Observation protocols: The deer in this population form sexually segregated herds occupying distinct home ranges for much of the year (Moore et al., 1995). Between August and September, whilst males still resided in a cohesive single-sex group (bachelor herd), they were monitored daily (between 9am-5pm) Monday to Friday by two to three observers. During late September, the bachelor herd gradually disperses to the female range and males increasingly exhibit typical rutting behaviour (e.g. fighting, vocalising, scent marking), and show a heightened interest in females (e.g. herding, sniffing, Chapman & Chapman, 1975). At the beginning of October, the number of observers and the observation schedule increased such that approximately 10 observers were in the field between dawn and dusk seven days per week.

Data Analysis. Daily variation in mating success was investigated in relation to three different regressors (see below for details) between the 14th – 31st of October when the majority of matings occur (Moore et al., 1995). We recorded the outcomes of aggressive interactions and the identities of the protagonists using all-event sampling (Altmann, 1974). Dyadic aggression was divided into two categories: (i) non-contact interactions where one male approached and displaced his opponent without making physical contact and (ii) fights.

The first regressor, the number of interventions suffered per day, represented the variable of interest in the present study (N = 600, Mean = 0.26, SD = 0.6 per male/day, Jennings et al., 2017). The second regressor was the number of dyadic fights each mature male engaged in that ended without suffering an intervention (N = 3548, Mean = 1.55, SD = 2.3 per male/day). The third regressor used the Elo-rating method (Elo, 1978) to investigate daily variation in dominance rank (see supplementary file for raw data). The Elo-rating method was selected as it differs from other methods because it does not calculate the hierarchy based on a summary matrix at the end of a defined period of time (Briffa et al. 2013). Rather it updates the dominance rank of individual males based on contests as they occur meaning that the order in which contests occur may influence the rating each individual is awarded. We calculated an initial Elo-rating for each male based on the outcome of all decisively resolved non-contact interactions recorded from late August/early September to October 14th. Thereafter, we recalculated the Elo-rating using only non-contact interactions each day until October 31st in order to estimate how dominance rank varied for each individual (see Figure 1).

Insert figure 1 about here

The present study analysed data using information on a day-by-day basis during the rut permitting us to account for the effects of day and year as categorical variables in the models. In addition, three random effects were included: individual identity of the males, and two interaction terms: (i) identity * day and (ii) identity * year (Jennings et al., 2017), because individual males can differ in both their willingness to engage in fighting and competitive ability over the course of the rut (e.g. refer to Figure 1 to see variability in dominance).

Three models are presented here: the first examined the association between variation in suffering an intervention and mating success on that day (a proximate model), and the second on the delayed association between suffering an intervention and mating success the following day (a delayed model). In the case of the delayed model, the outcome variable (mating success), and the two other regressors (dominance rank and number of fights) were offset by one day relative to the regressor for suffering an intervention; thus, interventions suffered on the 14th were regressed against mating success on the 15th. Dominance rank and number of fights on the 15th were regressed against mating success on the 15th and so on. We included a third model to investigate if there was any cumulative effect of suffering an intervention: in this model the summed number of interventions suffered every two days was regressed against daily mating success. Thus, interventions suffered on the 14th/15th of October were summed and regressed against mating success on the 15th and so on. The other two regressors were held constant as in the proximate and delayed models; therefore, dominance rank and number of fights recorded on the 15th were regressed against mating success on the 15th.

The statistical model: We used Bayesian methods to evaluate our data as it provides a more straightforward approach to analysing complex (e.g. hierarchical) models with latent structures (Kruschke 2015). The posterior distribution generated by MCMC was sampled using the freely available JAGS software package (4.2, Plummer, 2003) controlled within the RunJags package (2.0.4-

2, Denwood, 2015) in R (3.3.3). Following the analytic approach in Jennings et al. (2017), we investigated the association between suffering third-party intervention and variation in mating success using a hierarchical ‘hurdle’ model. The model consisted of two levels: the lower level (the hurdle) used a logistic regression to investigate the effects of each regressor based on whether a male achieved a mating or not. The upper level was a truncated Poisson regression (because inclusion at this level was conditional on a mating being achieved), that addressed the effects of the regressors with respect to the number of mating achieved (see supplementary files for model code).

