Personality and predictability in fallow deer fighting behaviour: the relationship with mating success

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Individuals often differ from each other in how they respond to environmental events: a feature of behaviour often termed animal personality. Furthermore, animals often show unpredictability in how much they respond to these events over time leading to the suggestion that personality and intra-individual variability (IIV) might have important fitness consequences. We investigated this hypothesis by focusing on the tendency for individually identifiable male fallow deer, *Dama dama*, to escalate low-level (noncontact) agonistic interactions to fighting during the rut. Males differed in their tendency to escalate noncontact interactions to fighting; however, repeatability in escalation rates was unstable over the rut suggesting that escalation rate is a poor measure of personality. There was no difference in the level of IIV in escalation rate shown by males. A comparison of IIV recorded over two consecutive annual ruts showed that IIV was highly correlated between years; therefore, over an extended time period individuals were consistent in their willingness to engage in fighting. There was a nonlinear relationship between IIV and mating success; specifically, individuals that showed either low or high IIV in escalation rate had lower mating success than individuals that showed intermediate levels of IIV. Aggression and the willingness to commit to fighting are important fitness correlates; nevertheless, our understanding of how personality and IIV are related to aggression is poorly understood. This study shows that although escalation rate appears to be a poor measure of personality in the fallow deer, IIV is related to increased fitness in individuals that show intermediate levels of predictability in their willingness to fight over the rut.

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The repeated observation of animals, usually within the same context, shows consistent individual differences in the magnitude of responses to environmental events or test stimuli (see Bell et al. 2009; Stamps et al. 2012; Carere & Maestripieri 2013). While the differences in behaviour across individuals have sometimes been considered a form of statistical noise (e.g. Wilson 1998), they might also be indicative of what are variously referred to as personality dimensions/traits or behavioural syndromes (Smith & Blumstein 2008; see also Gosling 2001; Sih et al. 2004; Bell 2007; Carter et al. 2013). Furthermore, individuals might differ not only between themselves in their response to events within their environment but also in the magnitude of their response to the same event on different occasions (e.g. Briffa et al. 2013). Thus animals can behave in an unpredictable manner even with the constraint of

relatively short intertrial intervals (in the seconds to days range, Bell et al. 2009; Stamps et al. 2012): a pattern of behavioural plasticity referred to as intraindividual variability (IIV; Siegler 1994; Salthouse 2007).

Research into animal personalities is considered to be important for a variety of reasons (see Carere & Maestripieri 2013) including the rationale that they may provide an insight into evolutionary processes via their effect on individual fitness (Biro & Stamps 2008; Smith & Blumstein 2008; Dingemanse & Réale 2013); for example, personality traits are associated with increased mating success (e.g. Ciuti et al. 2011) and survival (e.g. Boon et al. 2007; Réale et al. 2009). Although studies relating to the effect of behavioural predictability on fitness are less numerous, it has been shown that individuals that display low variability in signal structure have higher dominance rank and/or mating success (e.g. Byers 2007; Botero et al. 2009; Węgrzyn et al. 2010). Alternatively, studies of predator–prey interactions have shown that prey that show high variability have a greater probability of survival relative to those that display low variability (e.g. Bednekoff & Lima 2002; Jones et al. 2011) because unpredictable responses make it more difficult for

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predators to learn avoidance strategies. However, with the exception of some recent studies on hermit crabs and damselfish there is a clear lack of studies that have specifically investigated IIV in nonhuman animals (Stamps et al. 2012; Briffa et al. 2013).

In game-theoretic terms, consistency in the repetition rate of signals is expected because it might facilitate the assessment of individual quality: a central prediction of certain models of contest behaviour such as the sequential assessment model (e.g. Enquist & Leimar 1983). Aggression is a ubiquitous feature of animal social behaviour (see Hardy & Briffa 2013 and chapters within) and the decision to escalate an interaction to fighting represents a trade-off for males (Dall et al. 2004); specifically, individuals must determine whether to incur the costs of fighting with respect to any fitness implications that result as a consequence of fighting. The European fallow deer, *Dama dama*, is a seasonally breeding ungulate; the annual rut takes place from mid to late October in the Northern hemisphere. As the rut approaches, mature males become increasingly intolerant of each other and show an increased tendency to escalate low-level interactions to fighting (e.g. Jennings et al. 2006, 2009; Jennings & Gammell 2013). The males in our study population (see below) do not gather harems; rather, the most successful males employ a follower strategy moving with the female herds over the day range (Moore et al. 1995). As a consequence there are high male–male encounter rates and fighting is commonly observed. Nevertheless, not all interactions lead to fighting; the majority of interactions, although still identifiably aggressive, are resolved with one individual yielding before physical contact is made (Jennings et al. 2003, 2006).

