Queen's University
Belfast

Vocal rate as an assessment process during fallow deer contests

Published in:
Behavioural Processes

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
Link to publication record in Queen's University Belfast Research Portal

Accepted Manuscript

Title: Vocal rate as an assessment process during fallow deer contests

Authors: Dómhnall J. Jennings, Robert W. Elwood, Caitríona M. Carlin, Thomas J. Hayden, Martin P. Gammell
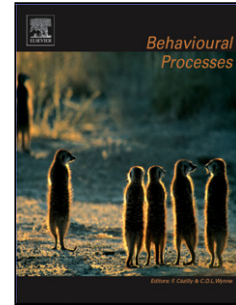
Please cite this article as: Jennings, D.J., Elwood, R.W., Carlin, C.M., Hayden, T.J., Gammell, M.P., Vocal rate as an assessment process during fallow deer contests, *Behavioural Processes* (2010), doi:10.1016/j.beproc.2012.07.003

1   Vocal rate as an assessment process during fallow deer contests

2

3   Dómhnall J. Jennings[a]*, Robert W. Elwood[b], Caitríona M. Carlin[c], Thomas J. Hayden[d] and Martin P.

4   Gammell[e]

5   [a] Institute of Neuroscience, Newcastle University, Newcastle upon Tyne

6   [b] School of Biology, Queen's University, Belfast

7   [c] Centre for Environmental Science, National University of Ireland, Galway

8   [d] School of Biology and Environmental Science, University College, Dublin

9   [e] Department of Life and Physical Sciences, Galway-Mayo Institute of Technology, Galway

10

11   *Correspondence: D. Jennings, Centre for Behaviour and Evolution, Institute of Neuroscience,

12   Newcastle University, Framlington Place, Newcastle upon Tyne, NE2 4HH, UK (email:

13   domhnall.jennings@ncl.ac.uk).

14

15   C. Carlin is at the Applied Ecology Unit, Centre for Environmental Science, National University of

16   Ireland Galway, University Road, Galway, Ireland (caitrona.carlin@nuigalway.ie). R. Elwood is at the

17   School of Biological Sciences, Queen's University, Belfast, BT9 7BL, UK (r.elwood@qub.ac.uk). T.

18   Hayden is at the School of Biology and Environmental Science, University College, Belfield, Dublin 4,

19   Ireland (tom.hayden@ucd.ie). M. Gammell is at the Department of Life and Physical Sciences,

20   Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland (martin.gammell@gmit.ie).

21

22

1

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.

36

37

38

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

40   only' assessment

41

42

2

42   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

3

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

4

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

5

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

6

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

7

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

8

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-likelihood of the best

190   fitting model)-(log-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).

197

198

199

200

9

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 ± 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 x 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).

10

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

11

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

12

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

13

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

14

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

15

339   References

340   Alvarez, F. 1993. Risks of fighting in relation to age and territory holding in fallow deer. Canadian

341   Journal of Zoology 71, 376-383.

342   Andersson, M. 1994. Sexual Selection. Princeton University Press. New Jersey.

343   Arnott, G. & Elwood, R.W. 2008. Information gathering and decision making about resource value in

344   animal contests. Animal Behaviour 76, 529–542.

345   Arnott, G. & Elwood, R.W. 2009. Assessment of fighting ability in animal contests. Animal Behaviour

346   77, 991-1004.

347   Bartoš, L., Fričová, B., Bartošová, J., Panamá, J., Šustr, P. & Šmidová, E. 2007. Estimation of

348   probability of fighting in fallow deer (Dama dama) during the rut. Aggressive Behaviour 33,

349   7-13.

350   Bosch, J. & Marquez, R. 1996. Acoustic competition in male midwife toads Alytes obstetricians and

351   Alytes cisternasii: response to neighbour size and calling rate. Implications for female choice.

352   Ethology 102, 841-855.

353   Briffa, M. 2008. Decisions during fights in the house cricket, Acheta domesticus: mutual or self

354   assessment of energy, weapons and size? Animal Behaviour 75, 1053-1062.

355   Briffa, M. & Elwood, R.W. 2009. Difficulties remain in distinguishing between mutual and self-

356   assessment in animal contests. Animal Behaviour 77, 759-762.

357   Briffa, M. & Sneddon, L.U. 2007. Physiological constraints on contest behaviour. Functional Ecology

358   21, 627-637.

359   Briffa, M. & Sneddon, L.U. 2010. Contest behaviour, in: Westneat, D.F. and Fox, C.W. (Eds),

360   Evolutionary Behavioral Ecology. Oxford University Press, Oxford, pp. 246-265.

16

361   Burnham, K.P. & Anderson, D.R. 2004. Model Selection and Multimodel Inference: A Practical

362   Information-Theoretic Approach, second ed. Springer, New York.

363   Clutton-Brock, T.H. & Albon, S.D. 1979. The roaring of red deer and the evolution of honest

364   advertisement. Behaviour 69, 145-170.

