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Freedom to choose: unconstrained mate-searching behaviour by female fallow deer (*Dama dama*)

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Abstract. Individuals can increase their fitness by searching for mates of an appropriate quality. We here report the results of a five-year study on the behaviour of peri-estrous female fallow deer to document examples of apparent mate-searching and the context in which it occurs. Using direct observation of 266 tagged does we collected spatial and behavioural data of does and the bucks with which they were seen, together with the identity of their mate. Movement of does was relatively unconstrained by bucks. Buck-switching by does was mostly due to apparently unprovoked movements by the does. Approximately half of the does were recorded with more than one buck on the day they mated. Mobile does encountered bucks at rates between 0.76 and 1.85 per hour and were more likely to transfer to a reproductively successful buck than an unsuccessful one. Does of all ages were equally likely to be recorded in multiple or in single consortships with no tendency for does to fall into the same category in two or more years. We suggest that the behaviour of fallow does in this population is consistent with the use of mate-searching by a variable proportion of the population as a condition-dependent mating tactic.

Key words: peri-estrus behaviour, mate encounters, conditional strategy

Introduction

In polygynous species, variance in fitness of females is lower than that of males and fitness is limited more by the quality, rather than the number of their mates, although multiple mating can play a part acting through sperm competition. By contrast fitness of males is constrained by the degree of access to mates and is correlated with the number of different females whom they fertilize. Therefore encounter rates influence the fitness of both sexes by either widening the menu of males from which a female might choose or increasing access by males to potential mates. On theoretical grounds it has been predicted that mate searching is a conditional strategy and one sex should invest more in improving encounter rates with the opposite sex (Hammerstein & Parker 1987, Kokko & Wong 2007). Because of the asymmetrical benefits of multiple mating (Bateman 1984), it is generally expected that males should be more likely to invest in the effort of searching for mates, unless male density is low (Hammerstein & Parker 1987). By contrast, females are more passive in the searching phase at least (Janetos 1980, Parker 1983) unless there is little cost associated with searching (Kokko & Wong 2007) but should be more choosy than males (Emlen & Oring 1977). The prevalence of mate-searching by females could increase if sampling potential mates improves mate quality particularly if there are many males to compare (Kokko & Wong 2007).

While the reproductive behaviour of males, in conventionally dimorphic species may be understood from the perspectives of access to females and female choice, and indeed in many cases the phenomenon of female choice is often inferred from the behaviour of males during the breeding season, demonstration of mate searching and mate choice by females has so far been less widespread. Nevertheless, over the last two or three decades evidence for active mate searching and choice has been obtained from females of species from many phyla (Andersson 1994). The most appropriate approach to demonstrate female searching and choice is an experimental paradigm (Kotiaho & Puurtinen 2007, Maklakov & Arnqvist 2009), firstly to identify that females have the capacity to discriminate between males and that, in fact, they do so (Reby et al. 2001, Charlton et al. 2007), secondly to identify and experimentally modify the traits on which the females base their decision (Morehouse & Rutowski 2010), thirdly to reveal the strategy by which females seek and compare potential mates and

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arrive at a decision (Parott et al. 2007) and fourthly to identify and quantify the net direct and indirect fitness benefits deriving from the exercise of choice (Oneal et al. 2007).

Much of the experimental evidence for searching and choice emphasises fitness benefits and is derived from studies of a number (increasing) of model organisms, usually innocuous and of small body mass, chosen in part because of their tractability to experimental manipulation. For large and/or free-ranging animals for example, evidence of mate-searching and/or mate choice by females is almost inevitably derived from careful behavioural analysis and is largely correlative in nature (Uy et al. 2001, Hoffman et al. 2007). Mate-searching and/or mate-choice behaviour of females has been described in only a few species from among the Cetartiodactyla. These are mostly lek-breeding species such as fallow deer (Clutton-Brock et al. 1989) and Uganda kob (Balmford et al. 1992). Apart from these, mate-searching behaviour by female ungulates has only been convincingly reported for bighorn sheep (Hogg 1987), pronghorn (Byers et al. 2006) and roe deer (Lieberg et al. 1998, Lovari et al. 2008).

In lekking populations females preferentially visit leks over isolated individual territories and an element of mate-searching by females can be inferred. Interpretation of female movements between males on the lek is more problematical (Apollonio et al. 1990, Clutton-Brock et al. 1992, Carbone & Taborsky 1996, Clutton-Brock et al. 1996). It is confounded by the difficulty in distinguishing between choice based on male phenotype, on the lek territory itself or on harem size (Carranza 2000). Nevertheless some potential elements of mate searching and mate choice by females have been identified in fallow deer. Bucks are highly vocal (McElligott et al. 1999) and their vocalisations are sufficiently different to act as a vocal signature (Reby et al. 1998, Vannoni & McElligott 2007). Captive does have the capacity to delay oestrus when given access to immature bucks only (Komers et al. 1999) and captive does show a preference for groups of does with or without a consorting buck over isolated bucks (Clutton-Brock & McComb 1993).

