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Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*)

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Abstract We used data from a long-term study (15 years) of fallow deer to report for the first time the lifetime mating success, overall variance in lifetime mating success, and age-specific mortality levels of males. Fallow bucks that gain matings have higher social dominance rank, higher rates of fighting, and invest more in vocal display during the breeding season than unsuccessful males. Therefore, we examined if mating was associated with trade-offs in terms of survival, lifespan, and mating potential. We found that the variance in lifetime mating success was very high: 34 (10.7%) males mated, and of those, the 10 most successful males gained 73% of all matings (n=934). Mortality rates were generally high and only 22.3% (71/318) of males reached social maturity, i.e., 4 years. The oldest male was 13 years old. We found that fallow bucks that mated were not more likely to die during the following year, did not suffer from a reduction in lifespan, and did not incur lower mating success later in life as a result of mating during the early years of social maturity. Our results show that mating males at age 5 years (and possibly 9 years) may be more likely to survive than non-mating males. Additionally, the number of matings gained by males during the first years of social maturity was positively correlated with lifespan. We suggest that mating males are of higher quality than non-mating males because they are not more likely to incur trade-offs as a result of their increased reproductive efforts.

Key words Fallow deer · Life history theory · Mating success · Survival · Trade-offs

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Introduction

Trade-offs resulting from reproduction are central to discussions of life history theory (Roff 1992; Stearns 1992). Since resources are generally considered to be limited, current investment in reproduction by iteroparous species must therefore be balanced against future survival and reproduction (Williams 1966; Kirkwood and Rose 1991). Many empirical studies involving a diverse array of taxa have been carried out to test hypotheses of life history theory (Reznick 1985). In mammals, and particularly polygynous mammals, females and males differ in the manner in which their genetic contributions to future generations are maximized and therefore the factors that might contribute to trade-offs are usually different (Trivers 1972; Michener and Locklear 1990).

In polytokous female mammals, litter size and litter mass have been examined to determine if trade-offs could result from variation in these factors (Mappes et al. 1995; Dobson et al. 1999; Huber et al. 1999). In monotokous female mammals, trade-offs are often investigated in relation to the number of offspring produced during an animal's lifetime, the age of primiparity, or the sex of the offspring produced (Clutton-Brock et al. 1983; Bercovitch and Berard 1993; Lunn et al. 1994; Festa-Bianchet et al. 1995; Bérubé et al. 1996, 1999; Birgersson 1998). By contrast, for polygynous male mammals, the number of matings or some other proxy indicators of the efforts to acquire matings are usually examined in order to determine if trade-offs result from reproduction (Clutton-Brock 1984; Clinton and Le Boeuf 1993; Arnould and Duck 1997). Because of the difficulty dealing with large and long-lived mammals, most studies of these species are correlational in approach. However, one study succeeded in experimentally investigating trade-offs resulting from reproduction by preventing a subsection of males from participating in the effort to acquire mates (Stevenson and Bancroft 1995).

For male mammals, some of the immediate costs associated with reproductive efforts include energy expenditure (Anderson and Fedak 1985; Bobek et al. 1990), loss of foraging time (Alberts et al. 1996), and injuries (Michener and Locklear 1990; Alvarez 1993). These costs may entail more long-term consequences by affecting mortality, lifespan, and/or future potential for reproduction. In addition, there may be less obvious costs arising from factors such as high social dominance rank (which is often closely related to reproductive success) and sexual size dimorphism (Promislow 1992; Owen-Smith 1993; Creel et al. 1996).