365   Clutton-brock, T.H., Albon, S.D., Gibson, R.M. & Guinness, F.E. 1979. The logical stag: adaptive

366   aspects of fighting in red deer. Animal Behaviour, 27, 211-255.

367   Clutton-Brock, T.H., Green, D., Hiraiwa-Hasegawa, M. & Albon, S.D. 1988. Passing the buck: resource

368   defence, lek-breeding and mate choice in fallow deer. Behavioral Ecology and Sociobiology

369   23, 281-296.

370   Crawley, M.J. 2007. The R Book. Wiley, Chichester.

371   Elias, D.O., Kasumovic, M.M., Punzalan, D., Andrade, M.C.B. & Mason, A.C. 2008. Assessment during

372   aggressive contests between male jumping spiders. Animal Behaviour 76, 901-910.

373   Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour. decision rules and assessment of

374   relative strength. Journal of Theoretical Biology 102, 387-410.

375   Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. 1990. A test of the sequential

376   assessment game. fighting in the cichlid fish Nannacara anomala. Animal Behaviour 40, 1-14.

377   Gammell, M.P., de Vries, H., Jennings, D.J., Carlin, C.M. & Hayden, T.J. 2003. David's score. a more

378   appropriate dominance ranking method than Clutton-Brock et al.'s index. Animal Behaviour

379   66, 601-605.

380   Goubault, M., Cortesero, A.M., Poinsot, D., Wajnberg, E. & Boivin, G. 2007. Does host value influence

381   female aggressiveness, contest outcome and fitness gain in parasitoids? Ethology 113, 334-

382   343.

17

383   Hammerstein, P. & Parker, G.A. 1982. The asymmetric war of attrition. Journal of Theoretical

384   Biology 96, 647-682.

385   Hardy, I.C.W. & Briffa, M. in press. Animal Contests. Cambridge University Press, Cambridge.

386   Hsu, Y., Lee, S.P., Chen, M.H., Yang, S.Y. and Cheng, K.C. 2008. Switching assessment strategy during

387   a contest. fighting in killifish Kryptolebias marmoratus. Animal Behaviour 75, 1641-1649.

388   Jennings, D.J. 2007. The effect of chemical immobilization on dominance rank in the fallow deer.

389   Animal Behaviour 74, 1107-1110.

390   Jennings, D.J. 2012. A right-sided bias in the decision to terminate fallow deer parallel walks.

391   evidence for lateralization during a lateral display. Animal Behaviour 83, 1427-1432..

392   Jennings, D.J., Carlin, C.M. & Gammell, M.P. 2009. A winner effect supports third-party intervention

393   behaviour during fallow deer, Dama dama, fights. Animal Behaviour 77, 343-348.

394   Jennings, D.J., Carlin, C.M., Hayden, T.J. & Gammell, M.P. 2010. Investment in fighting in relation to

395   body condition, age and dominance rank in the male fallow deer (Dama dama). Animal

396   Behaviour 79, 1293-1300.

397   Jennings, D.J., Carlin, C.M., Hayden, T.J. & Gammell, M.P. 2011. Third-party intervention behaviour

398   during fallow deer fights. the role of dominance, age, fighting and body size. Animal

399   Behaviour 81, 1217-1222.

400   Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J. 2002. Does lateral presentation of the

401   palmate antlers during fights by fallow deer (Dama dama) signify dominance or submission?

402   Ethology 108, 389-401.

403   Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J. 2003. Is the parallel walk between

404   competing male fallow deer (Dama dama) a lateral display of quality? Animal Behaviour 65,

405   1005-1012.

18

406   Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J. 2004. Effect of body weight, antler length,

407   resource value and experience on fight duration and intensity in fallow deer. Animal

408   Behaviour 68, 213-221.

409   Jennings, D.J., Gammell, M.P., Payne, R.J.H. & Hayden, T.J. 2005a. An investigation of assessment

410   games during fallow deer fights. Ethology 111, 511-525.

411   Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J. 2005b. Win, lose or draw. a comparison of

412   fight structure based on fight conclusion in the fallow deer. Behaviour 142, 423-439.

413   Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J. 2006. Is difference in body weight, antler

414   length, age or dominance rank related to the number of fights between fallow deer (Dama

415   dama)? Ethology 112, 258-269.

416   Komers, P.E., Pélabon, C. & Stenström, D. 1997. Age at first reproduction in male fallow deer: age-

417   specific versus dominance specific behaviors. Behavioral Ecology 8, 465-462.

