



**QUEEN'S
UNIVERSITY
BELFAST**

Third-party assessment of contestants during fallow deer fights increases with resource abundance and dominance rank

Jennings, D., Amin, B., & Gammell, M. (2021). Third-party assessment of contestants during fallow deer fights increases with resource abundance and dominance rank. *Animal Behaviour*, 177, 81-89.
<https://doi.org/10.1016/j.anbehav.2021.04.020>

Published in:
Animal Behaviour

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

Copyright 2021 Elsevier.

This manuscript is distributed under a Creative Commons Attribution-NonCommercial-NoDerivs License (<https://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits distribution and reproduction for non-commercial purposes, provided the author and source are cited.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access

This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: <http://go.qub.ac.uk/oa-feedback>

1 **Third-party assessment of contestants during fallow deer fights increases with resource**
2 **abundance and dominance rank**

3
4
5 Dómhnall J. Jennings

6 School of Biological Sciences

7 Queen's University Belfast

8
9 Bawan Amin

10 School of Biology and Environmental Science

11 University College Dublin

12
13 Martin P. Gammell

14 School of Science

15 Galway-Mayo Institute of Technology

16
17
18
19
20 Correspondence: d.jennings@qub.ac.uk

21

Abstract

22

23

24 The decision to engage in escalated fighting involves an interplay between the individual's estimate
25 of the value of the resource under dispute, and the ability of the combatants to invest sufficient time
26 and energy in the contest. Although fallow deer (*Dama dama*) contests usually take place between
27 pairs of individuals, they are sometimes terminated by the intervention of dominant third-party
28 individuals. Theory argues that these interventions prevent subordinates from gaining a competitive
29 boost via a winner-effect; thus, interveners benefit by removing this threat to their status. Prior to
30 intervention, third-party individuals often approach and closely follow the competing dyad before
31 either abandoning their interest in the contest, or physically targeting one of the contestants. This
32 study investigates the possibility that third-party following is an assessment process whereby
33 individuals monitor the quality of fighting rivals during the annual rut. We tested three hypotheses:
34 (i) that third-party followers are socially dominant individuals, that (ii) follow contests in order to
35 assess the current quality of high-ranking rivals (iii) when resource abundance (i.e. the number of
36 oestrus females) is high. Our results show that socially dominant individuals are most likely to follow
37 contests; however, contrary to expectation, third-party males tended to follow dyads consisting of
38 low-ranking rivals. We also show that as resource abundance increased in the population there was
39 an increased tendency for males to follow contests, and a reduction in the probability of engaging in
40 a third-party intervention of the contest. As expected by theory, dominance and resource
41 abundance were important correlates of third-party following. Our results support the idea that
42 socially dominant males monitor subordinate males who possess sufficient resources to expend in
43 fighting, and who thus may be a threat to their status.

44

45 **Key words: Assessment, Fighting, Resource abundance, Resource holding potential, Third-party**
46 **individual**

Introduction

47

48 Escalated aggressive encounters such as fights are a consequence of individuals motivated by the
49 need to possess or control access to scarce and valuable resources. However, fighting is a time
50 consuming and energetically costly activity that can result in serious injury or death (Briffa &
51 Sneddon 2007, see also Wilkinson & Shank 1976; Drews 1996; Piper et al. 2008; Kapranas et al.
52 2020). Thus, theory expects both the value of a resource and the quality of the contestant to be
53 central to the decisions that individuals make in relation to who to direct aggression towards, how
54 much to invest in a contest, and the point at which investment is withdrawn (e.g. Parker 1974;
55 Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Kokko 2013). These theories fall in two
56 broad classes of model (Taylor & Elwood 2003): one class expects that contestants compete based
57 on their ability to invest in costly fighting, and without reference to the competitive quality of their
58 opponent (self-assessment models: Mesterton Gibbons et al. 1996; Payne 1998). The second class of
59 model anticipates that individuals estimate their opponents' quality (resource holding potential,
60 RHP: Parker 1974) by monitoring signals associated with competitive ability and determining
61 whether this is at a higher level than their own (opponent assessment models: Enquist & Leimar
62 1993; Enquist et al. 1990). Thus, the underlying decision processes proposed by these models differ
63 fundamentally dependent on whether contestants gather information about their opponent.

64 Although dyadic competition tends to be ubiquitous in nature, there are numerous studies
65 showing that third-party individuals often intrude during ongoing contests (see Smith et al. 2010 for
66 a review). The theoretical approaches that seek to explain this behaviour have tended to differ
67 markedly from theories developed to explain dyadic contests (see Bissonnette et al. 2015 for a
68 review). Models of triadic behaviour have tended to focus on the idea that third-party individuals
69 intervene in order to establish, or cement coalitions (and alliances) with particular individuals in the
70 group (Harcourt & de Waal 1992). Thus, an individual might intervene in a dyadic contest to support
71 an established coalitionary partner by attacking its opponent in order to help secure access to, or
72 retain, a resource. The division between individuals of any resources that are secured can be either
73 on an egalitarian basis (e.g. Gavrilets et al. 2008) or according to individual RHP (e.g. Pandit & van
74 Schaik 2003; Whitehead & Connor 2005; Stamatopoulos et al 2009). One key driver of coalition
75 development rests on the social status of the individuals concerned which can take different forms:
76 so called 'all-down' where the partners outrank their target, 'bridging' where one partner outranks
77 the target and one is subordinate, and 'all-up' where both partners are subordinate to the target
78 (Bissonnette et al. 2015). Under such a rank driven system, there is an assumption that coalitionary
79 behaviour must be cognitively complex; specifically, group members know the social status of all
80 other group members relative to each other, have the capacity to track shifts in dominance status,

81 and to estimate the impact of these shifts on social relationships within the group (e.g. Cheney &
82 Seyfarth 1990; Tomasello & Call 1997).

83 It is, nevertheless, possible to account for such apparently complex interactions by arguing
84 that individuals intervene to protect their rank position (Dugatkin 1998 a,b). Under this approach,
85 high-ranking individuals block rivals from becoming a threat to their status by either preventing
86 them attaining a winner effect or by imposing a loser effect, i.e. the enhanced probability that
87 winners keep winning and losers keep losing (Hsu et al. 2006). This focus on fitness enhancement as
88 a key driver of aggression is a common approach to dyadic and triadic models with both traditions
89 expecting higher incidences of aggression and third-party behaviour when a contestable resource is
90 available. However, key areas of divergence rest on how individuals gather information about the
91 quality of potential opponents. For dyadic models, only certain models assume that information
92 concerning opponent quality is acquired; critically, this is achieved through direct interaction
93 between the competitors. Conversely, some triadic models assume that individuals monitor group
94 members as they interact with each other, thereby, gathering information concerning the quality of
95 rivals or potential allies (e.g. Johnstone & Dugatkin 2000; Mesterton Gibbons & Sherrat 2007; Broom
96 et al. 2009). The tendency for bystanding individuals to attend to information with fitness
97 implications has been shown many times. For example, subordinate male deer reduce their vocal
98 rates when presented with play-back vocalizations that simulate a larger opponent nearby (Reby et
99 al. 2005). When bystanders are permitted to view a fight, they adjust their subsequent behaviour
100 towards the observed individuals on the basis of information gathered and whether the opportunity
101 to compete against the winner or loser was given (e.g. McGregor 1993; Earley & Dugatkin 2002; Hsu
102 et al. 2006). However, the behaviour of the bystander may also be determined by its social status;
103 for example, low ranking geese (*Anser anser*) show heightened heart rates when observing higher
104 ranked non-affiliated individuals interact (Wascher et al. 2008), and interest in contest losers is
105 limited to dominant bystanders in the zebrafish (*Danio rerio*, Abril-de-Abreu et al. 2015).

106 The European fallow deer breeds annually with the period of heightened sexual activity
107 between mid-to-late October in the northern hemisphere (Moore et al. 1995). During this period
108 and in the lead-up to the rut, males become highly intolerant of each other, and exhibit a number of
109 stereotypical rutting activities including wallowing in scrapes, scent marking, vocalizing and an
110 increase in aggression including fighting (e.g. Clutton-Brock et al. 1988; Festa-Bianchet et al. 1990;
111 Moore et al. 1995; Fricová et al. 2007). These contests are structurally complex interactions: they
112 usually occur between two individuals and involve lateral displays (Jennings et al. 2002, 2003;
113 Jennings 2012), vocalizations (Jennings et al. 2012), and a series of attacking and defensive actions
114 (Jennings et al. 2002, 2003, 2005a) which satisfy theoretical predictions corresponding to both self-

115 and mutual assessment processes (Payne 1998; Taylor & Elwood 2003). Thus, male fallow deer
116 adjust their contest behaviour based on an assessment of the resource, their ability to invest in
117 fighting and the quality of their opponent (Jennings et al. 2010; Jennings 2020). Although fights are
118 dyadic interactions, contests are frequently interrupted by the intervention of third-party males
119 (Jennings et al. 2009). These interventions are associated with an increase in rank in favour of the
120 intervener (Jennings et al. 2009, 2011) while also negatively impacting on the mating success of the
121 males in the competing dyad (Jennings et al. 2018).