Fallow deer are polygynous and sexually dimorphic: mature males in our study population weigh up to 117 kg, and females weigh on average 45 kg (O'Connell 1993; T.J. Hayden, unpublished data). Distinct age- and dominance-related participation in activities associated with reproduction is also evident. During the rut, socially mature males (≥4 years old) fight at far higher rates than immature males (≤3 years old). Serious injuries such as blinding of one eye often occur during a fight, and occasionally males are killed (A.G. McElligott, personal observation). The majority of mature males vocalize, whereas most immature males do not. Among mature males, dominant individuals gain most of the matings, but they also fight more (McElligott et al. 1998). These males also invest more in vocal display, by doing so for longer during the breeding season, and at higher rates (McElligott and Hayden 1999; McElligott et al. 1999). In addition, mature males feed little and lose a substantial proportion of their body weight during the rut (Hayden et al. 1992; Moore 1993). Mating skew during breeding seasons is high (Moore et al. 1995a; McElligott et al. 1998), and thus males gaining large numbers of matings might be expected to incur higher costs, if they invest more resources than they can afford.

Fallow deer populations show a variety of mating systems and individual males may adopt a number of changeable tactics during the course of a breeding season in order to maximize their mating success (Thirgood et al. 1999). In our study population, males use different mating strategies during the breeding season but those that usually gain most matings adopt a low-fidelity territorial/follower strategy (Moore et al. 1995a). This involves males defending territories during the first half of October and abandoning them during the latter part of the month to mingle with female groups. The second half of October is also when most matings take place (Moore et al. 1995a; McElligott et al. 1998, 1999).

Here, we use data from a long-term study of fallow deer (15 years) to report for the first time the lifetime mating success, overall variance in lifetime mating success, and age-specific mortality levels of fallow bucks. We also test some of the assumptions of life history theory by examining the following questions: (1) Does current mating success affect survival and lifespan? (2) Does current mating success affect future reproduction?

In a field-based study such as ours, involving a large and long-lived species living under semi-natural conditions, experimental manipulations or genetic correlations to strictly measure trade-offs resulting from reproduction are neither feasible nor possible (Lessells 1991). Thus, we must rely on a study such as this to at least provide some indication of possible trade-offs resulting from reproduction. Our data allow us to compare possible trade-offs resulting from reproduction in same-aged males, at the ages when they are considered to be socially mature and have the potential to gain matings. Thus they provide a more rigorous examination of possible factors influencing life history than simple phenotypic correlation studies (Clinton and Le Boeuf 1993). However, evidence for positive correlations between fecundity and longevity, or between current and future fecundity do not necessarily show that there are no trade-offs resulting from reproduction. For example, high-quality individuals may be capable of producing and maintaining costly traits but also survive better than low-quality individuals (Promislow 1992; McNamara and Houston 1996). Moreover, all methods that attempt to measure trade-offs resulting from reproduction also have their limitations (Partridge 1992; Reznick 1992).

Methods

Study site, population, and observations

We conducted the study on a herd of European fallow deer in Phoenix Park (709 ha, 80% pasture, 20% woodland; 53°22′ N, 6°21′ W), Dublin, Ireland. The climate is temperate, with mean annual rainfall of 750 mm, and mean monthly temperatures ranging from 4.4°C in January to 15.0°C in July. Natural forage is abundant and therefore the deer are not provided with any supplementary food (Hayden et al. 1992).

Population size fluctuated during the present study (1984–1999), from its lowest level in 1984 of 322 to 689 in 1995. These numbers refer to the deer present in November of each year. From 1988 to 1999, we have accurate details of the population structure in terms of females ≥1 year old, males ≥1 year old, and fawns. The sex ratio of females to males (1988–1999) varied from 1.4 in 1993 to 2.7 in 1996. Population size, structure, and density are similar to those reported for other fallow deer populations (Clutton-Brock et al. 1988; Apollonio et al. 1989; Langbein and Thirgood 1989).

The park authorities have carried out ear tagging of fawns in June of each year since 1971 (T.J. Hayden, unpublished data). Therefore, the majority of the deer were of known age and individually recognizable. We recognized males that were not tagged using a combination of coat color and antler characteristics. The entire herd was captured in 1991 and any untagged individuals were tagged and aged (Moore et al. 1995b).