418   Koops, M.A. & Grant, J.W.A. 1993. Weight asymmetry and sequential assessment in convict cichlids.

419   Canadian Journal of Zoology 71, 475-479.

420   Logue, D.M., Abiola, I.O., Rains, D., Bailey, N.W., Zuk, M. & Cade, W.H. 2010. Does signalling mitigate

421   the cost of agonistic interactions? A test in a cricket that has lost its song. Proceedings of the

422   Royal Society 277, 2571-2575.

423   Maynard Smith, J. & Harper, D. 2003. Animal Signals. Oxford University Press, Oxford.

424   McElligott, A.G. & Hayden, T.J. 1999. Context-related vocalization rates of fallow buck, Dama dama.

425   Animal Behaviour 58, 1095-1104.

426   Mesterton-Gibbons, M., Marden, J.H. & Dugatkin, L.A. 1996. On wars of attrition without

427   assessment. Journal of Theoretical Biology 181, 65-83.

19

428   Oberweger, K. & Goller, F. 2001. The metabolic cost of birdsong. Journal of Experimental Biology

429   204, 3379-3388.

430   Parker, G.A. 1974. Assessment strategy and the evolution of fighting behaviour. Journal of

431   Theoretical Biology 47, 223-243.

432   Payne, R.J.H. & Pagel, M. 1996. Escalation and time costs in displays of endurance. Journal of

433   Theoretical Biology 183, 185-193.

434   Payne, R.J.H. & Pagel, M. 1997. Why do animals repeat displays? Animal Behaviour 54, 109-119.

435   Payne, R.J.H. 1998. Gradually escalating fights and displays. the cumulative assessment model.

436   Animal Behaviour 56, 651-662.

437   Prenter, J., Elwood, R.W. & Taylor, P.W. 2006. Self assessment by males during energetically

438   expensive contests over precopula females in amphipods. Animal Behaviour 72, 861-868.

439   Prenter, J., Taylor, P.W. & Elwood, R.W. 2008. Larger body size for winning and larger swords for

440   winning quickly in swordtail males, Xiphophorus helleri. Animal behaviour 75, 1981-1987.

441   Reddon, A.R., Voisin, M.R., Menon, N., Marsh-Rollo, S.E., Wong, M.Y.L. & Balshine, S. 2011. Rules of

442   engagement for resource contests in a social fish. Animal Behaviour 82, 93-99.

443   Reichert, M.S. & Gerhardt, H.C. 2011. The role of body size on the outcome, escalation and duration

444   of contests in the grey treefrog, Hyla versicolor. Animal Behaviour, 82, 1357-1366.

445   Rillich, J., Schilderberger, K. & Stevenson, P.A. 2007. Assessment strategy of fighting crickets

446   revealed by manipulating information exchange. Animal behaviour 74, 823-836.

447   Taylor, P.W. & Elwood, R.W. 2003. The mismeasure of animal contests. Animal Behaviour 65, 1195-

448   1202.

449   Todt, D. & Naguib, M. 2000. Vocal interactions in birds. the use of song as a model in

450   communication. Advances in the Study of Behavior 29, 247-296.

20

451   Wagner, W.E. 1989. Fighting, assessment, and frequency alteration in Blanchard's cricket frog.

452   Behavioral Ecology and Sociobiology 25, 429-436.

453   Wolff, J.O. 1998. Breeding strategies, mate choice, and reproductive success in American bison.

454   Oikos 83, 529-544.

455

456

457

21

457 List of Figures

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
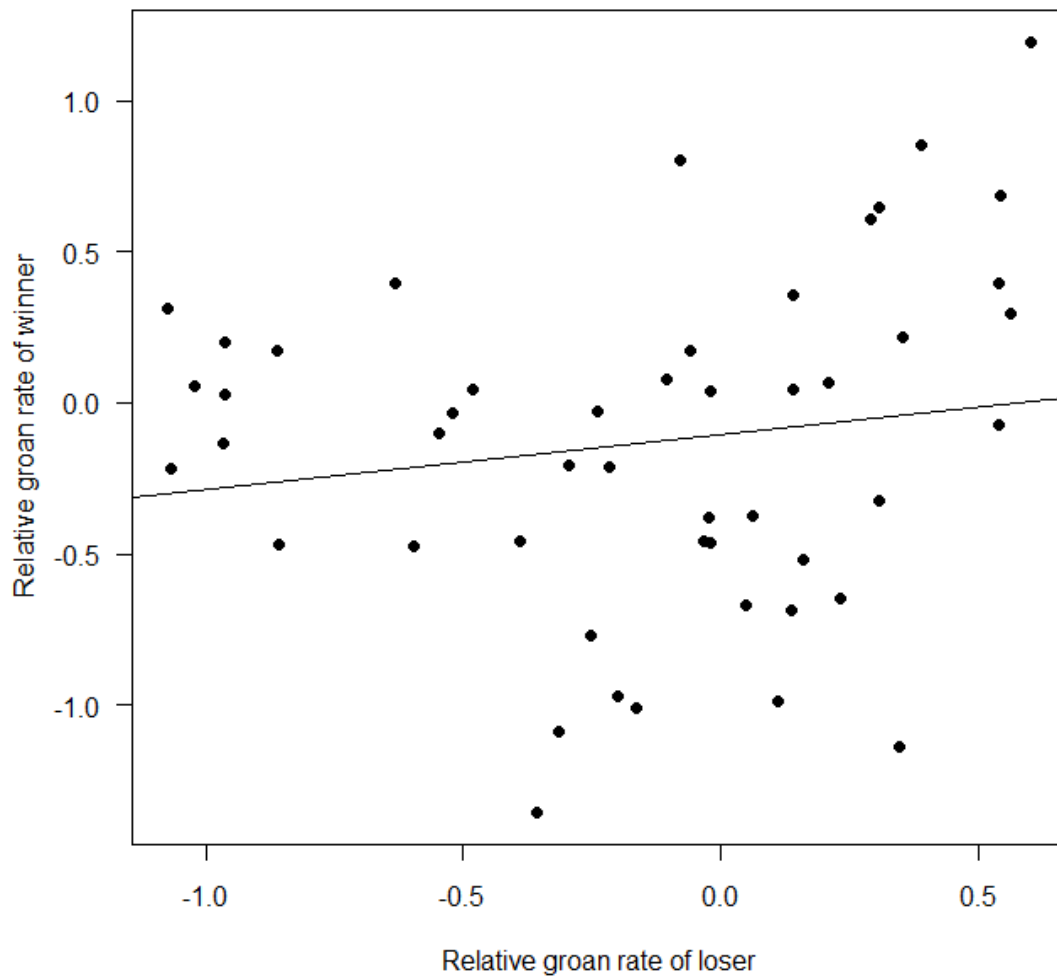
474 fixed factors.

