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Investigating variation in third-party intervention behavior during a fallow deer (Dama dama) rut

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Abstract

Pairwise contests are frequently disrupted by the intervention of third-party group members. However, little is known about whether an individual’s engagement in intervention behavior varies over time, or what factors might be associated with such variation. Using a hierarchical ‘hurdle’ model with two levels we investigated the conditions under which focal males: (i) would or would not engage in an intervention, and (ii) varied the number of interventions per day they engaged in. The lower level of the model showed that the proportion of unique opponents per day (estimated from the overall number of mature males in the herd) that focal males competed with, and the number of interventions suffered by a focal male were associated with an increased probability that this individual would itself engage in third-party intervention behavior. At the upper level of the model there was no association between these two variables and the rate at which individuals engaged in intervention behavior. The number of matings observed per day and aggression rate within the herd failed to contribute meaningfully to either level of the model. We also show that, although inconsistent over days and between years, some individuals displayed a greater propensity to intervene than others. The data from our study show that intervention behavior is more likely to occur as a results of individual directly experiencing aggressive behavior at a sufficiently high level, and not as a result of individuals monitoring aggressive or sexual activity in the wider social group.

Key words:
Aggression, Bayesian statistics, fallow deer, hierarchical hurdle model, third-party intervention, matings
A salient feature of group living behavior is that individuals will, to a greater or lesser extent, engage in aggressive acts with conspecifics as they seek access to valuable resources (Arnott & Elwood 2008). Nevertheless, within social groups not all aggressive encounters adopt a pair-wise structure and, in many instances contests can involve triads of individuals. Specifically, an ongoing dyadic interaction can be disrupted by the engagement of a third individual (Jennings et al. 2009). These triadic interactions have been reported across a wide range of species, and thus appear to represent a general feature of agonistic behavior (e.g. baboon (Papio cynocephalus), Seyfarth 1976; bottlenose dolphin (Tursiops sp.), Connor et al. 1992; African wild dog (Lycaon pictus), de Villiers et al. 2003; rhesus macaque (Macaca mulatta), Widdig et al. 2006; fallow deer (Dama dama), Jennings et al. 2011; chimpanzee (Pan troglodytes), von Rohr et al. 2012; raven (Corvus corax), Fraser & Bugnyar 2012).

Consistent with the volume and complexity of the empirical data, models of intervention behavior have proposed a number of functions regarding triadic aggression. It has, for example, been argued that individuals intervene in dyadic contests to support kin (e.g. Engh et al. 2005), to combine fighting value (e.g. Noë & Sluijter 1995), to increase access to food (e.g. Vogel et al. 2007) or mating opportunities (e.g. Bissonnette et al. 2011; Young et al. 2014), and to increase or maintain dominance rank (e.g. de Villiers et al. 2003; Higham & Maestripieri 2010; Jennings et al. 2011, see Bissonnette et al. 2015 for a review). Accordingly, a central theme of theoretical approaches to intervention behavior is the association between the intervention and the intervening subject’s fitness (Dugatkin 1998a; Mesterton Gibbons et al. 2011; Bissonnette et al. 2015). Although the study of intervention behavior is now well established in the literature, there are still considerable gaps at the theoretical and empirical levels, and a number of questions remain to be addressed (see reviews in Mesterton-Gibbons et al. 2011; Bissonnette et al. 2015). For example, little is known about how individuals vary in their willingness to engage in intervention behavior over time, and what variables contribute to such variation (but see Silk 1993; Schülke et al. 2010). We sought to address these
questions by investigating third-party intervention behavior of male fallow deer during their annual rut.

