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## Vocal rate as an assessment process during fallow deer contests

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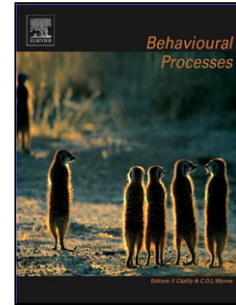
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1 Vocal rate as an assessment process during fallow deer contests

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22

22

Abstract

23

24 Two types of model propose that strategic decisions during contests are determined either by (i) a  
25 mutual-assessment process or (ii) a self-assessment process. Vocal signals are thought to convey  
26 information about the competitive abilities of individuals, the ultimate function of which is a  
27 reduction in costs associated with fighting consistent with the principle of mutual assessment.  
28 Nevertheless, the limited evidence that male ungulates engage in mutual assessment of vocal rates  
29 during dyadic contests has been questioned. Therefore, we examined the vocal rates of winners and  
30 losers during escalated dyadic contests between male fallow deer in order to further inform on this  
31 issue. Our results showed that winners and losers did not differ in vocal rate. The best model fit that  
32 accounted for individual vocal rates included a preponderance of factors related to the opponent  
33 indicating that contestants were attending to their opponent during fights. Vocal rate was,  
34 therefore, dependent on estimates of opponent quality without reference to self, supporting an  
35 'opponent-only' rather than a mutual assessment process.

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39 Keywords: Vocal rate, resource holding potential, fighting, self- and mutual-assessment, 'opponent-  
40 only' assessment

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## Introduction

43 Within the field of animal competition, a single theoretical account that accurately describes the  
44 strategic decisions made by animals during dyadic contests for resources remains somewhat elusive.  
45 While contestants typically use information concerning the value of the disputed resource and  
46 adjust their tactics in accordance with this estimate (e.g. Goubault et al. 2007; Arnott & Elwood  
47 2008), there is disagreement concerning the information gained about opponent fighting ability  
48 (Arnott & Elwood 2009). Models developed for this latter purpose can broadly be placed within two  
49 classes that differ fundamentally in how they describe the assessment process: one class emphasises  
50 the role of self-assessment whereas the other emphasises a process of mutual-assessment (Taylor &  
51 Elwood 2003; see Briffa & Sneddon 2010 for a review).

52 Under a self-assessment process no information is gathered about the quality of an  
53 opponent. Both contestants are expected to fight until they reach some cost threshold that the  
54 individual is willing to pay (e.g. time, energy or damage). This class of model assumes that there will  
55 be no difference in the repetition rate of aggressive actions between the opponents although rates  
56 are permitted to escalate and de-escalate over the duration of the contest (Briffa & Elwood 2009,  
57 Table 1). Therefore, under a self-assessment process, contestants illustrate their quality by matching  
58 action rates with their opponent (Briffa & Sneddon 2010). Whichever contestant reaches its cost  
59 threshold first will give up at that point and its opponent will either retain, or take control of the  
60 resource (e.g. energetic war of attrition: Payne and Pagel 1996; cumulative assessment model:  
61 Payne 1998). In line with predictions regarding competitor behaviour, there is considerable empirical  
62 evidence for self-assessment as a form of contest strategy in a variety of different species (e.g. fallow  
63 deer: Jennings et al. 2004, 2005a; amphipod crustacean: Prenter et al. 2006; house cricket: Briffa  
64 2008; jumping spider: Elias et al. 2008).

65 Models of mutual-assessment propose that each opponent gathers information about the  
66 other contestant and compares that with its assessment of its own ability or quality. One influential

67 account, the sequential assessment model (SAM, Enquist & Leimar 1983), is explicit as to how  
68 animals monitor the aggressive displays given by their opponent and, therefore, how opponent  
69 display rates affect the decisions that animals make during contests (Enquist et al. 1990). The model  
70 assumes that when two contestants enter into a contest that their respective estimate of each  
71 other's quality will be poor at the beginning; however, by repeated sampling of opponent display  
72 rates this error in assessment is reduced. Consequently, rather than continue until a maximum cost  
73 threshold is reached, a contestant is predicted to persist only until it determines that it will not  
74 succeed in winning and elects to abandon the interaction. Therefore, contest duration should be  
75 positively related to loser quality but negatively related to winner quality (Taylor & Elwood 2003).  
76 We would also expect a negative relationship between difference in opponent quality and contest  
77 duration (Enquist & Leimar 1983; Enquist et al. 1990) although this is not a diagnostic feature of  
78 mutual assessment (Taylor & Elwood 2003). A critical feature of the mutual assessment process is  
79 that information quality must be reliable and not easily faked; therefore, signals employed during  
80 dyadic contests are expected to be costly to produce (Maynard Smith & Harper 2003).

81 It has been shown that males of numerous species engage in vocal displays that apparently  
82 convey information about their quality and/or aggressive intent (Andersson 1994). For example,  
83 male songbirds' aggressive intent can be determined by song matching or countersinging between  
84 the prospective opponents (Todt & Naguib 2000). Similarly, interactions between males of several  
85 anuran species involve an increase in individual vocal rates in response to a potential rival (e.g.  
86 Wagner 1989; Bosch & Marquez 1996). When male ungulates are vocal (but not otherwise  
87 interacting) there can be a tendency towards very high vocal rates (e.g. McElligott & Hayden 1999)  
88 relative to the rates observed when males are engaged in multi-male vocal contests (e.g. Wolff  
89 1998) or in pairwise interactions (e.g. Clutton-Brock & Albon 1979). In the latter case it has been  
90 argued that high vocal rates inhibit vocal exchanges between individuals because one member of  
91 the interacting dyad is actively prevented from vocalizing (e.g. Clutton-Brock & Albon 1979; Clutton-  
92 Brock et al. 1988; Komers et al. 1997). This observation placed in theoretical terms suggests that a

93 mutual assessment process, which relies on cooperation between contestants, might hold. If this is  
94 the case, it seems unlikely that high vocal rates would facilitate mutual assessment of opponent  
95 quality in many of the contexts in which vocal behaviour has been observed (e.g. Clutton-Brock et al.  
96 1988; McElligott & Hayden 1999; see Enquist & Leimar 1983; Enquist et al. 1990).

97 A finding that has been cited in support of evidence for mutual assessment is the presence  
98 of a winner-loser disparity during vocal contests in red deer (Clutton-Brock & Albon 1979; Enquist  
99 & Leimar 1983); however, another key feature of mutual assessment was not, i.e. a stable rate of  
100 repetition over contest duration (Payne & Pagel 1997; Payne 1998; Briffa & Elwood 2009).  
101 Nevertheless, there is potentially a complex interplay between the context in which vocalizations are  
102 emitted and the form of assessment process being employed. For example, high repetition rates  
103 could support a self-assessment process subject to certain constraints; for example, matched rates  
104 where more than one male is vocal (Mesterton-Gibbons et al. 1996; Payne 1998; Briffa & Elwood  
105 2009; see for example Wolff 1998). Alternatively, if only a single male is vocal, a form of 'opponent-  
106 only' process but not mutual assessment might be applicable (Arnott & Elwood 2009). Therefore,  
107 while there is most likely some form of on-going assessment process related to vocal rates in  
108 ungulates, it is unclear what form that process takes and how this might be influenced by context.

109 The present study sought to investigate this issue by focussing on vocalizations emitted  
110 during a single defined context - the escalated contest. These contests involve the use of many  
111 different types of action that are potentially a source of information concerning opponent quality  
112 (Jennings et al. 2005a, 2010). However, the interaction between these actions and vocal behaviour  
113 have rarely been investigated (but see Logue et al. 2010); therefore, they could inform on any on-  
114 going assessment process. The present study addresses this issue. If a mutual assessment process is  
115 applicable to vocal rates during fallow deer contests then certain theoretical predictions must be  
116 met (Arnott & Elwood 2009). Specifically, vocal rate should be related to the competitive ability of  
117 the producer; therefore winners should out-produce losers and, furthermore, dominance rank

118 should be related to the vocal rate of both contestants. In keeping with mutual assessment, contest  
119 behaviour should be related to the disparity in vocal rates between the winner and loser;  
120 specifically, as winner quality increases relative to loser there should be a reduction in contest  
121 action rates since the disparity in quality should become clear early in the contest (Enquist &  
122 Leimar 1983; Enquist et al. 1990). If this is the case then contestants that are more closely matched  
123 in terms of competitive ability will vocalise at a higher rate. Conversely, if a self-assessment process  
124 is applicable then we would expect that contestants should match their vocal rates independent of  
125 dominance rank (Payne 1998; Briffa & Elwood 2009; Arnott & Elwood 2009). The present study was  
126 conducted to determine which of these alternative hypotheses best accounted for vocal rates during  
127 escalated contests in the fallow deer.

128



128

## Methods

129 Study site and population: This study was conducted over two consecutive rutting seasons (1996  
130 and 1997) on a herd of free-ranging European fallow deer resident in the Phoenix Park – a large  
131 enclosed city park consisting of 709 ha located at Dublin, Ireland (53° 22' N, 6° 21' W). The majority  
132 of the park (80%) is open grassland with the remaining 20% covered by mixed woodland. Fawns are  
133 tagged in each ear with unique colour/numbered tags shortly after birth in June and July each year.  
134 Identification of mature males in the population is facilitated by a combination of ear tags, coat  
135 colour and antler conformation.

136

137 Study System: The fallow deer is a seasonally breeding ungulate; the annual rut takes place from  
138 mid to late October in the Northern hemisphere. From late September and through October mature  
139 males show increasingly heightened levels of aggression with each other; there is an increasing  
140 tendency to escalate to fighting in relation to the number of matings observed in the population  
141 (Jennings et al. 2006, 2009). We addressed the function of groaning during contests that involved  
142 fighting in the present study. These contests could start with antler engagement following an  
143 approach by one male towards another or with a parallel walk that proceeded to antler contact  
144 (Jennings et al. 2003). To provide a clearly defined context and opponent in which to examine vocal  
145 rate as an assessment process, we recorded vocalizations from the point at which two males started  
146 to interact (e.g. started to parallel walk) and until the loser terminated the contest. In order to  
147 account for differences in contest duration we calculated winner and loser vocal behaviour as a rate  
148 per minute score (number of groans / non-contact duration \* 60). Because males do not vocalise  
149 when in antler contact we excluded the duration that contestants spent with antlers locked when  
150 calculating vocal rate per minute.

151

Fallow deer fights involve a range of aggressive actions, such as backward pushing, jump  
152 clashing and retreats (e.g. Alvarez 1993; Jennings et al. 2004, 2005a,b). Backward pushing involves

153 one animal forcing his opponent backwards while their antlers are locked, and jump clashing  
154 involves one animal initiating antler contact by jumping towards his opponent with his antlers  
155 lowered (Alvarez 1993). Retreats did not involve attacking an opponent; here one animal slowly  
156 backed away from his opponent with lowered antlers so that antler contact was broken. Once antler  
157 contact was broken the opponent often raised his antlers and slowly followed the retreating male  
158 (Jennings et al. 2005b). These actions are related to contest success and inform on assessment  
159 processes (Jennings et al. 2005 a,b), therefore, the approach adopted here was to include these  
160 data in the statistical models. This permitted us to examine whether vocal rates were determined by  
161 the action rates of either the opponent or self. Fights were recorded on video tape and screened  
162 using the Observer video analysis system (Noldus Information Technology, Wageningen, The  
163 Netherlands). We calculated the rate of these additional variables: the rate of backward pushes,  
164 jump clashes and retreats (per minute: number of actions / contact duration \* 60) for both contest  
165 winners and losers per fight using the duration that antlers were in contact.

166

167 Dominance ranking: Individual dominance ranks were calculated for each male in both years of the  
168 study using David's score (Gammell et al. 2003); we used all decisively resolved non-contact  
169 interactions recorded between mature males (4+ years) in that year to calculate dominance ranks.  
170 The two hierarchies are linear indicating that dominance relations between the males in both years  
171 were transitive (Jennings 2007). For pooled analyses involving dominance ranks, the David's scores  
172 were converted to ordinal ranks, the animal with the highest David's score in each year was assigned  
173 an ordinal rank of 1. Dominance rank provides a good measure of individual quality in the fallow  
174 deer and reliably correlates with mating success (e.g. Jennings et al. 2011).

175

176 Statistical analyses

177 We used generalized linear mixed models fitted with a restricted estimate maximum likelihood  
178 (REML) in the lme4 package for R (version 2.13.1). Because the dependent variables were  
179 transformed count data we used a Poisson distribution with Laplace parameter estimation for the  
180 models (Crawley 2007). Some individual males were recorded in more than one contest as a winner  
181 or loser and because vocal rate can change over the rut (e.g. Clutton-Brock et al. 1988, Table 4), we  
182 fitted the factor Day (calculated from the first day of October) within individual buck identity (winner  
183 and loser) as random effects to account for temporal pseudoreplication (Crawley 2007). There were  
184 42 individual males recorded on video tape that competed in 51 escalated contests with antler  
185 contact (fighting) and where at least one competitor was vocal. In order to test the different  
186 predictions outlined in the Introduction we ran separate models to explain winner and loser vocal  
187 rates. In order to reduce the full model to the best model (Burnham & Anderson 2004), we  
188 iteratively removed fixed factors from each model based on the z value score (removing the smallest  
189 value first) and then conducted a likelihood ratio (LR) test where:  $LR=2*[(\log\text{-likelihood of the best}$   
190  $\text{fitting model})-(\log\text{-likelihood of the worst fitting model})]$ , the best fitting model having the highest  
191 log-likelihood score. The significance of the LR is evaluated against a chi-square distribution with  
192 degrees of freedom equal to the difference in the number of predictors between the two competing  
193 nested models. The statistical models used here analyse the effect of several independent  
194 variables on the dependent variable; therefore the graphs presented show the relative effect of  
195 the independent variable of interest on the dependent variable (thus taking the effect of all  
196 independent variables into account; Jennings 2012).

