The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks?

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ABSTRACT

The somatic costs of reproduction are important for understanding the relationship between sexual selection and life-history evolution, and there are two main hypotheses used to explain the pattern of reproductive effort in ungulates. The terminal investment hypothesis predicts that reproductive effort should increase with age, because the value of each offspring increases as the number of future potential offspring decreases over the lifetime of an individual. In contrast, the mating strategy-effort hypothesis predicts that reproductive effort should be highest in prime-aged males, and lower in both younger and older males, since prime-aged males are most active in trying to gain matings. We examined reproductive effort among prime-aged (5–8 years old) fallow bucks (*Dama dama*) by comparing mass loss during the breeding season with mating success and activities associated with mating. Males lost about 26% of their body mass during the breeding season and mating success was strongly positively related to the time spent moving and in vocal display. However, mass loss was not related to either mating success or the behaviours associated with mating success. This indicates that males of higher quality were more efficient at converting energy into reproductive success, and is consistent with our earlier results showing phenotypic quality differences between males in our study population. Mass loss was positively correlated with initial mass. Therefore, body condition at the start of the breeding season was the most important determinant of reproductive effort. Mass loss was not related to age, in that it neither increased with age nor peaked in males that are usually the most reproductively active (ages 6 and 7). Thus, for reproductive effort in prime-aged males, our results do not support either the terminal investment hypothesis or the mating strategy-effort hypothesis.

Keywords: *Dama dama*, life history, mass loss, mating strategy-effort hypothesis, mating success, terminal investment.

INTRODUCTION

Reproduction is energetically expensive and mass loss during reproduction is common in both sexes of many species (Halliday, 1987). Variation in the ability to cope with energetic

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demands during the breeding season could be an important factor influencing reproductive success (Halliday, 1987; Andersson, 1994; Festa-Bianchet *et al.*, 1998). Therefore, energetic costs and the constraints they may impose are important for understanding the relationship between sexual selection and life-history evolution (Lindstedt and Boyce, 1985; Vehrencamp *et al.*, 1989; de Jong and van Noordwijk, 1992; Stearns, 1992).

In many male mammals, the period of reproduction is associated with an increase in energy expenditure with a concomitant decrease in foraging time (Mitchell *et al.*, 1976; Michener and Locklear, 1990; Newman *et al.*, 1998; Wolff, 1998). Therefore, the energy resources available for reproduction must accrue outside the breeding season and are generally considered finite. Males incur energetic costs mainly as a result of intrasexual competition and courtship. These costs reach their most extreme in some polygynous species of pinnipeds and ungulates in which males may stop feeding completely and lose up to 40% of their body mass (Leader-Williams and Ricketts, 1981; Anderson and Fedak, 1985; Deutsch *et al.*, 1990; Miquelle, 1990). The costs are also thought to be particularly high in sexually size dimorphic species, in which male body size exceeds female body size by 60% (Gittleman and Thompson, 1988; Key and Ross, 1999).

The fallow deer is a highly polygynous species with a similarly high level of sexual size dimorphism; mature males weigh on average 110 kg and females weigh on average 45 kg (McElligott *et al.*, 2001). Different mating systems are evident in different populations of fallow deer, and within those populations the mating strategies of individual males are very variable (Moore *et al.*, 1995; Thirgood *et al.*, 1999). The mating success of males is also highly variable and is related to factors such as age, body size and mass, vocal display, social dominance rank, fighting success and spatial strategies (Clutton-Brock *et al.*, 1988; Apollonio *et al.*, 1989; Moore *et al.*, 1995; McElligott *et al.*, 1998, 1999, 2001; McElligott and Hayden, 2000, 2001). Mating success peaks between the ages of 5 and 8 years, with 6- and 7-year-old males usually having the highest numbers of matings (McElligott and Hayden, 2000; McElligott *et al.*, 2002). However, it is not known to what extent the higher investment required to gain matings imposes additional somatic reproductive costs (Yoccoz *et al.*, 2002) on successful males. Research has already shown that successful males do not appear to suffer any long-term consequences (in terms of decreased survival or a reduction in fecundity) as a result of gaining matings (McElligott *et al.*, 2002).