Male and female fallow deer tend to reside in sexually segregated social groups outside of the breeding season. Prior to the onset of the rut the bachelor herd disbands; males congregate on the female range where they become increasingly intolerant of the presence of rivals leading to a marked increase in aggression (Clutton-Brock et al. 1988). The majority of agonistic interactions are non-contact displacements; however, as the number of oestrus females increases during the rut there is an increase in fighting (Festa-Bianchet et al. 1990; Moore et al. 1995; Jennings et al. 2009, 2013). The dominance hierarchy that is formed as a consequence of the outcome of these interactions is linear (Jennings et al. 2006, 2010), and mating success is highly skewed in favour of high ranking males (Moore et al. 1995). Although most fights tend to only involve pairs of males, approximately 10% of contests are disrupted by the approach and intervention of a third-party male (Jennings et al. 2009). There appear to be significant benefits accruing to males that intervene; they achieve an increase in dominance rank, are more likely to win subsequent contests and have greater mating success (Jennings et al. 2009, 2011). Nevertheless, these studies of intervention behavior focussed on the summed behavior and outcomes at the end of the rut for a limited sample of individuals. The rut is a complex and changing environment for males as they seek to outcompete rivals and attract females; given these challenges, it may be empirically and theoretically relevant to investigate variation in individual behavior and that of the wider social group in relation to intervention behavior.

According to some models, changes in competitive ability (RHP, resource holding potential: Parker 1974) are likely to be important drivers of intervention behavior. They suggest that individuals strategically intervene against certain rivals in order to secure or advance their dominance rank (e.g. Dugatkin 1998a, see Bissonnette et al. 2015 for a review). During the rut, male physical condition declines; rutting males are inapt, losing up to a third of their body mass in
addition to acquiring and recovering from injuries they sustain from fighting (e.g. Jennings et al. 2010). Thus, the RHP of individual group members is expected to change over time, and individuals should seek to update this RHP estimate through (aggressively) interacting with rival members of their group (Mesterton-Gibbons & Sherratt 2007). Accordingly, we test the idea that the proportion of unique opponents that individual males engage with on any given day in the rut will be associated with intervention behavior; specifically, we expect that as the proportion of unique opponents increases there will be an increased probability of engaging in intervention behavior.

Although fallow deer that engage in intervention behavior hold high rank (Jennings et al. 2009), it remains to be determined whether males that intervene selectively target low ranking males. In other words, is there a possibility that two sub-groups of males exist: one group that engages in intervention behavior and one that suffers from interventions. This is theoretically relevant, and certain models of intervention behavior suggest that this should be the case (e.g. Dugatkin 1998a). Therefore, engaging in intervention behavior and suffering from third-party interventions should be negatively associated; the present study tests this prediction.

We have shown elsewhere that intervention rates, albeit summed over the entire rut, predict mating success (Jennings et al. 2011). However, the question as to whether the presence of the oestrus female encourages intervention behavior has not been examined. In general, female fallow deer are not promiscuous maters and only a low proportion of females mate more than once within a single oestrus cycle; therefore, we used the number of matings observed as an index of resource abundance. We predict that males are sensitive to resource abundance (Arnott & Elwood 2008); therefore, as the number of matings increase we should see a corresponding increase in intervention behavior as individuals seek to maximise their access to reproductive opportunities (i.e. a direct benefits explanation, Smith et al. 2010). Alternatively, we note that rates of aggression fluctuate in relation to the number of matings (Jennings et al. 2006); therefore, intervention behavior could simply be mediated by opportunity to intervene, i.e. an increase in group-wide
aggression will coincidentally result in a greater number of potential targets and thus higher levels of intervention. Accordingly, we test the hypothesis that intervention behavior is associated with heightened levels of aggression within the social group.
Methods

Study site and population: The behavior of a herd of free-ranging European fallow deer in Phoenix Park, Dublin (Ireland) was investigated. The management plan for the herd involves tagging fawns shortly after birth during June-July with unique coloured and numbered ear tags. During this study there were approximately 394 and 349 females aged over one in either year. There are a number of different coat colours in the population, and mature males show distinct differences in antler size and shape; thus, we could identify individuals using a combination of coat colour, antler conformation and ear tag.

Data collection

We recorded aggressive behavior using all-event recording (Altmann 1974), and divided agonistic interactions into two categories depending on whether physical contact between the opponents was made: (i) non-contact interactions which involved the approach and displacement of an opponent, and (ii) fights where males locked antlers and engaged and took part in a vigorous pushing contest. In order to investigate the predictions of this study, the data were analysed using day as a factor from the 14th to the 31st of October, thus ensuring we covered the time period when all males were actively engaged in rutting. During this time-period we recorded 2645 (Mean = 146.9, SD = 55.1 per day; Range = 37-253) and 3462 (Mean = 192.33, SD = 86.5 per day; Range = 50-327) agonistic interactions in 1996 and 1997 respectively; there were 775 (29%) and 1076 (31%) fights recorded with the remaining interactions involving non-contact displacements. We also calculated the number of interventions of dyadic contests each day (i.e. the intervention rate per day), and the identities of the male that conducted the intervention and that of the competing males that suffered the intervention. The behavior of a combined total of 83 mature (4 yeas+) males were analysed in this
study (N = 69 and 67 males in 1996 and 1997 respectively with 53 males present in both years).