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.
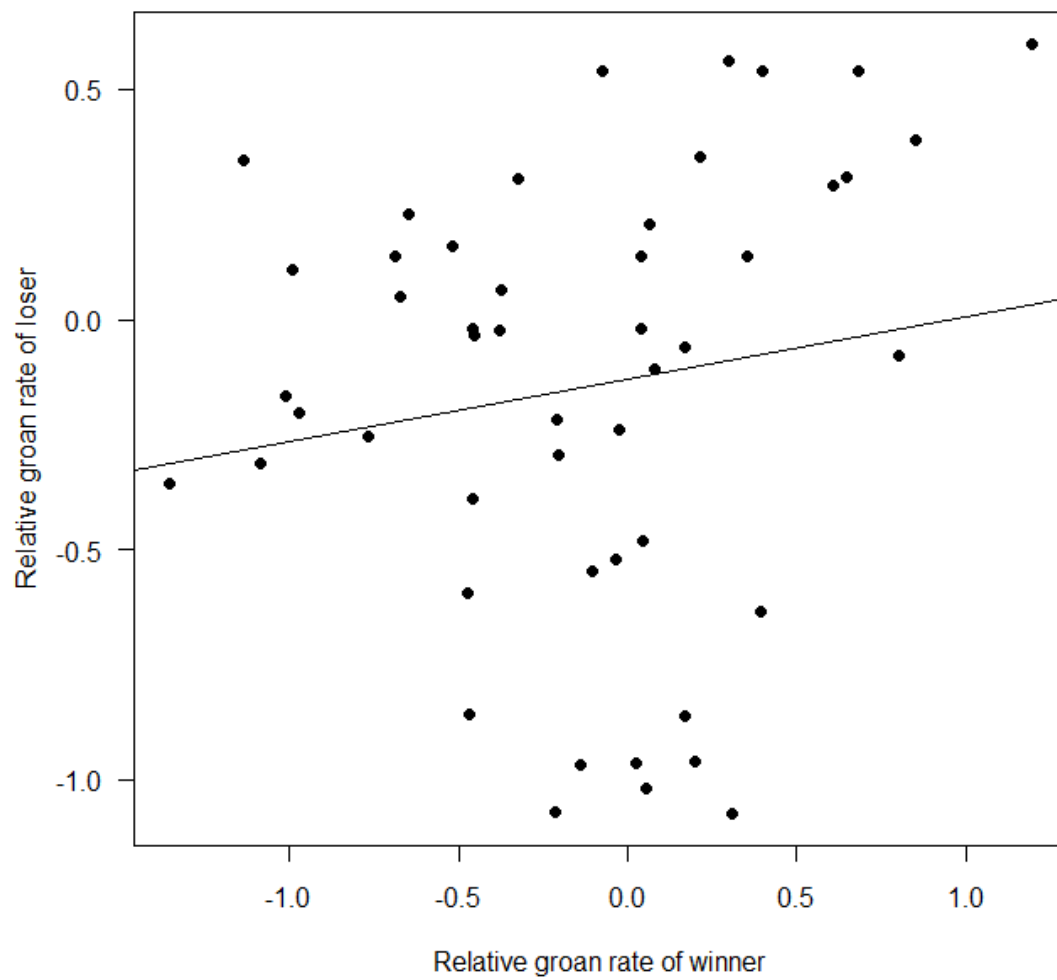
478