The mating system of fallow deer is highly plastic ranging from leks to free-ranging dominance systems (Clutton-Brock et al. 1988, Langbein & Thirgood 1989, Thirgood et al. 1999), male-male conflict is frequent and protracted (Apollonio et al. 1989, McElligott et al. 1998) and the variance in male mating success and fitness is universally highly skewed (Clutton-Brock et al. 1988, Apollonio et al. 1989, McElligott et al. 1998, Say et al. 2003). This provides the opportunity in some populations to identify mate-searching by does relatively unconfounded by territoriality.

In Phoenix Park fallow deer have never been recorded lekking and the mating system may best be described as a mixed non-territorial dominance/territorial system with 90 % of bucks using a follower strategy (Moore et al. 1995). The majority of matings are achieved by non-territorial bucks that are relatively vagile but show some area-fidelity within the grassland or parkland areas (Moore et al. 1995). Successful bucks accumulate harems of peri-estrous does by a combination of searching for and joining a group of does and spontaneous accumulation of peri-estrous does around the buck (Chapman & Chapman 1975). Mating success of bucks in all years is highly skewed and between 5 and 14 bucks achieve over 80 % of the matings recorded each year (Naulty 2006). High variance in male mating success does not reveal *per se* the mechanism by which females choose a mate or indeed if mate choice by females exists (Clutton-Brock et al. 1992). Within this mobile system does could encounter males in a variety of ways depending to an extent on the ability of bucks (i) to exclude rival bucks from an area frequented by does, (ii) the extent to which bucks can constrain the free movement of does and (iii) the extent to which bucks change their location.

The purpose of this paper is to present evidence of behaviour consistent with mate searching by females. If mate searching exists then a number of predictions may be made. 1. Doe movement during the rut is relatively unconstrained by bucks. 2. Does changing groups are more frequently recorded at the peak of the rut. 3. Does are more likely to initiate heterosexual encounters than bucks. 4. Does are more likely to terminate heterosexual encounters than bucks. 5. Does terminating an encounter are more likely to join a buck of high quality (defined *a posteriori* from his total copulatory score for the rut). 6. Does of all ages are equally likely to be recorded in encounters with multiple bucks. 7. Does are equally likely to be recorded in multiple encounters in different years.

Material and Methods

Study site and population

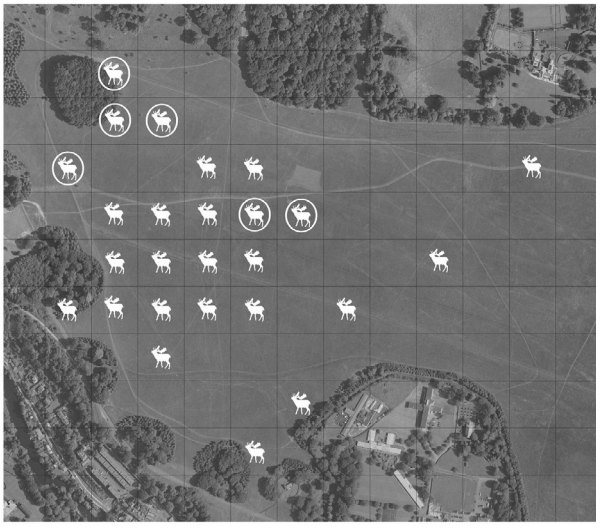
The study was conducted on a herd of fallow deer, mostly tagged at birth, in Phoenix Park (709 ha, 53°22′ N, 6°21′ W, 12-56m ASL), Dublin, Ireland. The herd was established in 1662 (Hayden et al. 1992) and was studied during five breeding seasons

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between 1998 and 2002 during which the herd size ranged from 548 to 630 and contained between 233 and 297 does aged one year or older. Population density ranged from 0.75 to 0.9 per ha, at the lower end of population densities for park herds (0.5 to 6 per ha; Langbein & Thirgood 1989). The sex ratio (F/M), excluding fawns varied between 1.28 and 2.26. The park consists of a mosaic of grassland (398 ha; 56 %), parkland (grassland areas with few scattered trees or shrubs: 96 ha; 14 %) and closed canopy mixed-species woodland (215 ha; 30 %) (OPW 2009). By day, does range over an area that covers about 130 ha and includes areas of open grassland, parkland and closed-canopy mixed woodland. Does are free to move at will within this area, subject only to their reluctance to spend much time alone. Matings may be recorded anywhere within the range of the does. During darkness the doe herds are more fragmented and more widely dispersed throughout the park. In late August to early September the bucks move from the southeast onto the does range and remain there until about early November.