Evidence from ungulates suggests that the pattern of reproductive effort differs markedly between the sexes. Studies of females provide support for the terminal investment hypothesis (Ericsson *et al.*, 2001). This predicts that reproductive effort or somatic reproductive costs should increase with age, because the value of each offspring increases as the number of future potential offspring decreases over the lifetime of an individual (Clutton-Brock, 1984; Evans, 1990). By contrast, the mating strategy-effort hypothesis, proposed by Yoccoz *et al.* (2002), predicts that somatic reproductive costs should be highest in prime-aged males, and lower in both younger and older males, since prime-aged males are most active in trying to gain matings. This is supported by their study of male red deer (*Cervus elaphus*).

In this study, we examined reproductive effort directly in prime-aged (5–8 years old) fallow bucks by weighing each individual before and after the breeding season, observing the mating success of each male and quantifying the behaviours associated with mating during this period. Our aim was to determine the somatic cost of reproduction to males of a highly polygynous mammal in a manner that has not been previously possible. Increasing mass loss between the ages examined would provide support for the terminal investment

hypothesis of reproductive effort. By contrast, mass loss peaking at ages 6 and 7, with less mass loss at both ages 5 and 8 years, would indicate support for the mating strategy-effort hypothesis of reproductive effort.

MATERIALS AND METHODS

Study site and population

The study was conducted on a herd of fallow deer in Phoenix Park (709 ha, 53°22′N, 6°21′W), Dublin, Ireland during the breeding seasons of 1996, 1997 and 1999. Full details of the population structure in these years are contained in McElligott *et al.* (2001). All males used in this study were of known age, tagged and individually recognizable.

Study animals and morphological measurements

We selected 32 different males (15 in 1996, 10 in 1997 and 7 in 1999) in mid-September each year based on their ages and approximate dominance ranks. The animals selected consisted of 7, 13, 8 and 4 males aged 5, 6, 7 and 8 years, respectively. We only included males between 5 and 8 years of age as they had reached their asymptotic size and mass, were not undergoing changes associated with senescence and account for the vast majority of matings (McElligott and Hayden, 2000; McElligott *et al.*, 2001, 2002). The mating success of males in our study population is highly skewed and related to dominance rank (McElligott *et al.*, 1998; McElligott and Hayden, 2000). Therefore, we tried to select males (based on approximate dominance ranks from field observations) that would be successful in gaining matings, when these occur during the second half of October. Later we analysed all agonistic interaction data to determine the exact dominance ranks. The males were immobilized by a veterinary surgeon using gas-propelled darts. Full details of the immobilizing, catching and measuring procedures are given in McElligott *et al.* (2001).

We caught males on 16 and 19 September 1996, on 16 and 17 September 1997, and 14 September 1999. These dates were chosen because they were before the expected onset of rutting activities and possible changes in mass (McElligott *et al.*, 1999). The males were caught again after the breeding season and weighed. This was carried out on 7 and 8 November 1996, 1 and 2 December 1997, and 23 November 1999. The average mass loss in 1999 was less than in the other 2 years (mean ± standard error: 29.6 ± 0.60 kg in 1996, 28.6 ± 1.29 kg in 1997, 24.6 ± 1.28 kg in 1999; see Results). However, this was not due to the date of recapture, because males in 1997 were caught at later dates than in 1999 and their average mass loss was greater. In addition, Asher *et al.* (1987) found that fallow bucks do not begin to regain the mass lost during the breeding season until the following spring.

Observations

We carried out all-event recording of matings and agonistic interactions. The matings were recorded from 16 October to 4 November 1996, from 15 October to 31 October 1997, and from 17 October to 31 October 1999. Our observation schedule was very similar each year and is detailed elsewhere (McElligott *et al.*, 2001). The mating success of males was based

on the number of directly observed copulations for each male, which provides a very good estimate of genetic paternity (Say *et al.*, 2003). For the total population, we recorded 337 matings in 1996, 278 matings in 1997 and 147 matings in 1999.

We also investigated the activity budgets of the males. The males were observed for periods of 1–2 h each day, noting at 2 min intervals the behaviour of the focal individual. We chose observation periods so that each male was observed at different times of the day throughout the study. We carried out focal watches from 1 October to 2 November 1996, from 3 to 29 October 1997, and from 29 September to 31 October 1999. Each male was observed for 24.1 ± 1.3 h. The following exclusive categories of behaviour were recorded during the focal watches: moving, fighting, feeding and resting (lying down). We also recorded if males were groaning. This could happen simultaneously with moving, but not with any of the other behavioural categories. These behavioural categories accounted for most of the activities of the males (see Results) and therefore we do not give details of the very small proportion of the overall activity budget that remained. In total, there were 771 focal hour observations.