122 Third-party behaviour is not, however, restricted to physical intervention against an ongoing
123 contest. During the course of dyadic fights, third-party males occasionally approach and follow a
124 competing dyad (hereafter *tp-follow(er/ing)*). This often has the effect that the contestants break off
125 physical contact, and proceed into a parallel walk followed by the third-party male. The *tp-following*
126 male can either intervene and potentially disrupt the ongoing contest by selectively targeting one of
127 the combatants or withdraw and take no further interest in the contest. We are not aware of any
128 study that has investigated *tp-following* in ungulates; however, because these males are attending to
129 a clearly identifiable dyadic contest, we suggest that it is a form of assessment process similar to
130 bystanding. The purpose of this study is to investigate this proposition and determine if *tp-followers*
131 gather information about rivals by testing predictions derived from models of dyadic and triadic
132 aggression. Therefore, we focus on the dominance status of the third-party male, the dominance
133 status of the males competing at the dyadic level, and the interaction with resource abundance (the
134 number of matings of oestrus females recorded each day) in relation to *tp-following*. Third-party
135 models argue that the dominance status of a third-party individual is central to the decision to
136 intervene in order to protect rank position (Dugatkin 1998 a,b; Bissonnette et al. 2015; Jennings et
137 al. 2009). Thus, we hypothesise that *tp-following*, as a form of triadic interaction, will be associated
138 with the rank of the third-party male; we predict that rank will be positively associated with *tp-*
139 *following*. In addition, theory assumes that competitors assess the competitive ability of rivals and
140 act on the basis of the information they acquire; specifically, that rivals approximating their own
141 quality will necessitate close visual scrutiny (e.g. Enquist & Leimar 1983; Enquist et al. 1990; Parker &
142 Rubenstein 1981). Thus, we test the hypothesis that *tp-following* facilitates this assessment process,
143 and test the prediction that contests containing high-ranking (i.e. high RHP) males will be more likely
144 to experience *tp-following* than contests containing low-ranking males. In addition, we examine the
145 effect of variation in the daily number of oestrus females in the population because contest theory
146 argues that resource abundance will also influence contest behaviour (Arnott & Elwood 2008). In
147 line with such thinking, it has been shown that males in this population increase their investment in
148 fighting as resource abundance increases (Jennings 2020). Thus, we expect that rivals should

149 increase their monitoring and assessment of potential rivals in line with the abundance of a high-
150 value resource such as the oestrus female; therefore, we predict that incidences of *tp*-following will
151 increase as resource abundance in the population increases.

152

Methods

153 **Study site and population:** This study was conducted on a population of European fallow deer
154 resident in Phoenix Park, Dublin (Ireland). The park encloses 707 hectares of mixed grass and
155 woodland with the majority of this area available to the deer. Under the management plan for the
156 herd, fawns are located and tagged with unique coloured and numbered tags when they are also
157 weighed, measured and sexed. Consequently, the identity of the majority of the deer in the park is
158 known with the identification of mature males also facilitated through a combination of coat colour,
159 and unique features of their antler conformation.

160

161 **Ethics statement:** The present study was observational in nature and at the time data were collected
162 no specific licensing was required by law. The study forms part of a long-term collaboration between
163 University College Dublin and the relevant Irish authorities (Office of Public Works and locally via the
164 Superintendent of Phoenix Park) into the behaviour and ecology of the deer herd.

165 As a major large urban park located close to the centre of Dublin, the park is readily
166 accessible to members of the public for recreational purposes. Thus, as long as they are not directly
167 approached the deer tend to tolerate the presence of humans in their vicinity. Observations of the
168 deer were conducted by fieldworkers using telescopes situated at static distances of between 20-30
169 metres at the initiation of observation sessions although the deer could move closer to the
170 fieldworkers over the course of a session. In so far as we could determine, our presence did not
171 affect the behavior of the deer and there were no environmental implications of the research.

172

173 Data collection

174 Observation of the males took place between late August to the end of October over three
175 consecutive field seasons between 1995-1997. The annual rut in this population occurs during the
176 last two weeks of October and during this time period matings were recorded with their date and
177 time, the location and the identity of the male and female (Moore et al. 1995). Thus, we recorded
178 the daily number of oestrus females that were observed to mate as a measure of resource
179 abundance, and the daily mating success of each male (Jennings 2020).

180 All-event sampling was employed to record agonistic behaviour between males (Altmann,
181 1974), and interactions were categorised depending on whether physical contact was made. If males
182 displaced a conspecific without physical contact we categorized the interaction as non-contact,
183 however, if physical contact with the antlers occurred the interaction was classed as a fight (e.g.

184 Jennings et al. 2006). When an interaction occurred, we recorded the type of interaction, the
185 identity of the two contestants, the outcome and the location, date and time. In order to analyse *tp*-
186 following behaviour, we focused on temporally extended aggressive interactions (e.g. parallel walks,
187 and fights, N = 6,708 contests: 5,768 dyadic, 552 third-party intervention and 388 *tp*-follow only) as
188 these types of contest allowed us to determine whether third-party males were indeed engaged in
189 *tp*-following rather than simply being in proximity to the contest. If the contest was followed, we
190 recorded the identity of the *tp*-following male and also whether the interaction was subsequently
191 disrupted by a third-party male intervening in the contest by aggressively targeting one of the
192 original competitors (a third-party intervention: Jennings, Boys & Gammell 2017, 2018).

193 **Dominance ranking:** Based on the outcomes of all decisively resolved (i.e. a clear winner and loser)
194 non-contact dyadic interactions between males we calculated the rank of all males using the Elo-
195 rating method (Elo 1978). The approach adopted here was as follows: an initial Elo-rating was
196 estimated for each male from decisively resolved non-contact interactions recorded between late
197 August/early September to the 14th of October each year - about the time that the first mating was
198 observed in the herd. The Elo-rating was then re-calculated from the 14th for each subsequent day
199 until the end of October (Jennings et al. 2017, 2018), permitting us to assign a daily Elo-rating to
200 each male in the population. This provided a daily estimate of each males' competitive ability, which
201 we used to assign each male as either the dominant or subordinate contestant in each contest
202 (Jennings 2020). By assigning males a dominance position within contests in such a manner we could
203 investigate the decision whether or not engage in *tp*-following, or to *t-p* intervene in a contest was
204 based on the current rank of the contestants. In some instances (i.e. to test our first prediction), we
205 needed to use a single measure of dominance; where this was the case we took the average Elo-
206 rating score for October.

207 Both *tp*-following and interventions were associated with mean Elo-rating (*tp*-following: $z =$
208 14.15, $p < .001$; *t-p* intervention: $z = 12.38$, $p < .001$) and these two factors were also highly
209 associated ($z = 21.48$, $p < .0001$). To address the first prediction, i.e. that high-ranking males were
210 more likely to follow competing dyads in order to gather information about potential rivals, we
211 subtracted the number of times a male was observed engaging in contest intervention from the
212 number of occasions they engaged in *tp*-following (hereafter referred to as the 'intervention score').
213 Thus, a negative value indicates a greater tendency for intervention than *tp*-following (i.e. not to
214 gather information via *tp*-following) with a positive value showing a greater tendency for *tp*-
215 following (i.e. to gather information via *tp*-following).

216

217 Data analysis

218 All analyses reported here were conducted using R (version 3.3.3, R Foundation for Statistical
219 Computing) running R Studio (version 1.1.423). We examined the association between the number
220 of fights an individual engaged in and its mean Elo-rating using a generalized linear mixed model. In
221 order to investigate whether dominant males were more likely to engage in *tp-following* of contests,
222 the relationship between mean Elo-rating and **the intervention score** ($N_{tp-follow} - N_{intervention}$)
223 was determined using a linear mixed effects model in *nlme* (version 3.1-131, Pinheiro et al. 2020),
224 while the consistency for individual *tp-following* of contests was examined using *rptR* (version
225 0.9.22, Stoffel, Nakagawa & Schielzeth, 2019). We ran these models with year and male identity set
226 as crossed random effects fitted with either a Poisson or Gaussian distribution as appropriate.

227 In order to investigate whether the decision to *tp-follow* a competing dyad was related to
228 contestant dominance status and resource abundance, we ran two logistic regressions using a
229 Bayesian framework with the posterior distribution generated by MCMC and sampled using
230 *MCMCglmm* (version 2.25, Hadfield 2010). We employed a Bayesian approach to evaluate these
231 data as it provides a straightforward approach to analysing (complex) hierarchical models with latent
232 structures (Kruschke 2015). The first model set as the decision to *tp-follow* or not (*tp-follow*) a
233 contest as the dependent variable, the second model set the decision to *tp-follow* or the decision to
234 intervene in a contest as the dependent variable. The independent variables included the number of
235 matings recorded that day (resource abundance), the dominance rank of the dominant and
236 subordinate contestants and their mating success on that day. Data relating to resource abundance
237 and daily mating success were log transformed and all data were centred prior to analyses (Kruschke
238 2015). We included three random intercepts in each model: the identity of the dominant and
239 subordinate males and the identity of each unique pairs of competing males (see supplementary
240 files for model code and data).