The reproductive activity takes place from about the beginning of October and matings usually occur between 14th October and 31st October. The majority of matings are achieved by non-territorial bucks that are relatively vagile but show some area-fidelity within the grassland or parkland areas or in woodland in years with a good acorn crop (Moore et al. 1995). Bucks tend to vary the centroid of their activity each day. For example, in 2000 the most dominant buck mated at least once in up to 6 different 1 ha squares on Oct 21 and in 26 squares overall during the rut which is equivalent to a mating range that may have been as large as 45 ha (Fig. 1a). Does in estrus moved between bucks often ignoring intervening animals (Fig. 1b).

(a)



(b)

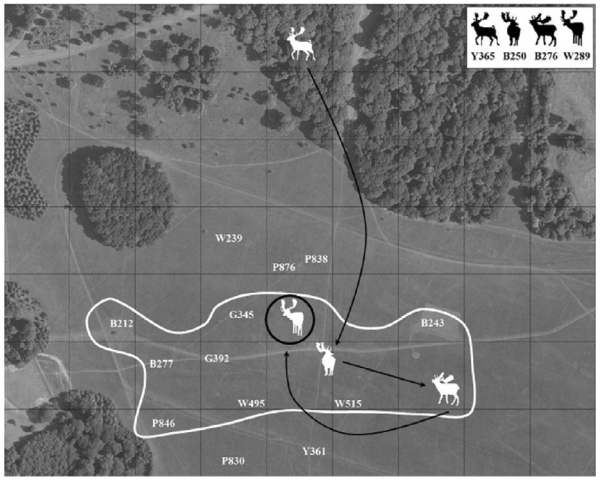


Fig. 1. (a) Locations (1 ha squares) in which the most successful buck mated on Oct 21, 2000 (icons in circles) together with all locations (plain icons) within which he mated during the entire rut. (b) Locations of 17 bucks (icons and alphanumerics) between 10.00 and 13.00 on the same day. The sequence of arrows represents the path of a spontaneously-moving doe who, over the same period, consorted with 4 bucks before mating (circled icon). The area enclosed by the white line represents the extent of the doe herd over this period.

Observations

We carried out all-event recording of agonistic interactions, rutting activities of bucks, matings and movements of does between groups during the rut, defined as the period when matings occur. In 11 ruts from 1989 to 1999, on average, 90.1 % of matings occur within the period 20-30 October (Moore et al. 1995, McElligott et al. 1999, Farrell 2001). We identify a group as an aggregation of does (i) in close proximity (within 10 metres, estimated as buck-lengths) to a buck either isolated from other does or (ii) if within a herd, in a noticeably higher density than that of the matrix of the remainder of the herd.

During this period, up to 13 observers were in the field daily, from dawn to dusk (c. 11 h). Observations were made using Kowa telescopes (X27-X40 lens magnification) and recorded onto Dictaphone or video tapes for later transcription and collation. Observers were in radio contact and spatially deployed to maximize coverage of animals and to help minimize duplicate recordings. Movements of does or bucks were communicated between observers in an attempt to compile a continuous record of the locations of deer for as long as possible.

Fallow does are extremely nervous when isolated (Clutton-Brock & McComb 1993) and whenever a doe or does left a group it was invariably to join another

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group. All instances and contexts of a doe or group of does entering or exiting a group were noted. Their identities were recorded as well as the identities of any other animals i.e. fawns, immature and mature bucks moving with them. A departing doe was monitored while in transit to record whether she encountered a buck, also in transit, and finally the location of her destination group was noted together with the identity of any consorting bucks in the group. Changes in buck locations were noted whenever movement occurred and all matings were recorded together with the identities of all females in the mating area/group.

An encounter is defined largely by behaviour and proximity. A doe is considered to have encountered a buck if there has been physical contact between them (e.g. sniffing and/or licking), if she has been recorded orienting towards a nearby buck, or if she is close enough (within 10 metres, estimated as buck-lengths) to make it unlikely that she could be unaware of his presence (Hovi et al. 1995).

