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Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population

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Abstract The rutting behaviour of bucks in an enclosed population was investigated between 1988 and 1990. A substantial proportion of the matings were observed. After preliminary observations in the 1987 rut we categorised bucks into one of four rutting strategies based mainly on their degree of territoriality. We investigate the effects of age, dominance and mating strategy on mating success. Territories were aggregated in an area of oak woods and mating success was highly skewed. Bucks of between 5 and 7 years old achieved the majority (over 90%) of observed matings. Mating success was highly correlated with dominance but only weakly related to fighting success. The possession of a territory was crucial to achieving high reproductive success, with a 38-fold difference between the most and least successful strategies. Bucks pursuing the different strategies also differed in the time they commenced groaning, timing of matings, mating interference and the locations where they achieved their matings. Although high-ranking males devoted considerable effort to obtaining and defending a territory only 36% of each buck's matings were achieved on his territory and males tended to abandon these sites when the tendency of females to visit them decreased.

Key words Fallow · Deer · Mating · Strategy

Introduction

It was formerly generally believed that a particular mating system was a species-specific phenomenon (Wilson 1975). However, it is now accepted that mating systems may vary substantially among different populations of the same species (Wilson 1975; Davies 1991). In mammals the mating system employed by a given species or population depends to a large extent on the pattern of female dispersion (which is at least partially dependent on the distribution of resources). This determines the way in which males can optimally compete for access to females (Emlen and Oring 1977; Davies 1991). Furthermore, within the mating system employed by a given population, individual males may pursue alternative mating strategies. Differences between the mating strategies of individuals within populations have been reported for species as diverse as damselflies (Waltz and Wolf 1984) and topi (*Damaliscus lunatus*; Gosling and Petrie 1990). Such variation led researchers to consider three general hypotheses (Rubenstein 1980; Dunbar 1982; Gosling and Petrie 1990). Firstly, particular strategies are optimal under specific conditions; secondly, the fitness payoffs for different strategies may be similar in the long run; and finally, some males are simply making the best of a bad job as they are at a competitive disadvantage to other males.

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Fallow deer are seasonal breeders and the annual onset of breeding condition is controlled by decreasing photoperiod. The rut takes place in the autumn (October in the northern hemisphere, April in the southern). Nevertheless males may remain fertile for at least 6 months, that is, until as late as April in northern latitudes. Does are seasonally polyoestrous and if conception does not occur will return to oestrus at approximately 22-day intervals until late spring. Thus females could, in principle, go through up to seven ovarian cycles before the return of seasonal anoestrus. The poor survival of late-born fawns has presumably been a potent factor selecting for an October rut in the northern hemisphere in which most of the matings take place over a 3-week period.

The mating system of fallow deer (*Dama dama*) is highly variable. The earliest studies described mating strategies based on discrete, relatively isolated, mating territories (rutting stands) (Espmark and Brunner 1974; Chapman and Chapman 1975). Since the early 1980s, much interest has centred on variation in mating systems between populations of fallow deer. A number of studies have attempted to determine the mating systems exhibited by populations and to identify the key features of the various systems and factors which may be responsible for the variation (Schaal and Bradbury 1987; Clutton-Brock et al. 1988; Appolonio et al. 1989; Langbein and Thirgood 1989).

The mating systems described to date range from non-territorial systems in which males defend mobile groups of females (Alvarez et al. 1975; Schaal 1986) to highly aggregated territorial systems such as leks (Schaal and Bradbury 1987; Clutton-Brock et al. 1988; Appolonio et al. 1989). The mating systems of male fallow deer (bucks) can be viewed as a continuum with many males within a population pursuing different strategies (Langbein and Thirgood 1989). Langbein and Thirgood (1989) divide the mating systems of fallow deer into seven different categories based on the type and degree of territoriality of the males that accounted for the majority of the matings. These seven categories are divided into three basic types, namely multiple territories, single territories and non-territorial mating systems. Multiple territories include leks and multiple stands where the lek is considered to function for display and mating only, whereas the stands or territories are larger in area and may contain resources of interest to does. Single territories include single stands which are more or less continuously occupied by a buck throughout the rut and temporary stands at which the buck is intermittently present. The non-territorial systems include (1) harem holding, (2) multi-male groups in which priority of access to females is determined at least in part by dominance relationships and (3) systems in which males forage for oestrous females by following female groups (Langbein and Thirgood 1989).

Even though many males pursue different strategies, one particular strategy usually predominates in populations in parks (Schaal and Bradbury 1987; Clutton-Brock et al. 1988; Langbein and Thirgood 1989). In contrast, there is greater variation in the strategies that individual males pursue in wild populations. In a free-ranging population in the New Forest in England, males may pursue three types of rutting strategy (they defend lek territories, single territories or are non-territorial; Thirgood 1991). They also altered their strategies as the rut progressed. Appolonio et al. (1992) described three types of territorial behaviour in a predominantly lekking population in Italy. Males pursuing these strategies neither differed in mean age nor copulatory success.

To date, the main focus of study has been on the lekking populations. Lekking was first described for fallow deer (and cervids in general) for a population in Jaegersbourg, Denmark (Schaal 1986; Schaal and Bradbury 1987) and subsequently leks have been reported, both from enclosed and feral populations, from Italy (Appolonio et al. 1989), Great Britain (Pemberton and Balmford 1987; Clutton-Brock et al. 1988) and Hungary (Pemberton and Balmford 1987). Several studies have examined the role of alternative mating strategies adopted by other bucks in the population (Clutton-Brock et al. 1988; Thirgood 1991; Appolonio et al. 1992). All other reports of mating systems have been part of studies involving many populations (Langbein and Thirgood 1989) or are notes on breeding behaviour (Espmark and Brunner 1974; Alvarez et al. 1975, 1990; Braza et al. 1986; Buschhaus et al. 1990). In only one of the studies was it possible to examine differences between alternative strategies in relation to age (Appolonio et al. 1992).