We used data from the males that were born from 1984 to 1988 (*n*=56, 68, 67, 67, 60, respectively; total *n*=318). When intensive observations of this population began in 1988, the males from the 1984 cohort were the oldest at 4 years old. Males younger than this age rarely gain matings (Moore et al. 1995a; McElligott et al. 1998), and we therefore assumed that none of the males in this study had mated prior to 1988. When the observations for this study were complete (November 1999), most males from the five cohorts were either dead or, if alive (*n*=2), considered to have little chance of gaining additional matings.

We tagged a large number of fawns born in each year between 1984 and 1988 shortly after birth (*n*=388). However, because it was not possible to find and tag all the young born, it was necessary to estimate the total number of males born each year. Therefore we used the ratio of tagged to untagged fawns to estimate the total number born in a year, and then we used the sex ratio of tagged fawns to estimate the total number of males.

Prior to 1988, records of dead deer were kept by the Phoenix Park authorities (T.J. Hayden, unpublished data). Since 1988, male mortality has been calculated using a combination of death records and dates when individual males were last observed. Deer do not move outside Phoenix Park and therefore if males were not seen for a period of 3 months and were never observed again, we assumed they had died.

The breeding season lasts from late August to November, with matings occurring from mid October until the beginning of November (the rut), (McElligott et al. 1998, 1999). During the breeding season, the deer live in an area of open pasture, with adjacent copses and open woodland. Each year (1988–1999), we carried out observations from dawn to dusk every day during the rut (ca 11 h). Observers were in radio contact and organized to maximize coverage of all animals, and observations were not biased towards particular individuals. Data were screened for duplicate recordings of the same events prior to analysis. For additional details of our observations, see Moore et al. (1995a), McElligott et al. (1998, 1999), and McElligott and Hayden (1999).

Male mating success is based on the number of directly observed copulations for each male. Copulations are clearly identifiable because a male mounts a female and jumps forward as he ejaculates, with both hind legs usually leaving the ground. We observed most females (≥60%) mating each year, and in some years this proportion was greater than 80% (Moore 1993; McElligott 1997; Kelly 1998; T.J. Hayden, unpublished data). In our study population, 84% of females mated once within the same estrous cycle (McElligott 1997). Of the remaining 16% that mate more than once, 86% of these mated twice, 12% mated three times, and 2% mated more than three times. Only 18% of the females that mated twice did so with the same male for their second mating (M.E. Farrell and T.J. Hayden, unpublished data). Because the majority of females only mate once, and also because females generally only mate once with any male, we did not adjust the mating success of males to take account of additional matings by females. Since our measure of male mating success is based on directly observed copulations (rather than indirect methods), and we observe the majority of females mating each year, our observations probably provide a good estimate of reproductive success. A genetic study of paternity is currently not feasible for this population. In addition, evidence from a study of red deer (*Cervus elaphus*) suggests that directly observed matings provide a very good estimate of reproductive success (Pemberton et al. 1992).

To examine any trade-offs between mating success and subsequent survival, lifespan, or mating, we only considered males that had reached 4 years old. This is the age at which males first participate in the rut by fighting and vocalizing, i.e., it is the age of social maturity (McElligott et al. 1998, 1999). The upper age limit considered was 9 years old, because only one 10-year-old male has ever gained a mating and the number of males surviving to this age is also low (McElligott 1997).