The overall movement patterns of does varied in duration and complexity. The intervals between a doe being first recorded with a buck and her mating ranged from 43 to 532 minutes and an individual doe may have been recorded in the presence of up to 11 bucks on the same day. Overall 552 records involving 266 tagged does who were observed mating only once in a particular rut between 1998-2002 were examined. Of these 194 records included the mating sequence only and were not considered further. For the remaining 358, it is necessary to distinguish between behaviours/events potentially involved in mate searching or mate choice, from those that may be triggered by other causes but that simultaneously happen to improve mate-encounter rates (Kokko & Wong 2007). We were particularly interested in, (i) the tendency of bucks to attempt to restrain the movements of does, (ii) the frequency and the circumstances under which does encounter a buck or bucks, (iii) the context of departure of a doe from her consort and (iv) whether the tendency of individual does to encounter multiple males varied across years.

Herding

The extent to which does can search for a mate depends on how their movements are constrained by bucks. All attempts (514) by a doe to leave a group, containing an adult buck, were partitioned into those in which he was unavailable (147; involved in a mount sequence or agonistic interaction) or otherwise unoccupied (367) and was therefore available to attempt to retain the doe. The vagility of does was assessed by comparing the number of group changes by single does with the number of matings recorded during each day of the rut (Pearson's correlation).

Initiation of encounters between does and bucks

The frequency of types of onset and termination of encounters were estimated from a data set containing 436 instances of a doe joining a buck. Individual does contributed on average 2.56 ± 0.19 encounters per year and 3.23 ± 0.26 overall. Four types of initiation were considered (i) movement of a doe into a group that included a buck, (ii) replacement of the resident buck by an interloper, (iii) an encounter while the doe was in transit and (iv) a doe coming into proximity with a buck as a consequence of a group of does moving *en masse*.

Termination of encounters between does and bucks

The frequency of types of termination of encounters were estimated from a data set containing 280 instances of a doe leaving a buck. Encounters that led to a mating have been excluded, since a buck had been accepted. Terminations were classified into three main types, (i) spontaneous departures by the doe (ii) event-associated departures (during an agonistic interaction involving the consorting buck or during a mount sequence between the buck and another doe) and (iii) as a result of the take-over of the group or harem by an intruder buck.

In an attempt to determine the time a doe takes to make a decision to reject a buck during an encounter, cases of encounters where the termination was the result of an apparent spontaneous movement of the doe were examined (n = 192). These were subdivided into those in which the encounter was initiated by the doe (n = 169) and those in which the buck initiated (n = 23). A Mann-Whitney U test was used to test for differences in stay duration. The data were also examined (Kruskal-Wallis test) with the encountered bucks grouped according to rank category (top 10 ranks, bucks ranked 11-20 and lower ranks). In this population, the top 10 ranked males typically account for > 80 % of the matings (McElligott et al. 1998). A logistic regression (enter method) was used to determine if encounter initiation type (buck/doe) was a good prediction of female behaviour (stay and mate/leave). A model including a measure of male status (dominance rank) was also analysed. David's score (David 1987, 1988) was used to calculate a global measure of dominance. All noncontact interactions that were decisively resolved prior to the first mating in that year were used to calculate dominance rank (e.g. Gammell et al. 2003, Jennings et al. 2009).

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Encounter rate of bucks by does

There were 78 cases (out of 358) of an identified mating doe with a continuous record for the three hours prior to mating. Encounter rates with bucks were estimated for these does. They formed two groups; 30 does had spent the entire 3-hour period in the presence of the buck with whom they mated, while 48 had been recorded with a minimum of two bucks. Records were further classified into those involving only spontaneous transitions between bucks and those involving encounters due to other circumstances (e.g. harem take-over) or a mixture of the two. The encounter rates were examined for an effect of year using an ANOVA.

Encounters and reproductive status of bucks

The final copulatory score, the total number of copulations recorded, for the active bucks in each year was used to estimate the reproductive skew using the Lambda index (Kokko & Lindström 1997) as calculated by the Skew Calculator 2003 (http://www.eeb.ucla.edu/Faculty/Nonacs/). Overall copulatory score is highly correlated with both dominance rank (McElligott et al. 1998) and paternity score in this population (Say et al. 2003). The number of mature bucks varied between 61 and 72 over the ruts of 1998-2002 and the mating skew among these ranged from 0.23-0.37 (Table 1).

Does searching for particular males might be expected to initiate encounters preferentially with those of high quality, i.e. those who have successfully mated. Encounters by spontaneously-moving does were partitioned into those with a male that had mated and those that had not (classified *a posteriori*) and the number of bucks in each category were compared to those expected from their relative abundance in the population. Over these years the number of bucks that mated at least once ranged from 18 to 27 and over the five years, 119 of the 334 mature bucks were successful at least once. Similarly, encounters initiated by movements of a buck were partitioned into those brought about by maters and non-maters and the number of bucks in each category were summed and similarly tested as for spontaneously-moving does.