The model was run over three parallel chains that employed dispersed initial values. We employed an adaptive phase of 11,000 iterations (including burnin), following which a posterior phase of 0.5 million iterations was sampled. The posterior was thinned by taking every 1000th iterate to reduce autocorrelation, and convergence was assessed using the Gelman-Rubin statistic (Gelman & Rubin, 1992) – a convergence level of <1.1 for each model parameter indicated that the adaptive phase of the model was sufficient (Kruschke 2015). We used independent weakly informative normal priors for the regression coefficients, and a half-t prior for the random effect variances to reduce the influence on the posterior distribution (Gelman, Jakulin, Grazia-Pittau & Su, 2008). Inferences concerning each model regressor were made based on the posterior mean and 95% credible confidence intervals. For the purpose of interpreting whether a regressor was meaningful, we inspected the central 95% posterior confidence intervals of each regressor and we considered there to be a meaningful effect of a regressor if less than 5% of the posterior distribution of the coefficients crossed zero (Allen, Street & Capellini, 2017; Capellini, Baker, Allen, Street & Venditti, 2015). Where the posterior mean of the regressor coefficient was low (i.e. less than 0.02), we considered there to be no meaningful biological effect (Bridger, Bonner & Briffa 2015).

Results

Inspection of the mean number of interventions suffered by individual males indicated that there was considerable variation across individuals (Figure 2): the total number of interventions ranged between 0-20 per male (Mean = 4.7, SE +/-: 0.36). There was daily variation in the number of interventions suffered over the course of the rut (Figure 3): there was a mean of 0.3 (SE +/-: 0.01) interventions suffered, with a range of between zero and six interventions recorded per male per day.

Insert figures 2 and 3 about here

The logistic model

We examined the correlations in the posterior distributions of the three regressor coefficients in the models. In general, these were weakly correlated with the strongest positive correlation between the coefficients of daily variation in dominance and number of fights in the three models: the proximate model ($r = 0.58$), the delayed model ($r = 0.35$) and the cumulative model ($r = 0.52$).

Inspection of the posterior distribution relating to the three models indicated that variation in dominance and number of fights were both positively associated with whether or not a male would achieve a mating (see Figure 4, the intercepts were excluded from the figure because the credible intervals were very wide: Proximate model: mean -35.78% CI = -45.6, -26.2; Delayed model: mean = -36.1, 95% CI = -46.2, -26.8; Cumulative model: mean = -37.4, 95% CI = -48, -28.1). However, since these models regressed essentially the same rank and daily fight rate data onto daily mating success this result is unsurprising. The association of interest here is the fate of the regressor relating to the number of interventions suffered: in all three models, there was no evidence of a direct association with variation in mating success. An examination of the percentage of the

posterior chains indicated that 23%, 80% and 73% of the proximate, delayed and cumulative models were negative. Reference to the interaction terms indicated that there was a negative interaction between variation in interventions suffered and daily fight rate in the proximate model (99% of the thinned posterior was negative) but no meaningful association in the delayed or cumulative models (45% and 93% of the thinned posterior chains were negative). No other meaningful interactions were observed. As expected in a population with a high skew in reproductive success the random effects component of the model showed a meaningful effect of individual and meaningful interactions between individual and year/day.

Insert figure 4 about here

In order to investigate the interaction between fighting and suffering an intervention in the proximate model we estimated, from the raw data, the proportion of matings achieved in relation to these two variables. We grouped the number of fights into three categories: no fights that day, 1-4 fights as this encompassed the average daily fight rate of males (2.3 fights per male per day), and five or more fights per day. As might be expected, the proportion of matings increased as males increased the number of fights per day they engaged in (Figure 5). Our data show that the proportion of matings was highest (47%) when males engaged in five or more fights per day, and no interventions were suffered. Where a single intervention was suffered and males engaged in five or more fights, the proportion of matings decreased to 40%. This decrease in mating success was more pronounced if two or more interventions were suffered; the proportion of matings was some 31% lower (0.16, Figure 5) relative to when no intervention was suffered.