Data analysis

We carried out all statistical tests using SPSS and used parametric and non-parametric tests when appropriate (Zar 1999). All tests were two-tailed and we considered results significant at the $P<0.05$ level. We calculated overall variance in lifetime mating success according to Brown's (1988, p. 448) method that specifically includes the contribution of non-mating individuals. This method of calculating overall variance differs substantially from statistical variance, and we chose it because of the high proportion of males in our population that do not gain any matings. The statistical variance of lifetime mating success, the mean of lifetime mating success, and the proportion of mating males, are used in its calculation. We used stepwise multiple-regression analysis to determine the variation (r^2) in lifetime mating success explained by the number of breeding seasons in which males gained matings and the age at death. However, because of collinearity between the two independent variables, we used Pearson partial correlations to check our result. Both lifetime mating success and the number of breeding seasons in which males gained matings were log-transformed to improve the normality of their distributions (Shapiro-Wilks test). We used a contingency test (phi, ϕ) to examine the association between mating in the current year and survival during the following year. In this analysis (Table 2), males are listed as either mating or non-mating, irrespective of the number of matings. In all other analyses, we used the actual number of matings. We used Spearman rank correlation (r_s) to examine the relationship between the total mating success of males at ages 4 and 5 years, and their subsequent lifespan. This was done for all males that reached age 5. We used Kendall's rank-order correlation coefficient (τ) to examine the relationship between current and future mating success. This coefficient was used because of the number of tied ranks (Siegel and Castellan 1988).

Table 1 Stepwise multiple-regression analysis. Lifetime mating success (log-transformed) is the dependent variable and the number of successful breeding seasons (log-transformed) and age at death are independent variables. Multiple $r=0.69$ (adjusted $r^2=0.47$), $n=34$, $P<0.001$

Variable	Coefficient	*T*	*P*
Constant	0.4	–	–
Number of successful breeding seasons	1.9	5.5	<0.001
Age at death	0.11	0.56	0.58

Results

Lifetime mating success

The successful males (34, 10.7%) gained 934 matings, with the 10 most successful males gaining 679 (73%) matings (Fig. 1); 284 (89.3%) males gained no matings. The highest lifetime mating success gained by one male was 171. The overall variance in lifetime mating success was 208.8. The proportion of the variance owing to the difference in mating success among males that mated was 0.65; the proportion as a result of the males that failed to mate was 0.35. We found that among the mating males, those that gained matings over several breeding seasons had the highest lifetime mating success; age at death was not a significant additional factor (Table 1). Partial correlation analysis confirmed this result. When the relationship between the number of successful breeding seasons and lifetime mating success was controlled, the age at death was not significantly related to lifetime mating success (Pearson correlation: partial $r=0.10$, $n=34$, $P=0.58$). Conversely, when the relationship between the age at death and lifetime mating success was controlled, the relationship between the number of successful breeding seasons and lifetime mating success remained significant (Pearson correlation: partial $r=0.50$, $n=34$, $P=0.003$).

Overall mortality and mating rates

The average age-specific mortality rates and mating rates of all males are shown in Fig. 2. At 4 years old, 247 (77.7%) males were dead, and no males survived more than 13 years. Although there was a small peak in mor-

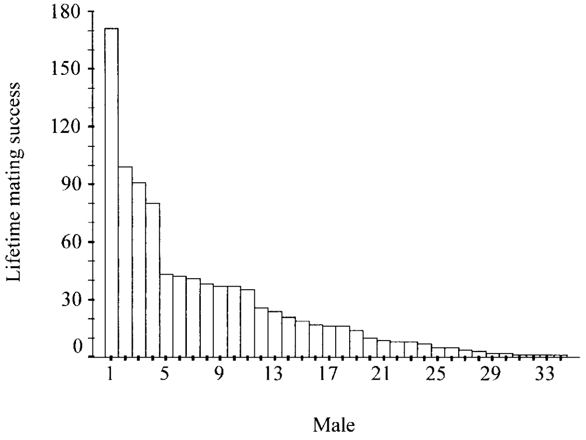

Fig. 1 Lifetime mating success of the successful males (*n*=34). The total numbers of males from 4 to ≥12 years old were 71, 59, 40, 33, 25, 18, 13, 5, and 1