241 Each logistic regression was run over three independent chains with dispersed initial values.
242 The adaptive burnin phase was set to 10,000 and a posterior length of 75,000 iterations. A thinning
243 interval was set to 500 to reduce autocorrelation (e.g. Jennings et al. 2017, 2018). We used a weakly
244 informative inverse Wishart prior for the regression co-efficients and random effects. Convergence
245 of the posterior chains was estimated using the Gelman-Rubin statistic (Gelman & Rubin 1992) with
246 a convergence level of <1.1 used to indicate that the adaptive phase was sufficient for each
247 parameter (Kruschke 2015). Interpretation of the model output was determined by reference to
248 posterior means and 95% credible intervals (e.g. Jennings 2020). If the 95% credible interval did not
249 cover zero, we concluded that there was a meaningful effect between that parameter and the

250 dependent variable. We set contests with *tp*-following as the lower category (i.e. 0) in both logistic
251 models, while contests that were either not followed by third-party males (model 1), or that suffered
252 intervention (model 2) were set at the higher category (i.e. 1). Thus, negative effects of a predictor
253 variable (posterior distribution with mean below zero) indicate an association with *tp*-following,
254 whereas a positive effect of a predictor variable (posterior distribution and mean above zero)
255 indicates a meaningful association with either (i) contests that were not third-party followed or (ii)
256 contests that suffered third-party intervention. Within the model we included an interaction effect
257 between resource abundance and the ranks of the two contestants because theory expects both
258 factors to be fundamental to contest behaviour, and because the presence of oestrus females
259 generates high levels of aggression between males in this population (Jennings et al. 2006; Jennings
260 2020).

Results

261
262
263
264
265
266
267
268
269
270
271
272

Association between dominance rank and third-party following

An initial examination of the relationship between investment in fighting (i.e. the total number of fights males engaged in) and mean Elo-rating indicated that there was a significant positive association between these two variables (Poisson GLMM: $z = 17.47$, $p < .001$, estimate = 0.35, std. error = 0.02). We regressed the mean Elo-rating against the intervention score for each male over three years ($N = 108$), and a linear mixed effects model indicated that there was a positive association between these two variables ($t = 6.33$, $p < .001$, estimate = 1.35, std. error = 0.21, Figure 1). Thus, although dominant males were more likely to engage in both *tp*-following and fight interventions, there was a greater tendency to engage in *tp*-following over interventions as male rank increased.

273

Figure 1 about here

275

The intervention scores of a sub-sample of males present in each of the three ruts ($N = 40$) was estimated in order to determine whether third-party behaviour was a repeatable property of individuals and/or related to dominance. An initial model that included only individual identity and year as crossed random effects indicated that *tp*-following behaviour was repeatable ($R = 0.20$, $SE = 0.09$, $CI = 0.02, 0.39$) and this was statistically significant ($D = 5.34$, $df = 1$, $P = 0.01$). However, when the mean Elo-rating for these individuals was entered as a fixed factor, the repeatability estimate for individual males declined ($R = 0.12$, $SE = 0.09$, $CI = 0, 0.32$) and was no longer significant ($D = 1.87$, $df = 1$, $P = 0.09$). The repeatability estimate for rank was higher ($R = 0.19$, $SE = 0.09$, $CI = 0.06, 0.41$) indicating that *tp*-following is more strongly associated with rank than individual identity.

285

The association between competitor dominance rank, mating success, resource abundance and third-party following

We also investigated the association between following and daily variation in dominance and mating success of the two competing individuals. We first examined the tendency for contesting dyads that were followed by third-party males against dyadic contests that were not followed. There was a meaningful association between daily variation in resource abundance and *tp*-following (Figure 2).

291

292 Further, contests that were not followed by third-party males showed a meaningful association with
293 both the Elo-rating and the number of matings achieved by dominant males. Thus, dominant males
294 that successfully mated were unlikely to be involved in contests that were followed by third-party
295 males.

296 Critically, there was also a meaningful interaction between resource abundance, and the Elo-ratings
297 of both the dominant and subordinate contestants (Figure 2). In order to investigate the interaction,
298 we examined the association between the Elo-rating of the dominant and subordinate dyad
299 members separately by incrementally increasing resource abundance (Figures 3 and 4). For ease of
300 interpretation, we manually set these increments as notional daily increases from 0 to 40 matings in
301 fixed steps of 10. Figure 3 illustrates two key points in relation to the dominant member of the dyad:
302 the first is that as the Elo-rating increased there was a decline in the likelihood that a contest would
303 be followed by a third-party male; the second shows that an increase in resource abundance was
304 associated with an increase in the likelihood of *tp*-following. Thus, dyads containing high-ranking
305 individuals were unlikely to be followed but as resource abundance increased, dyads containing
306 relatively lower ranked contestants had an increasing likelihood of *tp*-following. Figure 4 indicates
307 that the association between the likelihood of *tp*-following and the Elo-rating of the subordinate
308 contestant was weak although there was a slight tendency for *tp*-following to increase as dominance
309 increased. Reference to the association between subordinate dominance and *tp*-following in Figure
310 2 supports the conclusion that this relationship was not meaningful. Nevertheless, Figure 4 shows
311 that as resource abundance increased there was an increased likelihood that *tp*-following would be
312 observed. Therefore, while the dominance status the subordinate was not associated with *tp*-
313 following, there was an increased likelihood of following when resource abundance in the herd
314 increased.

315

316 **Figure 2 about here**

317

318 **Figure 3 and 4 about here**

319

320 We also investigated the association between *tp*-following and the decision by third-party males to
321 actively intervene in a contest. There was no evidence that third-party following males were basing
322 the decision to intervene on the dominance rank of the competing males; rather, a meaningful
323 association with resource abundance suggests that the number of matings in the herd on any given

324 day was a key factor (Figure 5). Specifically, that as the number of matings in the herd increased
325 there was a decrease in interventions and an increasing tendency for males to engage in *tp*-following
326 of contests (Figure 6).

327

328 **Figure 5 and 6 about here**

329

Discussion

330 The present study investigated decision making by males engaged as third-party followers of dyadic
331 contests. We proposed that following may function as a visual assessment strategy akin to that
332 proposed for parallel walks (Enquist et al. 1990; Enquist & Leimar 1983; Arnott & Elwood 2009).
333 However, *tp*-following behaviour has never been described in ungulates, and as a consequence, this
334 proposition has not been tested; accordingly, we tested three predictions related to this idea in the
335 present study. Our results show that high-ranking males were likely to engage in *tp*-following of
336 contests. Specifically, as rank increased there was an increasing tendency for *tp*-following over and
337 above the tendency to engage in third-party intervention indicating that high-ranking males invested
338 more effort in opponent assessment than lower ranking males. Furthermore, as expected by contest
339 theory, we show that *tp*-following has a complex relationship with daily variation in dominance rank
340 and resource abundance. Where *tp*-followers elected to escalate to intervention of an ongoing
341 contest, this study shows that resource abundance is a key factor in this decision. Taken together
342 our results provide evidence that *tp*-following is an assessment process, albeit more nuanced than
343 we initially expected.

344 The decision to escalate to fighting is expected to be costly in terms of energetic expenditure,
345 time and a heightened possibility of suffering a serious injury. In order to mitigate these costs,
346 contest theory allows that contestants assess the relative quality of a putative opponent, and the
347 value of the resource under dispute (Arnott & Elwood 2009). Thus, high-quality opponents are
348 expected to have sufficient resources to invest in fighting by either out-competing (e.g. Clutton-
349 Brock & Albon 1979; Enquist et al. 1990; Jennings et al. 2005a; Neat et al. 1998) or out-lasting a low-
350 quality opponent (e.g. Hack 1997; Marden & Rollins 1994; Smith et al. 1994). Conversely, the ability
351 to accurately assess an opponent's quality should enable weaker individuals to quickly withdraw
352 uninjured, and with potentially a lower energetic investment than might otherwise be the case.
353 Consistent with this argument is the observation that high-quality individuals are more likely to act
354 on information acquired as bystanders by attacking individuals they have previously seen fighting
355 (e.g. Johnsson & Ackerman 1998; Otter et al. 1999; Earley & Dugatkin 2002; Tibbetts et al. 2020).
356 Although we note that third-party intervention behaviour is associated with high rank (Jennings et
357 al. 2009, 2017), this study shows that as dominance rank increased there is an increasing tendency
358 for third-party males to favour *tp*-following over and above escalating to intervention. Accordingly,
359 our first prediction is supported. In theoretical terms, we argue that these results are consistent with
360 dyadic models that appeal to information gathering in aggressive contexts (e.g. Enquist & Leimar
361 1983), and the idea that third-party behaviour acts to prevent rivals from threatening the
362 intervener's social status (e.g. Dugatkin 1998a).

