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Suffering intervention and mating success in fallow deer

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

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Suffering intervention and mating success in fallow deer

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

33

34 Key words:

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

36

37 **Introduction**

38 The study of animal contest behaviour in relation to outcome and fight dynamics has tended to
39 focus on the importance of resource value and fighting ability (resource holding potential, RHP:
40 Parker, 1974). Such considerations have led to the development of a number of influential models
41 that focus on the decision processes used by combatants during fights (e.g. Payne, 1998; Taylor &
42 Elwood, 2003). A key aspect of these models is that they specifically address aggression at the dyadic
43 level. However, there is accumulating evidence that contest behaviour can involve more complex
44 forms of aggressive interaction. Specifically, a number of studies conducted on (semi-) captive (e.g.
45 African wild dog, *Lycaon pictus*: de Villiers, 2003; raven, *Corvus corax*: Fraser & Bugnyar, 2012;
46 gelada, *Theropithecus gelada*: Pallante, Stanyon & Palagi, 2016; Grant and Chapman zebra, *Equus*
47 *quagga boehmi* and *E. q. antiquorum*: Schilder, 1990), and field populations (e.g. fallow deer, *Dama*
48 *dama*: Jennings, Carlin, & Gammell, 2009; baboon, *Papio cynocephalus*: Silk, Alberts & Altmann,
49 2004; rhesus macaque, *Macaca mulatta*: Widdig et al., 2006), have shown that third-party
50 individuals frequently intervene and disrupt ongoing contests.

51 Theoretical explanations underpinning the study of intervention behaviour have been
52 largely driven by the extensive body of work conducted on primate species (Bissonnette et al., 2015;
53 Smith et al., 2010). Such accounts typically emphasise that intervention behaviour serves to
54 underpin the formation of coalitions; thus, individuals are expected to be able to track shifting
55 dominance relationships (e.g. Chapais, 1995) or to remember past relationships (i.e. who helped
56 who previously, e.g. Gavrilets, Duenez-Guzman & Vose, 2008). Alternative accounts hold that
57 individuals might simply disrupt dyadic fights in order to prevent successful rivals from advancing in
58 the hierarchy via a winner effect (Dugatkin, 1998). Therefore, rather than coalition formation,
59 intervention acts to maintain the social status quo by insulating high-ranking individuals from
60 challenges by lower ranking adversaries (Jennings et al., 2009). Nevertheless, regardless of whether
61 one appeals to a coalitionary or noncoalitionary account of third-party behaviour, the majority of

62 these theories tend to argue that interventions serve to improve fitness by helping the intervener
63 secure access to valuable resources.

64 Nonetheless, determining whether intervention confers fitness benefits has proven to be
65 difficult. For example, benefits might accrue directly (e.g. an increase in rank: Jennings, Carlin,
66 Hayden & Gammell, 2011), or indirectly (e.g. kin support: Engh, Siebert, Greenberg & Holekamp,
67 2005). However, despite numerous studies the relationship between reproductive opportunities and
68 triadic behaviour is not clear-cut. Consequently, few studies have shown that third-party
69 intervention behaviour benefits individuals with respect to mating success (but see Jennings et al.,
70 2011; Gilby et al., 2013). One possibility is that the lack of evidence supporting such a relationship
71 might be due to the temporal relationship between intervention behaviour and the fitness outcome
72 (Harcourt & de Waal, 1992). From a coalitionary perspective for example, it is possible that the
73 degree of (in)stability in the nascent relationship between individuals introduces a temporal lag
74 between intervention acts, and the accrual of any actual benefits. Although we are not aware of any
75 studies that focus specifically on the temporal relationships between intervention behaviour and
76 mating success, coalitionary behaviour (which includes third-party behaviour) tends to peak just
77 prior to the most likely day of conception in the baboon (Bercovitch, 1988). In terms of improvement
78 in rank the evidence is somewhat mixed; for example, temporal lag appeared to be minimal with
79 respect to male rank advancement in chimpanzees (e.g. de Waal, 1982; 1984), whereas in macaques
80 there was little evidence that intervention was associated with an increase in rank over time (e.g.
81 Silk, 1993). Given that there has been relatively little investigation of this question, one objective of
82 this study is to gain a more comprehensive understanding of the temporal association between
83 intervention behaviour and mating success.