479

22

479   Figure 1a
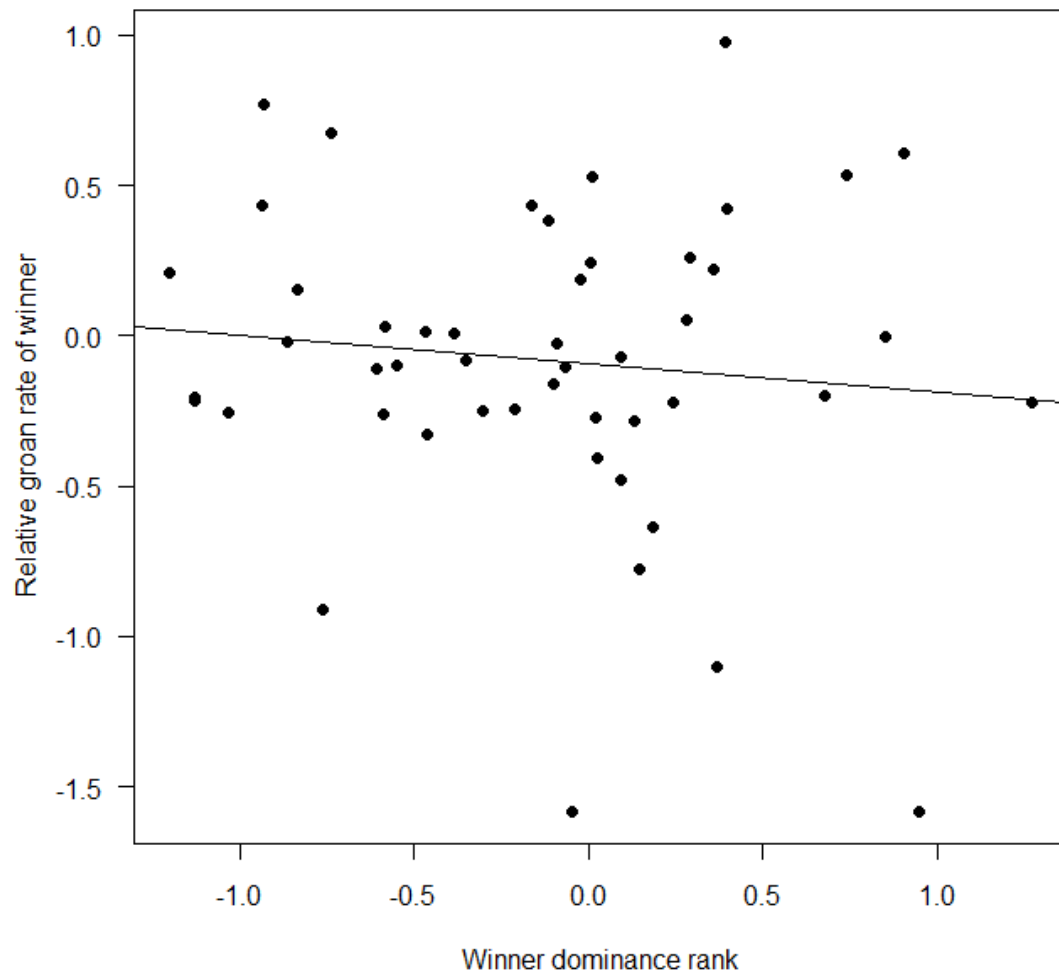

480

481

482

23

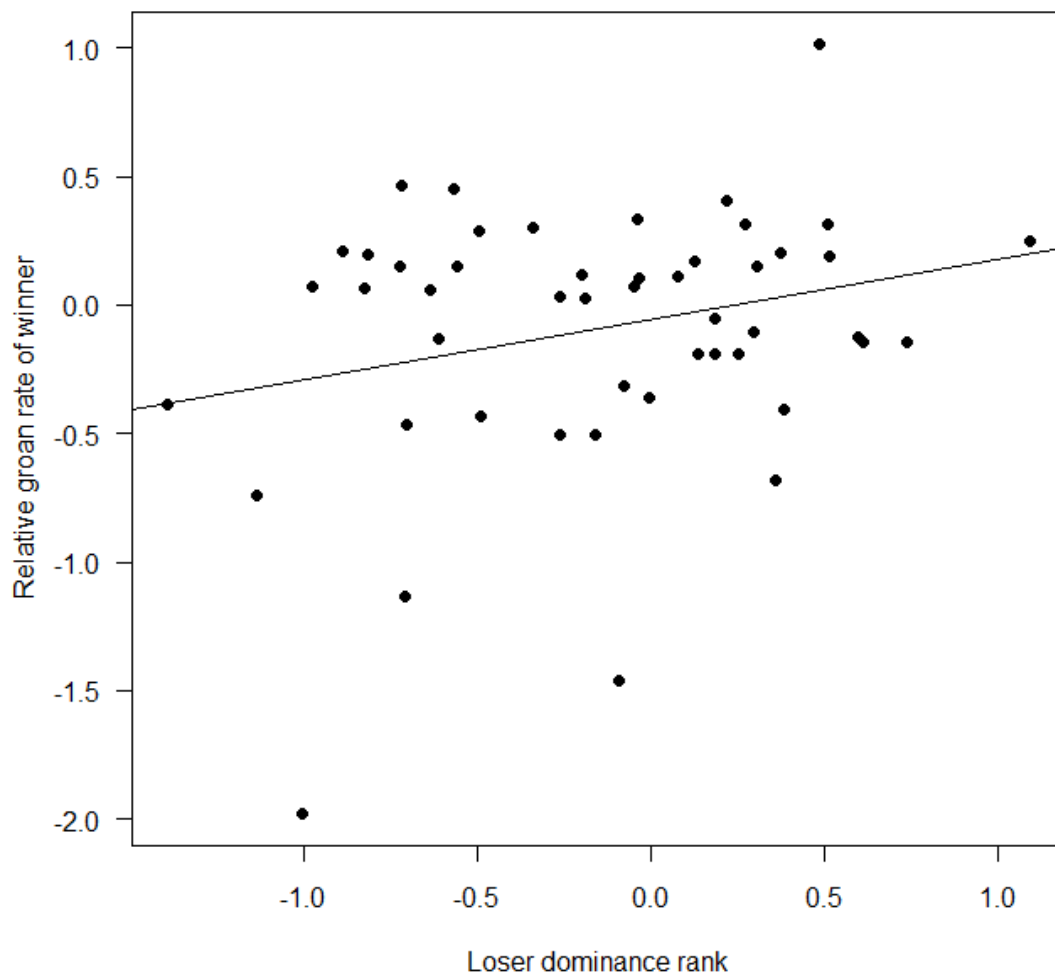482   Figure 1b

483

