Animal Behaviour 79 (2010) 1293–1300

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Investment in fighting in relation to body condition, age and dominance rank in the male fallow deer, *Dama dama*

Dómhnall J. Jennings[a,*], Caitríona M. Carlin[b,1], Thomas J. Hayden[c,2], Martin P. Gammell[d,3]

[a] *Institute of Neuroscience, Newcastle University, Newcastle upon Tyne*
[b] *Centre for Environmental Science, National University of Ireland Galway, Galway*
[c] *School of Biology and Environmental Science, University College, Dublin*
[d] *Department of Life and Physical Sciences, Galway-Mayo Institute of Technology, Galway*

A R T I C L E I N F O

Article history:
Received 13 November 2009
Initial acceptance 8 January 2010
Final acceptance 19 February 2010
Available online 8 April 2010
MS. number: 09-00730R

Keywords:
body condition
contest structure
Dama dama
fallow deer
fighting
life history
reproductive effort

According to life history theory, males of iteroparous species are expected to trade off investment between current and future reproduction based on age (mating strategy or terminal investment hypotheses) or body condition (individual quality hypothesis). However, although central to this latter model, the question concerning whether and to what extent condition regulates competitive investment in polygynous species is unknown. Consequently, we investigated this issue with reference to fight structure in fallow deer contests. Support for the individual quality hypothesis was limited: males with larger necks as determined by prerut neck girth fought for longer than males with smaller necks. However, prime-aged males had higher investment in fighting than preprime- or postprime-aged males indicating that investment in fighting might be age related. Other aspects of our results also failed to support condition-related predictions; although we found that jump clashing and vocal rate were related to weight loss and decline in neck girth, respectively, there was no relationship between investment in fighting and prerut measures of body size. Moreover, we also found that rank was predicted by investment in fighting (backward pushing) rather than body condition. Our results show that, in addition to body condition and age, variation in competitive investment between individuals also influences reproductive effort in the fallow deer.

Although game-theoretical models of animal competition differ fundamentally in their predictions concerning the process by which animals reach a decision to continue or quit a contest, there is a common assumption that competition imposes a range of costs on the individual (Arnott & Elwood 2009). Theoretical approaches such as that proposed by the sequential assessment model (SAM) predict that individuals will escalate contests through phases that increase in both intensity and cost as contestants seek to assess the quality of their opponent (Enquist & Leimar 1983). It is the ability of individuals to match their opponent's within-phase behaviour that increases the likelihood that the contest will continue through phases thus increasing the costs that are incurred (e.g. DeCarvalho et al. 2004). Similarly, the war of attrition (WOA) predicts that opponents match each other in behavioural rates until one contestant reaches a maximum cost threshold and elects to abandon the contest (e.g. Mesterson-Gibbons et al. 1996). Costs associated with fighting include time directed away from tending a resource and the risk of serious injury or death (Riechert 1998), but also arise from the energetic constraints imposed by repeatedly signalling during these interactions (Briffa & Sneddon 2007). Recent studies focusing on this aspect of competitive behaviour have shown that investment in competitive behaviour is compromised by increases in lactic acid, depletion of glucose and anaerobic constraints (e.g. Thorpe et al. 1995; Hack 1997; Briffa & Elwood 2001; Matsumura & Murai 2005; Dissanayake et al. 2009).

It seems reasonable to assume that there could be cumulative costs associated with repeated incidences of escalated competition. This should be particularly true in polygynous ungulates; here mature males adopt a capital breeding strategy relying on stored energy during the breeding season during which they compete over access to reproductive opportunities (Festa-Bianchet et al. 1998; Forsyth et al. 2005). While game-theoretical models address the tactical aspects of competition as a means to understand contest structure and decision rules, life history models tend

---

[*] Correspondence: D. J. Jennings, Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Framlington Place, Newcastle upon Tyne NE2 4HH, U.K.

E-mail address: domhnall.jennings@ncl.ac.uk (D. J. Jennings).

[1] C. M. Carlin is at the Applied Ecology Unit, Centre for Environmental Science, National University of Ireland Galway, University Road, Galway, Ireland.

[2] T. J. Hayden is at the School of Biology and Environmental Science, Science Centre West, University College, Belfield, Dublin 4, Ireland.

[3] M. P. Gammell is at the Department of Life and Physical Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland.

0003-3472/$38.00 © 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2010.02.031

to emphasize the role of competition in terms of optimizing reproductive success. From this latter perspective reproductive effort can potentially have two effects on an individual's fitness: it can result in decreased survival and also deplete future investment in offspring by diverting resources towards current offspring (Charnov et al. 2007). In males, it has been proposed that one major source of the reproductive costs that are incurred arise from an escalation in incidences of intrasexual competition as competitors seek to gain, and monopolize, access to territories and receptive females (e.g. Maher & Byers 1987; Yoccoz et al. 2002; Pelletier et al. 2006).

