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Animal behaviour

Weapon damage is associated with contest dynamics but not mating success in fallow deer (*Dama dama*)

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Antlers function as primary weapons during fights for many species of ungulate. We examined the association between antler damage and (i) contest dynamics: the behavioural tactics used during fighting including fight duration, and (ii) mating success, fighting rate and dominance. Structural damage of the antlers was associated with contest dynamics: damage was negatively associated with jump clash attacks by individuals with damaged antlers, whereas opponents were more likely to physically displace individuals with damaged antlers during fighting. We found a positive association between dominance and damage indicating that high-ranking individuals were likely to have breaks to their antlers. We found no evidence that damage was associated with either mating success or the number of fights individuals engaged in. Our study provides a new perspective on understanding the association between contest dynamics and weapon structure, while also showing that damage has limited fitness consequences for individuals.

1. Introduction

Aggressive behaviour is frequently observed when individuals seek to gain access to scarce resources such as food, territories and reproductive opportunities. Contest theory assumes that individuals will persevere against an opponent dependent on the costs of persistence, versus the benefits that might accrue from continued investment in the contest [1]. While fighting involves costs relating to time and energy expenditure, contestants also run the risk of incurring physical damage (e.g. [2]). But although there have been many studies into the temporal and energetic costs of fighting, there have been relatively few studies that address how damage costs might influence behaviour [3]. Furthermore, only a single theoretical model has addressed this issue [4]; critically, however, the model assumes that while opponents can suffer damage costs, the potential for individuals to self-inflict damage by their actions is not considered.

Although not incorporated into theory, a recently proposed framework suggests that self-inflicted damage can be investigated across three axes: (i) likelihood as consequence of fighting, (ii) severity as it impacts on fitness, and (iii) its reversibility [3]. For example, self-inflicted damage costs in the sea anemone (*Actinia equina*) accumulate during contests because pieces of the attacker's stinging nematocyte remain adhered to the opponent; thus, self-inflicted damage costs increase as attacks increase [5]. Similarly, in deer, there is an increased likelihood of damage occurring to the bearer's antlers due to the repeated engagement of these structures during fighting [6,7]. Therefore, an examination of weapon structure following fighting should give an insight into the likelihood of self-inflicted damage.

Depending on severity, there may be immediate costs associated with damage because fighting and weapon structure have coevolved [8]. Many species compete

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by mutual engagement of their weaponry, and damaged or missing structures may affect the ability of contestants to engage with an opponent if they cannot properly compensate for these acquired asymmetries (e.g. [9]). Consequently, individuals with damaged weapons may be restricted in their use of behavioural tactics, leading to altered contest dynamics. In line with such thinking, several reports show that damage (either acquired or artificially imposed) is linked with a tendency for individuals to avoid engaging in fights [9–11]. The effects of withdrawing from competitive behaviour can be profound, and individuals with damaged weapons suffer a rapid decline in dominance rank, with a consequent decline in the number of matings achieved ([9–11], but see [7]).

This study investigates two objectives relating to both the likelihood and severity of the effects of antler damage on the contest behaviour of fallow deer. As we are unaware of any study that has investigated the association between damage and contest dynamics, the first objective of this study is to investigate whether contest tactics and contest duration (i.e. behavioural dynamics) are associated with antler damage in fallow deer fights. The second objective seeks to clarify whether damage is associated with the propensity for individuals to engage in fighting, and additionally to determine whether damage is associated with mating success and dominance.

2. Material and methods

(a) Study population and data collection

The behaviour of a herd of free-ranging fallow deer in Phoenix Park, Ireland, was recorded prior to and during the annual rut. Mature males (minimum of 4 years old) were identified by a combination of unique coloured and numbered ear tags, coat colour and differences in antler shape and size. From late August, all-event sampling was employed to record non-contact interactions (usually displacement of the opponent) and fights between males. From these data, we estimated the total number of fights each male had, while all decisively resolved non-contact interactions were used to estimate each male's dominance status using David's score [12]. Mating success was recorded as the number of matings achieved by each male during the October rut. In the following Spring, we collected cast antlers and matched these to specific males ($N = 48$ pairs of antlers) using photographic records of the males. Antlers were considered damaged if one of the structures was broken at the palm, the main beam or trez/brow tine.

Fights were recorded opportunistically on videotape and analysed using the observer [12] ($N = 30$ males with antler records). We extracted data concerning tactical actions (jump clashes and backward pushes) and the duration that protagonists locked their antlers during fights. These tactical actions occur frequently, are associated with contest victory and have been used to investigate assessment process during fights [13,14]. Because mature males engaged in multiple fights, the data for each male were summed and the average of their actions and antler contact duration calculated. Following this, the data on actions were calculated as responses per minute (time from first to last antler contact) prior to analysis [13].