Dominance relationships

The outcomes of agonistic interactions were used to calculate a dominance rank for all mature males for the pre-rut (before matings started) in each year, according to Clutton-Brock *et al.* (1979). In September, we did not record agonistic inter-actions involving our study males for up to 5 days after they had been caught. This avoided recording the outcome of any agonistic interactions that may have been affected by any short-term effects of the handling. According to the pre-rut dominance rank, we found that in 1996 the males selected included 8 of the top 10 ranked males and 8 others distributed throughout the lower ranking individuals. In 1997, our selection included 5 of the top 10-ranked males and 5 others distributed throughout the lower ranking individuals. In 1999, the males were ranked at regular intervals between 4 and 31. Because of the lower average mass loss, and the generally lower ranks of males in 1999 compared with the other 2 years, we controlled for the effect of year in our later analyses (see Results). The total number of males ranked in the pre-rut in 1996, 1997 and 1999 was 61, 63 and 69, respectively.

Statistical analysis

The data were analysed using general linear models (GLM). Initially, we evaluated the effects of time spent moving, fighting, groaning and feeding on mating success. We then investigated the determinants of mass loss. This model initially included male age, mating success [entered as either a nominal (yes/no) or continuous variable (number of matings)], dominance rank, initial mass, leg length (as an indicator of skeletal body size), and time spent moving, fighting, groaning and feeding. In these analyses, variables were removed from the final model in order of least significance if they did not explain a significant amount of the variance. Because of our limited sample size and to minimize the number of independent variables, we did not include resting in the GLM analyses. All data were normally distributed (Kolmogorov-Smirnov test, all $P > 0.5$), except for age ($P = 0.049$) and number of matings ($P < 0.01$), both of which were normalized after log transformation [log age, $P = 0.095$; log (number of matings + 1), $P = 0.11$].

RESULTS

Summary of the overall activity budget, mating success, mass and mass loss

A summary of the overall activity budget is given in Table 1. Of the 32 males that we selected, 19 (59.4%) gained matings. These males gained 251, 88 and 9 matings in 1996, 1997 and 1999, respectively (total = 348). This represents 76.8% (1996), 31.7% (1997) and 6.1% (1999) of the total matings in each year. The most successful male gained 104 matings in one year. The total number of matings gained by each age class from 5 to 8 years old was 14, 285, 22 and 27, respectively. On average, males weighed 110.5 ± 0.7 kg in September and 82.3 ± 0.9 kg when weighed later. This represents an average total mass loss of 28.2 ± 0.6 kg ($25.5 \pm 0.5\%$ of body mass). Mass loss ranged from 20 to 34.5 kg.

Mating success as a function of moving, fighting, feeding and groaning

The overall model with mating success as the dependent variable was significant ($F_{4,27} = 4.93$, $P = 0.004$, $r^2 = 0.42$). However, none of the independent variables tested were significant (all $P > 0.16$), indicating a potential problem of collinearity (Zar, 1999). Further investigation revealed a strong relationship between moving and groaning ($F_{1,30} = 83.0$, $P < 0.0001$, $r^2 = 0.74$). Therefore, we carried out the analysis again, but in each case only included either moving or groaning, along with the other independent variables. We found that mating success was positively associated with the amount of time males spent moving, when groaning was not included ($t = 4.1$, $n = 32$, $P = 0.0003$; $F_{3,28} = 6.10$, $P = 0.0025$, $r^2 = 0.40$; Fig. 1a). Mating success was not related to either feeding or fighting (both $P > 0.24$). Similarly, mating success was positively associated with the amount of time males spent groaning, when moving was not included ($t = 3.9$, $n = 32$, $P = 0.0005$; $F_{3,28} = 5.71$, $P = 0.0035$, $r^2 = 0.38$; Fig. 1b). Again in this model, mating success was not related to either feeding or fighting (both $P > 0.41$).