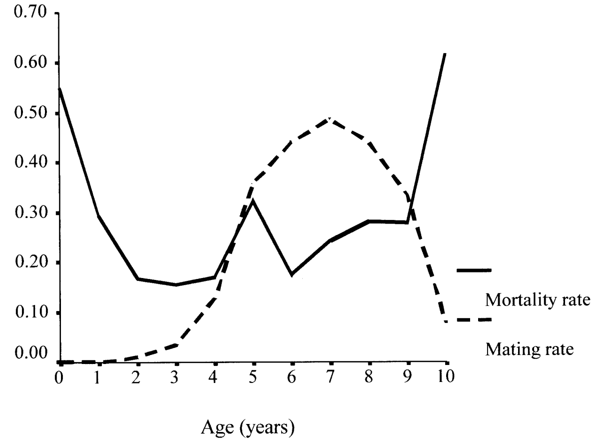

Fig. 2 Age-specific mortality and mating rates of all males (*n*=318 at age 0). Five males that survived beyond 10 years are not represented in this figure; two were still alive in November 1999, two died aged 11 years, and one at age 13. The mortality rates from 0 to 10 are 0.55, 0.29, 0.17, 0.15, 0.17, 0.32, 0.18, 0.24, 0.28, 0.28, and 0.62. The mating rates, i.e., the proportion of males gaining matings at each age from 0 to 10 are 0, 0, 0.01, 0.04, 0.13, 0.36, 0.44, 0.48, 0.44, 0.33, and 0.08

Table 2 Association between mating success and survival during the following year

Age at rut (years)	Survival to next rut	Mating males	Non-mating males	ϕ	*P*
4	Died	2	10	–0.05	0.65
	Survived	7	52		
5	Died	3	16	0.29	0.03
	Survived	18	22		
6	Died	2	5	0.15	0.34
	Survived	16	17		
7	Died	4	4	–0.07	0.92
	Survived	12	13		
8	Died	2	5	0.19	0.33
	Survived	9	9		
9	Died	0	5	0.44	0.06
	Survived	6	7		

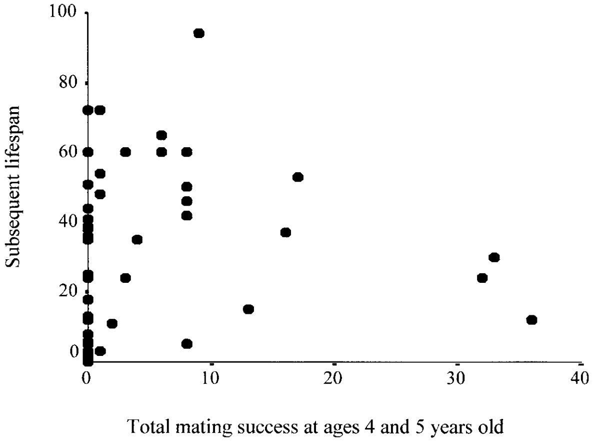

Fig. 3 Relationship between the total mating success of males at ages 4 and 5 years and their subsequent lifespan

tality at age 5, the numbers of animals dying in this age class (19/59) were not significantly higher than those dying at age 4 years (12/71; contingency test: ϕ=–0.13, *P*=0.11) or 6 years (7/40; contingency test: ϕ=0.11, *P*=0.21). The proportion of males gaining matings at each age, i.e., the mating rate, was highest at ages 6, 7, and 8 years old. The mortality rate was not related to the mating rate (Spearman rank correlation: r_s=–0.11, *P*=0.77, *n*=11; Fig. 2).

Mating success, survival, lifespan, and future mating

The relationship between mating success and mortality during the following year was examined for males aged 4–9 years. Males that mated were not significantly more likely to die during the following year than those that did not mate (Table 2). In fact, at age 5, the non-mating males were significantly more likely to die than the mating males. We found a similar, but marginally significant relationship at age 9. It was not possible to determine if the number of matings of successful males was related to survival to the following breeding season because of the low number of mating males dying at each age. We also examined the relationship between the total mating success of males aged 4 and 5 years and their lifespan after age 5. We found a weak, but significant positive relationship between the matings that males gained at 4 and 5 years and their subsequent lifespan (Spearman rank correlation: r_s=0.29, *P*=0.03, *n*=59; Fig. 3). When the three males with the highest mating success were removed (see Fig. 3), this relationship was even stronger (Spearman rank correlation: r_s=0.35, *P*=0.008, *n*=56).