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198

199

200

200 Results

201

202 The effect of contest action rate on groan rate

203 Winners and losers displayed similar rates of vocalizing over contest duration (Means = 3.8 and 5.2  
204 per minute, SE  $\pm$  0.8 and 0.9 respectively) and there was no difference in groan rate ( $t = 0.65$ ,  $p = 0.5$ )  
205 and no effect of contest duration ( $t = 1.17$ ,  $p = 0.2$ ) and no outcome  $\times$  contest duration interaction ( $t$   
206 =  $-0.20$ ,  $p = 0.8$ ). Within each model, both winner and loser groan rate were predicted by the  
207 opponent's groan rate (Table 1, Figure 1a and 1b). Winner vocal rate was predicted by both own and  
208 the loser's dominance rank (Table 1, Figure 2a and 2b); however, loser rate was not predicted by  
209 either own or winners rank. Winner vocal rate was negatively associated with backward push rate of  
210 the loser (Table 1, Figure 3a) and positively related to loser jump clash rate (Table 1, Figure 3b).  
211 Loser vocal rate was negatively related to winner retreat rate (Table 1, Figure 4); no other fixed  
212 factors were significant contributors to the model. Simplifying the models was attained by removing  
213 the weakest fixed factors in order to determine the best (most parsimonious) model relative to the  
214 full model: four variables were removed from both the full winner and loser models. For the winner  
215 model: winner jump clash rate, backward push rate, retreat rate and loser retreat rate were  
216 removed without a significant effect on the model (LR = 6.78,  $df = 4$ ,  $p = 0.15$ ). Removal of a fifth  
217 fixed factor, loser backward push rate, resulted in a model with significantly less explanatory power  
218 than the full model (Full model: AIC = 147.14, log likelihood = -57.59; Reduced model: AIC = 150.02,  
219 log likelihood = -64.01; LR = 12.89,  $df = 5$ ,  $p = 0.025$ ). For the loser model: loser retreat rate, jump  
220 clash rate and winner backward push rate, jump clash rate were removed without a significant  
221 decline in explanatory power (LR = 2.32,  $df = 4$ ,  $p = 0.7$ ). The additional removal of winner  
222 dominance rank yielded a significant reduction in explanatory power (Full model: AIC = 158.05, log  
223 likelihood = -63.02; Reduced model: AIC = 161.58, log likelihood = -69.79; LR = 13.53,  $df = 5$ ,  $p =$   
224 0.019).

225

226 Insert Table 1 about here

227 Insert Figures 1a and 1b, 2a and 2b, 3a and 3b, 4

228

229 Contest duration and dominance rank

230 The rank of the contest winner was related positively to contest duration ( $t = 2.45, p = 0.01$ ), i.e. as  
231 winner rank declined losers competed for longer (rank decreases with increasing number), but  
232 there was no relationship between duration and loser dominance rank ( $t = 0.67, p = 0.5$ ) and there  
233 was no interaction ( $t = -1.49, p = 0.1$ , see Figure 5). There was no relationship between duration of  
234 antler contact and winner rank ( $t = 1.15, p = 0.3$ ) or loser rank ( $t = 0.23, p = 0.8$ ) and no interaction ( $t$   
235  $= -1.15, p = 0.3$ ).

236

237 Insert Figure 5 about here

238

238

## Discussion

239 Game theoretic models divide into two main categories that differ fundamentally with regard to the  
240 type of assessment process adopted by contestants. In order to differentiate between these forms  
241 of assessment process, a commonly employed approach focusses on contestants' rates of action  
242 repetition over contest duration (Briffa & Elwood 2009). Nevertheless, despite underlying theoretical  
243 differences, it is an expectation of both types of model that the assessment process adopted will  
244 continue until the loser determines that it cannot defeat its opponent, and abandons the contest  
245 (Enquist & Leimar 1983; Mesterton-Gibbons et al. 1996; Payne & Pagel 1996, 1997; Payne 1998).  
246 Escalated contests in ungulates are characterised by a range of offensive and defensive actions that  
247 can inform on the strategic decisions adopted by contestants (Alvarez 1993; Clutton-Brock et al.  
248 1979; Jennings et al. 2003, 2004, 2005a,b; Jennings 2012); however, despite potentially shedding  
249 light on this process, vocal repetition rates have received comparatively little attention (but see  
250 Clutton-Brock & Albon 1979). Moreover, because contests are energetically costly to the  
251 competitors (Briffa & Sneddon 2007), vocal rate could provide an accurate index of current rather  
252 than overall quality (e.g. dominance rank: Jennings et al. 2010, 2011). The present study addressed  
253 these issues; specifically, we investigated the function of vocal rate within the context of escalated  
254 contests and asked whether it corresponded with a mutual assessment process. Such an approach  
255 permitted us to test predictions derived from game theoretic models of contest behaviour,  
256 specifically that individuals employ mutual assessment of opponent quality during contests (Enquist  
257 & Leimar 1983; Payne & Pagel 1996, 1997; Payne 1998).

258 As noted above, individual vocal rates in male ungulates appear to be influenced by context.  
259 It has been noted that very high rates have been recorded when vocal males are in proximity to each  
260 other but not obviously engaged in agonistic interactions (e.g. McElligott & Hayden 1999), relative to  
261 vocal rates during dyadic contests (e.g. Clutton-Brock & Albon 1979; Wolff 1998). In the present  
262 study, the vocal rate of this population of deer approximated that of red deer engaged in dyadic

263 competition; therefore, by reference to the parameters established by Clutton-Brock and Albon  
264 (1979), vocal rates in this population appear to fall into a general optimum range that permits an  
265 exchange of information. We note that the data reported by Clutton-Brock and Albon (1979) are  
266 derived from interactions that precede antler contact whereas the present study takes its data from  
267 interactions that have escalated to contact. However, this discrepancy is not relevant in theoretical  
268 terms; only the SAM anticipates phases of escalating intensity; however, contest actions are  
269 permissible over all phases subject to the models theoretical constraints (Enquist & Leimar 1983;  
270 Enquist et al. 1990; Koops & Grant 1993 but see Hsu et al 2008). Nevertheless, the question as to  
271 whether red deer vocal rates during the pre-antler contact phase support a mutual assessment  
272 process has been challenged. The SAM predicts that both competitors should signal at a constant  
273 rate in order to facilitate the assessment process and this core prediction concerning repetition  
274 rate stability was not met (Payne 1998). Furthermore, it is important to note that evidence for vocal  
275 exchanges is not in itself evidence for mutual assessment; self-assessment models require  
276 monitoring of opponent action rates and because this requires matching of action rates they can  
277 comfortably account for such patterns of vocal exchange (Arnott & Elwood 2009; Briffa & Elwood  
278 2009). We note that there is evidence of such matching in the present study.