Doe age-class and encounters

To examine if there was a relationship between doe age-class and tendency to encounter bucks, 653 mating records for 278 individual does (yearlings and older between 1998 and 2002) were sorted by age-class and whether they were recorded either with one buck only (their mate) or with more than one. In this case, 115 cases of multiply-mating by does, i.e. those that were recorded mating more than once on the same day were included since they had encountered at least two bucks. Individual does contributed data for on average 2.35 ± 0.08 years. A Chi-square test was used to test for an association between age and encounter behaviour (mate only or multiple encounters).

Of the 278 individual tagged does, 102 were only observed mating in only one year. Data were available for 176 does from more than one year: sixty were observed in two years only, 56 in three years only, 37 in four years only and 23 in all five years. Does observed in only one year (102) were divided into those recorded with one (45) or more than one buck (57). The proportion 57/102 (0.56) was taken to be the probability that any doe would be recorded with more than one buck and used to estimate the probability of being so classified in two or more years. These were used to estimate, of the remaining 176, the numbers expected to be always recorded with more than one buck (41), never recorded with more than one buck (17) and recorded with more than one buck in one year and not in another (118). These were compared to the observed numbers by a Chi-square test.

Yearly variations in encounter behaviour

To determine if encounter behaviour is related to context, the data (n = 653) were examined for effects

Table 1. Yearly variation in the context of encounters.

Year	1998	1999	2000	2001	2002	Total
Mature bucks (≥ 4 years of age)	72	68	63	70	61	334
Number of bucks that mated	27	18	20	27	27	119
Mating skew (λ)*	0.36	0.30	0.37	0.27	0.23	
Mating bucks (non-mating) encountering spontaneously moving does	17(1)	15(3)	16(2)	15(1)	12(1)	75(8)
Mating bucks (non-mating) encountering oestrous does after buck movement	2(7)	2(3)	2(3)	1(1)	1(1)	8(15)

* Calculated according to Kokko & Lindström (1997).

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of year. Within each year, females were classed according to their encounter behaviour (multiple encounters or mate only). A Chi-square test was used to determine if there was an association between year and behaviour. The relationship between reproductive skew (λ: calculated according to Kokko & Lindström 1997) and encounter behaviour was examined using a Pearson's correlation. The relationship was also examined with multiple encounters separated into multiply mating females and single mating females with multiple encounters.

Statistical analysis

All statistical tests were carried out using SPSS version 18 (SPSS Inc., Chicago). Means are expressed ± SE. Distributions were tested using Chi-square contingency tests. Logistic regression (enter method) was used to determine if variables significantly predicted female behaviour. Datasets were tested for normality using the Kolmogorov-Smirnov test. The relationship between variables were tested by correlation analysis (Pearson's). Differences between variables were tested using Mann-Whitney tests, Kruskal-Wallis tests and ANOVA depending on normality.

Results

Group changes by fallow does during the rut (predictions 1 and 2)

Group changes by single does, that is does travelling alone, increases approximately 5-fold at the peak of the rut when the frequency of daily matings was at its highest. For example in 2000 the number of movements of estrous does recorded was highly correlated with the number of matings recorded on that day (Fig. 2; Pearson's correlation; $r = 0.881$, $n = 18$, $P < 0.001$). Movement of does is hardly constrained by the bucks. Of these 367 instances when he might have intervened, in only 52 (14 %) cases did a buck attempt, by herding behaviour, to prevent the doe from leaving and in only 17 (33 % of attempts) was he successful.

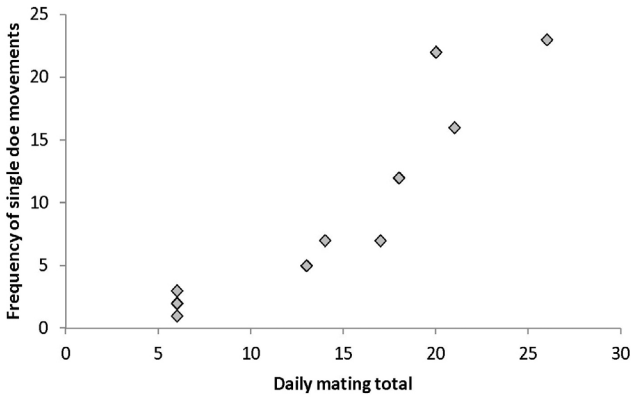


Fig. 2. Relationship between the number of lone movements by estrous females (N = 100) and the number of matings recorded on each day of the rut in October 2000.