We examined the relationship between current and future mating success by comparing the total mating success of individual males at ages 4 and 5 years, with their mating success at age 6 and older. We found that when all males that reached at least age 6 were included, there was a significant positive relationship between their total mating success at ages 4 and 5 and their mating success at 6 and older (Kendall rank correlation: τ=0.33, P=0.009, n=40). However, when the males that gained no matings were excluded from the analysis, this relationship was no longer significant (Kendall rank correlation: τ=–0.02, P=0.88, n=27). Overall, of the 34 males that mated from the five cohorts, 26 (76.5%) gained matings during more than one rut.

Discussion

This is the first study to report lifetime mating success of fallow bucks. We found that the overall variance in lifetime mating success of fallow bucks in our study population was very high. To our knowledge, it is the highest overall variance in lifetime mating success reported for any mammal, calculated according to the Brown's (1988) method (Clutton-Brock 1988). The next highest level of overall variance in lifetime mating success was found in Northern elephant seals (*Mirounga angustirostris*), a species with a similarly high level of polygyny and intense competition among males for matings (Le Boeuf and Reiter 1988; Haley et al. 1994). Although the vast majority of males (89.3%) in our study gained no matings, there was potential for a very high mating success for some males. While only one male gained 171 matings, ten others gained between 35 and 99 matings (Fig. 1). The most successful male was the only one to achieve the highest social dominance rank and the highest individual total for matings during two successive ruts (1993 and 1994; McElligott 1997). For males that mated, the relationship between lifetime mating success and the number of breeding seasons in which they gained matings is similar to that reported for Northern elephant seals (Clinton and Le Boeuf 1993). However, in contrast to the findings for elephant seals, lifetime mating success was not related to the age at death of the successful males in our study (Table 1). This indicates that simply surviving through the years in which males might be expected to gain matings did not ensure that they gained large numbers of matings. Earlier research on this study population has already shown that high dominance rank and large investment in vocal display by males are critical to gaining matings (Moore at al. 1995a; McElligott et al. 1998, 1999).

Only a few studies have succeeded in measuring the lifetime mating success of complete cohorts of males, e.g., red deer (Rose et al. 1998) and soay sheep (*Ovis aries*; Coltman et al. 1999). This is essential both for estimating the true levels of sexual selection in a population and also the effective population size (Nunney 1993; Andersson 1994). It is interesting to note that Coltman et al. (1999) found that the potential for the loss of genetic variation from their study population was highest when population density was highest. The distribution of matings among males during single breeding seasons in our study population is similar to populations of fallow deer in which males lek (Clutton-Brock et al. 1988; Apollonio et al. 1989; McElligott et al. 1998, 1999). Therefore, the lifetime mating success and thus the extent of sexual selection of fallow bucks in non-lekking and lekking populations may be similar.