Insert figure 5 about here

The Poisson model

Inspection of the correlations of the posterior distributions of the three coefficients indicated weak or negative relationships. For the proximate model the correlation between interventions suffered and dominance was weak ($r = 0.23$); for the delayed model and cumulative models, the relationship between dominance rank and fighting was weak ($r = -0.31$ and -0.21 respectively). The upper level of the model showed that dominance rank was meaningfully associated with daily variation in mating success (see Figure 6, the intercepts were excluded from the figure because the credible intervals were very wide: Proximate model: mean -0.2 , 95% CI = $-4.5, 4.8$; Delayed model: mean = -0.2 , 95% CI = $-5.8, 4.6$; Cumulative model: mean = -0.4 , 95% CI = $-5.3, 4.8$). With respect to the objectives of this study, however, the coefficient for variation in interventions suffered showed no meaningful main or interaction effects. The effect of individual identity and the interaction between identity and year/day was limited due to the low mating success of many individual males achieved during the rut.

Insert figure 6 about here

Discussion

The present study investigates a variation on a question posed by Bissonnette et al. (2015): what are the potential fitness consequences of not participating (in coalitions)? Although fallow deer do not form coalitions, we note that coalitionary models are often underpinned by data derived from third-party behaviour. Therefore, we examined the fitness consequences of suffering from third party interventions. Thus, for the first time as far as we are aware, this study addresses the consequences of being an unwilling (or unwitting) recipient of a third-party interaction. The lower logistic level of our model showed that both dominance rank and fight rate were positively associated with whether or not a male would achieve a mating on any given day. At the upper level of the model, only variation in dominance rank was positively associated with mating success over the three statistical models. We chose dominance rank and fight rate because their relationship with mating success has been established in this population (e.g. Jennings et al., 2006; Moore et al., 1995), other ungulate populations (e.g. Clutton-Brock et al., 1979; Hogg & Forbes, 1997; Wolf, 1998), and other species (e.g. Dewsbury, 1982; Ellis 1995; Colishaw & Dunbar, 1991). Nevertheless, although they are not in themselves of concern here, they are theoretically relevant to the hypotheses examined. We wished to know whether the effects of suffering from interventions interacted with dominance rank or fighting, and whether any effects of suffering an intervention were immediate or delayed.

Studies that have addressed the effects of intervention behaviour have generally examined time-periods ranging between months and years (e.g. de Waal, 1984; Silk, 1993); however, these long time-periods are less appropriate for this system. Intervention behaviour in this population occurs mainly during the relatively short duration of the annual rut where the oestrus female acts as a highly contestable resource that varies in abundance over days. Moreover, it is during this restricted time-period that the vast majority of fighting occurs (Jennings et al., 2009; Moore et al., 1995). Therefore, we concentrated our investigation to a more temporally proximate scale (i.e. variation on a day-by-day basis, Jennings et al., 2017). The analytic approach adopted here

permitted us to investigate the relationship between suffering from intervention and mating success on two levels: a logistic model addressed whether individuals achieved a mating or not while the Poisson model addressed whether suffering intervention was associated with how many matings a male achieved.

From an inspection of the lower level of the model, it is evident that the effect of suffering an intervention differ between the three models as a function of the temporal relationship with mating success. There are immediate consequences at the lower level of the model for mating success as represented by the negative interaction between suffering an intervention and fight rate. Both the delayed and cumulative models showed no meaningful association, as either a main effect or interaction, indicating that the effects of suffering an intervention are temporally limited. It has been shown that estimates of the probability of mating are associated with age, dominance rank, fight rate, time of arrival at mating sites, ability to hold and defend a territory, body and antler size (e.g. Ciuti & Apollonio 2016; Ciuti, de Cena, Bongi & Apollonio, 2011; Jennings et al., 2006, 2011; Moore et al., 1995). The present study adds to this body of work. However, although we show that suffering from intervention behaviour affects the likelihood of mating, in common with many studies, our analytic approach failed to shed any light on the number of matings achieved by individual males. It may be that focussing solely on components of male aggression is too limited an approach and that further investigation of this issue may benefit by the inclusion of factors relating to female choice (e.g. Bro-Jørgensen, 2002).