The main aim of this paper is to describe the mating system in a non-lekking population. Firstly, we outline the overall pattern of rutting activity in a multiple-stand system over 3 years in terms of overall mating success and mating behaviour of the males. Secondly, we assess the relative importance of different strategies within the population with regard to the number of males that adopt them and the number of matings these bucks achieve. Of particular importance is the payoff to an individual male (in terms of matings) that pursuit of a given strategy will produce. Finally the effects of age, dominance and mating strategy on mating success are investigated.

Methods

Study site

Phoenix Park is a large city park of 709 ha in Dublin, Ireland (Hayden et al. 1992). Of this, 569 ha are available to the deer. Much of the park consists of open pastures but woodland covers 20% of the area. There are no other large herbivores in the park. Herd size increased during the study period from 381 (90 males, 222 females and 69 fawns) to 525 (118 males, 288 females and 119 fawns) and the sex ratio varied from 2.22 to 2.41 females per male. Approximately 50% of the males were individually recognisable as they had been marked at birth with coloured and numbered ear tags. The remaining males were recognised by particular facial or antler features.

Observational data

Observations were carried out between early September and late November in 1988, 1989 and 1990. Usually one or two observers were in the field from the beginning of September to mid-October. During this period the bucks were in their bachelor herd and moving onto the does' range. Between two and four observers were in the field each day during the peak of rutting activity (mid-October to early November). The total hours of observation were 545 in 1988, 684 in 1989 and 812 in 1990. Three main types of data were collected: interactions between males, location of individual males and matings. The time, location and the identities of the male and female involved in all matings were noted. Time, location and outcome of all interactions (both contact and non-contact) between males were noted. Contact interactions refer to all agonistic encounters in which the males engage antlers. Non-contact interactions refer to agonistic encounters with no antler contact. These include "parallel walks" and "threat and retreats". The identities of both participants were noted, where possible. The location of adult bucks was noted as frequently as possible during the day (every 5th minute for focal bucks and half-hourly for non-focal adult bucks).

Observations were carried out in two ways

1. It was originally decided to sample focal bucks. Between 7 and 11 adult bucks were observed focally between sunrise and sunset on 51–60 days between September and November each year. Adults are more interactive than yearlings, 2- and 3-year old

bucks. Thus the focal bucks were generally 4 years of age or older. However, since most of the adult bucks were together in the bachelor herd during September, interaction data were collected for all bucks. Later, when the bucks were somewhat more dispersed, each focal buck was still close to a number of others so that the whole population of bucks was still sampled.

2. Observation of the main herd of does took place as follows. By day most of the does are found in a large, loosely aggregated herd ranging over the pasture area. One to three people, appropriately located, observed the main doe herd each day during daylight hours between 18 October and 4 November in 1989 and 1990. This further ensured collection of data on mating success that was not biased towards particular males, since all observed matings were recorded.

Dominance assessment

Data on agonistic encounters between bucks were collected during observations of the bachelor herd during August and September and throughout the rut in October and early November. All agonistic encounters in which both males were identified were used in this analysis. Younger males were less frequently involved in agonistic interactions and therefore only males more than 2 years old were included in the assessment of rank.

An index of dominance was calculated according to Clutton-Brock et al. (1979). This assigns a dominance index to a male based not only on his number of subordinates but also on the relative dominance of these subordinates and the relative dominance of animals dominant to him. Dominance rank was assessed for September based on non-contact interactions, which take place largely in the bachelor herd. This measure is made before the does begin to exhibit oestrus. Fights are not observed until early October and thus the data set for October contained both non-contact interactions and fights. Both were used to assess dominance rank in October. Fighting success was also assessed using the method of Clutton-Brock et al. (1979) but in this case only fights, as defined by the criteria of Alvarez (1993), were used to determine the index.

Identification of strategies

Based on preliminary observations made in 1987, four broad rutting strategies were distinguished according to the overall behaviour of the buck during the rut. The most important criteria were (1) site fidelity of a buck, (2) defence of an area and (3) occupancy. Site fidelity was defined as the maximum distance between daily centres of activity. Centres of activity were determined by kernel analysis (Worton 1989; P.F. Kelly unpubl.). Territorial defence was identified by the existence of areas in which a particular buck was dominant to all others and fought to drive out intruders although the relationship might be reversed in other locations. Occupancy was quantified as the proportion of time spent in a defended area during the day. These four strategies were termed high-fidelity territorial, low-fidelity territorial, satellite and follower. High-fidelity (territorial) bucks exhibited centres of activity 60–90 m apart, were locally dominant to all others and had occupancy scores of 90% or greater. Low-fidelity (territorial) bucks had centres of activity 80–130 m apart, were locally dominant to all other bucks and had occupancy scores between 25 and 100%. These bucks spent variable periods of the day elsewhere beyond what could be identified as the limits of their territories, usually with the doe herd. Satellite bucks was the term applied to a number of middle- to low-ranking bucks who could regularly be found on or in the vicinity of the aggregated territories of the more dominant bucks. These satellites were usually tolerated by the territory-holders from whom they experienced less overt aggression than occurred between the holders of adjacent territories. Satellites, although they had centres of activity 80–140 m apart, had no area of total dominance and thus did not occupy a territory. Followers were those adult bucks which did not hold a territory either because they failed or did not attempt to do so. Their centres of activity were over 200 m apart. Throughout the rut they were regularly in attendance with the doe herd and therefore often were to be found on or near the territories in the oak wood if the does were in the vicinity. For analysis of the ruts of 1988–1990 bucks were assigned to a particular strategy based on their behaviour during the rut according to the criteria above. Within a strategy, however, tactics may vary from day to day or within a given day or a particular tactic may be predominant at one time but not another.