The overall pattern of age-specific mortality of fallow bucks that we found is similar to some polygynous mammals (see review Ralls et al. 1980; Clinton and Le Boeuf 1993; Owen-Smith 1993) and higher than others (Rose et al. 1998; Loison et al. 1999). Although on an overall basis, the number of males dying at age 5 years did not differ from the numbers dying at either ages 4 or 6 (Fig. 2), our results suggest that the numbers of non-mating males dying at age 5 were significantly higher than the numbers of mating males dying at age 5 (Table 2). This coincides with the time when the vast majority of a cohort first participates in the efforts to acquire mates. For example, the proportion of each cohort vocalizing during the breeding season increases greatly through ages 3, 4, and 5 (41.9, 78.1, and 96.3%, respectively; McElligott et al. 1999). Increased mortality associated with the onset of social maturity has also been found in male elephant seals (Clinton and Le Boeuf 1993) and bighorn sheep (*O. canadensis*; Jorgenson et al. 1997). The findings of Clinton and Le Boeuf (1993) differ in one important respect from our study. They found that elephant seal males that died at the beginning of social maturity tended to be ones that had mated at those ages. By contrast, our results show that the males that died at age 5 were predominantly those that had not mated (84.2%; Table 2). The mating status of males in the bighorn sheep study was not known (Jorgenson et al. 1997). Although our study does not include an analysis of female life history, there are indications that mortality levels are lower in females than in males. For example, females as old as 15 years have been recorded raising fawns to weaning age, and the oldest female known was 22 years old (T.J. Hayden, unpublished data).

The increasing levels of mortality for older males in our study (Fig. 2) are in keeping with the concept of senescence (Loison et al. 1999). However, because of the low numbers of males surviving to old age, the data from our study cannot be used for a detailed analysis aimed at examining the occurrence of senescence. The obvious deterioration in general body condition and decrease in antler size of old fallow bucks also point to senescence through physiological decline in this species (Abrams 1991; Kelly 1998; A.G. McElligott personal observation).

Fallow bucks are capable of producing viable sperm at 16 months and this coincides with the rut in their second year (Chaplin and White 1972). If the potential for mating success among immature males was high, mating as soon as physiologically possible could become a viable strategy, even if there was a trade-off in terms of mortality. For example, juvenile male soay sheep gained up to 15% of matings during some breeding seasons, but also had higher mortality rates in those years (Stevenson and Bancroft 1995). By refraining from reproduction and avoiding the risks associated with reproductive effort, younger males may reduce the mortality associated with developing sexually selected traits, and thus might increase their potential for reproduction in later life (Clinton and Le Boeuf 1993; Kokko 1997a). However, recent evidence suggests that the main reason for the lack of matings among immature males is competitive exclusion by mature males (Komers et al. 1997; McElligott et al. 1998).

We found that fallow bucks that mated were not more likely to die during the following year, did not suffer from a reduction in lifespan as a result of mating during the early years of social maturity, and similarly did not incur lower mating success as a result of mating during the early years of social maturity. We provided some evidence that mating males (at ages 5 and 9 years) may in fact be more likely to survive than non-mating males (Table 2). Similarly, the number of matings gained by males during the first years of social maturity (ages 4 and 5 years) was positively correlated with subsequent lifespan.

Although many studies have shown that animals may compromise longevity for reproductive success (Partridge and Harvey 1985), this is not necessarily the case for all species. In some birds in which males do not provide any parental care, the males that gain matings are also the ones that are more likely to survive (Alatalo et al. 1991; Petrie 1992). Similarly in mammals, a number of studies involving mainly indirect methods of measuring mating success showed that mating males were also the ones that tended to survive (Clutton-Brock 1984; Clinton and Le Boeuf 1993; Arnould and Duck 1997). The most common explanation for the lack of any costs is a suggested link between traits or qualities that confer advantages during intrasexual competition for mates and traits that are important for viability.

In our study population we have already found that the majority of females mate with males of high dominance rank, which also invest more in vocal activity during the breeding season (Moore et al. 1995a; McElligott et al. 1999). Although the subject of mate choice in fallow deer remains controversial (Carbone and Taborsky 1996; Clutton-Brock et al. 1996), there is evidence that fallow does may exercise an element of choice when accepting a mate (Komers et al. 1999; McElligott et al. 1999). Our results here suggest that females could benefit by gaining genes for longevity for their offspring, since lifespan itself may be heritable (Kokko 1997b; Horne and Ylönen 1998; Møller and Alatalo 1999). This is particularly important for females that produce female offspring, because one of the most important factors determining lifetime reproductive success of females is their lifespan (Birgersson 1998). However, to test this hypothesis, studying the heritability of traits that are important both for reproduction and for offspring viability is necessary (Møller and Alatalo 1999; Wedell and Tregenza 1999).