Individual males were included dependent on whether they were present for 18 days of the study irrespective of whether or not they engaged in third-party intervention behavior. We note that a small number of males were excluded (N = 4 and 7 males respectively) from this study because they were only intermittently present, suffered severe injury (e.g. blinding) or died during the rut.

With respect to the regressors used in the analysis, we used the number of different opponents (1996: range = 0 – 29 (0 – 39.7% of potential opponents); 1997: range = 0 – 18 (0 – 24.3% of potential opponents)) to calculate the proportion of unique opponents in the herd with which each individual interacted on each day. When third-party males approached and disrupted ongoing fights we recorded the number of times the focal male was subjected to an intervention. We also calculated the number of dyadic contests (non-contact interactions and fights) in the population on each day minus the number of contests for each male on that day; thus, the question as to whether intervention behavior is a consequence of variation in aggression rate over time within the population could be addressed. The number of matings was variable over days (1996: N= 315 matings observed, Mean = 17.5, SD = 16.7, Range = 0 - 48 matings per day; 1997: N = 275, Mean = 14.72, SD = 11.7, Range = 0 - 33 matings per day) permitting us to investigate whether variation in number of matings was associated with intervention behavior.

Data analysis

Three regressors (number of interventions suffered by the focal male, aggression rate in the population and number of matings per day) were log transformed prior to analysis to ensure that very large values were not overly influential. The fourth regressor, the proportion of unique opponents that the focal male interacted with per day, was subjected to an empirical logit transformation (log((p+0.5/n)/(1-p+0.5/n))) where the proportion is calculated as observing x (number of opponents) out of n (number of males in the herd) events, i.e. p = x/n). This transform was used to ensure that small or large values were not overly influential, and uses a correction term
0.5/n to remove the problem when transforming a zero response (no opponents recorded on a particular day). In addition to these four regressors, year and day were entered into the model as categorical variables. Three random effects were also entered into the model: individual identity, the interaction between individual and year, and the interaction between individual and day.

Intervention behavior was analysed using Bayesian methods with Markov Chain Monte Carlo (MCMC) sampling. In order to sample the posterior distribution of the model’s parameters, we used the freely available JAGS software package (version 4.2, Plummer 2003) which was controlled from within the RunJags package (version 2.0.1-4, Denwood 2015) in R (version 3.1.3). We modelled the distribution of number of interventions across all mature males in the population per day including a substantial number of zero rated cells (see Figure 1) by using a hierarchical ‘hurdle’ model (e.g. Falk et al. 2015). This model has two levels in the hierarchy: the lower level focusses on the probability that an intervention takes place and the higher level models the number of interventions (conditional on an intervention taking place). Both levels of the model investigate the effects of the regressors on the observed outcomes; the first via a logistic regression and the second via a (truncated) Poisson regression (see supplementary materials for the model setup and code).

The hurdle model was run with an adaptive phase (including burn in) of 11,000 iterations over three parallel chains that employed dispersed initial values following which, a posterior phase consisting of 1,000,000 iterations was sampled. The posterior sample was thinned by taking every 1000th iterate in order to reduce autocorrelation, and convergence in the model chains was assessed using the Gelman-Rubin statistic (Gelman & Rubin 1992). The parameters of the models were given a weakly informative prior with a half-t model in order to reduce influence on the posterior distribution and allowing the information in the data to dominate (Gelman et al. 2008). A
convergence level of <1.1 for each model parameter indicated that the adaptive phase of the model
was sufficient (Kruschke 2015). This gave a posterior sample with an effective sample size of 1000
for inference, that is, information corresponding to an un-autocorreled sample of 1000
observations. Inferences regarding the importance of each model parameter were made based on
the posterior mean and the 95% credible confidence intervals. Following Bridger et al. (2015), where
an individual parameter’s posterior mean effect was below 0.02 we determined that there was no
evidence for a biologically meaningful effect.
Results

Inspection of the correlations in the posterior distribution revealed that generally the coefficients in the models were weakly correlated, with the strongest (positive) correlation between the coefficients for the proportion of unique opponents and interaction rate in the herd for the upper level Poisson model (see Table 1a and 1b). However this largest correlation was not sufficiently high to make the estimation procedure for the regressor coefficients unstable.

Insert Table 1a and 1b about here

The estimates relating to each regressor for both levels of the model are shown in Figures 2a and 2b.

With respect to the lower logistic level of the model (Figure 2a) regressors relating to the individual’s day-to-day agonistic behavior - the proportion of unique opponents, and the rate at which the focal individual suffered third-party interventions were associated with an increased probability that this individual would itself engage in third-party intervention behavior. There was no meaningful association between intervention behavior and either the number of aggressive contests in the herd or the number of daily matings. The random effects component of the model showed that individual identity contributed meaningfully to intervention behavior; moreover, there was also a meaningful interaction between both year and day indicating that intervention behavior at the level of the individual was highly variable over days in the rut and between years.

The upper (truncated Poisson) level of the model showed that there was no meaningful association between the model regressors and the rate of intervention behavior (Figure 2b). An examination of the effect of both day and year on intervention behavior for the logistic level showed a meaningful effect for one day early in the second rut (see supplementary file). There was no meaningful effect of day or year for the Poisson level (see supplementary file: Figure 3a and 3b).

Insert Figure 2a and 2b about here
Discussion

Theory has stressed the importance of intervention behavior in relation to fitness benefits that accrue to the individual (see Smith et al. 2010 for a review), and empirical studies have shown that engagement in third-party interventions can be beneficial for the intervener (de Villiers et al. 2003; Engh et al. 2005; Flack et al. 2006; Jennings et al. 2011). Nevertheless, it has been suggested that the study of triadic relationships have tended to omit potentially important information (Bissonnette et al. 2015). To the best of our knowledge few studies have studied variation in intervention behavior (but see Silk 1993 for rank related change). Therefore, we tested a number of predictions in relation to day-to-day variation in intervention behavior in a herd of fallow deer during their annual rut. This study shows that daily variation in the proportion of unique opponents and the number of interventions suffered by the focal male was associated with the occurrence but not the number of interventions engaged in. Conversely, daily variation in group-wide aggression rate and the number of matings in the herd were not associated with the occurrence or number of interventions.

Third-party disruption of ongoing fights may be a strategy used by high-ranking individuals to prevent subordinates from advancing in the hierarchy (Dugatkin 1998a). One interpretation of this theoretical approach suggests that individuals fall within two groups: those that intervene and those that suffer intervention. However, intervention behavior in this population is associated with an increase in dominance rank early in the rut (Jennings et al. 2011), indicating that intervention behavior is a bottom-up process (Dugatkin 1998a,b; Bissonnette et al. 2015). Moreover, individuals that intervene tend to also hold a higher rank than individuals that did not (Jennings et al. 2009). Thus, intervention behavior might be used strategically by (already) high ranking individuals to edge themselves higher in the hierarchy suggesting that intervention and suffering intervention might represent an inter-related strategy. The present study confirms this: where focal males suffered an intervention of their own contests, they were also highly likely to engage in third-party interventions themselves. Such a strategy might be expected in large and highly competitive systems such as ours.
where rank is associated with mating success, and where mating success is highly skewed in favour
of a small number of males (Moore et al. 1995). In short, intervention against a rivals of similar RHP
would be strategically more beneficial than intervention against rivals of low RHP; whereas the
former would be a threat if they achieved a winner effect, the latter would not.

In large and highly competitive populations we expect individual RHP to decline over time
(e.g. Clutton Brock & Albon 1979; Jennings et al. 2010). We also note that there is little evidence to
support choice of specific opponents based on rank, age or other RHP correlates such as body and
weapon size and this is expected where RHP changes over time (Jennings et al. 2006). Therefore, if
intervention to maximise individual fitness (e.g. Dugatkin 1998a), those individuals may benefit from
an estimate of RHP based on current opponent quality (Mesterton-Gibbons & Sherratt 2007). Given
this we might expect individuals to sample the competitive quality of a range of rivals and use this
update to inform intervention behavior. Our results support this prediction. We show that the
occurrence, although not the number of interventions, is associated with daily variation in the
proportion of unique opponents. Our analytic approach also afforded us the opportunity to address
the behavior of individual males over the rut. This showed a meaningful effect of identity; moreover,
there was also an interaction between identity and both day and year indicating that intervention
was highly variable between and within individuals. Taken together, this suggests that intervention
behavior is driven by a complex interplay between dyadic and triadic aggression and individual
factors.