484

485

486

486   Figure 2a

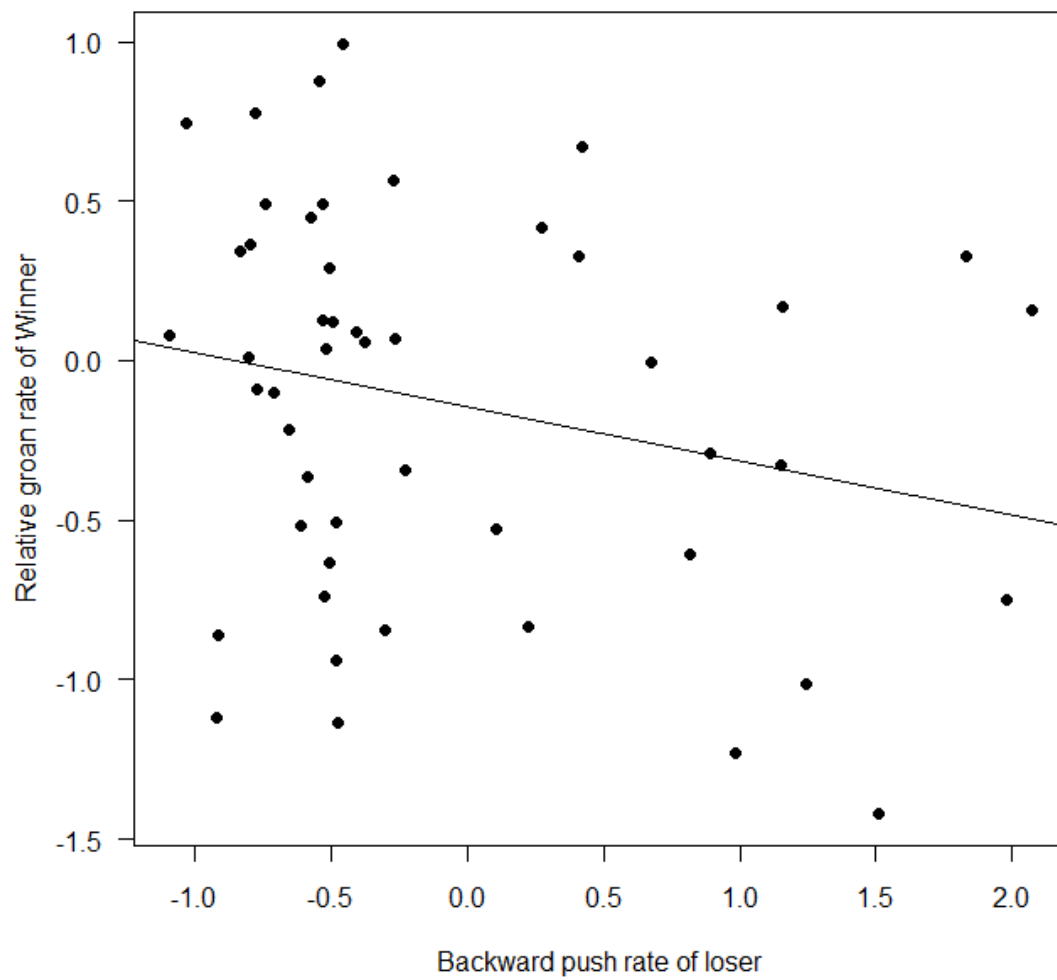487

488

489

489   Figure 2b

490

491

26

491   Figure 3a