279 Escalated contests generally involve many different forms of aggressive action (Hardy &  
280 Briffa in press); however, the relationship between contest actions and acoustic behaviour has rarely  
281 been investigated (but see Logue et al. 2010). Moreover, during fights, energetic costs are expected  
282 to increase as a consequence of an increase in the number of repetitions of an action or suite of  
283 actions (Briffa & Sneddon 2007). The production of vocalisations is thought to be costly (e.g.  
284 Oberweger & Goller 2001) and it is possible, therefore, that vocal rates might be affected by the  
285 current RHP of each contestant. However, there is inconsistent evidence to support this point; for  
286 example, when contestants remain silent there is a greater level of aggression than contests where  
287 males emitted acoustic signals (Logue et al. 2010) while the reverse has also been shown (e.g. Bartoš  
288 et al. 2007). Our results, suggest that vocal rate is unrelated to contest cost in terms of attacking

289 contest actions: the best model fits indicated that in both instances only slight support for the idea  
290 that attacking actions are positively related to vocal rate.

291 Under a mutual assessment process contest winners are expected to out-produce their  
292 opponent while holding vocal rates consistent over time (Enquist & Leimar 1983). This was not the  
293 case; winners did not out-produce losers and although vocal rates did not differ over contest  
294 duration, this aspect of repetition rate can be accounted for by a self-assessment process (Briffa &  
295 Elwood 2009). Therefore, consistent with one theoretical interpretation of red deer vocal contests  
296 (e.g. Payne 1998) a preliminary interpretation of repetition rates in this study do not support a  
297 mutual assessment process. However, during contests, vocal rate is expected to be related to  
298 resource holding potential of the producer (RHP: Parker 1974; Enquist & Leimar 1983, see Clutton-  
299 Brock & Albon 1979; Wolff 1998); therefore, we expect that vocal rate should be related to  
300 individual dominance rank. This was the case for winners but not losers (Table 1), although a  
301 simplification of the models that reduced the number of fixed factors indicated that winner and  
302 loser rank was an important factor in determining winner and loser vocal rates. Based on this  
303 somewhat restricted view of the data, i.e. focussing simply on the evidence for altering vocal rate  
304 based on both self and opponent dominance rank, our results show support for a mutual  
305 assessment process (Enquist & Leimar 1983; Payne 1998).

306 Examination of the full winner model shows that five of the nine fixed explanatory variables  
307 contributed significantly to the model; subsequent iterative removal of the four weaker factors  
308 indicated that these five factors should be retained in the best model (Burnham & Anderson 2004).  
309 With the exception of winner dominance rank, the remaining variables related to loser contest  
310 action rates and dominance rank. Under self-assessment we would expect winner vocal rate to be  
311 related to winner contest actions rates including dominance. From a theoretical perspective  
312 attending to the rate of behavioural actions of an opponent rather than the difference in rates falls  
313 outside predictions made by current models – both self- and mutual-assessment - and suggests an



314 “opponent-only” rather than mutual-assessment process (Arnott & Elwood 2009). The effect of  
315 action rate on loser vocal rate was more equivocal; in addition to the rank of both opponents, two  
316 winner factors and a single loser factor were retained in the best model while two winner and two  
317 loser variables were excluded. This suggests that there is some evidence to support an opponent-  
318 only assessment process. To further examine this possibility we regressed contestant dominance  
319 rank against contest duration. Only winner rank was related to duration: as winner rank, (i.e. quality)  
320 declined there was an increase in contest duration. Therefore, losers were sensitive to winner rank  
321 without reference to their own rank, which is consistent with an opponent-only assessment process.  
322 Perhaps because such predictions are not encompassed within traditional models there has been  
323 little attempt to formally investigate opponent-only assessment either as a contest strategy or to  
324 define it within a theoretical model. However, the present findings add to a number of empirical  
325 studies that demonstrate opponent-only assessment in insects (e.g. Rillich et al. 2007) and fish  
326 (Prenter et al. 2008; Reddon et al. 2011; reviewed by Arnott & Elwood 2009).

327 In conclusion, we have found that vocal rate during fallow deer contests do not conform to  
328 the theoretical prediction of either a self or a mutual assessment process. Rather, our results suggest  
329 that it is the action rate of the opponent during contests that is central to determining both winner  
330 and loser vocal rates. For both contestants it was evident that vocal rate was influenced by the  
331 motivation or willingness of their opponent to invest in the contest (see also Rillich et al. 2007;  
332 Reddon et al. 2011). Since methods were proposed to objectively discriminate modes of assessment  
333 in contests (see for example Briffa & Elwood 2009; Taylor and Elwood 2003), there have been a  
334 number of studies that indicate opponent-only assessment (see above) or no assessment at all (e.g.  
335 Reichert & Gerhardt 2011). The present study adds to these accounts in contradicting the pervasive  
336 view that animal contests are settled by a process of mutual assessment. Nevertheless, it still  
337 remains to be established whether such a process governs vocal behaviour over the range of  
338 contexts in which vocalizations occur.

339

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## List of Figures

457

458

459 Figure 1. The relationship between winner and loser vocal rate controlling for the effects of the  
460 other contest actions and dominance rank. Panel A shows the relationship between winner groan  
461 rate and loser groan rate. Panel B shows the relationship between loser groan rate and winner  
462 groan rate.

463

464 Figure 2. The relationship between winner vocal rate and dominance rank after controlling for the  
465 effects of the remaining contest actions. Panel A shows the relationship between the winner's groan  
466 rate and dominance rank. Panel B shows the relationship between winner vocal rate and loser  
467 dominance rank.

468

469 Figure 3. The relationship between winner vocal rate and loser contest actions rates. Panel A shows  
470 the relationship between winner vocal rate and loser backward push rate. Panel B shows the  
471 relationship between vocal rate and loser jump clash rate.

472

473 Figure 4. The relationship between loser vocal rate and winner retreat rate controlling for the other  
474 fixed factors.