84 While a general finding shows that dominance rank is positively associated with mating
85 success in many species (Dewsbury, 1982; Ellis, 1995), the evidence that the relationship between
86 third-party behaviour and fitness is influenced by dominance rank is more limited (e.g. de Waal
87 1984), albeit theoretically expected (e.g. Chapais, 1995; Dugatkin, 1998; van Schaik, Pandit, & Vogel,

88 2006). Whether the same relationships hold for recipients of third-party intervention behaviour has
89 received little attention. While it has been reported that the costs to individuals of suffering an
90 intervention can be severe in terms of consortship with females (e.g. Noë, 1992), we are unaware of
91 any detailed studies that have investigated the relationship between suffering third-party
92 intervention, dominance and fitness. We might speculate that depending on the way in which
93 dominance interacts with intervention behaviour, a negative (lower ranks depose higher ranks -
94 revolutionary) or positive (higher ranks defeat lower ranks - conservative) interaction between
95 suffering an intervention and dominance should hold in relation to fitness. Nonetheless, theory is
96 generally silent on the matter; therefore, one possibility investigated here is whether suffering
97 intervention is associated with fitness via an interaction with dominance rank.

98 However, if we ignore the bulk of theoretical and empirical work on third-party behaviour,
99 perhaps the most parsimonious explanation is that irrespective of rank, a direct negative impact of
100 suffering intervention on mating success is expected. Specifically, the intervener behaves
101 opportunistically in disrupting ongoing fights (Jennings et al., 2009, 2011); therefore, rather than
102 interacting with dominance, suffering an intervention should be directly associated with reduced
103 mating success. An alternative possibility is that intervention behaviour forms part of the general
104 aggressive repertoire of males as they compete for mating opportunities (Jennings, Boys, &
105 Gammell, 2017). Therefore, suffering from intervention might well interact with other aspects of
106 competitive behaviour such as fighting (see de Waal & Harcourt, 1992 for a discussion of facial and
107 vocal signals aligned with triadic behaviour); therefore, in relation to fitness, an interaction between
108 fighting and suffering from intervention might be expected.

109 Male fallow deer display a heightened tendency to fight with conspecifics during the
110 annual rutting season (e.g. Apollonio, Festa-Bianchet, Mari, Mattioli & Sarno, 1992; Clutton-Brock,
111 Green, Hiraiwa-Hasegawa & Albon, 1988; Moore, Kelly, Cahill & Hayden, 1995), and approximately
112 ten percent of fights are disrupted by the intervention of third-party males (Jennings et al., 2009). To
113 date, studies have focussed almost exclusively on intervention behaviour in relation to the

114 intervener rather than the recipient of the intervention; these have shown that intervention is
115 associated with increased mating success (Jennings et al., 2011), and is most likely to be committed
116 by high-ranking males (Jennings et al., 2009). Furthermore, the tendency for individuals to engage in
117 interventions varies based on aggression experienced, rather than resource access. Therefore, the
118 number of different opponents fought, and whether the individual itself suffered from fight
119 interventions on a given day, rather than the number of mating opportunities available are
120 important correlates of intervention behaviour (Jennings et al., 2017). Taken together, these findings
121 indicate that it is males at the upper end of the hierarchy (Jennings, Gammell, Carlin, & Hayden,
122 2006), i.e. those most likely to mate, that are most likely to disrupt each other's fights. The question
123 we ask here is why, and to what end? Given the lack of empirical studies on this question, and in the
124 absence of theoretical direction, we sought to investigate a number of possibilities in relation to the
125 impact of suffering third-party behaviour on fitness.

126 We sought to determine whether there was evidence for any detrimental effect of
127 suffering an intervention on mating success by examining whether any association between
128 suffering intervention and mating success was direct or via an interaction with dominance and
129 fighting - two variables that correlate with mating success (Clutton-Brock, Albon, Gibson & Guinness,
130 1979; Moore et al., 1995). Given that numbers of oestrus females represent a variable resource over
131 the course of the rut, we also investigated the temporal relationship between variation in suffering
132 from intervention and any potential fitness gain (e.g. Bercovitch, 1988; de Waal, 1984; Silk, 1993).
133 Therefore, we investigated whether any association between suffering an intervention and mating
134 success was temporally proximate (evident on the same day) or delayed (evident on the following
135 day).

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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.

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

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

181

182 **Insert figure 1 about here**

183

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

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

204

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

209 2, Denwood, 2015) in R (3.3.3). Following the analytic approach in Jennings et al. (2017), we
210 investigated the association between suffering third-party intervention and variation in mating
211 success using a hierarchical ‘hurdle’ model. The model consisted of two levels: the lower level (the
212 hurdle) used a logistic regression to investigate the effects of each regressor based on whether a
213 male achieved a mating or not. The upper level was a truncated Poisson regression (because
214 inclusion at this level was conditional on a mating being achieved), that addressed the effects of the
215 regressors with respect to the number of mating achieved (see supplementary files for model code).

216 The model was run over three parallel chains that employed dispersed initial values. We
217 employed an adaptive phase of 11,000 iterations (including burnin), following which a posterior
218 phase of 0.5 million iterations was sampled. The posterior was thinned by taking every 1000th iterate
219 to reduce autocorrelation, and convergence was assessed using the Gelman-Rubin statistic (Gelman
220 & Rubin, 1992) – a convergence level of <1.1 for each model parameter indicated that the adaptive
221 phase of the model was sufficient (Kruschke 2015). We used independent weakly informative
222 normal priors for the regression coefficients, and a half-t prior for the random effect variances to
223 reduce the influence on the posterior distribution (Gelman, Jakulin, Grazia-Pittau & Su, 2008).
224 Inferences concerning each model regressor were made based on the posterior mean and 95%
225 credible confidence intervals. For the purpose of interpreting whether a regressor was meaningful,
226 we inspected the central 95% posterior confidence intervals of each regressor and we considered
227 there to be a meaningful effect of a regressor if less than 5% of the posterior distribution of the
228 coefficients crossed zero (Allen, Street & Capellini, 2017; Capellini, Baker, Allen, Street & Venditti,
229 2015) . Where the posterior mean of the regressor coefficient was low (i.e. less than 0.02), we
230 considered there to be no meaningful biological effect (Bridger, Bonner & Briffa 2015).

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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.

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241

Insert figures 2 and 3 about here

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243

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

257 posterior chains indicated that 23%, 80% and 73% of the proximate, delayed and cumulative models
258 were negative. Reference to the interaction terms indicated that there was a negative interaction
259 between variation in interventions suffered and daily fight rate in the proximate model (99% of the
260 thinned posterior was negative) but no meaningful association in the delayed or cumulative models
261 (45% and 93% of the thinned posterior chains were negative). No other meaningful interactions
262 were observed. As expected in a population with a high skew in reproductive success the random
263 effects component of the model showed a meaningful effect of individual and meaningful
264 interactions between individual and year/day.

265

266 **Insert figure 4 about here**

267

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

279

280 **Insert figure 5 about here**

281

282 **The Poisson model**

283 Inspection of the correlations of the posterior distributions of the three coefficients indicated weak
284 or negative relationships. For the proximate model the correlation between interventions suffered
285 and dominance was weak ($r = 0.23$); for the delayed model and cumulative models, the relationship
286 between dominance rank and fighting was weak ($r = -0.31$ and -0.21 respectively). The upper level of
287 the model showed that dominance rank was meaningfully associated with daily variation in mating
288 success (see Figure 6, the intercepts were excluded from the figure because the credible intervals
289 were very wide: Proximate model: mean -0.2 , 95% CI = $-4.5, 4.8$; Delayed model: mean = -0.2 , 95% CI
290 = $-5.8, 4.6$; Cumulative model: mean = -0.4 , 95% CI = $-5.3, 4.8$). With respect to the objectives of this
291 study, however, the coefficient for variation in interventions suffered showed no meaningful main or
292 interaction effects. The effect of individual identity and the interaction between identity and
293 year/day was limited due to the low mating success of many individual males achieved during the
294 rut.

295

296 **Insert figure 6 about here**

297

Discussion

298

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

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

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

327 From an inspection of the lower level of the model, it is evident that the effect of suffering
328 an intervention differ between the three models as a function of the temporal relationship with
329 mating success. There are immediate consequences at the lower level of the model for mating
330 success as represented by the negative interaction between suffering an intervention and fight rate.
331 Both the delayed and cumulative models showed no meaningful association, as either a main effect
332 or interaction, indicating that the effects of suffering an intervention are temporally limited. It has
333 been shown that estimates of the probability of mating are associated with age, dominance rank,
334 fight rate, time of arrival at mating sites, ability to hold and defend a territory, body and antler size
335 (e.g. Ciuti & Apollonio 2016; Ciuti, de Cena, Bongi & Apollonio, 2011; Jennings et al., 2006,
336 2011; Moore et al., 1995). The present study adds to this body of work. However, although we show
337 that suffering from intervention behaviour affects the likelihood of mating, in common with many
338 studies, our analytic approach failed to shed any light on the number of matings achieved by
339 individual males. It may be that focussing solely on components of male aggression is too limited an
340 approach and that further investigation of this issue may benefit by the inclusion of factors relating
341 to female choice (e.g. Bro-Jørgensen, 2002).

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

349 coalitions, numerous interactions are required before a rank change may occur (van Schaik et al.
350 2006). Moreover, although individuals that engage in interventions in this population show increase
351 in rank, there is little evidence that interveners are targeting specific individuals (Jennings et al.,
352 2009, 2011). Therefore, it is possible that suffering from interventions do not occur at a sufficiently
353 high level to interact with rank in this population.

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

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

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

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

389

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394

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539 Figure 1. The Elo-ratings achieved for each male on each day of the rut in both years of the study
540 (panel A shows data from 1996 and panel B shows data from 1997). Each line represents the rating
541 for one male.

542 Figure 2. The mean (95% CI) for the number of interventions suffered by individual males between
543 the 14th – 31st October in each year of the study (panel A shows data from 1996 and panel B shows
544 data from 1997). Each bar represents one male.

545 Figure 3. The mean (and 95% CI) for the number of interventions suffered between October 14th –
546 31st for each year of the study (panel A shows data from 1996 and panel B shows data from 1997).

547 Figure 4. Summary of the parameter posterior distributions showing the dependence between the
548 daily variation in mating success for individual males (0 = no mating, 1 = mating), and three
549 regressors (including two interaction terms) for the logistic model. The three models showing the
550 mean and 95% credible intervals for the proximate model (■), the delayed model (●), the
551 cumulative model (▲) are included. For each parameter the mean is denoted by the black shape and
552 the 95% credible intervals by the thin line.

553 Figure 5. The proportion of matings achieved in relation to the number of fights engaged in, and the
554 number of interventions suffered. Bars represent the 95% confidence intervals. Because the
555 numbers of interventions suffered and fights engaged in per day decrease substantially at high
556 values, we grouped the number of fights and number of interventions suffered in order to reduce
557 the effect of outliers.

558 Figure 6. Summary of the parameter posterior distributions showing the dependence between the
559 daily variation in mating success for individual males and three regressors (including two interaction
560 terms) for the Poisson model. The three models showing the mean and 95% credible intervals for
561 the proximate model (■), the delayed model (●), the cumulative model (▲) are included. For each
562 parameter the mean is denoted by the black shape and the 95% credible intervals by the thin line.