Third-party behaviour can involve subordinate individuals acting as interveners, although the most commonly observed form of intervention tends to involve high-ranking individuals acting against subordinates (Bissonnette et al., 2015; Smith et al., 2010). Correspondingly, in the fallow deer it is high-ranking males that engage in third-party intervention behaviour against lower ranked individuals (Jennings et al., 2009), and experience a limited increase in dominance rank (Jennings et al., 2011). Critically, we failed to show the anticipated interaction between suffering from intervention behaviour and dominance. We note that in the particular case of rank changing

coalitions, numerous interactions are required before a rank change may occur (van Schaik et al. 2006). Moreover, although individuals that engage in interventions in this population show increase in rank, there is little evidence that interveners are targeting specific individuals (Jennings et al., 2009, 2011). Therefore, it is possible that suffering from interventions do not occur at a sufficiently high level to interact with rank in this population.

As noted above, the proximate model showed an interaction between suffering an intervention and fight rate at the lower level of the model. Previously we have shown that there are small margins associated with both a winner effect, and increased mating success in relation to intervention behaviour (Jennings et al., 2009). The effects of disruption of an ongoing fight on the combatants are unknown in terms of a loser effect (Hsu & Wolf, 1999); however, the interaction we observed might be explicable by appealing to the effects of previous experience. For example, the effect of prior experience on contest behaviour determines whether the individual will subsequently initiate a contest (e.g. Franck & Ribowski, 1987; Schuett 1997, Hsu & Wolf, 2001; McDonald, Heimstra & Damkot, 1968). Although these studies relate to the effects of losing a contest, they are relevant in a general sense because suffering an intervention prevents an individual from winning as discussed by Dugatkin (1998), whilst incurring at least some of the costs associated with fighting (Briffa & Sneddon, 2007). In line with such thinking, we have shown elsewhere that there is an increased probability of subsequent fights ending without victory, if the preceding fight is drawn (Jennings, Gammell, Carlin & Hayden, 2004). Given that access to resources is often determined by the ability to successfully compete for that resource (Arnott & Elwood, 2009; Parker, 1974), suffering an intervention may have a loser-like effect on the competitive ability of the recipient. It would be of theoretical and empirical interest to investigate this question in more detail.

The question as to whether third-party behaviour impacts on subsequent fitness has rarely been addressed (but see Gilby et al. 2013 for an investigation over seasons). As noted above, we have shown that suffering an intervention (as an interaction with fighting) is negatively associated with mating success. A central aspect of our findings is that this relationship is temporally

short-lived. Given the unpredictable distribution in the number of oestrus females per day over the course of the rut (e.g. Apollonio et al. 1992), our results emphasise the complex interplay between different forms of competition and fitness over time. Whereas, previous studies have highlighted this complexity (e.g. Gilby et al., 2013), the present study underlines how short-term variation in competitive dynamics interact to affect fitness.

In conclusion, the present study represents an attempt to understand a neglected aspect of intervention behaviour: how does suffering from interventions affect fitness? We anticipated that suffering from third-party interventions might interact with dominance rank to reduce the probability of achieving a mating; however, this was not the case. Rather, this study presents two key findings: (i) that suffering third-party intervention interacts with fighting to reduce the probability of mating, and (ii) that this effect is temporally limited to the day on which the intervention(s) occur. We suggest that there is a compelling need for further study into the effects of suffering an intervention, and that studies of this type will provide a more complete understanding of the evolution of third-party intervention behaviour.

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