Initiation of encounters between does and bucks (prediction 3)

Encounters of does and bucks occur mainly by translocation of the doe. Of 436 cases of a doe encountering a buck, most (343/436, 79 %) were as a result of a doe moving to a group containing a resident buck (Fig. 3). The remainder occurred in different

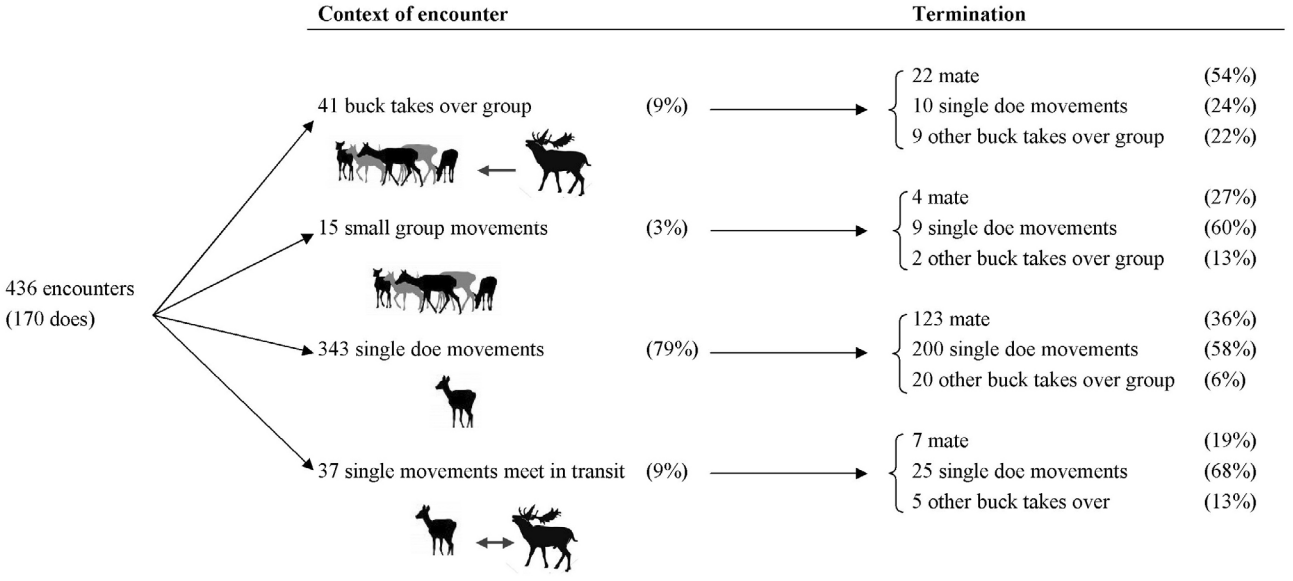


Fig. 3. Context of encounter initiation and termination.

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contexts. In 41 the resident buck was driven from the group by the entry of an interloper who now assumed consortship. In another 37 cases a doe encountered a buck while in transit between groups and in 15 cases the group moved as a whole, into the area controlled by another buck, leaving the resident buck behind. Overall, 20 % (67/343) of cases of encounters initiated by a spontaneously moving doe resulted in her moving to a male who was involved in a mount sequence at the time she moved. A further 79 (23 %) spontaneously moving does had the opportunity to move to a simultaneously mounting male but did not do so.

Termination of encounters between does and bucks (prediction 4)

To quantify how encounters ended we examined 280 cases which did not lead to a mating. Overall, 87 % (244/280) of encounters terminated due to the doe leaving (Fig. 3). Spontaneous movements by the doe with no obvious cause accounted for 168 (69 %) cases; in 44 (18 %) cases the doe left during an agonistic interaction and in 32 (13 %) cases she left while the buck was mounting another doe. In the remaining 36 (13 %) cases the encounter ended due to harem take-over either because the buck lost an agonistic interaction (24 cases, 9 %) or because the buck spontaneously left the group and another buck entered (12 cases, 4 %).

The duration of encounters prior to a doe leaving spontaneously differed depending on the context of the encounter. When classified into two groups, those in which the doe moved to the buck (88 %: 169/192) and those in which the buck moved (12 %: 23/192), does remained for a significantly longer period prior to leaving in cases where they had initiated the encounter (Fig. 4a; doe initiated: $\bar{x} = 30.06 \pm 3.93$ minutes; buck initiated: $\bar{x} = 5.13 \pm 1.41$ minutes: Mann-Whitney U = 1031.500, n = 192, $P < 0.001$). The stay duration was related to the category of buck she was with (Kruskal-Wallis test: $\chi^2 = 7.326$, DF = 2, $P < 0.05$). Does remained with top ranked bucks for significantly longer than low ranked animals (top ranked: $\bar{x} = 31.50 \pm 4.42$ minutes; low ranked: $\bar{x} = 11.32 \pm 3.89$ minutes). For does whose encounter ended by mating, the mean stay interval prior to a mount sequence commencing was 58.03 ± 6.02 minutes (n = 156).