363 We note, however, that because this argument is explicit with respect to both information
364 gathering and status retention, examination of the quality of the dyadic competitors will be central
365 to any conclusions regarding the role of *tp*-following behaviour. Differences in RHP as expressed
366 through differences in body and weapon size, age or fighting ability can be determined by calculating
367 individual dominance rank based on contest outcome (Arnott & Elwood 2009; Broom et al. 2009).
368 The use of lateral displays during contests can allow mutual comparison of size (e.g. Clutton-Brock et
369 al. 1979; Bartoš et al. 2007, Jennings 2012) while the rate of attacking actions are often predictive of
370 contest outcome (Jennings et al. 2005 a,b). We suggest that once sufficient information has been
371 gathered, the *tp*-follower is free to (de)escalate their involvement in the ongoing contest.
372 Accordingly, we predicted that dyads containing rivals possessing high dominance rank should be
373 preferentially followed by third-party males, as these individuals should present a more immediate
374 threat than low-ranking individuals. A comparison of contests that experienced *tp*-following and
375 those that were not indicated that contestant rank shares a complex relationship with resource
376 abundance. Focusing on the association between *tp*-following and dominance showed that as the
377 rank of the dominant (dyadic) contestant increased, there was a decline in the likelihood that the
378 contest would be followed. Moreover, the association between the likelihood of *tp*-following and
379 daily mating success showed a similar trend: individuals that achieved matings fought in dyads that
380 had a lower likelihood of being followed. Reference to the dominance status of the subordinate
381 contestant indicated a less obvious association suggesting a weak relationship between following
382 and rank. Further, when we examined contests that suffered an intervention we found no
383 relationship with dominance or mating success of either contestant. Taken together these results fail
384 to support the prediction that males use *tp*-following to facilitate assessment of high-quality
385 opponents.

386 During dyadic contests high quality individuals have substantially higher action rates than their
387 opponent (Jennings et al. 2005a), and attacks on opponents increase as resource abundance
388 increases (Jennings 2020). The association between *tp*-following and the higher ranked of the two
389 contestants is consistent with the idea that third-party males are attending to the higher action rates
390 of dominant contestants. However, this does not explain why dyads with socially dominant males
391 had a lower likelihood of being followed; critically, it is contrary to our expectation that third-party
392 males engage in low-cost monitoring of high-quality rivals (e.g. Parker 1974; Parker & Rubenstein
393 1981; Enquist & Leimar 1983). The answer may depend on the ability of individuals to assess
394 opponent quality. Theory predicts that closely matched opponents are less likely to be able to
395 resolve a conflict without escalation, and there are a number of studies that show that individuals of
396 similar quality tend to display a preference for fighting with each other (e.g. de Wall 1991; Clutton-

397 Brock et al. 1982; Freeman et al. 1992; Jennings et al. 2006). This is not the case for mis-matched
398 opponents where disputes are expected to be resolved through less costly, non-contact displays
399 (e.g. Clutton-Brock & Albon 1979; Enquist et al. 1990; Hoffman & Schildberger 2001). Under this
400 interpretation of theory, dominant individuals might be able to determine the quality of competing
401 subordinates without the necessity for physical confrontation. There is a second complimentary
402 explanation that is relevant here; specifically, that rank is positively associated with fighting, and as
403 social status decreases there is a decline in investment in fighting. Because individuals tend to fight
404 with similarly ranked opponents in this population (e.g. Jennings et al. 2006), in this context,
405 subordinate males who commit to fighting might represent new 'players on the pitch'. It may be
406 strategically beneficial to monitor low-ranked opponents who can expend resources on fighting
407 because such individuals could theoretically become a threat (Dugatkin 1998 a,b; Briffa & Sneddon
408 2007).

409 This impression is strengthened when we consider the association between *tp*-following and
410 resource abundance. While individual quality is a central factor in contest theory, the importance
411 that resource value plays in contest behaviour has long been recognized (Parker 1974; Maynard
412 Smith & Parker 1976; Arnott & Elwood 2008). Our results support this key hypothesis. We show that
413 resource abundance (i.e. the number of matings in the herd per day) plays an important role in
414 contestant decisions regarding third-party following; both logistic models show that the likelihood of
415 following increased when resource abundance increased. Individuals take resource abundance and
416 ownership into account when making contest decisions; for example, males increase their
417 assessment of opponents if females are present (e.g. Clutton-Brock & Albon 1979) and when they
418 hold a territory (Alvarez 1993). In this population, there is an increase in attack rates during fights
419 when females begin to enter oestrus, and this is associated with increased mating success for
420 dominant contestants (Jennings 2020). Thus, third-party monitoring of the threat posed by
421 subordinate rivals could be beneficial to dominant males when mating opportunities are available.

422 The decisions underlying engagement in third-party behaviour are complex and have resulted in
423 a diverse range of theoretical models and an increasing number of empirical studies on the subject
424 (Smith et al. 2010; Bissonnette et al. 2015). The present study investigated whether *tp*-following of
425 an ongoing dyadic contest acted as a third-party assessment process. We reasoned that if this were
426 the case, that dominance status and the decisions made by the third-party individual in relation to
427 contestant quality and resource abundance, would be important correlates of following. Our results
428 confirmed that dominant males had a greater tendency for *tp*-following and this decision was
429 associated with both the dominance status of the contestants and resource abundance. Although *tp*-
430 following was predominantly directed towards lower-ranked contestants contrary to our

431 expectations, these findings are consistent with the idea that dominant males monitor individuals
432 that may at some later stage become a threat to them. Taken together, these findings are consistent
433 with the predictions of contest theories that focus on information gathering and rank protection.

References

- 434
- 435 Abril-de-Abreu, R., Cruz, A.S. & Oliveira, R.F. (2015). Social dominance modulates eavesdropping in
436 zebrafish. *Royal Society Open Science*, 2, 150220.
- 437 Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49, 227-267.
- 438 Alvarez, F. (1993). Risks of fighting in relation to age and territory holding in fallow deer. *Canadian*
439 *Journal of Zoology*, 71, 376-383.
- 440 Arnott, G. & Elwood, R.W. (2008). Information gathering and decision making about resource value
441 in animal contests. *Animal Behaviour*, 76, 529-542.
- 442 Arnott, G. & Elwood, R.W. (2009). Assessment of fighting ability in animal contests. *Animal*
443 *Behaviour*, 991-1004.
- 444 Bartoš, L., Fričová, B., Bartošová-Víchová, J., Panamá, J., Šustr, P. & Šmídová, E. (2007). Estimation of
445 the probability of fighting in fallow deer (*Dama dama*) during the rut. *Aggressive Behaviour*,
446 33, 7-13.
- 447 Bissonnette, A., Perry, S., Barrett, L., Mitani, J.C., Flinn, M., Gavrilets, S. & de Waal, F.B.M. (2015).
448 Coalitions in theory and reality: a review of pertinent variables and processes. *Behaviour*, 152,
449 1-56.
- 450 Briffa, M. & Sneddon, L.U. (2007). Physiological constraints on contest behaviour. *Functional*
451 *Ecology*, 21, 627-637.
- 452 Broom, M., Koenig, A. & Borries, C. (2009). Variation in dominance hierarchies among group-living
453 animals: modelling stability and the likelihood of coalitions. *Behavioral Ecology*, 20, 844-855.
- 454 Cheney, D.L. & Seyfarth, R.M. (1990). *How monkeys see the world*. Chicago: University of Chicago
455 Press.
- 456 Clutton-Brock, T.H. & Albon, S.D. (1979). The roaring of red deer and the evolution of honest
457 advertisement. *Behaviour*, 69, 145-170.
- 458 Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. & Guinness, F.E. 1979. The logical stag: adaptive aspects
459 of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour*, 27, 211-225.
- 460 Clutton-Brock, T.H., Green, D., Hiraiwa-Hasegawa, M. & Albon, S.D. (1988). Passing the buck:
461 resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and*
462 *Sociobiology*, 23, 281-296.