Although our study did not strictly measure costs of reproduction for fallow bucks, we suggest that such research is usually not feasible on this or a similarly large and long-lived species. Nevertheless, a study of contiguous cohorts of individually identifiable males from birth until death, over a long period (in our case 15 years, with 12 years of intensive behavioral observations), can provide information on factors influencing life history strategies. Because of the high levels of mortality experienced before social maturity, and particularly during the first year of life, data from several cohorts are usually needed to sample the males adequately. In addition, using contiguous cohorts helps control for possible fluctuations in environmental factors that can also affect life history strategies (Festa-Bianchet et al. 1995; Loison and Langvatn 1998).

The setting for this study should also be considered when discussing the implications of our results. In Phoenix Park, natural predators of mature deer are absent and the most common cause of death among these individuals is collisions with vehicles (Hayden et al. 1992). Some males are also the indirect victims of predators, due to misadventure following worrying and chasing by domestic dogs (*Canis familiaris*) (A.G. McElligott, personal observation). However, it is not unusual for studies like this to be carried out in situations where natural predators of mature animals are either absent (Rose et al. 1998; Coltman et al. 1999) or have little impact (Jorgenson et al. 1997). In addition, one cannot assume that males in our study population are killed indiscriminately, since they are probably more likely to die if they are in generally poor condition or suffering from physical impairment. For example, there is an approximately threefold higher incidence of tuberculosis (TB; *Mycobacterium bovis*) in animals killed by vehicles than in the general population (Hayden et al. 1992). Moreover, even in what could be considered a more natural setting, Owen-Smith (1993) found that the sex ratios of male to female kudus (*Tragelaphus strepsiceros*) were similar in areas where mature animals both were and were not subject to natural predation. Newborn and very young fallow fawns in our study population are killed by foxes (*Vulpes vulpes*) and domestic dogs. The level of predation is not easy to quantify because of the difficulty in recovering remains of kills, although the available evidence suggests that it is no higher than 5% (Hayden et al. 1992). In addition, food is not a limiting factor even though the population density has fluctuated during the present study. Therefore, natural selection is not likely to be as great a factor influencing male life history patterns as in other comparable studies (Rose et al. 1998; Coltman et al. 1999).

In conclusion, our results suggest that life history trade-offs do not result from mating in fallow bucks because the males that gain matings are not more likely to die than males that do not gain any matings. If any trade-offs exist, our data suggest that they may occur at 5 years old (and possibly at age 9), and are associated with participation in the breeding season, and not mating success. This is despite the fact that the males that gain matings generally invest more in efforts to acquire mates in terms of fighting and vocalizing (McElligott et al. 1998, 1999; McElligott and Hayden 1999). Thus investment in reproduction at certain ages for some fallow bucks may not always be set at an optimal level (McNamara and

Houston 1996; Kokko 1997a). However, the high proportion of males dying before 4 years old (77.7%) indicates that males are already subject to strong selection before they reach social maturity. Therefore, all the males examined for any trade-offs resulting from mating may already be of higher quality than those that did not survive to social maturity. In addition, our results support the concept of "increasing returns," recently introduced to the literature from human economic systems (Dobson et al. 1999). In this scenario, Dobson et al. (1999) equated positive relationships among fitness traits in life history to the very rapid increase in market share by some technological products because of early advantages. In animal mating systems, it would mean that individuals investing more in reproduction would survive better, and they would therefore gradually increase in numbers until dominating a population. Finally, we suggest that fallow bucks that gain matings are not only of higher quality in terms of their dominance rank, but also of higher quality because they are not more likely than non-mating males to incur trade-offs as a result of their efforts (Ellis 1995; McNamara and Houston 1996).

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