475

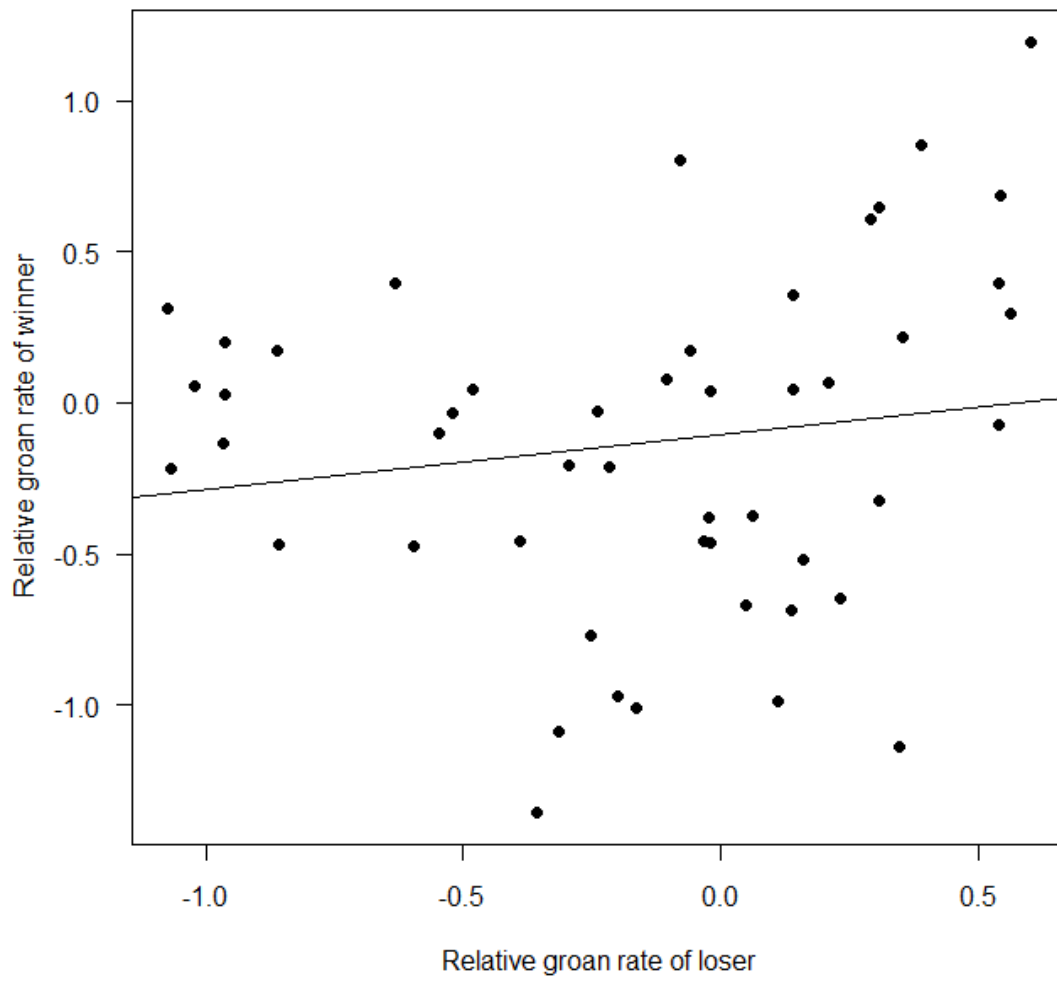
476 Figure 5. The relationship between dominance rank and contest duration during contests where  
477 winners (solid line) and/or losers (dashed line) engaged in groaning.