(b) Statistical analysis

We applied linear logistic regression models to the probability that an individual's antler was damaged using Bayesian methods with Markov chain Monte Carlo sampling. We allowed each individual to have different regression coefficients (around a population level) by using a random slopes model. Prior to analyses, we standardized the model covariates [15]. The posterior distribution was sampled using JAGS (4.2, [16]), controlled from within the RunJags package (2.0.4–2, [17]) in R (v. 3.3.1). The model used dispersed initial values with a burn-in and adaptive phase of 20 000 iterations across three independent chains. Then a posterior phase consisting of 4 000 000 iterations was sampled at every 40th iterate, leaving 100 000 un-autocorrelated realizations from the posterior distribution (see the electronic supplementary material for model code). Convergence of the posterior chains was examined using the Gelman–Rubin statistic [18], with a level of less than 1.1 for each covariate taken as evidence for model convergence [15]. The covariates were given a weakly informative prior with a half-*t* model in order to reduce influence on the posterior distribution [19]. Inferences concerning the covariates were based on the posterior mean and 95% credible intervals.

3. Results

There was no association between the time that males spent antler contact or between engagement in backward pushing by the focal individual. However, a positive association between backward pushing by the opponent and antler damage indicates that individuals with damaged antlers were more likely to be displaced backwards during fights. There was a meaningful negative association between jump clashing by the focal individual and damage; thus, individuals with undamaged antlers were more likely to attack their opponent using high-risk tactics. Damage was not associated with the use of the jump clash by opponents (figure 1).

A second model showed a meaningful positive association between individual dominance and damage indicating that dominant individuals were more likely to have damaged antlers (figure 2). There was no association between the number of fights and mating success, and no meaningful interactions between mating success and fighting or dominance.

4. Discussion

The effects of self-inflicted damage vary in relation to likelihood, severity and reversibility [3]. As antler damage is permanent within that season, we did not address reversibility. There is limited evidence suggesting that damage likelihood increases with fighting frequency [20]. However, our results show that damage likelihood was not associated with either fight duration or the number of fights individuals were involved in. Moreover, our results are consistent with studies that show no association between damage and mating success (e.g. [7]), and contrary to previous work (e.g. [11,20]), we show a positive association between damage and dominance status. Thus, although high-ranking males were most likely to suffer damage, this did not result in a decline in either dominance or mating success. Overall, our results show that antler damage does not lead to individuals being less competitive, as has previously been argued [9,10]. Critically, these results challenge the idea that individuals suffering antler damage are unable to compensate for this loss [9].

It has been argued that damage influences contest behaviour (e.g. [10,11,20]). However, these studies relate to the tendency for damage to negatively impact on the individuals engagement in contests rather than contest dynamics. We show that there was no meaningful association between damage and contest duration; however, there was a positive association between damage and the rate at which opponents, but not the focal male, achieved a backward

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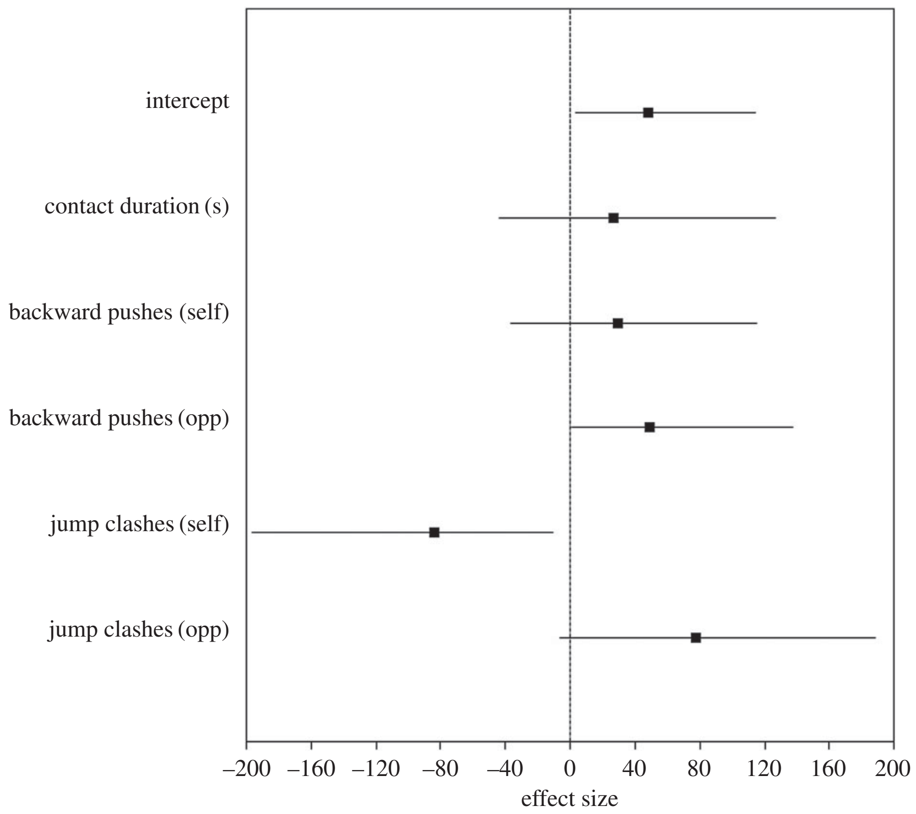

Figure 1. Summary of the parameter posterior distributions in the logistic model, which show the size and importance of the regressors for contest actions and duration (means are denoted by the black squares, and the 95% credible intervals by the thin lines).