However, while actual costs might stem from competitive behaviour, age (terminal investment hypothesis: Pianka & Parker 1975; mating strategy effort hypothesis: Yoccoz et al. 2002) and body condition (individual strategy hypothesis: Pelletier 2005) have been considered key factors regulating investment in reproductive effort. In terms of current life history models, the terminal investment hypothesis predicts that investment in reproduction should increase with increasing age (after prime age is reached) as residual value decreases (Mysterud et al. 2005). The mating strategy effort account is more related to mating strategy than specifically to age (Mysterud et al. 2005); however, in the context of male fallow deer which peak in mating success within a restricted age range (e.g. Moore et al. 1995; see also Yoccoz et al. 2002 for red deer, *Cervus elaphus*), the model predicts that reproductive effort should be greatest in prime-aged animals. This is because individuals within this age class are better able to acquire and defend a resource than older individuals. The individual strategy hypothesis differs from the two preceding accounts in that it predicts that reproductive effort will be greatest in individuals that possess the highest phenotypic quality before the onset of the breeding season. While these life history accounts of reproductive effort are broadly concerned with the costs of competition as a function of reproductive effort, investigation of these models tends to focus less on moment to moment behavioural actions of competition in favour of more indirect measures of competitive behaviour.

These indirect measurements are favoured primarily because direct observation and quantification of contest behaviour in field populations is extremely difficult (Vervust et al. 2009). Consequently, investment has been inferred from weight loss (e.g. Yoccoz et al. 2002; Mysterud et al. 2005), physical damage (e.g. Vervust et al. 2009), or through behavioural activities expressed as a percentage of a focal watch (e.g. Maher & Byers 1987; Mainguy & Côté 2008). Nevertheless, as noted above, experimental studies have shown that it is the rate and intensity of behavioural actions during fighting that index how costly a contest is to the individual. Therefore, engaging in high-cost, risky or fatiguing tactics and persisting for longer during fights would provide a direct measure of investment in reproductive effort. To the best of our knowledge no study has directly investigated this fundamental question and, consequently, the relative importance of competitive investment as a gauge of reproductive effort in males of polygynous species has remained speculative.

The tendency for male fallow deer to engage in escalated competition is common during the annual rut (e.g. Apollonio et al. 1992; Moore et al. 1995; Fričová et al. 2007). The majority of aggressive interactions between males involve noncontact dyadic contests although a proportion do escalate to fighting, some of which are disrupted by the intervention of third-party males (Jennings et al. 2006, 2009; Jennings & Gammell, in press). Studies of the structure of fallow deer fights have illustrated the highly complex nature of these encounters; they involve a range of vocal (Bartoš et al. 2007) and visual displays (Alvarez 1993; Jennings et al. 2002, 2003) in addition to a range of behavioural actions during physical engagement in bouts of antler contact (Alvarez 1993; Jennings et al. 2004, 2005a, b; Bartoš et al. 2007). These fights can last for several minutes and are considered to be extremely fatiguing suggesting that fighting is a key variable associated with mass loss in male ungulates (Yoccoz et al. 2002; Jennings et al. 2004). Given the frequency and complexity of fights, we sought to investigate whether male fallow deer regulate their investment in fighting based on body condition by directly quantifying individual behaviour during escalated fighting. The objectives of the present study were therefore two-fold. First, we investigated whether investment in fighting was related to body condition. Therefore, support for the individual quality hypothesis would be evident by a positive relation between prerut body condition and investment in fighting. Second, consistent with recent studies (e.g. Mainguy & Côté 2008) and because the individual quality hypothesis is not exclusive of age-related models, we investigated whether there was evidence for age-related differences in contest structure. Specifically, we sought to determine whether investment in fighting was highest in prime-aged fallow bucks (a mating effort strategy) or in older, postprime-aged males (a terminal investment strategy).

METHODS

Study Site and Population

This study was conducted over two consecutive ruts (1996 and 1997) on a herd of free-ranging European fallow deer resident in the Phoenix Park: a large enclosed city park consisting of 709 ha in Dublin, Ireland. Most of the park (80%) is open grassland with the remaining 20% covered by mixed woodland; the deer are free to range over much of this area but usually confine themselves to certain areas of the park. Annual tagging of the herd began in 1971, and the entire herd was rounded up and tagged between 1991 and 1992. The majority of fawns are tagged in each ear with unique colour/numbered tags shortly after birth in June and July each year. Identification of mature males in the population is facilitated by a combination of coat colour, antler conformation and identity tag. The number of females was similar over both years of the study (1996: $N = 394$; 1997: $N = 349$). The age structure of the males remained relatively stable over the two field seasons (1–3 years: 1996: $N = 100$ males; 1997: $N = 126$ males; 4–5 years: 1996: $N = 34$; 1997: $N = 27$; 6–7 years: 1996: $N = 24$; 1997: $N = 29$; 8+ years: 1996: $N = 14$; 1997: $N = 15$).

Data Collection

From the time that velvet was shed from the antlers in late August, two to three observers monitored the males that were usually resident in a single aggregated (bachelor) herd on their home range. We used all-event recording of agonistic interactions (Altmann 1974). Interactions were divided into two distinct 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. 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 information on the age of the interacting males, the total number of noncontact interactions and the number of fights for each male in the population. From these data we first 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