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

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2   **fallow deer**

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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).

136 **Methods**

137

138 **Study population:** Aggressive behaviour in a herd of free-ranging fallow deer resident in Phoenix

139 Park, Ireland ($53^022'N$, $6^021'W$) was recorded from late August/early September and throughout the

140 annual rut in the latter half of October during two successive years (1996/1997). The park encloses

141 709 hectares; the majority of the area of the park (80% approximately) is open grassland with the

142 remaining area consisting of mixed woodland. The management plan for the deer involves tagging

143 fawns shortly after birth (annually between June and July) with a uniquely coloured and numbered

144 ear tags. Approximately 95% of mature males (4 years or above) retained possession of their ear

145 tags, and we used these in combination with coat colour and differences in antler shape and size to

146 identify individuals. There were 79 individually identifiable males included in this study: 65 males in

147 1996 and 62 males in 1997, with 48 males present in both years, and 31 present in only one year of

148 the study. We excluded males from the analysis because they joined the rut late, thus, had no

149 ranking for some days, or they died prior to or during the rut.

150

151 **Observation protocols:** The deer in this population form sexually segregated herds occupying

152 distinct home ranges for much of the year (Moore et al., 1995). Between August and September,

153 whilst males still resided in a cohesive single-sex group (bachelor herd), they were monitored daily

154 (between 9am-5pm) Monday to Friday by two to three observers. During late September, the

155 bachelor herd gradually disperses to the female range and males increasingly exhibit typical rutting

156 behaviour (e.g. fighting, vocalising, scent marking), and show a heightened interest in females (e.g.

157 herding, sniffing, Chapman & Chapman, 1975). At the beginning of October, the number of

158 observers and the observation schedule increased such that approximately 10 observers were in the

159 field between dawn and dusk seven days per week.

160

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).

231   **Results**

232

233   Inspection of the mean number of interventions suffered by individual males indicated that there

234   was considerable variation across individuals (Figure 2): the total number of interventions ranged

235   between 0-20 per male (Mean = 4.7, SE +/-: 0.36). There was daily variation in the number of

236   interventions suffered over the course of the rut (Figure 3): there was a mean of 0.3 (SE +/-: 0.01)

237   interventions suffered, with a range of between zero and six interventions recorded per male per

238   day.

239

240
241   **Insert figures 2 and 3 about here**

242

243   **The logistic model**

244   We examined the correlations in the posterior distributions of the three regressor coefficients in the

245   models. In general, these were weakly correlated with the strongest positive correlation between

246   the coefficients of daily variation in dominance and number of fights in the three models: the

247   proximate model (r = 0.58), the delayed model (r = 0.35) and the cumulative model (r = 0.52).

248   Inspection of the posterior distribution relating to the three models indicated that

249   variation in dominance and number of fights were both positively associated with whether or not a

250   male would achieve a mating (see Figure 4, the intercepts were excluded from the figure because

251   the credible intervals were very wide: Proximate model: mean -35.78% CI = -45.6, -26.2; Delayed

252   model: mean = -36.1, 95% CI = -46.2, -26.8; Cumulative model: mean = -37.4, 95% CI = -48, -28.1).

253   However, since these models regressed essentially the same rank and daily fight rate data onto daily

254   mating success this result is unsurprising. The association of interest here is the fate of the regressor

255   relating to the number of interventions suffered: in all three models, there was no evidence of a

256   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.

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