- 463 Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982). Red deer: the behaviour and ecology of two
464 sexes. Chicago University Press: Chicago.
- 465 De Waal, F.B.D.M. (1991). Rank distance as a central feature of rhesus monkey social organisation: a
466 sociometric analysis. *Animal Behaviour*, 41, 383-395.
- 467 Drews, C. (1996). Contexts and patterns of injuries in free-ranging male baboons (*Papio*
468 *cynocephalus*). *Behaviour*, 133, 443-474.
- 469 Dugatkin, L.A. (1998a). Breaking up fights between others: a model of intervention behaviour.
470 *Proceedings of the Royal Society, London, B*, 265, 433-437.
- 471 Dugatkin, L.A. (1998b). A model of coalition formation in animals. *Proceedings of the Royal Society,*
472 *London, B*, 265, 2121-2125.
- 473 Earley, R.L. & Dugatkin, L.A. (2002). Eavesdropping on visual cues in green swordtail (*Xiphophorus*
474 *helleri*) fights: a case for networking. *Proceedings of the Royal Society, London, B*, 269, 943-
475 952.
- 476 Elo, A.E. (1978). *The Rating of Chess Players, Past, present and Future*. New York: Arco.
- 477 Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of
478 relative strength. *Journal of Theoretical Biology*, 102, 387-410.
- 479 Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. (1990). A test of the sequential
480 assessment game: fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, 40, 1-14.
- 481 Festa-Bianchet, M., Apollonio, M., Mari, F. & Rasola, G. (1990). Aggression among lekking male
482 fallow deer (*Dama dama*): territory effects and the relationship with copulatory success.
483 *Ethology*, 85, 236-246.
- 484 Freeman, L.C., Freeman, S. & Romney, A.K. (1992). The implications of social structure for
485 dominance hierarchies on red deer. *Animal Behaviour*, 44, 239-245.
- 486 Fričová, B., Bartoš, L., Bartošová, J., Panamá, J., Šustr, P. & Jozífková, E. (2007). Females presence
487 and males agonistic encounters in fallow deer, *Dama dama* during the rut. *Folia Zoologica*, 56,
488 253-262.
- 489 Gavrilets, S., Duenez-Guzman, E.A. & Vose, M.D. (2008). Dynamics of coalition formation and the
490 egalitarian revolution. *PLoS One* 3, e3293.

- 491 Gelman, A. & Rubin, D.B. (1992). Inference from iterative simulation using multiple sequences.
492 Statistical Science, 7, 457-511.
- 493 Hack, M.A., Thompson, D.J. & Fernandes, D.M. (1997). Fighting in males of the autumn spider,
494 *Metellina segmentata*: effects of relative body size, prior residency and female value on
495 contest outcome and duration. *Ethology*, 103, 488-498.
- 496 Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the
497 MCMCglmm package. *Journal of Statistical Computing*, 33, 1-22.
- 498 Harcourt, A.H. & de Waal, F.B.D.M. (1992). Coalitions and alliances in humans and other animals.
499 Oxford University Press: Oxford.
- 500 Hoffmann, H.A. & Schildberger, K. (2001). Assessment of strength and willingness to fight during
501 aggressive encounters in crickets. *Animal Behaviour*, 62, 337-348.
- 502 Hsu, Y., Earley, R.L. & Wolf, L.L. (2006). Modulation of aggressive behaviour by fighting experience:
503 mechanisms and contest outcomes. *Biological Review*, 81, 33-74.
- 504 Jennings, D. J., Boys, R. J., & Gammell, M. P. (2017). Investigating variation in third-party intervention
505 behaviour during a fallow deer (*Dama dama*) rut. *Behavioral Ecology*, 28, 288-293.
- 506 Jennings, D. J., Gammell, M. P., Carlin, C. M. & Hayden, T. J. (2002). Does lateral presentation of the
507 palmate antlers during fights by fallow deer (*Dama dama*) signify dominance or submission?
508 *Ethology*, 108, 389-401.
- 509 Jennings, D. J., Gammell, M. P., Carlin, C. M. & Hayden, T. J. (2003). Is the parallel walk between
510 competing male fallow deer, *Dama dama*, a lateral display of quality? *Animal Behaviour*, 65,
511 1005-1012.
- 512 Jennings, D. J., Gammell, M. P., Carlin, C. M. & Hayden, T. J. (2010). Investment in fighting in relation
513 to body condition, age and dominance rank in the male fallow deer, *Dama dama*. *Animal*
514 *Behaviour*, 79, 1293-1300.
- 515 Jennings, D. J., Gammell, M. P., Payne, R. J. H. & Hayden, T. J. (2005a). An investigation of
516 assessment games during fallow deer fights. *Ethology*, 111, 511-525.
- 517 Jennings, D. J., Gammell, M. P., Carlin, C. M. & Hayden, T. J. 2005b. Win, lose or draw: a comparison
518 of fight structure based on fight conclusion in the fallow deer. *Behaviour*, 142, 423-439.

519 Jennings, D. J., Gammell, M. P., Payne, R. J. H. & Hayden, T. J. (2006). Is difference in body weight,
520 antler length, age or dominance rank related to the number of fights between fallow deer
521 (Dama dama)? *Ethology*, 112, 258-269.

522 Jennings, D.J. (2012). Right-sided bias in fallow deer terminating parallel walks: evidence for
523 lateralization during a lateral display. *Animal Behaviour*, 83, 1427-1432.

524 Jennings, D.J. (2020). Contest behaviour varies in relation to reproductive opportunities and
525 reproductive success in the fallow deer. *Animal Behaviour*, 163, 95-103.

526 Jennings, D.J., Boys, R.J. & Gammell, M.P. (2018). Suffering third-party intervention during fighting is
527 associated with reduced mating success in the fallow deer. *Animal Behaviour*, 139, 1-8.

528 Jennings, D.J., Carlin, C.M. & Gammell, M.P. (2009). A winner effect supports third-party intervention
529 behaviour during fallow deer, *Dama dama*, fights. *Animal Behaviour*, 77, 343-348.

530 Jennings, D.J., Carlin, C.M., Hayden, T.J., Gammell, M.P. (2011). Third-party intervention behaviour
531 during fallow deer fights: the role of dominance, age, fighting and body size. *Animal*
532 *Behaviour*, 81, 1217-1222.

533 Jennings, D.J., Elwood, R.W., Carlin, C.M., Hayden, T.J., Gammell, M.P. (2012). Vocal rate as an
534 assessment process during fallow deer contests. *Behavioural Processes*, 91, 152-158.

535 Johnsson, J. & Ackerman, A. (1998). Watch and learn: preview of the fighting ability of opponents
536 alters contest behaviour in rainbow trout. *Animal Behaviour*, 56, 771-776.

537 Johnstone, R.A. & Dugatkin, L.A. (2000). Coalition formation animals and the nature of winner and
538 loser effects. *Proceedings of the Royal Society London, B*, 267, 17-21.

539 Kapranas, A., Zenner, A.N.R.L., Mangan, R. & Griffin, C.T. (2020). Objective and subjective
540 components of resource value in lethal fights between male entomopathogenic nematodes.
541 *Animal Behaviour*, 164, 149-154.

542 Kokko, H. (2013). Dyadic contests: modelling flights between two individuals. In. *Animal Contests*
543 (ed. I.W.C. Hardy and M. Briffa), pp. 5-32. Cambridge University Press: Cambridge.

544 Kruschke, J.K. (2015). *Doing Bayesian Data Analysis*. Amsterdam: Academic Press.

545 Marden, J.H. & Rollins, R.A. (1994). Assessment of energy reserves by damselflies engaged in aerial
546 contests for mating territories. *Animal Behaviour*, 48, 1023-1030.

- 547 Maynard Smith, J. & Parker, G.A. (1976). The logic of asymmetric contests. *Animal Behaviour*, 24,
548 159-175.
- 549 McGregor, P.K. (1993). Signalling in territorial systems: a context for individual identification, ranging
550 and eavesdropping. *Philosophical Transactions of the Royal Society, London, B*, 340, 237-244.
- 551 Mesterton-Gibbons, M., Marden, J.H. & Dugatkin, L.A. 1996. On wars of attrition without
552 assessment. *Journal of Theoretical Biology*, 181, 65-83.
- 553 Mesterton-Gibbons, M. & Sherratt, T.N. (2007). Coalition formation: a game-theoretic analysis.
554 *Behavioral Ecology*, 18, 277-286.
- 555 Moore, N.P., Kelly, P.F., Cahill, J.P. & Hayden, T.J. 1995. Mating strategies and mating success of
556 fallow (*Dama dama*) bucks in a non-lekking population. *Behavioral Ecology and Sociobiology*,
557 36, 91-100.
- 558 Neat, F.C., Huntingford, F.A. & Beveridge, M.M. (1998). Fighting and assessment in male cichlid fish:
559 the effects of asymmetries in gonadal state and body size. *Animal Behaviour*, 55, 883-891.
- 560 Otter, K., McGregor, P.K., Terry, A.M.R., Burford, F.R.L., Peake, T.M. & Dabelsteen, T. (1999). Do
561 female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive
562 song playback. *Proceedings of the Royal Society, London, B*, 266, 1305-1309.
- 563 Pandit, S.A. & van Schaik, C.P. (2003). A model of levelling coalitions among primate males: towards
564 a theory of egalitarianism. *Behavioral Ecology and Sociobiology*, 55, 161-168.
- 565 Parker, G.A. & Rubenstein, D.I. (1981). Role assessment, reserve strategy, and acquisition of
566 information in asymmetric animal conflicts. *Animal Behaviour*, 29, 221-240.
- 567 Parker, G.A. 1974. Assessment strategy and evolution of fighting behaviour. *Journal of Theoretical*
568 *Biology*, 47, 223-240.
- 569 Payne, R.J.H. 1998. Gradually escalating fights and displays: the cumulative assessment model.
570 *Animal Behaviour*, 56, 651-662.
- 571 Piper, W.H., Walcott, C., Mager, J.N. & Spilker, F.J (2008). Fatal battles in common loons: a
572 preliminary analysis. *Animal Behaviour*, 75, 1109-1115.
- 573 Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W.T. & Clutton-Brock, T. (2005). Red deer
574 stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings*
575 *of the Royal Society, London, B*, 272, 941-947.