Age determination

For males that achieved matings, 47.5% (n = 19) were of known age as they had been tagged at birth. A further seven bucks had their ages estimated post mortem using a measure of incisor height (Moore 1993). Together, these bucks accounted for 82.7% of the matings observed.

Statistical procedures

Kruskal-Wallis tests were used to test for differences between the four rutting strategies with respect to mating success, timing of matings and the timing of commencement of groaning (vocalisations made by males during the rut). The analysis was carried out in two ways. In the first instance, where a buck was assigned to the same category in more than 1 year, only 1 year's data were included in the analysis. On the other hand, where a buck was sampled in more than 1 year and exhibited different strategies he was included once for each strategy. Where statistical differences were found, pairwise comparisons were conducted using a non-parametric Tukey test. Contingency tables were used to test for differences in the spatial distribution of matings as well as the proportion of matings achieved by bucks of each strategy during the peak rut and recycles. Pearson's correlation coefficient was used to determine the relationships between dominance and mating success and fighting success and mating success. The dominance and fighting success indices were all log-transformed.

Results

General description of the rut

For 11 months of the year the sexes remain in separate herds. During September the bachelor herd (which contains over 95% of the adult bucks) joins the doe herd on its usual range. They may be joined during this month or in early October by a small number of bucks which were more solitary and remained in more secluded areas of the park during the spring and summer. The rut vocalisations (groaning) are first heard in the 3rd week in September. From early October some males attempt to defend territories in an oak wood at the periphery of the does' daytime range but near the centre of their overall range (the does are more dispersed and use more of the available range during the hours of darkness). These territories are contiguous and contain substantial resources (shelter and acorns) but are not sufficiently small to be considered a lek. The number of territories ranged from three to five in any year and their areas ranged from 2.5 to 20 ha. Thus the mating system could be classed as a multiple stand system. All territorial bucks defend their territories for a minimum of 2–3 weeks in October. Some abandon their territories in late October to consort with the doe herd which by day occupies an open pasture area of

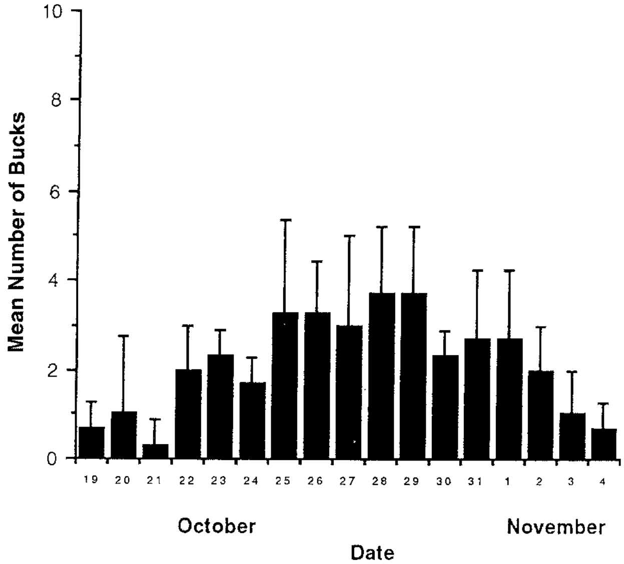


Fig. 1 The mean number of males seen to mate on each day during the main peak of the rut (mean of 3 years). *Error bars* represent 1 SD

about 150 ha. All other territorial bucks abandon their territories in early November. Here they mingle with the does and attempt to defend groups of females from the attention of other males.

The rut for the 3 years was similar in the overall timing of events. The first matings were seen in the third week in October in each year (22 October in 1988, 19 October in both 1989 and 1990). The median mating dates were virtually identical between the years (28 October in 1988 and 27 October in 1989 and 1990). During the peak days of the rut, up to five bucks achieved matings on any one day (mean 2.1, SD 1.10; Fig. 1). Matings continued until the 1st week in November. Matings resumed in mid-November as some does completed their next oestrous cycle (secondary or recycle peak). A total of 462 matings were seen over the 3 years. This represents between 38 and 62% of all females but about 70% of all the breeding females, based of the numbers of yearling and older females present each year and the fertility of these two age categories, 0.7 and 0.92 respectively.

Male participation in the rut

Not all the males actively participated in the rut. Indeed, a substantial proportion showed little or no rutting behaviour. If groaning is used as an indicator of minimum participation then, on average, only 31% (SD 1.8%) of bucks actively participated in each years' rut. No yearling or 2-year-old was heard to groan over the 3 years and only 35% ($n = 20$) of 3-year olds did so.

Skew in mating success

The distribution of matings among the bucks in each of the 3 years was highly skewed. Only a small proportion of the males (1 year old and older) achieved any matings. In all years, less than 15% (mean 11.7%, SD 1.18%) of the total number of males achieved matings, and even of those bucks that did actively take part in the rut (as defined by vocalisations) less than 40% of them obtained any matings. Among the bucks that did mate, and these were 4 years old or older, there was a very large variance in success (mean skewness 2.1, SD 0.64). The five most successful males accounted for over 80% of the matings each year (mean 84.3%, SD 2.50%), while the ten most successful accounted for over 95% (mean 96.9%, SD 1.00%). The proportion of observed matings achieved by the most successful buck varied between the 3 years, ranging from 26.1% to 51.0%.

Table 1 The number of bucks pursuing each strategy in each of the three years

Year	High fidelity territorial	Low fidelity territorial	Satellite	Follower
1988	3	2	2	27
1989	2	3	4	26
1990	2	1	4	28
Total	7	6	10	81

Relative frequency of strategies

In each of the three years, no more than five bucks defended territories during the rut (Table 1). This represents less than 5% of the total number of bucks in the herd. In 1988, 4.8% ($n = 5$) of the bucks defended territories, in 1989, it was 4.3% ($n = 5$) and in 1990, only 2.5% ($n = 3$) of the bucks did so. The satellite strategy was also a rarely chosen option in this population (mean 2.9%, SD 0.85%). The majority of bucks (over 90% in all years) pursued a follower strategy.