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479 Figure 1a

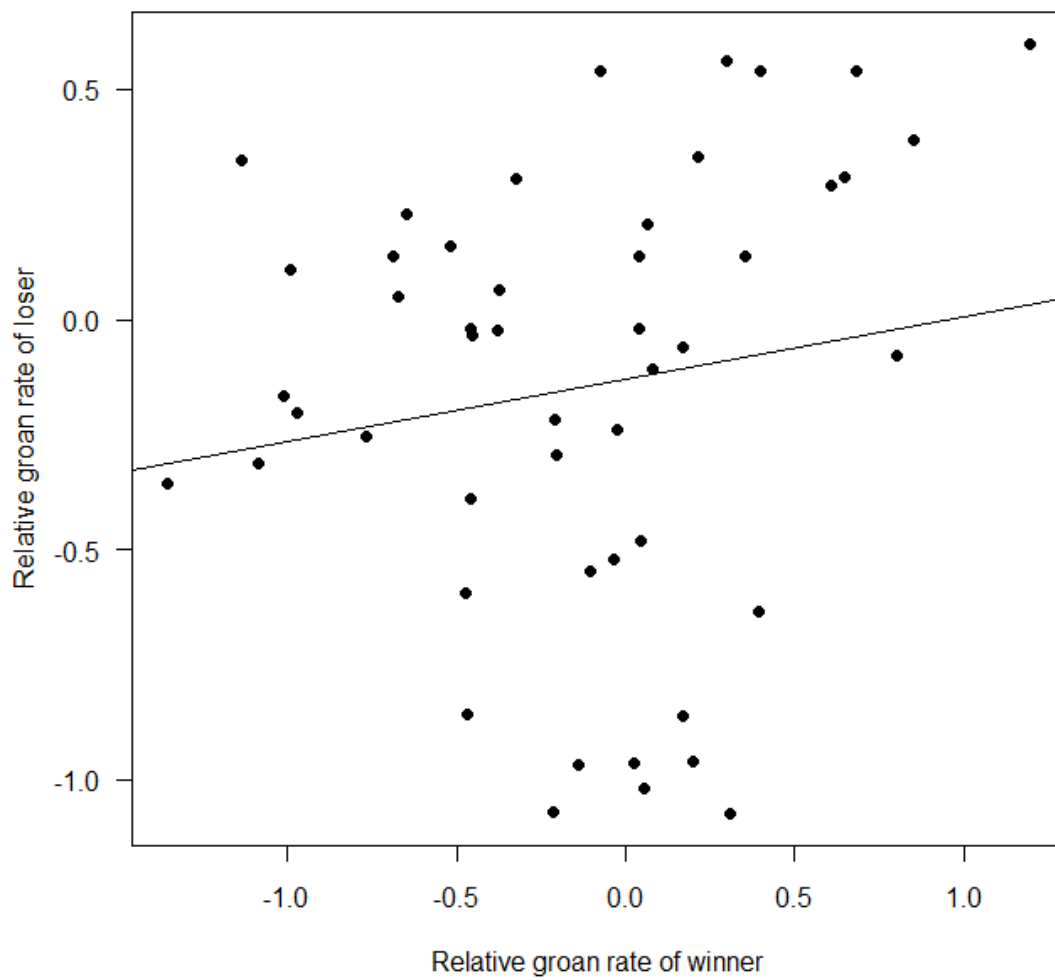


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482 Figure 1b



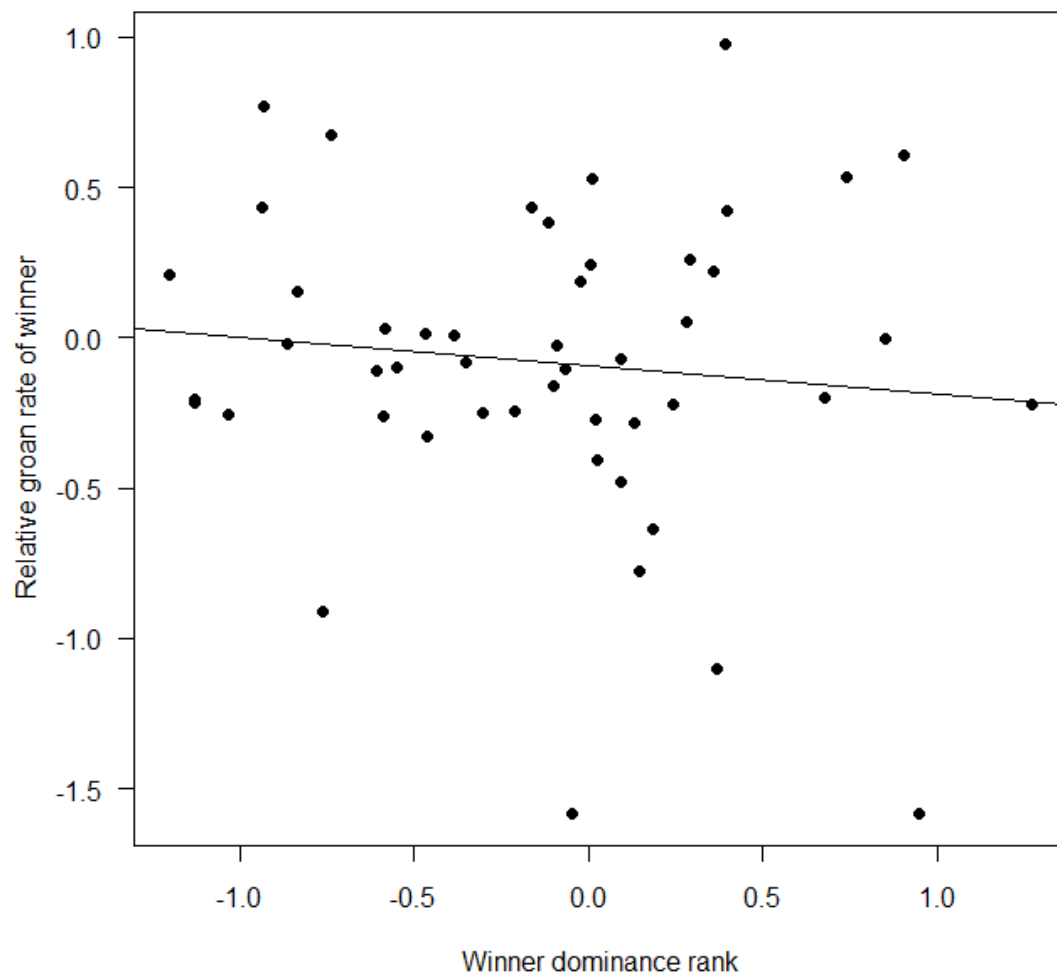
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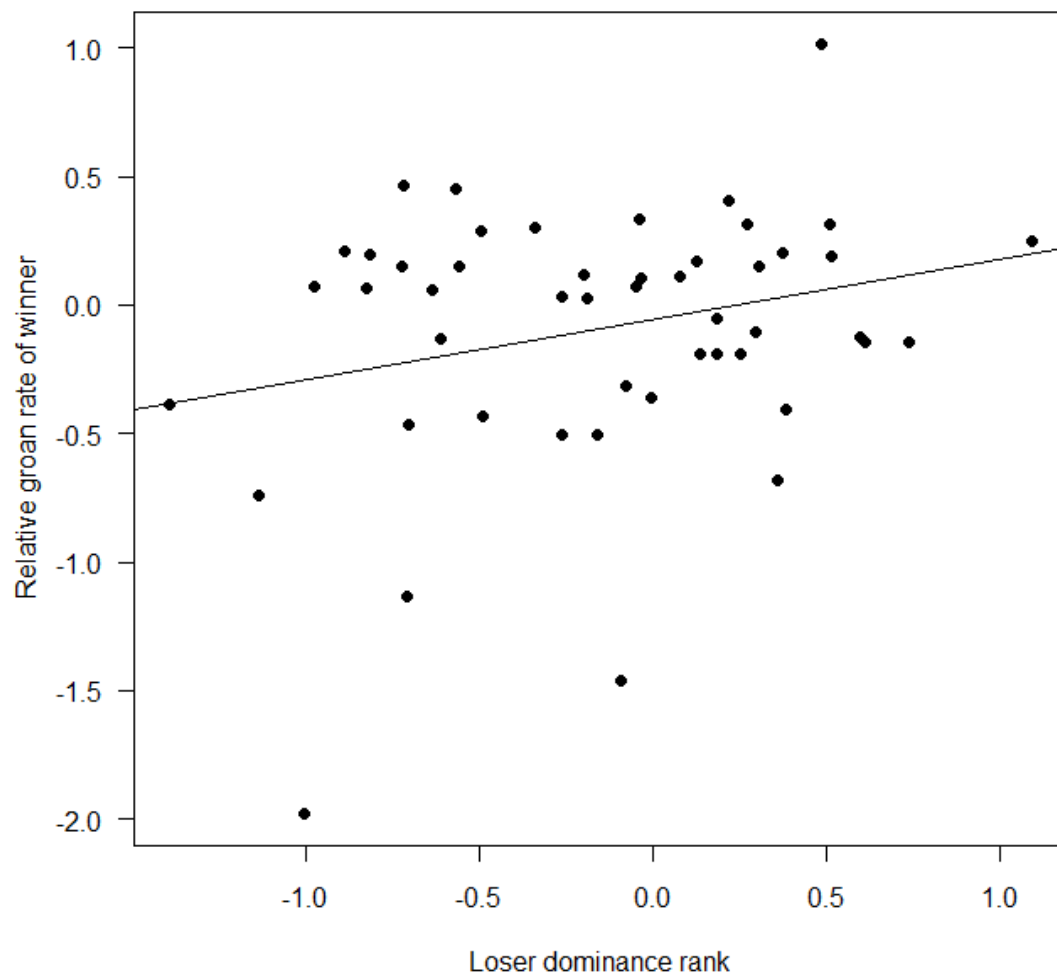


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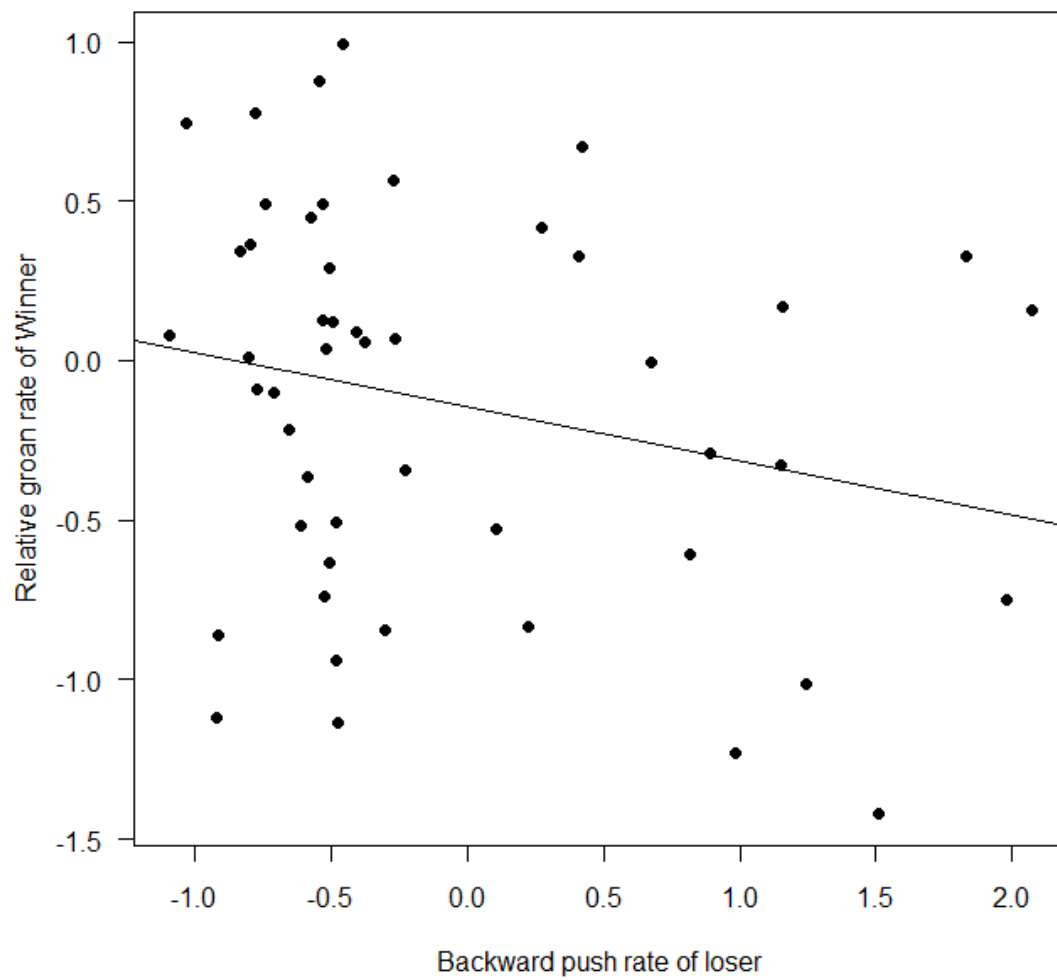


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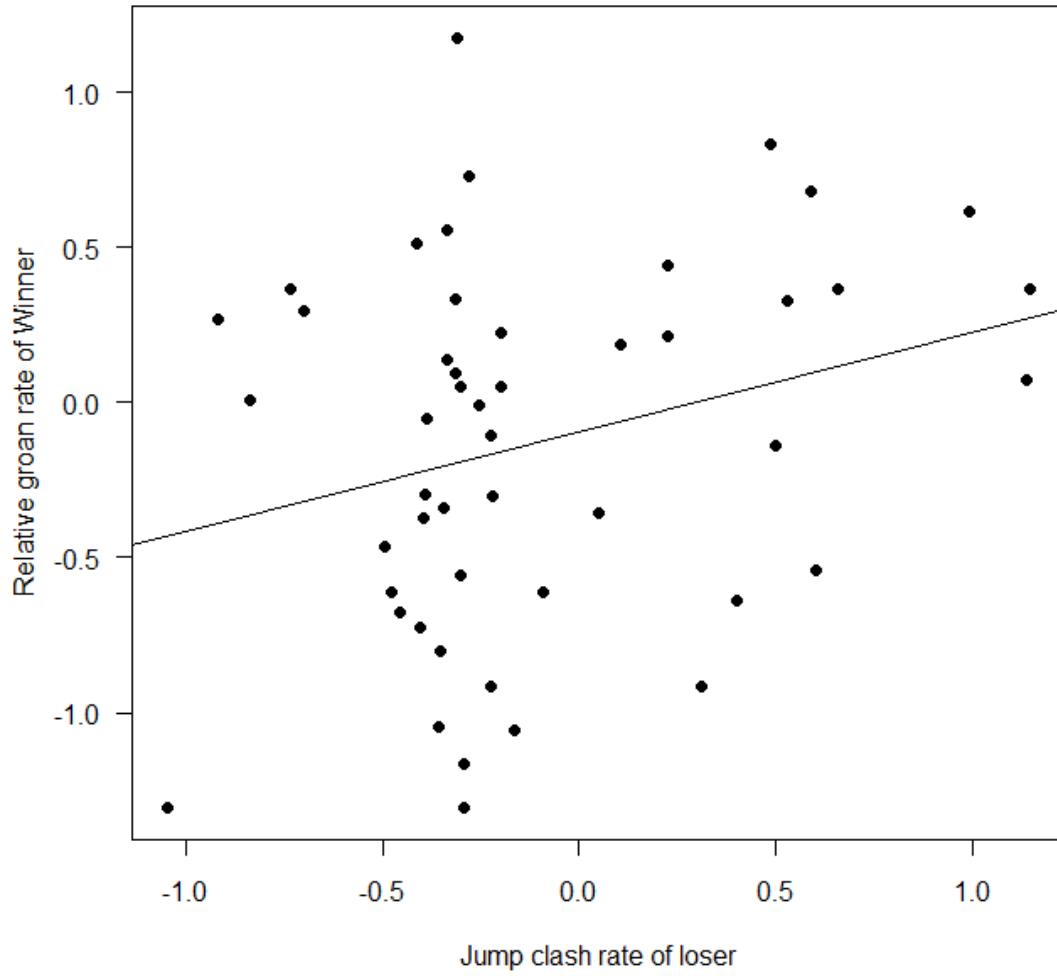