576 Smith, I.P., Huntingford, F.A., Atkinson, R.J. & Taylor, A.C. (1994). Strategic decisions during agonistic
577 behaviour in the velvet swimming crab, *Necora puber* (L.). *Animal Behaviour*, 47, 885-894.

578 Smith, J.E., van horn, R.C., Powning, K.S., Cole, A.R., Graham, K.E., Memenis, S.K. & Holekamp, K.E.
579 (2010). Evolutionary forces favouring intragroup coalitions among spotted hyenas and other
580 animals. *Behavioral Ecology*, 21, 284-303.

581 Stamatopoulos, G., Sengupta, A., Vogel, E. & Janson, C. (2009). A game-theoretic model of coalition
582 formation. *Journal of Bioeconomics*, 11, 165-183.

583 Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance
584 decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*,
585 8, 1639-1644.

586 Taylor, P.W. & Elwood, R.W. 2003. The mismeasure of animal contests. *Animal Behaviour*, 65, 1195-
587 1202.

588 Tibbetts, E.A., Wong, E. & Bonello, S. (2020). Wasps use social eavesdropping to learn about
589 individual rivals. *Current Biology*, 30, 1-4.

590 Tomasello, M. & Call, J. (1997). *Primate Cognition*. Oxford: Oxford University Press.

591 Wascher, C.A.F., Scheiber, I.B.R. & Kotrschal, K. (2008). Heart rate modulation in bystanding geese
592 watching social and non-social events. *Proceedings of the Royal Society, London, B*, 275, 1653-
593 1659.

594 Whitehead, H. & Connor, R. (2005). Alliances I. How large should alliances be? *Animal Behaviour*, 69,
595 117-126.

596 Wilkinson, P.F. & Shank, C.C. (1976). Rutting-fight mortality among musk oxen on Banks Island,
597 Northwest Territories, Canada. *Animal Behaviour*, 24, 756-758.

598

List of Figures

599

600

601 **Figure 1.** The association between mean Elo rating for individual males and **their intervention scores**
602 **(N *tp*-follows – N interventions) over three consecutive ruts.**

603

604 **Figure 2.** The mean distribution and 95% credible intervals showing the binary association of a
605 contest being *tp*-followed (0) or not (1) and daily resource abundance, dominance rank and mating
606 success of the dyadic opponents. We excluded the intercept from this figure in order to aid visual
607 clarity (Intercept: Mean = 1.73, 95% CI = 1.6, 1.88).

608

609 **Figure 3.** The relationship between whether a contest was followed (0) or not (1) and the Elo-rating
610 of the dominant contestant (**shown as centred scores**). Lines represent an iterative daily increase in
611 the number of matings (0 matings = solid line, 10 = dashed line, 20 = dotted line, 30 = dot-dash line,
612 40 = two-dash line).

613

614 **Figure 4.** The relationship between whether a contest was followed (yes=0, no=1) and the
615 dominance rank of the subordinate contestant (**shown as centred scores**). Lines represent an
616 iterative daily increase in the number of matings (0 matings = solid line, 10 = dashed line, 20 = dotted
617 line, 30 = dot-dash line, 40 = two-dash line).

618

619 **Figure 5.** The mean distribution and 95% credible intervals showing the binary association of a
620 contest being followed (0) or suffering an intervention (1) by a third-party male and daily resource
621 abundance, dominance rank and mating success of the dyadic opponents.

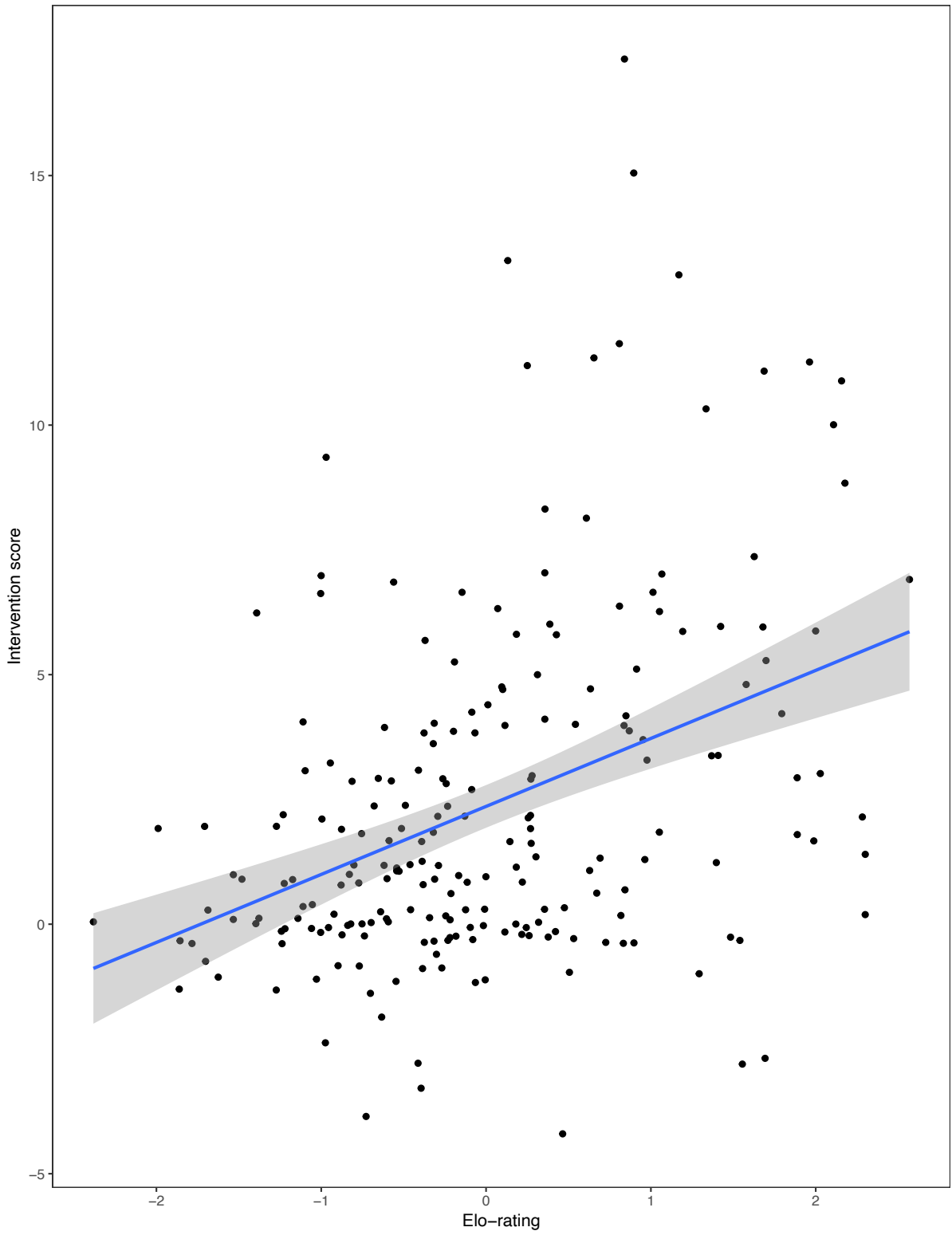
622

623 **Figure 6.** The **logistic relationship between daily matings (shown as mean centred scores) recorded**
624 **during the rut and whether there was either *t-p* intervention (1) or *tp*-following (0) of contests.**
625 **The negative relationship shown in the figure illustrates there is an increasing tendency towards**
626 ***tp*-following.**