The above results include all bucks in the herd. However, the same general picture applied when only actively rutting males (i.e. vocal bucks) were included. Territorial bucks still accounted for less than 15% of the rutting males in each of the three years (Table 1). The majority (77.9%) of these actively rutting bucks still pursued a follower strategy.

Change in strategy between successive ruts

In all, 31 different bucks were seen mating over the three ruts studied. Table 2 shows the strategies pursued and the number of matings achieved by a selection of these bucks. No male achieved a substantial number of matings in more than 1 year. Furthermore, all territorial males in a given year failed to hold territories the following year: 70% had died or were injured before the following rut, while the remaining 30% pursued a follower strategy. Only one male achieved matings in all 3 years, eight other males obtained matings in each of 2 years and a further 22 were seen to mate in 1 year only. This latter group includes eight bucks who were still alive when this phase of the study ended in spring 1991.

Table 2 Individual histories of successful bucks that participated in more than one rut. The numbers show the number of matings observed per year and the strategy they adopted in each rut is given after this number; 'f' denotes that the buck pursued a follower strategy in that rut, 's' denotes a satellite buck, HF denotes high-fidelity territorial and LF denotes low-fidelity territorial. **** denotes death prior to the following rut

Buck	Year		
	1988	1989	1990
Eras.	3 f	23 HF	****
Swal.	3 s	68 LF	****
Vince	3 HF	0 f	0 f
Droopy	1 HF	0 f	****
B23	1 f	41 LF	2 f
O58	1 f	9 f	****
Peg.	0 f	29 LF	****
O38	0 f	11 f	0 f
Claw	0 f	9 HF	****
Spike	0 f	4 f	****
O37	0 f	2 s	****
Pyt.	0 f	1 f	19 f
W117	0 f	1 f	18 f
W146	0 f	1 f	42 HF
W148	0 f	1 f	0 f
W156	0 f	1 f	13 f
Peter	0 f	0 s	43 LF

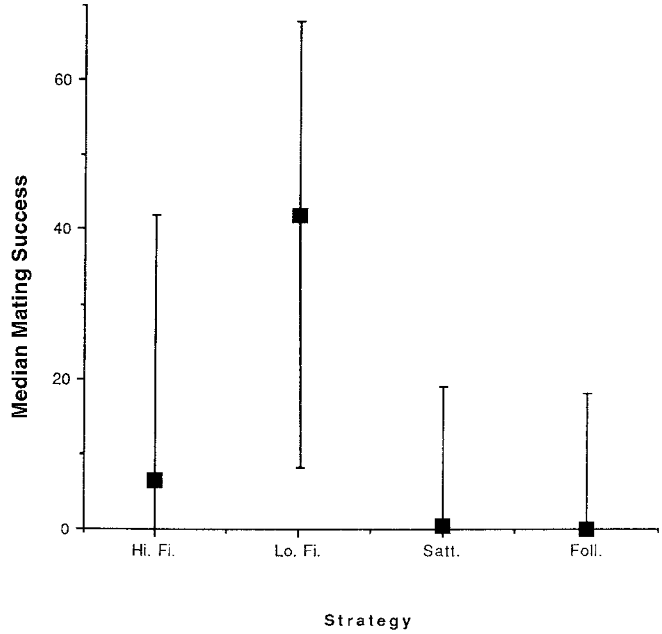


Fig. 2 The median mating success of bucks pursuing each strategy. *Error bars* represent the range of mating success observed per strategy over the 3 years (*Hi.fi.* high-fidelity territorial, *lo.fi.* low-fidelity territorial, *satt.* satellite, *foll.* follower)

Mating success of each strategy

Despite the low number of bucks (three to five) that pursue territorial strategies, they accounted for far more matings than either follower or satellite bucks. In the first two ruts, the proportion of matings achieved by follower bucks was less than 10%. In 1990, they accounted for 33% of the matings. In all 3 years, the majority of the matings (mean 75%, SD 19.8%) were achieved by bucks which had defended a territory. Low-fidelity bucks were the most successful overall, achieving 56.2% while followers obtained 19.5%, high-fidelity bucks 17.5% and satellite bucks 6.9% of matings.

Of more significance than the percentage achieved by each strategy, is the mean mating success of bucks pursuing each strategy. By dividing the total number of matings per strategy by the number of bucks pursuing that strategy we can quantify the mean number of matings per individual buck in each category. Low-fidelity bucks are the most successful followed by high-fidelity, satellite and followers (Fig. 2). There is a 38-fold difference between the least and most successful strategies in terms of mating success per individual buck. Pairwise comparisons showed that bucks using either of the territorial strategies achieved significantly more matings than followers (non-parametric Tukey test; $Q = 4.77$, $P<0.001$ for low-fidelity and $Q = 3.30$, $P<0.01$ for high-fidelity). Low-fidelity holders also differed significantly from satellites ($Q = 3.02$, $P<0.02$). Followers were not different from satellites ($Q = 1.36$, NS). The two territorial strategies were also not significantly different ($Q = 1.29$, NS).