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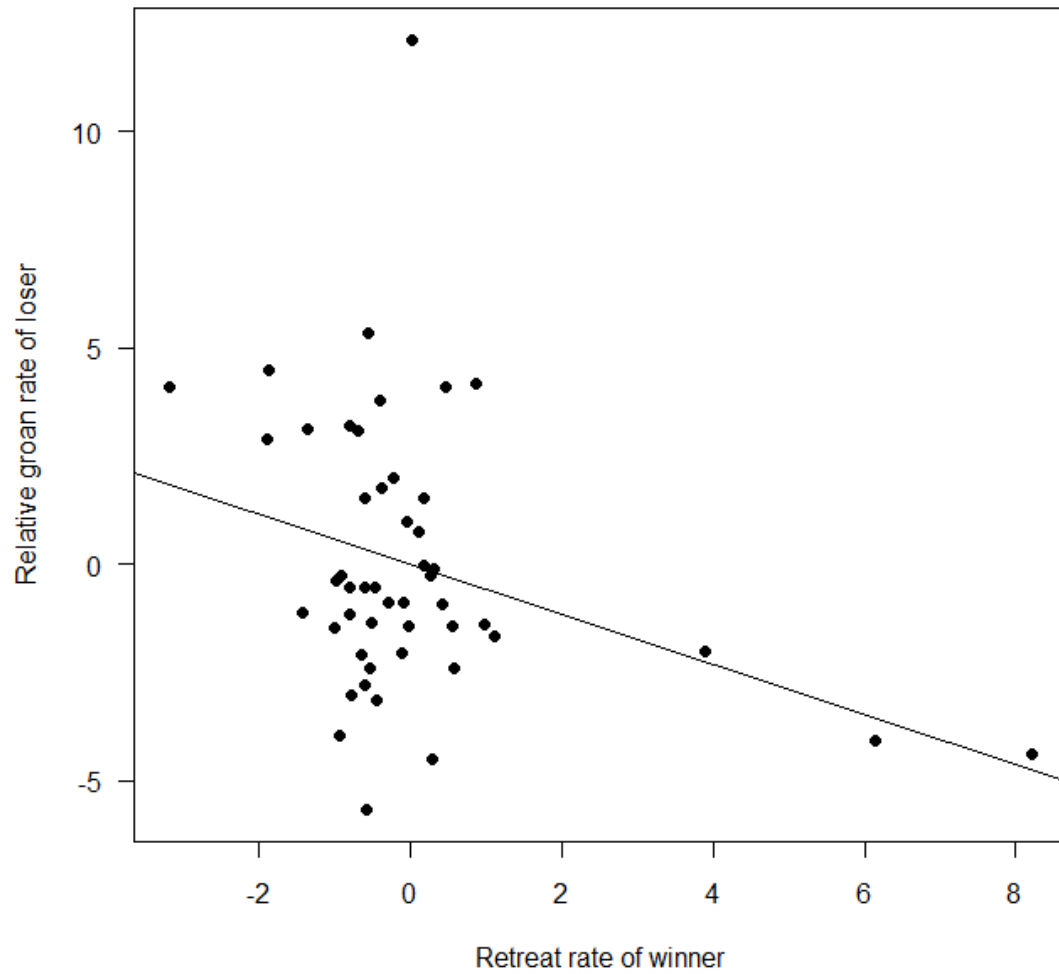
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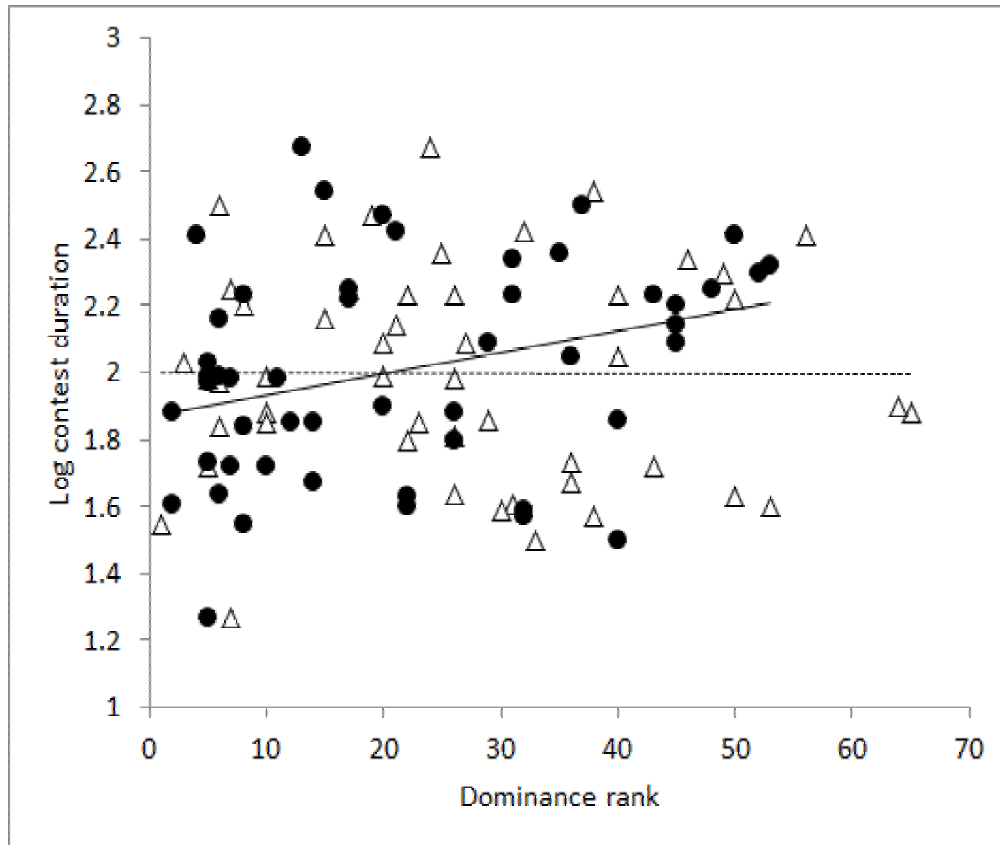
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501 Figure 5

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1 Table 1. Two generalised linear mixed models describing the contribution of nine fixed factors to winner and loser groan rate.

Fixed effects	Winner vocal rate	Estimate	SE	Loser vocal rate	Estimate	SE
Intercept	$z = 0.38, p = 0.7$			$z = 2.76, p = .006$	1.22	0.44
Opponent groan rate	$z = 3.19, p = 0.001$	0.07	0.02	$z = 2.00, p = 0.048$	0.07	0.03
Winner dominance rank	$z = -3.80, p = 0.002$	-0.04	0.01	$z = -0.85, p = 0.4$	-0.01	0.01
Loser dominance rank	$z = 3.19, p = 0.001$	0.04	0.01	$z = -1.05, p = 0.3$	-0.01	0.01
Winner backward push rate	$z = 1.01, p = 0.3$	0.05	0.05	$z = 0.304, p = 0.8$	0.02	0.05
Loser backward push rate	$z = -3.01, p = 0.003$	-0.42	0.14	$z = 1.64, p = 0.1$	0.20	0.12
Winner jump clash rate	$z = -1.00, p = 0.3$	-0.04	0.04	$z = 0.62, p = 0.5$	0.03	0.04
Loser jump clash rate	$z = 3.14, p = 0.002$	0.28	0.09	$z = -0.300, p = 0.8$	-0.03	0.11
Winner retreat rate	$z = 1.64, p = 0.1$	0.14	0.08	$z = -2.25, p = 0.02$	-0.39	0.17
Loser retreat rate	$z = -1.38, p = 0.2$	-0.03	0.02	$z = -0.11, p = 0.9$	-0.001	0.01

2 Winner rate model. AIC = 147.1, log likelihood = -57.57; Loser rate model. AIC = 158, log likelihood = -63.02.

3

1

3 Highlights

- 4 1. Investigates the relationship between vocal rate and assessment during escalated contests
- 5 2. Examines the role of contest behaviour of both contestants on vocal rate
- 6 3. Shows that vocal rate does not conform to a mutual assessment process
- 7 4. Results show that fallow deer vocal rate follows an opponent-only process
- 8 5. Results do not conform to traditional assumptions concerning the function of vocal rates during ungulate contests

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