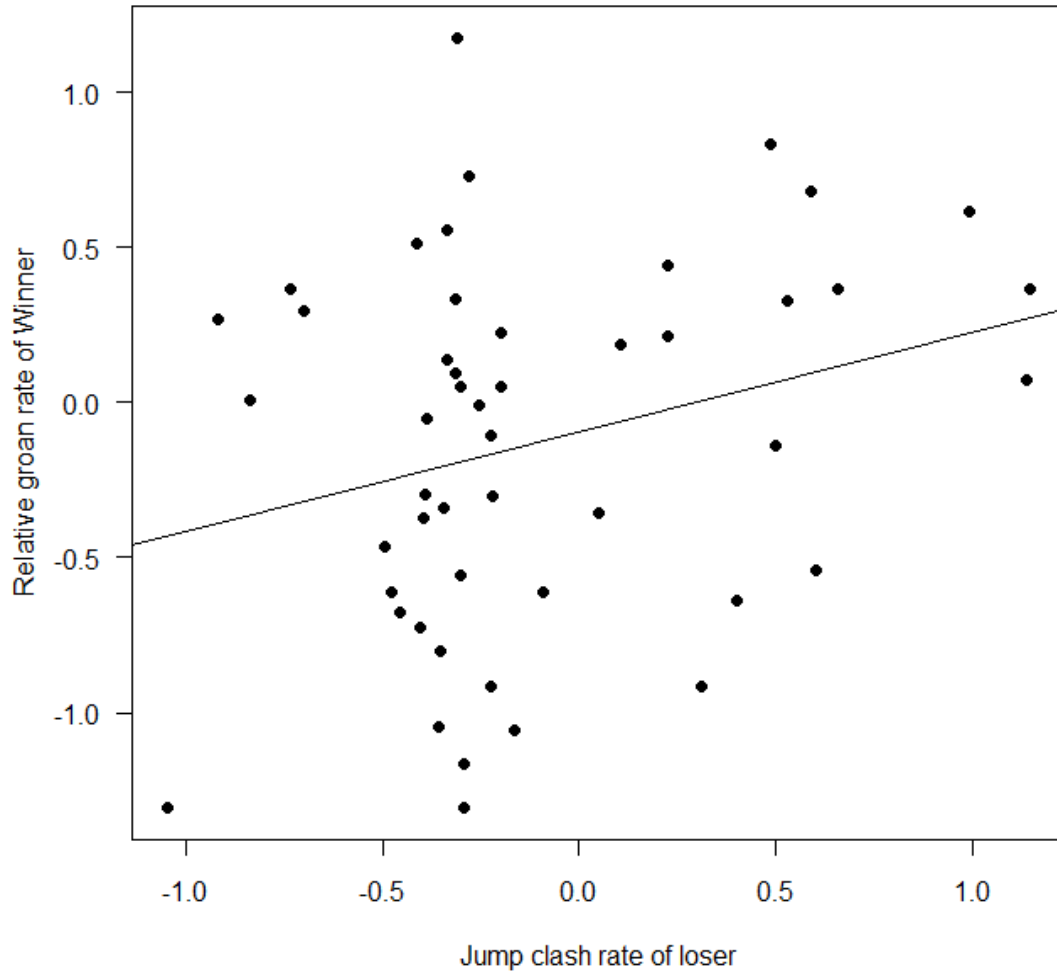

492

493

494

494   Figure 3b
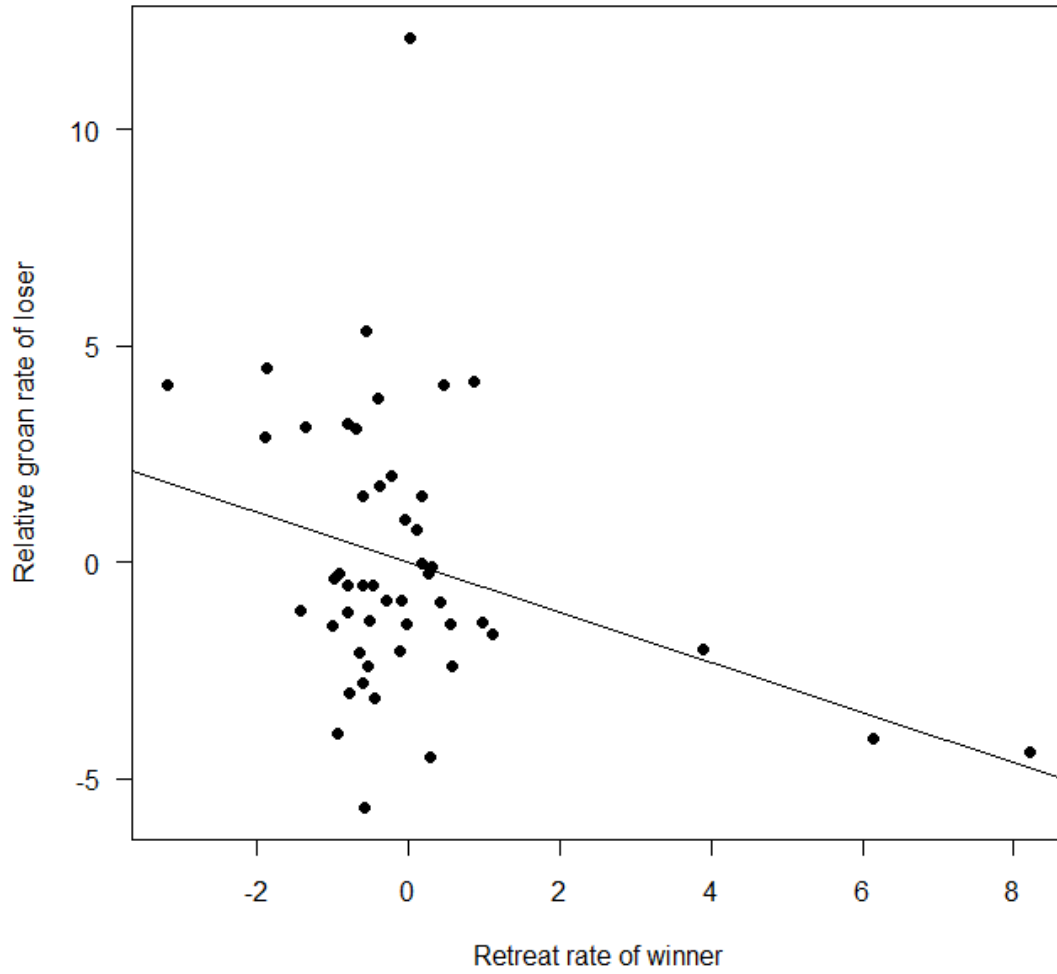

495

496

497

28

497   Figure 4