Territories and spatial distribution of matings

The oak woodland is traditionally the site of territorial behaviour by the bucks. The boundaries of territories were not constant from one year to the next but it was possible to identify a particular area of woodland, the owner of which consistently achieved the highest number of matings. This territory, which included at least a 10-ha section of the wood, was defended by the most successful buck (a different individual each year) in each of the 3 years. However, overall only 39.5% of matings took place in the woodland. Thus the majority of matings (mean 60.5%, SD 10.00%) in each year took place in areas outside the aggregated territories. Even on the territories matings were not necessarily achieved by the owner of the territory. Of 194 matings on territories, 81.4% were obtained by territorial bucks, 56.1% were achieved by the owners of the territories, 25.3% were achieved by other intruding territorial bucks, 6.2% by satellite bucks and 12.4% by followers (Table 3). There was considerable inter-year variation. In 1988 and 1990 no matings were achieved on any territory by territorial bucks other than the owner but in 1989, 49% of the matings that took place on territories were achieved by intruding territorial bucks.

Table 3 The number of matings that took place on territories that were achieved by the owner of the territory, other territorial bucks, satellite bucks and followers

Year	Owner	Other territorial buck	Satellite	Follower	Matings on territories	Total matings per Year
1988	23	0	3	0	26	88
1989	39	49	2	10	100	202
1990	47	0	7	14	68	172
Total	109	49	12	24	194	462

Table 4 The distribution of all matings achieved by each category of buck divided into those achieved on a buck's own territory, on that of another buck and on neutral ground

	Own territory	Other territory	Neutral
High-fidelity territorial	21 (32.3%)	16 (24.6%)	28 (43.1%)
Low-fidelity territorial	87 (37.0%)	32 (13.6%)	116 (49.4%)
Satellite		15 (53.6%)	13 (46.4%)
Follower		21 (29.6%)	50 (70.4%)

We then examined the distribution of all matings to assess if there were differences between the strategies in the spatial distribution of matings (Table 4). The matings of all the territorial bucks were divided into those achieved on their own territory, on that of another buck and on neutral ground (areas not defended by bucks). The matings of the non-territorial bucks (followers and satellites) were divided into those obtained on neutral ground and on territories as defined by the territorial bucks. The locations of matings for both low-fidelity and high-fidelity territory holders were not significantly different ($\chi^2 = 4.85$, NS). Overall, only 36% of the territorial bucks' matings were on their own territories, 48% were on neutral ground while 16% were on the territory of another buck. If one then compares the territorial bucks with non-territorial bucks (followers and satellites) with just two categories (matings on any territory versus matings on neutral ground), the pattern was significantly different ($\chi^2 = 12.73$, $P<0.01$). Territorial bucks did not differ from satellites ($\chi^2 = 0.03$, NS) but these combined differed greatly from follower bucks ($\chi^2 = 11.90$, $P<0.0001$). The followers achieved a higher proportion of their matings on neutral ground than bucks pursuing the other strategies.

Dates of matings

The median mating dates of bucks pursuing each strategy were significantly different (Kruskal-Wallis $H = 18.36$, $df = 3$, $n = 40$, $P<0.0001$). Pairwise comparisons showed that follower bucks were the most different (median: 1 November), mating later in the rut than both low-fidelity territory holders (26 October; $Q = 3.59$, $P<0.002$) and satellite bucks (27 October; $Q = 2.82$, $P<0.05$). There were no significant differences between any of the other categories. The distribution of matings among the strategies differed between the secondary and the main mating peaks ($\chi^2 = 27.74$, $P<0.0001$). Both categories of territorial bucks and satellite bucks achieved slightly lower proportions of matings in the second peak ($\chi^2 = 3.60$, NS) but followers achieved a far higher proportion of the matings with females which did not conceive in the main peak ($\chi^2 = 20.17$, $P<0.0001$).

This tendency towards later matings by bucks of the least successful strategy was paralleled by the tendency of follower bucks to commence groaning later than bucks pursuing the other strategies (Kruskal-Wallis $H = 19.94$, $df = 3$, $n = 40$, $P<0.0001$). Pairwise comparisons showed that bucks which subsequently pursued territorial and satellite strategies started groaning at roughly the same time (medians: high-fidelity, 3 October; low-fidelity, 5 October; satellite, 10 October). Follower bucks started groaning significantly later (23 October) than bucks of the other two strategies ($Q = 3.30$, $P<0.01$ for high-fidelity, $Q = 3.34$, $P<0.01$ for low-fidelity and $Q = 3.00$, $P<0.02$ for satellites).

Mating interference

Mating interference, defined as interference during the mounting sequence resulting in the loss of the doe before successful copulation by the original suitor, was a rare phenomenon in the Park. Only eight incidents were recorded in the two ruts of 1989 and 1990 (interference was not specifically recorded in 1988). This represents 2.2% of the matings seen in the 2 years. Follower bucks were subjected to more interference (6 out of 88 matings) than would be expected by the total number of matings they achieved (Fisher's exact test; $P<0.005$). Since only two cases (out of 286) were observed for the bucks of the other three strategies, it was impossible to test if this level of interference differed significantly from expected.

Ages of mating bucks

The median and range of the number of matings achieved per successful male in each age-class is shown in Fig. 3. Overall a successful 6-year-old mated with more than 3 times as many does as a successful 5-year-old. Successful 7-year-olds also mated with more than twice as many does as 5-year-olds although the variation between 7-year-olds was quite high. Successful 6-year-old bucks were most likely to have the highest mating success.

No male younger than 4 years old was seen to achieve a successful mating. The majority (94.4%) of the matings were achieved by bucks between the ages of 5 and 7 years. Bucks older than 7 years accounted for few (3.8%) of the matings. The oldest known-age buck that was seen to mate was 9 years old.

Relationship between age and mating strategy

All of the territorial bucks were at least 5 years old at the time they defended their territories. None was older than 8 years. Satellite bucks ($n = 4$) which were of known age were all 5 years old. Followers that actively participated in the rut tended to be either younger or older than the territorial and satellite bucks. Only 35% of these were between 5 and 7 years of age (Table 5).

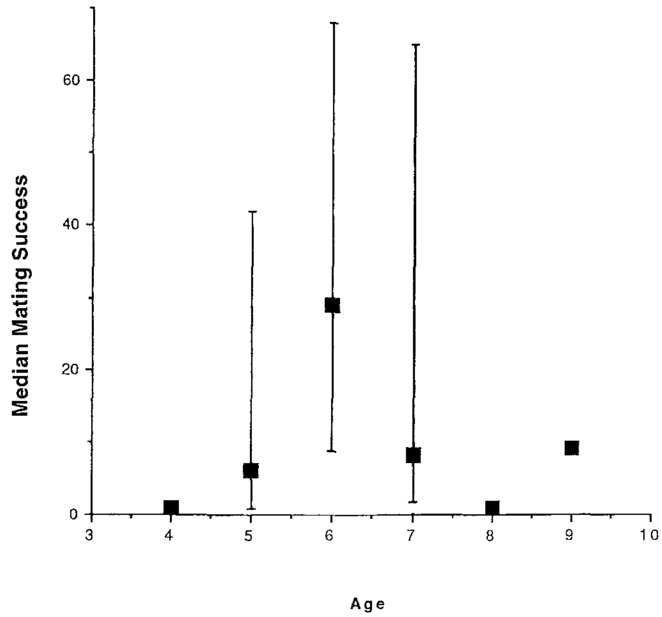
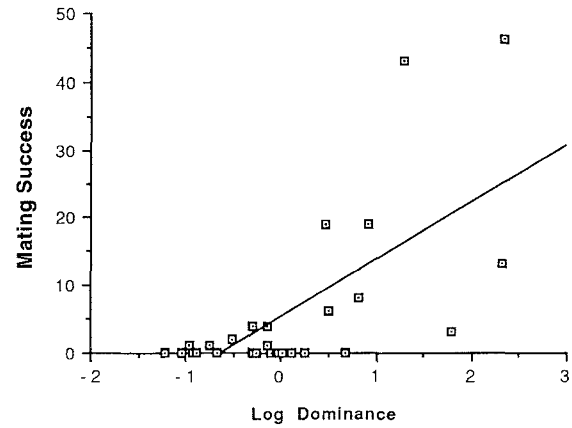


Fig. 3 Median mating success of males seen to mate in each age-class. *Error bars* represent the range of the number of matings that bucks in each age-class achieved

Table 5 The ages of bucks pursuing the four strategies over the years 1988 to 1990

Age class	Strategy			
	Hi-fi territorial	Lo-fi territorial	Satellite	Follower
3	0	0	0	7
4	0	0	0	16
5	1	0	4	9
6	1	3	0	3
7	0	1	0	1
8	1	1	0	3
9	0	0	0	1



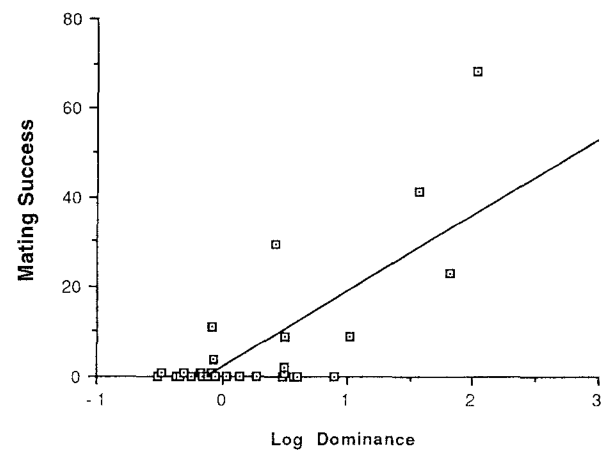


Fig. 4 The relationship between dominance index assessed in October (log-transformed) and mating success for 1989 (*above*) and 1990 (*below*)

Relationship between dominance and mating success

The mating success of the 30 most dominant bucks was plotted against their dominance index to investigate how much of the variation in mating success of bucks was explained by dominance. Dominance assessed in both September and October was highly correlated with overall mating success in both 1989 and 1990 (September: $r = 0.63$, 0.68 for 1989 and 1990 respectively, $P<0.001$ for both; and for October: $r = 0.73$, 0.67 for 1989 and 1990, $P<0.0001$ for both 1989 and 1990). Figure 4 shows this relationship for October in both years.

Relationship between dominance and mating strategy

In general, the bucks that held territories during the rut in Phoenix Park were highly dominant and this was true if one considered either September or October dominance ranks. There were highly significant differences in rank of bucks (assessed in both September and October) which pursued different strategies (September: Kruskal-Wallis $H = 16.31$, $df = 3$, $n = 39$, $P<0.0001$ and October: Kruskal-Wallis $H = 17.52$, $df = 3$, $n = 57$, $P<0.0001$) when one includes the top 30 ranked bucks. Bucks which held low rank in September and October were most likely to pursue a follower strategy. Follower bucks had median ranks of 19.5 in September and in October. In contrast, both high- and low-fidelity territorial bucks were generally high-ranking while satellite bucks were of middle rank (Table 6). Analysis of the differences in rank between the strategies was hampered by the very small sample size for the territorial bucks, some of which could not be ranked in September due to their absence from the bachelor herd.

Relationship between fighting success and mating success

The correlation between fighting success and mating success was investigated using all fights observed during October for both 1989 ($n = 104$) and 1990 ($n = 176$).

Table 6 The median rank of the four strategies assessed in September and October. The numbers in brackets indicate the ranges. For September, the rank represents the median of 1989 and 1990. For October the rank represents the median of 1988, 1989 and 1990. Superscripts indicate significant pairwise differences

	High-fidelity territorial	Low-fidelity territorial	Satellite	Follower
Sept. rank	2 (1–10)[a]	3 (1–8)	8 (3–16)	19.5 (4–30)[a]
Oct. rank	3.5 (2–16)[b]	1.5 (1–13)[c]	9.5 (5–16)	19.5 (2–30)[bc]

[a] $P<0.02$, [b] $P<0.01$, [c] $P<0.05$

There was a significant correlation between fighting success and mating success in 1989 ($r = 0.52$, $P<0.01$) but no correlation was found for 1990 ($r = 0.23$, NS).

Discussion

The mating system in Phoenix Park is a multiple-stand system with between three and five males defending contiguous territories for a 2–3 week period in mid-October. This territorial aggregation occurs at slightly lower densities in this population than would be predicted by Langbein and Thirgood's model using buck density, doe numbers and cover availability (Langbein and Thirgood 1989). It was, however, pointed out by both Appolonio (1989) and Langbein and Thirgood (1989) that the resource distribution in an area was also a major influence on the mating system adopted by a fallow population, i.e. territorial aggregation could occur at relatively low population densities if resources were patchily distributed. In Phoenix Park the territories are located in the only large area of oak woodland in the Park, which is also at the centre of the does' overall range.

The distribution of matings among the bucks in Phoenix Park is highly skewed; the most successful male achieves 26–51% of observed matings. By comparison the most successful male obtained 14.5–16% of matings in Petworth and 21–52% in San Rossari (both lekking populations). A small number of the most successful males also accounted for the majority of matings in these studies (the six most successful mating bucks in Phoenix Park obtained 85–90% of the matings, 57% in Jaegersbourg, 64% in Petworth and over 90% in San Rossari). This is in agreement with Langbein (1990), who believed that the skew in mating success among bucks in lekking populations (though high) was lower than in some of the less aggregated mating systems. Furthermore, as in the other well-studied fallow populations, most of the males in Phoenix Park that actively participated in the rut failed to breed in a given year despite being in close proximity to the females throughout.

What are the factors that cause this high skew in mating success? Age, dominance and mating strategy are all factors that influence mating success in this population. All three variables are highly inter-related. Bucks reach their peak in mating success at 6 years old at the same time that they are most likely to attain high rank and are most likely to defend a territory (Moore 1993). Age is clearly an important factor affecting dominance and therefore mating success in bucks. Bucks must be between 5 and 7 years of age to be highly dominant in this population. Similarly Appolonio et al. (1992) found that territorial males had a mean age of 5–6 years. Whether the distribution of matings among the age classes is similar in other fallow populations is unknown and it is obviously highly related to the age structure of the population. In Phoenix Park there is a high mortality rate among bucks (due mostly to collisions with cars) and 75% of male fawns die before their 4th birthday (Moore 1993). There are thus few middle-aged and old males in the herd.

Dominance, assessed using all interactions, in both September and October was highly correlated with mating success. All lower-ranking bucks pursued a follower strategy. Fighting success, on the other hand, was less correlated with mating success than was a dominance index derived from all agonistic interactions (both contact and non-contact). A similar situation occurs on the lek in San Rossari where a ranking of bucks based on their fighting success (similar to the one used in this study) was not correlated with mating success but on inclusion of all non-contact interactions the correlation became significant (Appolonio et al. 1989). In Petworth, fighting success was significantly correlated with mating success (Clutton-Brock et al. 1988) as it was in 1 of the 3 years studied here. The lowered correlation for fighting success is probably due to the fact that the outcome of a fight often depends on the particular location and context, while dominance rank, assessed by considering all interactions, more closely indicates the overall dominance in each period. Furthermore it may be that escalated interactions are more likely to occur between particular pairs of bucks as appears to be the case for red deer stags (Freeman et al. 1992).

Dominance alone explains approximately 50% of the variation in mating success among bucks in this population. There are a number of factors which may explain why it was not more important. Some males that were highly dominant in September and early October achieved few or no matings. For some, this is because they sustained an injury or serious antler breakage which led to a decrease in their rutting activity. Other bucks could not be ranked prior to or early in the rut as they were more solitary outside the breeding season and were not present in the bachelor herd. Much of the remaining variation can be explained in terms of the strategy adopted by bucks. In Phoenix Park a high social rank (not lower than 13th) is necessary for holding a territory, but not all dominant bucks did so. Those that failed to defend a territory were not highly successful.

The rutting area in Phoenix Park is a traditional site which has been used by the deer for at least several decades (M. O'Brien, personal communication). The same area also remained the focus of most of the rutting activity during the three years of the current study and all the territories (with one exception) were defended in this area. Such faithfulness to traditional rutting sites seems to be a notable feature of many populations of fallow deer (Cadman 1966; Appolonio et al. 1989; Clutton-Brock 1991). The wood may be important for three reasons: it provides shelter, a seasonally abundant food source (acorns) and is at the centre of the does' range in their pattern of daily movements (Moore 1993). This means that the does tend to linger in the wood for variable periods of the day and the bucks may hold their territories here in order to defend resources of value to the females. This might explain the very active defence of these territories for two to three weeks before the does come into oestrus. Territorial activity is unlikely to clarify dominance relations, as in Phoenix Park the outcomes of interactions between territorial bucks are highly dependent on context and encounter. This has also been shown in other studies (Dewsbury 1982). Thus the purpose of setting up territories to clarify relationships among males seems unlikely.

Why is defence of a territory so crucial to achieving high mating success since only 36% of matings were achieved on territories? In 2 of the 3 years the majority of matings in the early part of the rut took place on the territories. Later, at the peak of the rut, most matings occurred in the pastures and the successful males were largely those which had previously been territorial but had now switched tactics to follow the does for varying periods. It is tempting to speculate that the bucks were forced to change tactics due to a change in the quality of their territories, i.e. diminution of the acorn resource. The oak wood, in absolute terms, is small (c. 25 ha) and the deer population increased from 381 to 525 in the course of the 3 years. This aspect of resource availability is currently under investigation. If the males use the resource to influence mate choice by does then presumably female choice is influenced by other criteria when bucks are in the pastures.

Is the high variance in mating success within individual years also detectable in the lifetime reproductive success of bucks? Within a single year mating success ranges from 0 to 68 observed matings and is undoubtedly higher in reality as a number of matings were not seen. The majority (75%) of males die before they reach breeding age (4 years old in this population) and the mean life expectancy of male fawns (at birth) is only 2.3 years (Moore 1993). Of those bucks that do survive to breeding age not all of them reproduce in any one year. Only approximately 30% of 4-year-olds and 55% of those between 5 and 7 years old were seen to mate in any given year. Within individual year classes there is still a large variation in mating success. Furthermore, males that achieve high dominance and rut successfully are unlikely to survive to the next rut. We are as yet not in a position to determine whether achieving high mating success in a particular rut decreases survivorship to the next rut below that of the non-breeding males of the same cohort. However, the large differences in mating success between bucks plus the fact that few males survive to old age precludes those bucks which were initially less successful from eventually catching up with their highly successful fellows. Clearly then, in Phoenix Park, a small number of males contribute massively to the next generation and the skew in mating success seen in a single year greatly influences the pattern of relative lifetime reproductive success.

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References

Alvarez F (1993) Risks of fighting in relation to age and territory holding in fallow deer. Can J Zool 71:376–383

Alvarez F, Braza F, Norzagary A (1975) Estructura social del gamo (*Dama dama*, Mammalia, Cervidae), en Doñana. Ardeola Especial 21:1119–1142

Alvarez F, Braza F, San Jose C (1990) Coexistence of territoriality and harem defence in a rutting fallow deer population. J Mammal 71:692–695

Appolonio M (1989) Lekking in fallow deer: just a matter of density? Ethol Ecol Evol 1:291–294

Appolonio M, Festa-Bianchet M, Mari F (1989) Correlates of copulatory success in a fallow deer lek. Behav Ecol Sociobiol 25:89–98

Appolonio M, Festa-Bianchet M, Mari F, Mattioli S, Sarno B (1992) To lek or not to lek: mating strategies of male fallow deer. Behav Ecol 3:25–31

Braza F, Garcia JE, Alvarez F (1986) Rutting behaviour in fallow deer. Acta Theriol 31:467–478

Buschhaus NL, Lagory KL, Taylor DH (1990) Behaviour in an introduced population of fallow deer during the rut. Am Mid Nat 124:318–329

Cadman WA (1966) The fallow deer. HMSO, London

Chapman DI, Chapman NG (1975) Fallow deer: their history, distribution and biology. Terence Dalton, Suffolk

Clutton-Brock TH (1991) Lords of the lek. Nat Hist 10:34–41

Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). Anim Behav 27:211–225

Clutton-Brock TH, Green D, Hiraiwa-Hasegawa M, Albon SD (1988) Passing the buck: resource defence, lek breeding and mate choice in fallow deer. Behav Ecol Sociobiol 23:281–296

Davies NB (1991) Mating systems. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 263–294

Dewsbury D (1982) Dominance rank, copulatory behaviour and differential reproduction. Q Rev Biol 57:135–159

Dunbar RIM (1982) Intraspecific variations in mating strategy. In: Bateson PPG, Klopfer PH (eds) Perspectives in ethology. V. Ontogeny, Plenum, New York, pp 385–431

Emlen ST, Oring LW (1977) Ecology, sexual selection and the evolution of mating systems. Science 197:215–223

Espmark Y, Brunner W (1974) Observations on rutting behaviour in fallow deer (*Dama dama*). Saeugetierk Mitt 22:135–147

Freeman LC, Freeman SC, Romney K (1992) The implication of social structure for dominance hierarchies in red deer, *Cervus elaphus* L. Anim Behav 44:239–245

Gosling LM, Petrie M (1990) Lekking in topi: a consequence of satellite behaviour by small males at hotspots. Anim Behav 40:272–287

Hayden TJ, Moore N, Kelly PF (1992) The fallow deer of the Phoenix Park: an evolving management plan. In: Bullock DJ, Goldspink CR (eds) Management, welfare and conservation of park deer, Proceedings of the Second Deer Park Symposium, Potters Bar, UFAW, pp 27–45

Langbein J (1990) Effects of density and age on body condition, reproductive performance, behaviour and survival of fallow deer. Ph.D. thesis, University of Southampton

Langbein J, Thirgood SD (1989) Variation in mating systems of fallow deer in relation to ecology. Ethology 83:195–214

Moore NP (1993) Mating success in fallow (*Dama dama*) bucks in Phoenix Park, Ireland. Ph.D. thesis, National University of Ireland

Pemberton JM, Balmford AP (1987) Lekking in fallow deer. J Zool Lond 213:762–765

Rubenstein DJ (1980) On the evolution of alternative mating strategies. In: Stadden JER (ed) Limits to action: the allocation of individual behavior. Academic Press, New York, pp 1–44

Schaal A (1986) Mise en evidence d'un comportement de reproduction en arene chez le daim d'Europe (*Dama dama dama*). C R Acad Sci Paris 303:729–732

Schaal A, Bradbury JW (1987) Lek breeding in a deer species. Biol Behav 12:28–32

Thirgood SJ (1991) Alternative mating strategies and reproductive success in fallow deer. Behaviour 116:1–10

Waltz EC, Wolf LL (1984) By Jove!! Why do alternative mating tactics assume so many different forms? Am Zool 24:333–343

Wilson EO (1975) Sociobiology: the new synthesis. Belknap, Cambridge

Worton BJ (1989) Kernel methods for estimating the utilisation distribution in home range studies. Ecology 70:164–168

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