627

628 Figure 1.

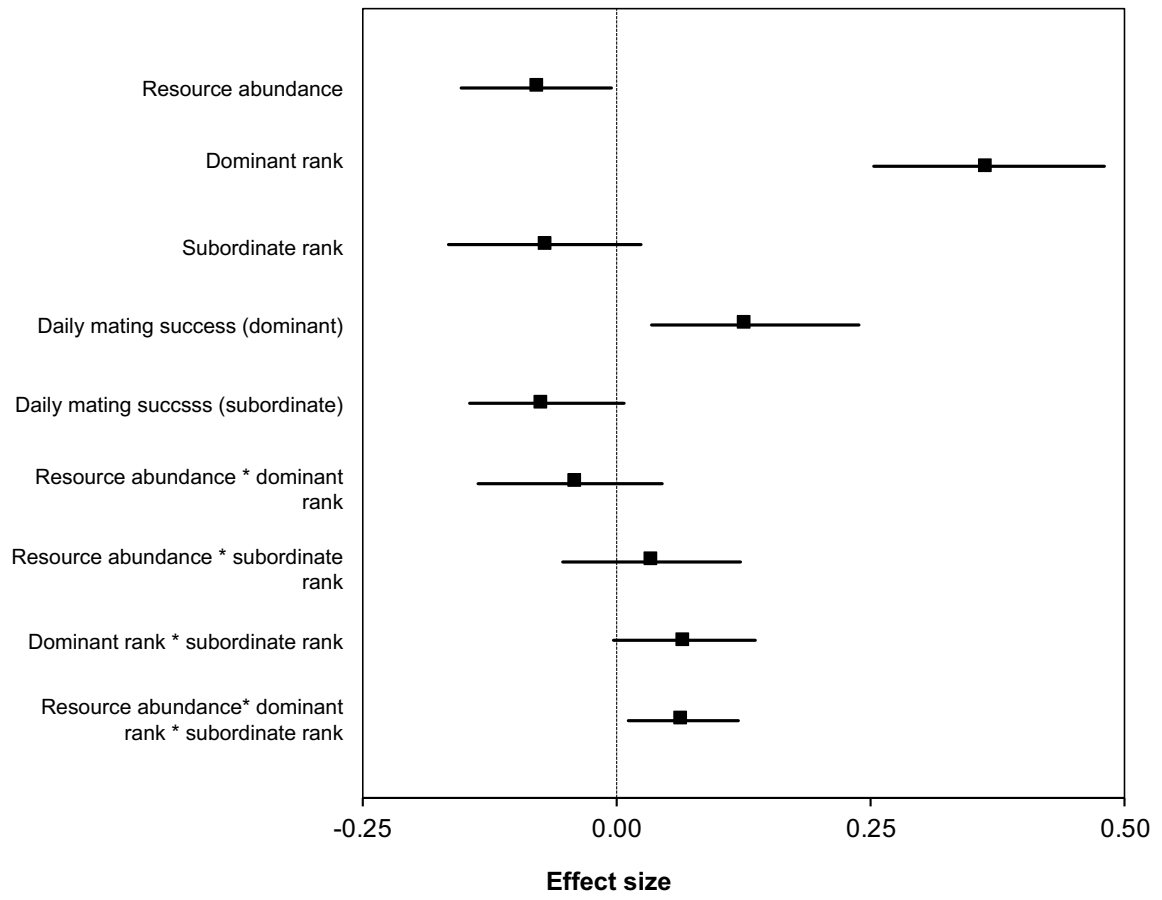
629



630

631

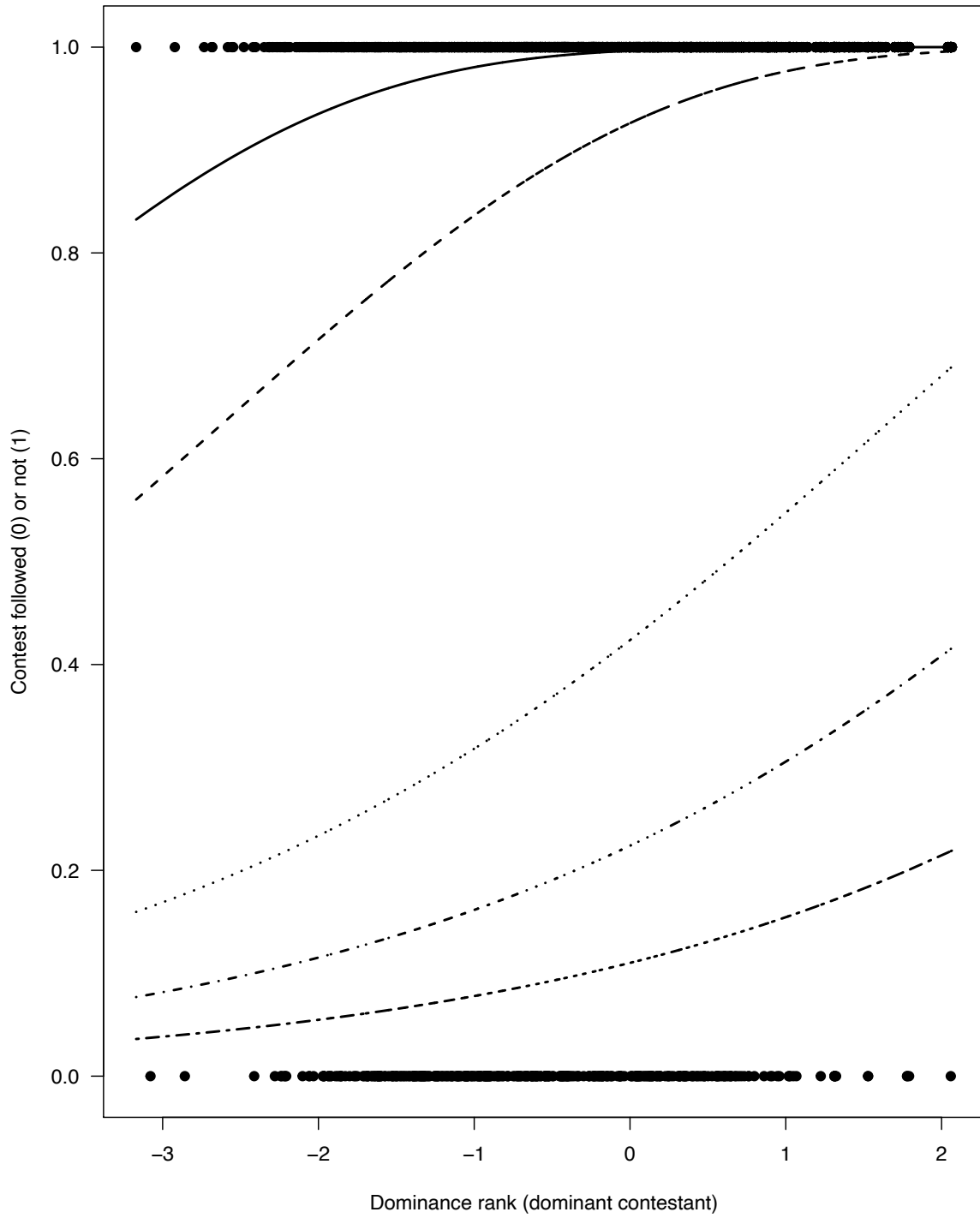
632 Figure 2.



633

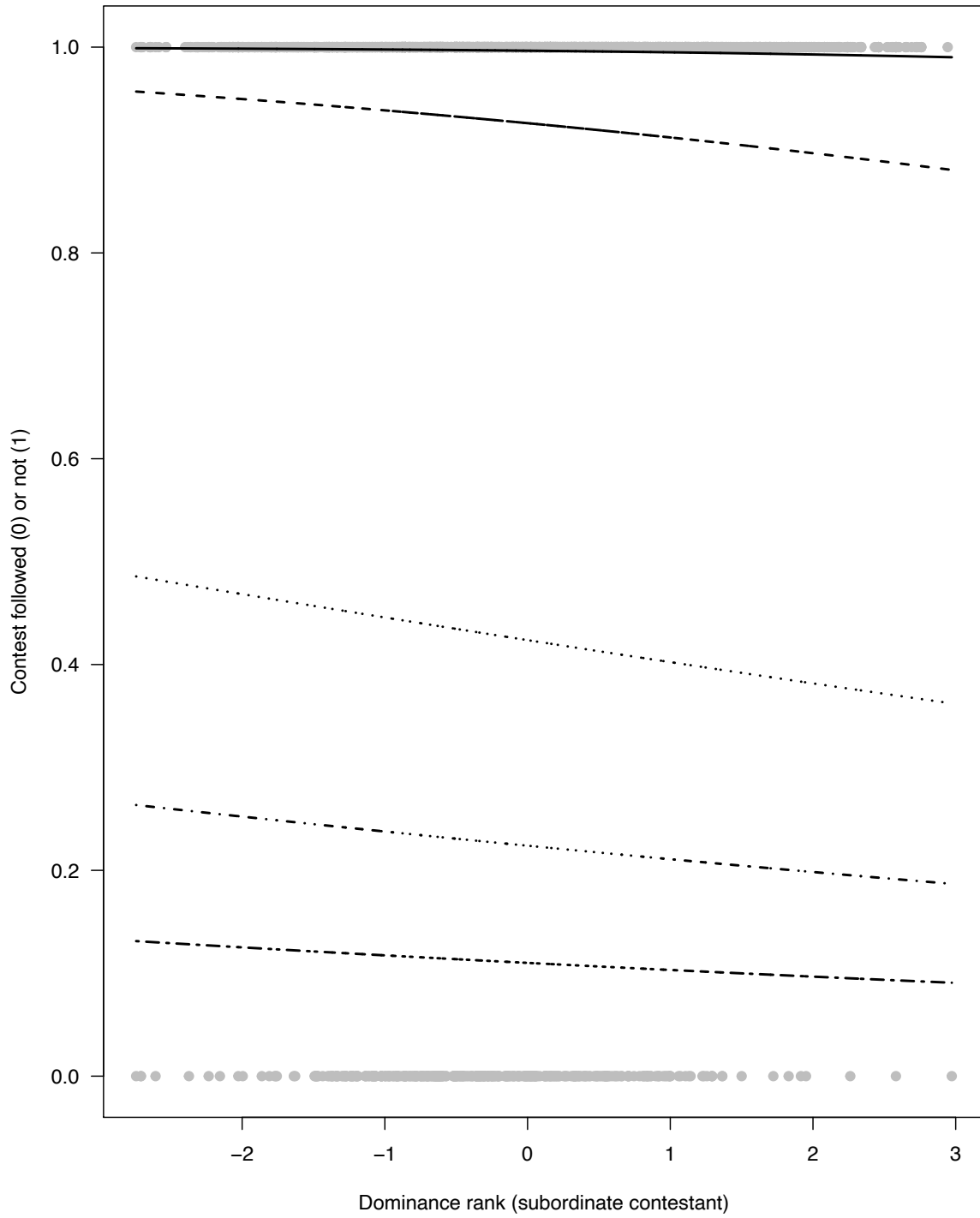
634

635 Figure 3



636

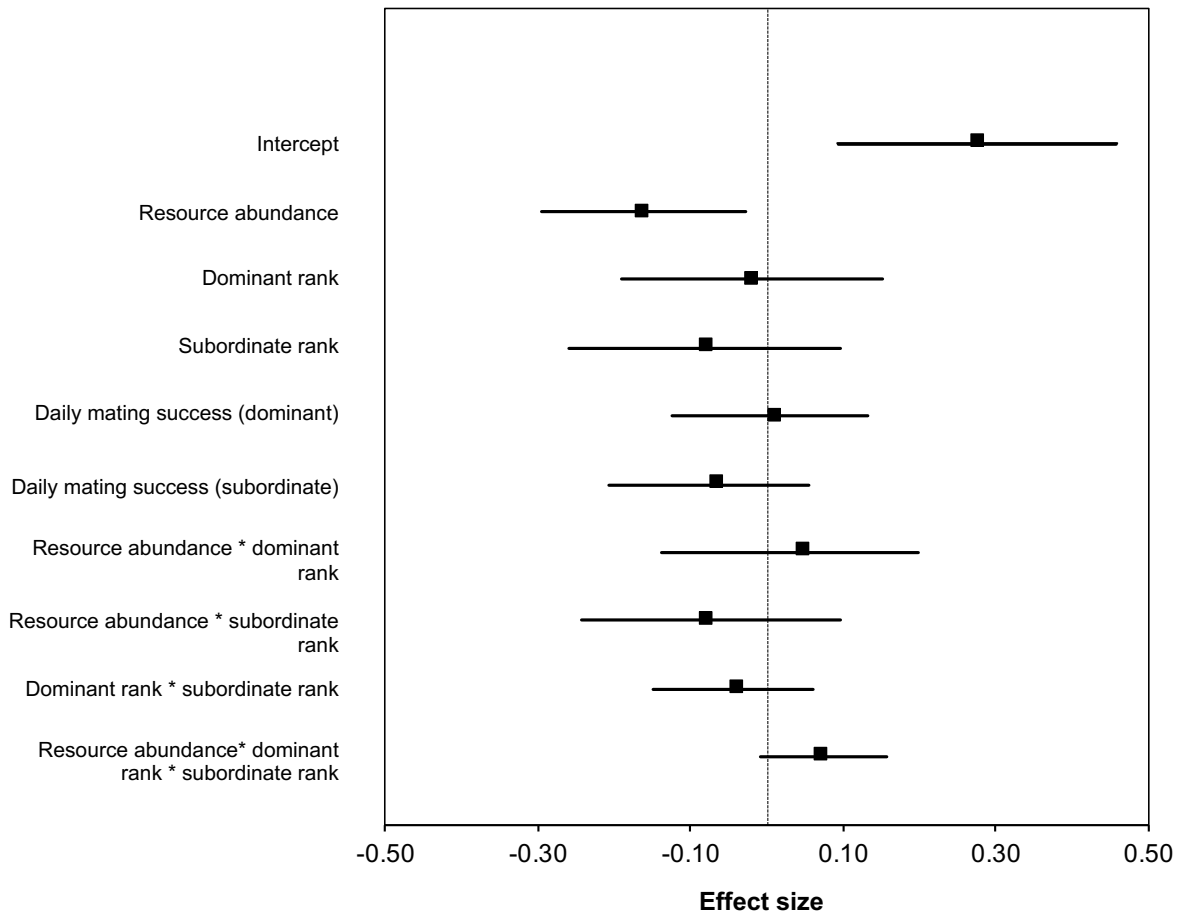
637 Figure 4.



638

639

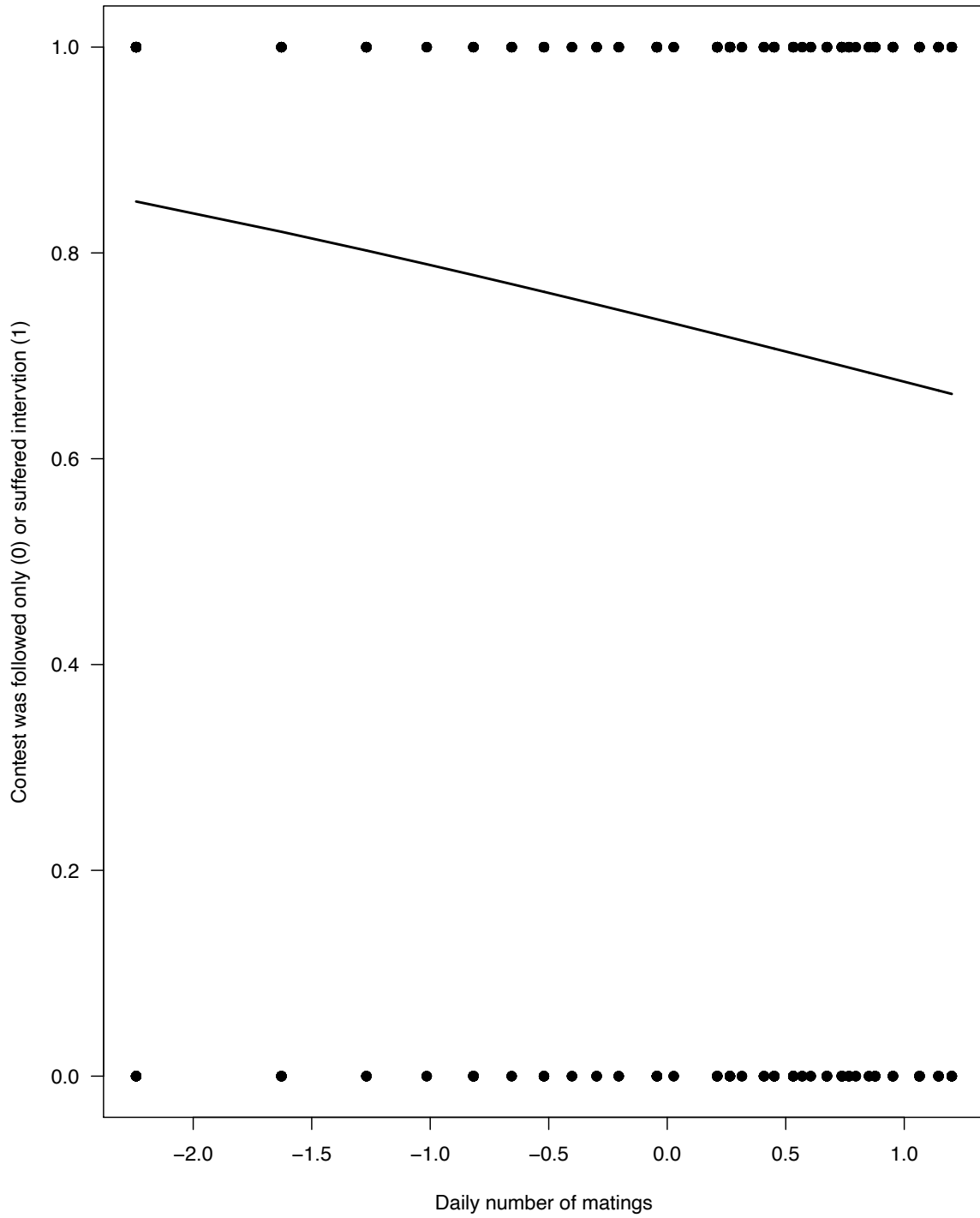
640 Figure 5.



641

642

643 Figure 6.



644

645