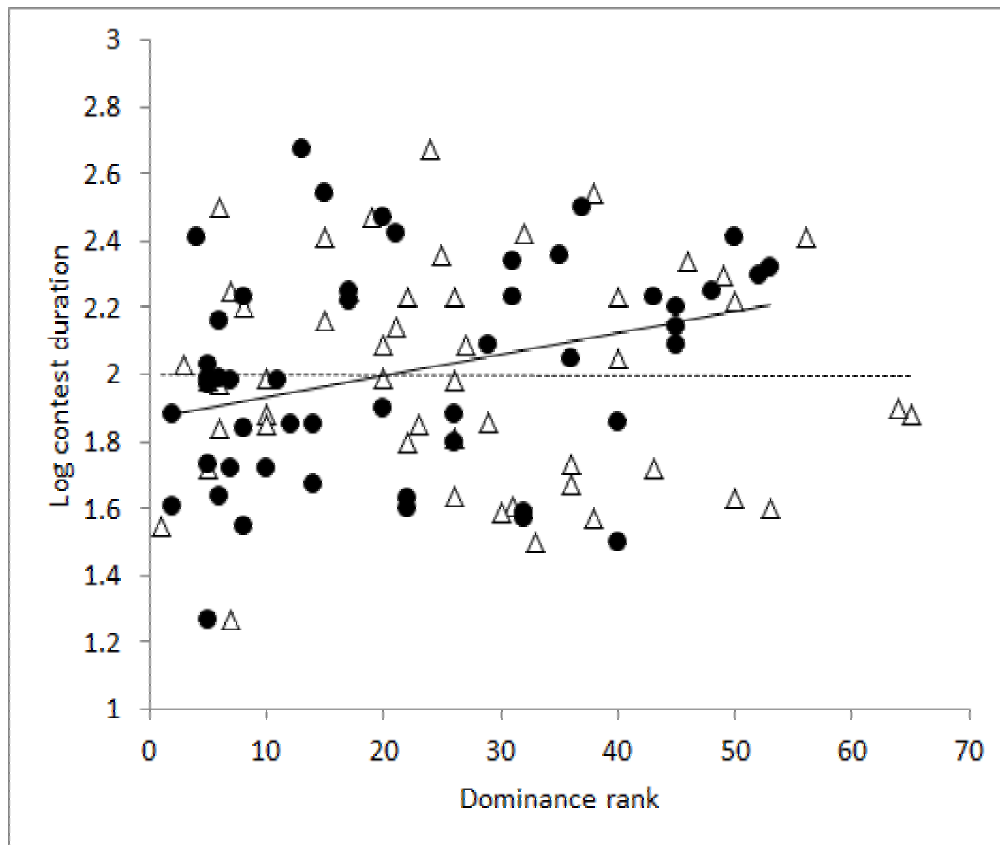

498

499

500

501

29

501   Figure 5

502

503

504

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

9

2