Mass loss as a function of initial mass, age, mating success, dominance rank, leg length, moving, fighting, groaning, feeding and year

There was a relationship between year and mass loss ($F_{1,30} = 1.21$, $P = 0.002$; see also Methods). Therefore, we controlled for year and examined the relationships between mass

Table 1. Summary statistics of the activity budgets of the males ($n = 32$; the total for the first four behaviour categories is 95%)

Activity	Mean ± standard error (%)	Range
Moving	25.1 ± 1.0	8.8–43.3
Fighting	3.8 ± 0.5	0–9.3
Feeding	14.4 ± 0.07	6.8–20.3
Resting	51.7 ± 1.0	37.9–66.9
Groaning[a]	15.5 ± 2.0	0–34.6

[a] Groaning can also occur simultaneously with moving and, therefore, when this is included the total is 110.5%.
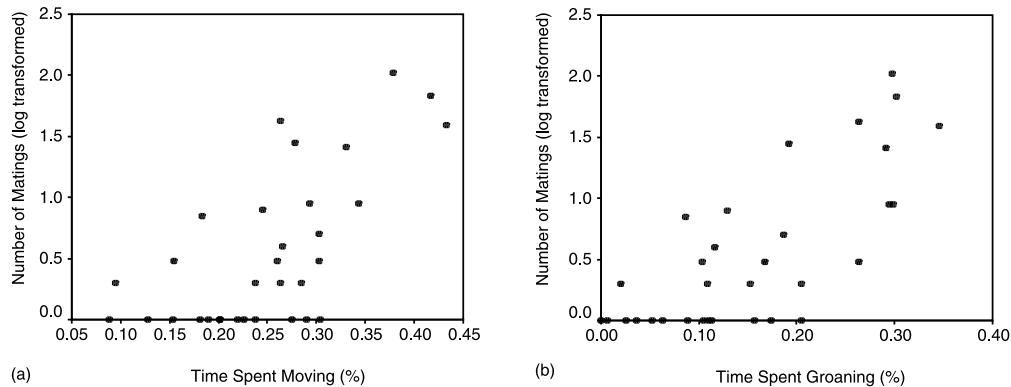
Fig. 1. The significant associations between mating success and the proportion of time a male spent (a) moving and (b) groaning.

loss and the other variables that we measured. We found that only initial mass was significantly positively related to the mass lost, with the overall model explaining 43% of the variation (Table 2; Fig. 2). Mating success was entered as a nominal (yes/no) in this analysis. We then repeated the analysis with mating success (log transformed) entered as a continuous variable. We found that initial mass was related to mass loss ($F_{1,22} = 3.43$, $P = 0.08$) at a marginally non-significant level. Therefore, we carried out backward elimination and found that the relationship between initial mass and mass loss became stronger, and the relationship between the amount of time spent fighting and mass loss was marginally positively significant (Table 3). The final model explained 34% of the variation in mass loss. Plots showing mating success in relation to mass loss, and age in relation to mass loss, illustrate the lack of associations between these variables (Fig. 3). Overall, these analyses show that heavier males lose more mass, and the amount of time spent fighting may be weakly positively associated with mass loss.

DISCUSSION

We found that males lose a large proportion (*c.* 26%) of their body mass during the breeding season. Mating success was very strongly related to the proportion of time that males spent moving and groaning, but not related to the other variables that we tested (Fig. 1). If we assume that these activities incur energetic costs, then we would predict that mating success should be related to mass loss. However, we found that mass loss was not related to either mating success or the behaviours associated with mating success (Tables 2 and 3). The proportion of time spent fighting was not related to mating success, but was weakly positively related to mass loss, when mating success was entered in the model as a continuous variable (Table 3). Mass loss was positively related to initial mass. Therefore, heavier males lost more mass during the breeding season than other males, and there is weak evidence to suggest that males that spent more time fighting lost marginally more mass than other males. The lack of a relationship between mass loss and activities strongly associated with mating suggests that some males are more efficient at utilizing their fat stores. This is in keeping with our earlier results showing phenotypic quality differences between males

Table 2. GLM analysis of mass loss as a function of initial mass, age, mating success, dominance rank, leg length, moving, fighting, groaning and feeding[a]

	Mean square	$F_{1,22}$	P
Initial mass	35.67	4.55	0.04
Age[b]	21.64	2.76	0.11
Mating success[c]	19.45	2.48	0.13
Dominance rank	5.53	0.71	0.41
Leg length	7.19	0.92	0.35
Moving	0.84	0.11	0.75
Fighting	13.71	1.75	0.20
Groaning	9.26	1.18	0.29
Feeding	10.49	1.34	0.26

[a] The effect of year is controlled. [b] Log-transformed. [c] Entered as a nominal variable (yes/no).
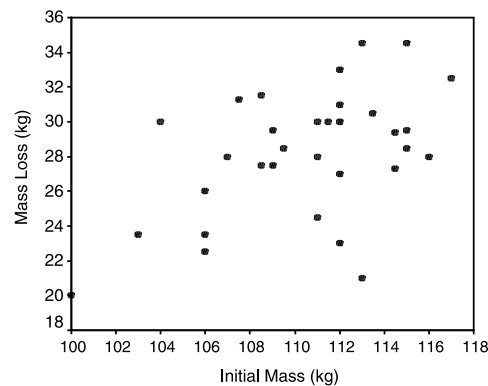
Fig. 2. The significant association between mass loss and initial mass.

in our study population and possible positive correlations between fitness correlates (Houle, 1991; Dobson *et al.*, 1999; McElligott *et al.*, 2002).

It is generally assumed that sexual displays are condition-dependent if they are honest quality signals (Andersson, 1994; Kokko, 1997). Consistent with this prediction, energy expenditure in male lekking sage grouse (*Centrocercus urophasianus*) was positively related to display rate and the time spent on the lek (Vehrencamp *et al.*, 1989). Similarly, several studies of pinnipeds, rodents and ungulates have found a relationship between mass loss and some indirect measure of male mating success, or another proxy indicator of mating success for males (Anderson and Fedak, 1985; Deutsch *et al.*, 1990; Michener and Locklear, 1990; Boyd and Duck, 1991; Salsbury and Armitage, 1995; Kovacs *et al.*, 1996; Millesi *et al.*, 1998; Wolff, 1998; Bro-Jørgensen and Durant, 2003). Our results show that the mass that males attained before the breeding season was an important determinant of mass lost during the breeding season, thereby providing some evidence for a link between condition and mass loss. However, neither initial mass nor mass loss has been shown to correlate with mating success (McElligott *et al.*, 2001; this study). It has been suggested that activities such

Table 3. GLM analysis (with backward elimination) of mass loss as a function of initial mass, age, mating success, dominance rank, leg length, moving, fighting, groaning and feeding [a,b]

	Mean square	$F_{1,26}$	P
Initial mass	3.85	5.08	0.03
Age[c]	2.06	2.73	0.11
Fighting	33.51	4.42	0.05
Groaning	5.55	0.73	0.40
Feeding	3.88	0.51	0.48

[a] The effect of year is controlled. [b] Mating success (continuous variable), dominance rank, leg length and moving were removed after backward elimination. [c] Log-transformed.
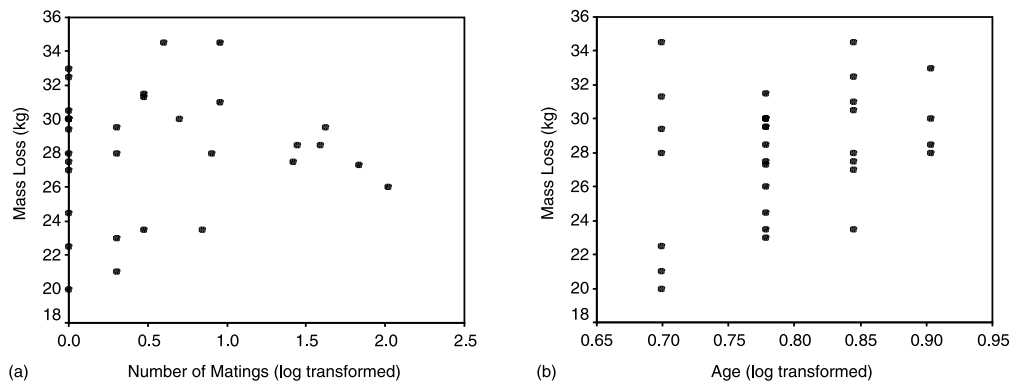

Fig. 3. The non-significant associations between mass loss and (a) mating success and (b) age.

as display and fighting probably account for the mass losses of male ungulates during the breeding season (Yoccoz *et al.*, 2002). However, ours is the only study to provide individual data on mass loss, mating success and activity budgets, and our results show that there is little or no evidence for this, at least in fallow deer. The positive relationship between the time spent fighting and mass loss is too weak to allow any firm conclusions to be drawn. Males in our study population have access to naturally abundant food before the breeding season. Therefore, it is possible that most males reach a body condition that does not limit activities associated with mating success or mating success itself. We already know from our study population that mating success is related to behavioural and quality differences among males (Moore *et al.*, 1995; McElligott *et al.*, 1998, 1999).

One of the most significant problems in measuring reproductive effort is the underlying variation in individuals in terms of stored resources and how these may mask possible costs (Parker, 1982; van Noordwijk and de Jong, 1986; de Jong and van Noordwijk, 1992; Doughty and Shine, 1997). This could also explain why we did not detect a relationship between mass loss and mating success, or behaviours associated with mating success. The large mass loss experienced by all males clearly indicates that they incur net energetic costs during the breeding season. Some of the successful males had very high mating success

together with associated high levels of activity, and lost similar or even less mass than unsuccessful males (Fig. 3a). This is in line with our earlier results from the same population showing clear differences in male quality, in terms of survival and mating probabilities (McElligott *et al.*, 2002). Given that non-mating males in our study population have lower survival rates than mating males (McElligott *et al.*, 2002), but lose similar mass during the breeding season, it is possible that there is a trade-off between survival and reproductive effort for these individuals. This contrasts with the suggestion that red deer males do not trade survival for reproductive effort (Yoccoz *et al.*, 2002). Yoccoz and co-workers found that reproductive effort was reduced at high population densities due to a reduction in body condition, particularly for prime-aged and very old males.

It is important to test for associations between mass loss and activities associated with mating success and not simply with mating success itself. This is because the behaviour and, therefore, the activity budgets of the males change from late September, while matings occur during the latter half of October (McElligott *et al.*, 1999). Even for prime-aged males, there are differences in the onset of behaviours associated with reproduction. Males that later gain matings exhibit reproductive behaviours earlier than unsuccessful males (McElligott *et al.*, 1999) and, therefore, it is especially surprising that these males do not incur greater somatic costs. We tested for an effect of feeding on mass loss because even though feeding is greatly reduced during the breeding season (Moore, 1993; Newman *et al.*, 1998), it is possible that males could feed to compensate for the energy expended trying to gain matings. For example, Vehrencamp *et al.* (1989) found that actively displaying male sage grouse lost less weight per day than other males because their foraging efficiency away from the lek was more efficient. Again, we found no evidence that feeding was associated with mass loss.

We specifically targeted males between the ages of 5 and 8 years (*c*. 26% body mass loss), since these are the males that account for the vast majority of matings in our study population (McElligott and Hayden, 2000; McElligott *et al.*, 2002). We do have some mass loss data for four younger males (three 3-year-olds and one 4-year-old) showing that these lose a lower proportion ($14.7 \pm 1.6\%$) of their body mass over the same period. Because males at these ages have not yet reached full size and data on the activity budgets of these males are not available, they were not included in our analyses (Moore, 1993; T.J. Hayden, unpublished data). Similarly, we have some indication that fallow bucks older than 8 years also lose a smaller proportion of their body mass than prime-aged males. Data for two 9-year-old males show that they lost on average 22.2% of their body mass during the breeding season (T.J. Hayden, unpublished data). One of the 9-year-old males was weighed in 2 years and his data when aged 8 were used in our detailed analysis. As an 8-year-old, this male weighed 112 kg and he then lost 29.5% of his body mass during the breeding season. The following year, the same male weighed 106 kg and lost 25.5% of his body mass. This limited data set for six males (four before prime-age and two after prime-age), showing that they lost less mass than prime-aged males, suggests tentative support for the mating strategy-effort hypothesis (Yoccoz *et al.*, 2002). However, a larger data set is required to determine if the mating strategy-effort hypothesis could be valid across a wider range of ages for fallow bucks, and this could be an interesting route for future research.

In conclusion, our results show that mass loss neither increases with age in prime-aged (5–8 years old) fallow bucks nor peaks at ages 6 and 7 years. Therefore, our study does not provide support for either the terminal investment or the mating strategy-effort hypotheses of reproductive effort within these age classes of fallow bucks (Fig. 3b). Thus it may not be

possible to distinguish between the main hypotheses of reproductive effort between the ages of 5 and 8 years. Recent evidence from red deer males of all ages provides support for the mating strategy-effort hypothesis of reproductive effort (Yoccoz *et al.*, 2002). Our finding that mass loss is not associated with mating success (Fig. 3a), despite huge differences in mating success, provides additional support for the idea that there are strong phenotypic quality differences between males in our study population (McElligott *et al.*, 2002).

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