However, encounter initiation type (buck/doe) was not a good predictor of the decision of the female (stay and mate/leave: Logistic regression: $\chi^2 = 2.943$, DF = 1, P = 0.086, NS). When a measure of male status (dominance rank) was included in the analysis, encounter initiation type was not a significant predictor (Wald criterion, P = 0.123) whereas male quality was (Wald criterion, $P < 0.01$). However, the model was a poor fit (Nagelkerke $R^2 = 0.066$) and only correctly classified 11 % of does deciding to leave in contrast to 96 % of those deciding to mate (overall correct classification = 69 %).

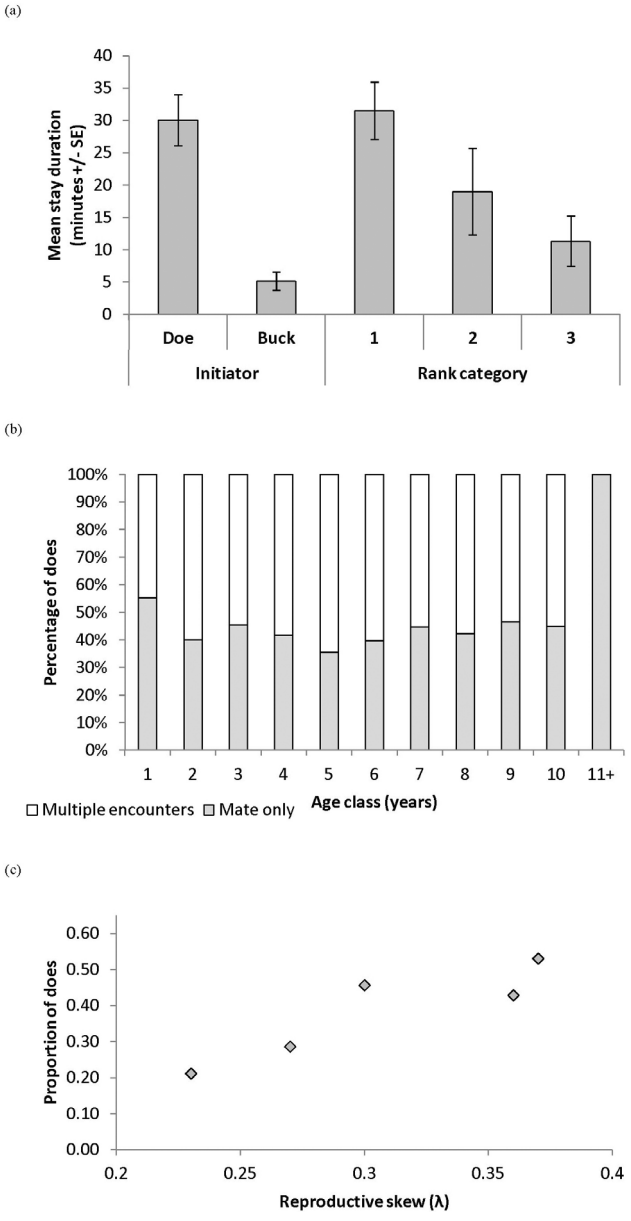


Fig. 4. (a) Duration of encounters (minutes) prior to spontaneous doe terminations. (b) Relationship between encounter behaviour (multiple encounters or mate only) and age, for 11 age categories (1-10 and 11+ years (N = 653). (c) Relationship between the proportion of single mating with multiple encounters and male reproductive skew (λ) calculated according to Kokko & Lindström 1997.

Encounter rates of bucks by does and reproductive status of bucks (prediction 5)

Encounter rates were calculated for 78 does with continuous records for three hours before they mated.

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Thirty does spent the entire period in the company of the buck with whom they mated. The remaining forty-eight does encountered on average 4.18 ± 0.33 bucks. Of these 32 had moved apparently spontaneously at least once and up to 11 times between bucks, that is without any obvious associated context that might have precipitated the moves and encountered 3.5 ± 0.28 (1.17 hr^{-1}) bucks before mating. There was no effect of year on encounter rate ($F_{2\text{-}20}$ = 1.541, P = 0.229, NS). The remainder, does moving for mixed reasons (n = 16) encountered 5.56 ± 0.72 (1.85 hr^{-1}) bucks over the same period. If the does that were only seen with their subsequent mate over the previous three hours are included, the encounter rates are 0.76 and 0.99 bucks hr^{-1}, respectively.