Group members at the top of the hierarchy more often than not gain priority access to
resources at the expense of individuals lower down in the dominance order (e.g. Englehardt et al.
2006; Holekamp et al. 1996; Moore et al. 1995; Stahl et al. 2001). Intervention models anticipate
that individuals strategically engage in intervention behavior in order to enhance or retain access to
resources (Smith et al. 2010; Bissonnette et al. 2015), and there is evidence that intervention
behavior is associated with reproductive success (e.g. Gilby et al. 2013). Therefore, individuals
should be sensitive to changes in resource availability; for example, as matings increase in frequency
during the rut there is generally also an increase in fighting (e.g. Clutton-Brock et al. 1979; Moore et
al. 1995). However, although intervention behavior is associated with mating success in fallow deer
(Jennings et al. 2011), variation in the number of matings within the herd over the course of the rut
was not. Thus, while males gain appreciably by engaging in intervention behavior, they do not alter
strategic decisions concerning how they engage with rivals (i.e. dyadic versus triadic interactions)
based on the distribution of matings.

This latter point is supported by our analysis of group-wide aggression. We tested the
hypothesis that intervention behavior may be an opportunistic response to a rise in the rate of
contest behavior in the social group (e.g. von Rohr et al. 2012 and references therein). In this
population the number of aggressive interactions between males increases in response to the
number of matings (e.g. Moore et al. 1995; Jennings et al. 2006). However, there was no association
between dyadic aggression in the herd and the propensity for individual males to engage in
intervention behavior. Therefore, we find little evidence to support the idea that individuals monitor
either changes in the level of aggression or mating opportunities in the social group.

We attempted to determine what factors might be associated with individual variation in
intervention behavior. To do so we examined a number of variables attributable to aggressive
behavior experienced directly by the individual, that of the wider herd and the distribution of
matings over time. Our results show that it is daily variation in aggression that is associated with
intervention behavior: an increase (proportionally) in the number of unique opponents and the
number of interventions suffered was associated with a greater probability that males would
intervene. We found no effect of variation in matings within the herd; therefore, we fail to support
those models that emphasise resource access as factor in intervention behavior. Our results re-
emphasise the complexity of intervention behavior (Bissonnette et al. 2015). This is underlined by
our failure to account for variation in the number of interventions over time - an issue that will need to be addressed in future studies.

Acknowledgments

The authors would like to extend our thanks to colleagues at the Mammal Research Group at University College Dublin for their help in the field. We would also like to thank the anonymous referees for their helpful comments on an earlier draft of this paper.

Data Accessibility

Analyses reported in this article can be reproduced using the data provided by Jennings et al. 2016.
References


Table 1a. Correlations between the coefficients of the four regressors entered into the lower (logistic) level of the statistical model.

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<th>Interactions in herd</th>
<th>Matings</th>
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Table 1b. Correlations between the coefficients of the four regressors entered into the upper (truncated Poisson) level of statistical model.

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<tr>
<td>Interactions in herd</td>
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<td></td>
<td>-0.19</td>
</tr>
</tbody>
</table>
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Figure 1. A count of the number of third-party interventions performed by males per day over two consecutive ruts (N = 301 interventions recorded within the sample period, October 14th – 31st).

Figure 2a. Summary of the parameter posterior distributions showing the association between daily variation in the occurrence of intervention behavior and the four regressors for the logistic model. For each parameter the mean is denoted by the black square and the 95% credible intervals by the thin line.

Figure 2b. Summary of the parameter posterior distributions showing the association between daily variation in the rate of intervention behavior and the four regressors for the Poisson model. For each parameter the mean is denoted by the black square and the 95% credible intervals by the thin line.
Figure 1
Figure 2a.
Figure 2b.