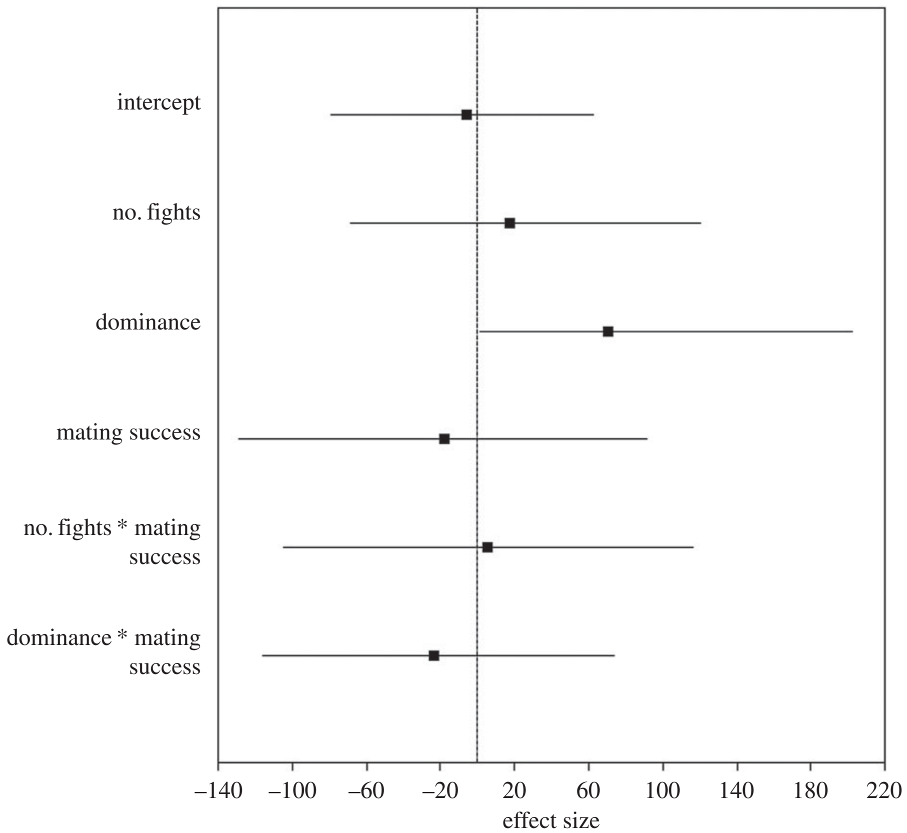

Figure 2. Summary of the parameter posterior distributions showing the size and importance of mating success, fighting and dominance with respect to antler damage.

push. Given that backward displacements are associated with victory [13], weapon damage appears to confer a tactical advantage on the focal individual's opponent. Damage was negatively associated with jump clashing for the focal individual but not the opponent, indicating that intact antlers are a critical feature of the use of this high-risk tactic [13,14]. Therefore, not only is damage associated with contest dynamics, we show that it also influences the use of tactical

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actions adopted by both the focal individual (jump clashing) and the opponent (backward pushing).

The study of contest strategy and contestant decision-making often focuses on individual action rates, and therefore, the impact of damage and its severity have theoretical implications [3,4]. For example, in the case of the fallow deer, the rates at which the jump clash and backward push occur during fights can help to distinguish between opposing theoretical models [13], while the analysis of fighting bouts can similarly provide an insight into the decision rules used by contestants (e.g. [21,22]). Nevertheless, while theory accepts that individuals may inflict injuries on each other [4], no model currently addresses how self-inflicted damage affects decision-making [3]. Consequently, there has been little theoretical consideration of how damage acquired through fighting might affect strategic behaviour [3]: this study shows that damage and its association with contest dynamics may be a fruitful avenue for further research.

To conclude, although the tactical dynamics of fighting are associated with damage, damage likelihood is not associated with how often individuals fight, and critically, this does not appear to have any fitness consequences for the bearer of the damaged weapons. In order to improve our understanding of contest dynamics and the evolution of fighting, we need to understand how damage interacts with aggressive behaviour [3]. We endorse this statement, and trust that the present study represents a movement towards this goal.

Data accessibility. Datasets reported here have been uploaded as the electronic supplementary material.

Authors' contributions. D.J.J., R.J.B. and M.P.G. drafted the manuscript; D.J.J. and R.J.B. analysed the data; D.J.J. and M.P.G. collected the data. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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