Comparatively few studies have investigated the relationship between repeatability and aggression (e.g. Riddell & Swain 1991; Clarke & Moore 1995; Wilson et al. 2011), although it is possible that these differences might be related to individual fitness (Biro & Stamps 2008; Smith & Blumstein 2008). Therefore, we investigated aggressive interaction rates between mature males in order to establish whether the tendency to engage in fighting might be representative of animal personality (see Mowles et al. 2012; Rudin & Briffa 2012). The question as to whether high or low IIV has fitness implications depends on the behaviour under investigation (Stamps et al. 2012), although limited evidence suggests that males that show high consistency are more dominant and have greater mating success (e.g. Botero et al. 2009). We are not aware of any study that has specifically addressed IIV in relation to fighting and mating success; nevertheless, in line with findings from previous research we tested the prediction that individuals with low IIV in escalation rate should have greater mating success than conspecifics with high IIV in escalation rate.

METHODS

Study Site and Population

The study was conducted over two consecutive rutting seasons in 1996 and 1997 on a population of European fallow deer resident in the Phoenix Park: a large enclosed city park consisting of 709 ha in Dublin, Ireland (53°22′N, 6°21′W) under the local management of the Office of Public Works. As part of the management strategy for the deer herd, fawns are tagged with a uniquely numbered and coloured plastic tag (Allflex medium) shortly after birth (early June to early July). Observation of the doe herd throughout the tagging period to record mother–fawn behaviour has shown that the tagging regime does not have an impact on fawn survival. As a consequence, mature males in the population are individually identifiable through a combination of their ear tags, coat colour and antler conformation.

Study System

A team of 10–12 trained observers were in the field from dawn to dusk during the rut; all-event recording of agonistic interactions was adopted throughout the study period (Altmann 1974). These interactions were divided into two distinct behavioural categories: (1) noncontact interactions where one individual displaced his opponent but no physical contact occurred and (2) fights. During fights two individuals locked antlers and engaged in a protracted interaction involving a vigorous pushing contest that could be separated into several different bouts of fighting (Jennings et al. 2005). When an interaction of either type was observed we recorded the category of interaction, the identity of the interacting males, the outcome, the location and the time of the interaction. Recording agonistic interactions in this manner therefore provided the total number of noncontact interactions and number of fights for each male in the population.

Between the end of August and the end of October in each year we recorded the following data (1996: 5494 interactions between 73 mature males, 61% of all possible dyads interacted; 1997: 7202 interactions between 74 mature males, 69% of possible dyads interacted). We then calculated the tendency for individual males to escalate to fighting by dividing the total number of fights they had by the total number of interactions (noncontact and fights). Because dyadic encounters such as fights involve two individuals, this measure includes information on fighting behaviour from the wider population of over 70 mature males; thus males contributed to each other's measure of escalation rate to varying degrees. For the purposes of the present study we divided the rut into 2-day blocks and selected males for inclusion based on whether they had engaged in at least one fight in each block. Thus there were seven consecutive 2-day observation periods within which an escalation rate score per block was calculated for each male. Males that did not satisfy this criterion were excluded from the study; this approach was adopted to avoid a floor effect in the data that can result in biased measures of IIV (Stamps et al. 2012). To allay concerns that our approach restricted the data to a limited number of values we checked the interaction rates of each male in the sample. The majority of males interacted at a high rate in each 2-day block: 63, 61, 72, 80, 85, 96 and 80% of the sample of males had 10 interactions or above; a further 20, 30, 21, 15, 13, 3 and 15% of the sample engaged in 5–10 interactions. On average only two males had a low (less than five) interaction rate per 2-day block. There was a total sample of 56 males recorded over two consecutive ruts (20 and 36 males, respectively) that satisfied the criterion for inclusion. Following initial screening of the data as described above, we noted that 10 males satisfied the criterion for inclusion in both ruts; we removed these males from the second rut to avoid pseudoreplication issues. Nevertheless, because we also examined escalation rate across ruts we used data from these 10 males' escalation rates to assess repeatability and IIV over an extended period of 1 year that included two annual ruts.

Statistical Analyses

Measures of repeatability (R_a) were assessed as described by Lessells & Boag (1987); specifically, R_a was calculated from the variance components derived from a one-way ANOVA in which individuals were treated as the group factor and escalation rate as the dependent variable. The total number of fights recorded on each day during the rut was correlated with the total number of matings recorded (1996: $r_S = 0.767$, $N = 16$, $P = 0.001$; 1997: $r_S = 0.664$, $N = 17$, $P = 0.004$); moreover, overall interaction rate per male (all mature males in population) was correlated with mating success (1996: $r_S = 0.540$, $N = 73$, $P < 0.001$; 1997: