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Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success?

Abstract Sexual size dimorphism may evolve as a result of both natural and sexual selection. In polygynous mammals, the main factor resulting in the evolution of large body size in males is the advantage conferred during competition for mates. In this study, we examined whether sexual selection acts on body size in mature fallow bucks (*Dama dama*) by examining how the following traits are inter-related: age, body (skeletal) size, body mass, prerut dominance rank, rut dominance rank and mating success. This is the first study to examine how all these factors are together related to the mating success of a large sexually dimorphic and polygynous mammal. We found that male mating success was directly related to body size, but not to body mass. However body mass was related to prerut dominance rank which was in turn strongly related to rut dominance rank, and thus there was an indirect relationship between mating success and body mass. Rut dominance rank was the variable most strongly related to mating success. Mating success among mature males was unrelated to age. We conclude that larger mature fallow bucks have advantages over other males when competing for matings, and sexual selection therefore continues to act on sexual size dimorphism in this species. Heavier fallow bucks also have advantages, but these are mediated through the dominance ranks attained by males before the rut.

Keywords Body size · Body mass · Dominance rank · Fallow deer · Mating success · Sexual selection

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Introduction

Many factors may contribute to individual reproductive success, but one of the more important is body size, which can affect both reproduction and survival. Accordingly, sexual size dimorphism may evolve as a result of either natural selection, sexual selection or both (Hedrick and Temeles 1989; Andersson 1994; Blanckenhorn, in press). Among polygynous mammals, ungulates and pinnipeds provide some of the most striking examples of sexual size dimorphism, males being much larger than females (Jarman 1983; Modig 1996). In these and many other species, the main factors resulting in the evolution of large body size are the advantages conferred on males during competition for mates, i.e. sexual selection. These advantages can operate in a number of different ways, but one of the main routes is through intrasexual competition leading to enhanced or prolonged access to females and/or resources attractive to females (Gosling and Petrie 1990; Andersson 1994). Recent research on ungulates suggests that although sexual selection is the most important factor influencing the evolution of sexual size dimorphism in these species, natural selection can also play a role in maintaining levels of dimorphism (Post et al. 1999).

Several extensive review papers, some using a comparative approach, have focused on sexual size dimorphism in ungulates (Jarman 1983; Weckerly 1998; Loison et al. 1999). However, among ungulates, very few studies have been specifically designed to examine the relationship between size and mating success of the same individuals. For example, as part of a larger study, Clutton-Brock et al. (1988a) found that mating success

was related to body size in red deer stags (*Cervus elaphus*). This is in contrast to the several similar studies on pinnipeds in the literature (Anderson and Fedak 1985; Le Boeuf and Reiter 1988; Deutsch et al. 1990; Haley 1994; Haley et al. 1994; Modig 1996).

In this study, we investigate whether sexual selection acts on body size in mature male fallow deer (*Dama dama*). This species is a large sexually size-dimorphic cervid, with different populations exhibiting a variety of mating systems. However, a high level of polygyny is common to all (Thirgood et al. 1999). In addition, and for the first time in any cervid, we aim to distinguish between the relative contributions of skeletal size and body mass to the mating success of fallow bucks. Because of competitive exclusion by mature males, males must be at least 4 or 5 years old before they have a chance of gaining matings in naturally age-structured populations (Komers et al. 1997; McElligott et al. 1998; McElligott and Hayden 2000). However, the extent to which variation in body size is related to mating success among mature males is not known. In our non-lekking study population, mature males weigh up to 117 kg (average 110 kg), and females weigh on average 45 kg (O'Connell 1993; Moore et al. 1995; this study).

Research to date has shown that reproductive effort and mating success among male fallow deer are related to factors such as age, social dominance rank, fighting success, vocal display and spatial strategies (Clutton-Brock et al. 1988b; Apollonio et al. 1989; Moore et al. 1995; McElligott et al. 1998, 1999). To fully assess the role of skeletal size and/or body mass in mating success, social dominance rank must be included in the analysis because an association between size and/or mass and mating success could be mediated by rank (Haley et al. 1994). Because this study uses marked animals whose ages are known, we also include age, in addition to skeletal size, body mass and social dominance rank. This is the first study of its kind to examine how all these factors together are related to the mating success of a large sexually dimorphic and polygynous cervid.

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. In 1996, the herd consisted of 142 fawns, 390 females (≥1 year old) and 147 males (≥1 year old). In 1997, there were 100 fawns, 319 females (≥1 year old) and 136 males (≥1 year old). In 1999, there were 126 fawns, 234 females (≥1 year old), and 188 males (≥1 year old). All males used in this study were of known age, tagged and individually recognizable.

Study animals and morphological measurements

We selected 38 different males (16 in 1996, 11 in 1997 and 11 in 1999) primarily based on their age. The animals selected consisted of 8, 17, 8 and 4 males, aged 5, 6, 7 and 8 years, respectively. There are strong age effects on skeletal size and body mass and thus we excluded males younger than 5 years and older than

8 years (Moore 1993; Fischer 1996). This ensured that all males had reached their asymptotic size and body mass but were not undergoing changes associated with senescence.

Because of the very large skew in mating success among males in this population and the fact that most males fail to gain any matings throughout their entire life, we tried to select at least some males each year that we thought had a chance of gaining some matings, i.e. those of generally high social dominance rank (McElligott et al. 1998; McElligott and Hayden 2000). In addition, our aim was to select males with a wide range of ranks. If we selected males purely at random, we would have risked sampling only males that gained no matings. Exact dyadic dominance relationships were not known at the time of selection, but we knew from our observations that some males were higher ranking than others. All agonistic interaction data were later compiled and analysed to determine the exact dominance rank of each male.

The males were immobilized by a veterinary surgeon (J.T.W.) using gas-propelled darts (1.5 ml, Daniject) to deliver a mixture of etorphine hydrochloride (18–20 µg kg^{-1}; C-Vet Veterinary Products) and xylazine (360–420 µg kg^{-1}, Rompun Dry Substance; Bayer) intramuscularly. We then weighed the males, and using calipers, measured a segment of one hind leg for each male. This was used as a proxy indicator of skeletal size and corresponds to measurements that have also been used as indicators of body size for other ungulates such as red deer and soay sheep (*Ovis aries*), (Clutton-Brock et al. 1988a; Coltman et al. 1999). The hind leg was measured from the caudal end of the calcaneal tuberosity to the cranial surface of the proximal phalanx when both the tibio-metarsal and the metarso-phalangeal joints were held in the fully flexed position. For simplicity, we henceforth use the term 'body size' when referring to this measurement. The effect of the tranquilizing drugs was then reversed by intravenous administration of a mixture of the antagonistic drugs diprenorphine hydrochloride (Revivon, 24–28 µg kg^{-1}; C-Vet Veterinary Products) and anti-pamazole hydrochloride (Antisedan; Pfizer) in a total volume of less than 2 ml. The males in this study did not appear to suffer any long-lasting effects as a result of being handled. Subsequently, a large proportion of them gained a large number of matings during the rut (see Results).

We carried out darting on 16 and 19 September 1996, on 16 and 17 September 1997, and on 14 September 1999. These dates were selected so that the males were at their annual maximal weights and before the expected onset of rutting activities, such as vocalizing, which usually begin during the final week of September (McElligott et al. 1999).

Observations

We carried out all-event recording of agonistic interactions and matings. We divided the breeding season into two periods: prerut and rut. The prerut began in late August when all males had cleaned the velvet from their antlers, and ended on the day before the first mating in each year. The rut is the time when matings occur, during the second half of October. Over the 11 ruts from 1989 to 1999, on average, 90.1% of matings occur within the period 20–30 October (Moore 1993; McElligott 1997; Kelly 1998; T.J. Hayden, unpublished data). For this study, the matings were recorded during the following periods: 16 October to 4 November 1996, 15 October to 31 October 1997, 17 October to 31 October 1999. Initially, 2 to 4 observers were in the field while the males were still in an aggregated bachelor herd on their summer range. From late September onwards, the males move onto the females' range and become more dispersed (Moore et al. 1995). During this period, more observers were recruited, such that up to 13 were in the field each day. Observations usually began at dawn. During October and the early days of November in 1996, we carried out observations every day from dawn to dusk (ca 11 h). Observers were in radio contact and deployed to maximize coverage of all animals. The mating success of males is the number of directly observed copulations for each male. For the total population, we recorded 327, 278 and 147 matings in 1996, 1997 and 1999, respectively.

Dominance relationships

The outcomes of agonistic interactions were used to calculate a dominance rank for all mature males for each phase of the breeding season (prerut and rut), according to Clutton-Brock et al. (1979). Immature males (<4 years old) were not ranked because of their low frequency of interaction with mature males (McElligott et al. 1998). We did not record agonistic interactions involving our study males for up to 5 days after they had been darted. This avoided recording the outcome of any agonistic interactions that may have been influenced by any short-term effects of handling.

We calculated dominance ranks of the males for both phases of the breeding season, prerut and rut. This was important for a number of reasons. The prerut rank is assessed at a time when the vast majority of agonistic interactions are non-contact displacements among males and before they begin to lose weight. By contrast, the rut dominance rank is calculated using a large proportion of results from fights and also at a time when the body condition of males is declining (McElligott et al. 1998, 1999). For additional details of the agonistic interactions of fallow bucks, see McElligott et al. (1998).

According to the prerut dominance rank, we found that in 1996, the males sampled included 8 of the top-ten-ranked males and 8 others distributed throughout the lower-ranking individuals. In 1997, our sample included 6 of the top-ten-ranked males and 5 others distributed throughout the lower-ranking individuals. In 1999, our sample included 5 of the top-ten-ranked males and 6 others distributed throughout the lower-ranking individuals. The total number of males ranked in the prerut in 1996, 1997 and 1999 were 61, 63 and 69, respectively. The total number of males ranked in the rut in 1996, 1997 and 1999 were 67, 68 and 62, respectively. For simplicity, the term 'rank' henceforth refers to social dominance rank.

Statistical analysis

We carried out statistical tests using SPSS and Excel. We checked variables for normality (Shapiro-Wilks test) and considered results significant at the $P<0.05$ level (all two-tailed). We used the Kendall rank-order correlation coefficient (τ) and the Kendall partial rank-order correlation coefficient to examine the relationships between mating success, dominance rank, body size and body mass (Siegel and Castellan 1988). We used these methods for a number of reasons; some data were not normally distributed, there were tied ranks, and there was also collinearity between some of the variables. In addition, partial correlations allowed us to determine the relationship between each independent variable and the dependent variable, while controlling for any association between other independent variables and the dependent variable. The use of a unique set of males each year and application of non-parametric ranking procedures allowed us to pool data across years.

To reach the final goal of determining the relationships between mating success, body size, body mass and rank, we divided our analysis into three main parts. First, we determined the relationships between prerut rank and age, body size and body mass. Second, we examined the relationships between rut rank and age, body size, body mass and prerut rank. Finally, we included all these variables in an analysis using mating success as the dependent variable. By carrying out the analysis in this manner, we could identify variables that might not be directly related to mating success, but instead operate indirectly through one of the other factors considered.

Results

Summary of mating success and morphological traits

A summary of the overall mating success and the morphological data of the study animals is given in Table 1. Body size and mass of the males ranged from 92 to 105% and from 85 to 105%, of the respective medians

Table 1 Summary statistics of morphological traits and mating success of males; mating success was not normally distributed and therefore only the median is given

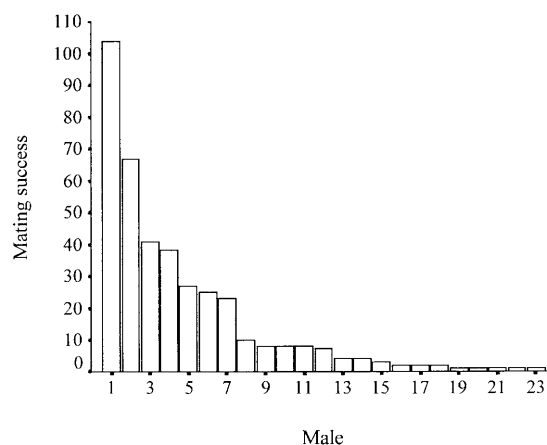|	Mean±SE	CV	Median	Range	n
Body size (cm)	32.4±0.2	3.5	32.5	30.0–34.0	38
Body mass (kg)	110.2±0.7	4.2	111.3	94.5–117	38
Mating success	–	–	1	0–104	38

Fig. 1 Mating success of the males that gained matings (*n*=23). The males that gained no matings (*n*=15) are not represented in this figure

(Table 1). In addition, the level of variation in mass was slightly higher than in size (Table 1). Body size and mass did not differ with age ($F_{3,34}=0.57$ and $F_{3,34}=0.31$, $P=0.82$ and $P=0.64$, respectively). In addition, body size was related to body mass ($\tau=0.28$, $P=0.02$, $n=38$). Of our sample of 38 males, 23 (60.5%) gained matings: 7 (43.7%) in 1996, 10 (90.9%) in 1997 and 6 (54.5%) in 1999. These males gained 251, 96 and 41 matings in 1996, 1997 and 1999, respectively. The number of matings gained by each of the successful males is shown in Fig. 1. This represented 76.8% (1996), 34.5% (1997) and 27.9% (1999) of the total matings in each year.

Age, body size, body mass and prerut rank

We found that prerut rank was significantly related to both body size and body mass (Table 2). Prerut rank was not related to age. When the relationship between prerut rank and either size or mass was controlled, the relationship between prerut rank and either of the other variables remained significant. Thus, body size and body mass were idependently related to prerut dominance rank (Fig. 2).

Age, body size, body mass, prerut rank and rut rank

When all factors were considered independently, we found that rut rank was significantly related to body size, body mass and prerut rank; rut rank was not related to

Table 2 Kendall rank-order correlation coefficients, with prerut rank as the dependent variable (n=38)

	Prerut rank		
	Simple τ	Partial τ[a, b]	Partial τ[a, c]
Age (years)	0.061		
Body mass	0.324**	0.254*	–
Body size	0.339**	–	0.274**

*P<0.05; **P<0.01; ***P<0.001
[a] Age excluded
[b] Controlled for body size
[c] Controlled for body mass

Table 3 Kendall rank-order correlation coefficients, with rut rank as the dependent variable (n=38)

	Rut rank		
	Simple τ	Partial τ[a]	Partial τ[b]
Age	0.067		
Body mass	0.232*	0.087	
Body size	0.345**	0.217*	–
Prerut rank	0.495***	–	0.428***

*P<0.05; **P<0.01; ***P<0.001
[a] Controlled for prerut rank; age excluded
[b] Controlled for body size; age and body mass excluded

age (Table 3). When prerut rank was controlled, rut rank was no longer significantly related to body mass and this factor was excluded. When the relationship between either rut rank and prerut rank, or rut rank and body size were controlled, the remaining bivariate relationship was significant. Thus, rut rank was related independently to both prerut rank and body size, unrelated to age, and not directly related to body mass (Fig. 2).

We also considered the relationships between body size, body mass and rut rank, while excluding prerut rank from the analysis. When the relationship between

Fig. 2 Summary of the main results, presenting the hypothetical direction of causality. Age is not included in the figure because it was not related to any of the other variables. The levels of significance for the partial correlations are included (*P<0.05, **P<0.01, ***P<0.001, NS non-significant). For additional details, see Tables 2, 3 and 4

Table 4 Kendall rank-order correlation coefficients, with mating success as the dependent variable (n=38)

	Mating Success		
	Simple τ	Partial τ[a]	Partial τ[b]
Age	0.065		
Body mass	0.128		
Body size	0.451***	0.318**	–
Prerut rank	0.369**	0.070	
Rut rank	0.652***	–	0.593***

**P<0.01; ***P<0.001
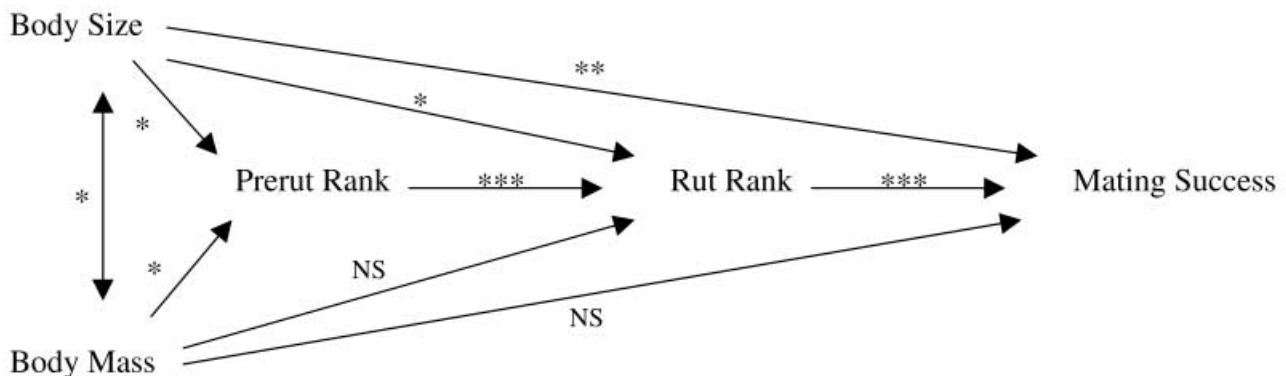[a] Controlled for rut rank; age and body mass excluded
[b] Controlled for body size; age, body mass and prerut rank excluded

body size and rut rank was controlled, body mass was not significantly related to rut rank (Kendall correlation: partial τ=0.15, n=38, P>0.05). Conversely, when the relationship between body mass and rut rank was controlled, the relationship between body size and rut rank remained significant (Kendall correlation: partial τ=0.30, n=38, P<0.01). This confirmed the result that body size was related to rut rank. Body mass was not directly related to rut rank, but was instead related to rut rank through the prerut rank.

Age, body size, body mass, prerut rank, rut rank and mating success

When all factors were considered independently, we found that mating success was related to body size, prerut rank and rut rank (Table 4). Mating success was not related to age, and not directly related to body mass. These variables were therefore excluded from further analysis. When rut rank was controlled, mating success was no longer related to prerut rank and this factor was then excluded. Mating success remained significantly related to body size when rut rank was controlled and, similarly, rut rank remained significantly related to mating success when body size was controlled. Thus, mating success was independently related to rut rank and body size, and unrelated to age. The relationship between mating success and prerut rank was mediated by rut rank. The relationship between mating success and body mass was mediated by prerut rank and, subsequently, rut rank (Fig. 2).

Discussion

In this study, we found that male mating success was directly related to body size, and indirectly related to body mass (Fig. 2, Table 4). The variation in body size was slightly less than in body mass (Table 1), which suggests that our methods did not inadvertently control for a direct relationship between body mass and mating success. Social dominance rank during the rut was the factor most strongly related to mating success. This is in keeping with earlier results from the same population (Moore et al. 1995; McElligott et al. 1998, 1999). Similarly, Komers et al. (1997) found that dominance rank was the most important factor influencing the expression of reproductive behaviors. We found that mating success was not directly related to body mass, but since this factor was related to prerut rank (Table 2), which was in turn strongly related to rut rank (Table 3), there is evidence for an indirect relationship between mating success and body mass. Once we controlled for rut rank, mating success was no longer related to prerut rank because of the close relationship between the two ranks. Mating success among mature males was unrelated to age, as we had previously shown (McElligott et al. 1999).

Since the dominance rank that was assessed during the prerut was mainly the result of non-contact agonistic interactions (McElligott et al. 1998), we might predict that it would not necessarily be strongly related to either body size or mass. By contrast, the dominance ranks assessed during the rut were calculated using the results of a large number of fights, and therefore we would predict that rank at this time should be more closely related to body size and mass (Parker 1974; Haley 1994; McElligott et al. 1998). We found that body size was related to both ranks to a similar extent. In addition, body mass was related to prerut rank but not to rut rank. This apparent anomaly can be explained by the phenotypic changes experienced by fallow bucks during the rut. As in male pinnipeds such as grey seals (*Halichoerus grypus*: Anderson and Fedak 1985) and elephant seals (*Mirounga angustirostris*: Deutsch et al. 1990) and other ungulates such as red deer (Mitchell et al. 1976) and bison (*Bison bison*: Wolff 1998), food intake of fallow bucks declines dramatically at this time of increased activity, and therefore their body condition (mass) also decreases (Moore 1993; McElligott et al. 1999). By contrast, skeletal size is likely to remain stable. Thus, males possibly do not maintain relative masses, and differences in prerut weights are too remote to affect the dominance asymmetries between dyads during the rut. The only means of resolving this matter would be to monitor mass changes of males throughout the rut. However, this would be very difficult in the semi-natural setting of our study.

According to Andersson (1994), there are four main routes through which sexual selection can lead to the evolution of sexual size dimorphism, with males larger than females: (1) advantages during combat, (2) advantages in endurance rivalry, (3) female preferences for larger males and (4) advantages during sperm competition.

However, one of the major problems determining which factors are most important in a particular system is that they do not necessarily have opposing predictions (Hedrick and Temeles 1989). In addition, traits can also be simultaneously involved in a number of different intrasexual and intersexual processes (Berglund et al. 1996).

We found that among mature males, body size and body mass were related to dominance relationships during the prerut. These relationships are in turn tested and modified by fights during the rut to produce the dominance ranks that influence mating success (Moore et al. 1995; McElligott et al. 1998). Thus, our study provides evidence of advantages resulting from direct intrasexual competition. However, predetermined dominance relationships are not always necessary for a relationship between body size and mating success, since in some species males do not form dominance hierarchies prior to the breeding season, and yet male body size is related to mating success (Fisher and Lara 1999).

The relationship we found between mating success and body size (independent of rank) suggests that endurance rivalry may also be a factor in the mating success of fallow bucks (Bartholomew 1970; Lindstedt and Boyce 1985). Large size would help males sustain reproductive efforts such as vocal display at a time when their food intake is very limited (McElligott and Hayden 1999, in press; McElligott et al. 1999). This is because the amount of stored fat becomes a larger proportion of body mass, as body size increases in mammals (Lindstedt and Boyce 1985).

Evidence is increasing for active female mate choice in fallow deer, and particularly in non-lekking populations (Komers et al. 1999; McElligott et al. 1999). Our results cannot be used to determine if fallow does prefer larger males, but they may provide a useful indication. However, an experimental study is required to test conclusively for female preferences for larger fallow deer males. Fallow does produce very large neonates relative to their own mass and male-biased maternal investment either pre- or postnatally plays a role in the development of sexual size dimorphism (Pélabon et al. 1995; Jabbour et al. 1997; Birgersson et al. 1998; Braza et al. 2000). Therefore, if females choose to mate with generally larger males, they may be selecting for larger offspring, since this trait is likely to be heritable (Horne and Ylönen 1998).

Body size represents a measure of the successful acquisition of resources by males, particularly during the early years of life. In our study population, males achieve 90% of their skeletal growth in their first year of life and have completed the process by age 4 (Moore 1993). The body size variable thus emphasizes early life processes and includes a component of maternal investment (Birgersson et al. 1998). Mature male body mass on the other hand, represents successful acquisition of resources each year and is not a static trait. Male body size could therefore be a potentially better indicator of overall male quality than body mass, even though the two factors are related (Kodric-Brown and Brown 1984; Sullivan 1990; Hill et al. 1999).

In some species, the number of sperm per ejaculate is directly related to body size (Møller 1991; Wedell 1997). Therefore, larger size would possibly also lead to advantages if there is sperm competition. In our study population, 16% of females mate more than once during the same oestrous cycle, and sperm competition may affect the reproductive success of males in a low proportion of cases (McElligott and Hayden 2000).

Fallow deer are probably the most sexually dimorphic cervid; the mass ratio of males to females from different populations ranges from 1.7. to 2.2 (Carranza 1996; Loison et al. 1999). In our population, this ratio is even higher at 2.4 (O'Connell 1993; this study). High variance in male mating success and high levels of sexual size dimorphism are often associated with higher levels of mortality among males (Promislow 1992; Owen-Smith 1993). However, an interspecific comparison of mortality rates will be needed to determine if males in our study population have comparatively high mortality levels as a result of the high level of sexual size dimorphism. At the intraspecific and population level, the males that gain matings in our study population, therefore generally the larger ones (this study), do not have increased levels of mortality compared to unsuccessful males (McElligott and Hayden 2000).

This study provides unique insight into the relationship between body size (in this context meaning both skeletal size and mass) and social dominance rank, and how these factors are related to the mating success of fallow bucks. In answer to the first part of the question posed in the title, yes, larger males do have advantages when it comes to gaining matings. Skeletal size is directly related to the mating success of fallow bucks. The second part of the question posed in the title regarding heavier males is more complex. If we did not have data on prerut dominance rank, we might conclude that body weight is not related to mating success. However our evidence has shown that body weight is related to the prerut dominance rank of males. The prerut dominance rank is in turn strongly related the rut dominance ranks of males, and this is one of the most important factors affecting the mating success of males in our study population (Moore et al. 1995; McElligott et al. 1998, 1999). Therefore we conclude that sexual selection continues to act on sexual size dimorphism in this species.

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