Spontaneously-moving does were significantly more likely to move to a successful buck (75/83; 90.4 %) than expected from their relative abundance in the population (119/334; 35.6 %) (Chi-square test; χ^2 = 80.05, DF = 1, P < 0.001). By contrast, in encounters precipitated by incursion of a buck, a doe encountered mating and non-mating bucks as often as expected from their relative abundance in the population (8/23, 34.8 % and 119/334, 35.6 %; Chi-square test; χ^2 = 0.007, DF =1; P = 0.935, NS).

Doe age-class and encounters (prediction 6)

When the numbers of cases of does exhibiting multiple encounters were compared to those not so doing (mate only), in eleven age categories (1-10 and 11+), there was no relationship between age-class and encounter behaviour (Fig. 4b; Chi-square test; χ^2 = 4.250, DF = 10, P = 0.935, NS). Yearling does, mating for the first time, were equally likely to be recorded in one encounter (16/29, 55 %) or in more than one (13/29, 45 %; χ^2 = 0.310, DF = 1, P = 0.577, NS).

Encounters with bucks in different breeding seasons (prediction 7)

The distribution of does between those always recorded in more than one encounter (41), never recorded in more than one encounter (17) and those that recorded in an encounter in one year and not so recorded in another (118) was not significantly different from that expected based on the proportion of does observed in one year only that were recorded in more than one encounter (0.56) (expected: 34, 18 and 124 respectively; Chi-square test; χ^2 = 0.831, DF = 2, P = 0.66, NS).

Yearly variations in encounter behaviour

There was a significant association between year and encounter behaviour (multiple encounters or mate only; Chi-square test; χ^2 = 33.162, DF = 24, P < 0.001). The proportion of females with multiple encounters varied from 0.39 to 0.65. There was no relationship between the proportion of females with multiple encounters and male mating skew (Pearson's correlation: r = 0.872, n = 5, P = 0.54, NS). However, when the behaviour was subdivided into multiply-mating females, single mating females with multiple encounters and single mating females seen with their mate only, there was a significant relationship between the proportion of single mating females with multiple encounters and mating skew (Fig. 4c; Pearson's correlation: r = 0.901, n = 5, P < 0.05). As mating success became more skewed with few males achieving the majority of matings, the proportion of females with multiple encounters increased.

Discussion

How female fallow deer encounter males

The behaviour of fallow does reported here is consistent with mate searching as part of the process of mate choice. The evidence may be summarised as follows. Does are relatively unconstrained in their movements; bucks are comparatively inefficient at herding females back into the groups with which they are consorting (prediction 1). In this they differ markedly from red deer stags (Clutton-Brock et al. 1982) although 43 % of hinds were recorded in different harems on successive days (Stopher et al. 2011). Both the total number of group switching events (transitions) and the number of does recorded in such transitions are most frequent when matings are most frequent (prediction 2). In this they resemble pronghorn, roe deer and red deer (Byers et al. 1994, Lovari et al. 2008, Stopher et al. 2011). Most encounters between bucks and estrous does are as a result of movement by the does (prediction 3). In total 87 % of instances of group switching are due to movements by the doe. Encounters between does and bucks were not random events that occurred as a result of group turnover or male-male competition. When does switched groups they were significantly more likely than expected to move to a buck that was known *a posteriori*, to have mated during the rut with does other than the focal individual (prediction 5). In this population reproductively successful bucks have been shown to have high social rank prior to the rut (Moore et al. 1995). By contrast in red deer harem switching was not associated with a move to more preferred males (Stopher et al. 2011).

Most of the departures were initiated by the doe (prediction 4; 244/280, 87 %). In 69 % of departures

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there was no associated context to which causality might be attributed. A similar proportion (0.70) of unprovoked moves has been reported for pronghorn females (Byers et al. 1994). By contrast female roe deer tend to make extraterritorial excursions when a male is courting another female suggesting that the temporary unavailability of a male might be the trigger for a move (Lovari et al. 2008) particularly since roe deer are monoestrous and the estrus rarely lasts longer than 36 hours (Hoffmann et al. 1978). There is little support for the possibility that fallow does change groups because the resident male is occupied courting another doe because in only 13 % of departures (32/280) the doe left while the male was involved in a mount sequence with another doe. Fallow deer may be less time-constrained than roe deer since they are seasonally polyestrous although an individual estrus is of similar duration to that of roe, about 24 hours (Asher et al. 1993). Nevertheless fallow does appear to be quite prepared to wait for a mating opportunity. Over one-third of the does with continuous records for three hours were recorded only in the presence of their mate before they mated. During this 3-hour period the resident male mated with 3.4 ± 0.62 (range 0 to 8) other does. The longest 'wait' recorded was of a doe who spent over eight hours with the same male during which time he mated with eleven other does before mating with her.

Movement of fallow does between territories on a lek has been attributed to avoidance of harassment by younger males mainly by seeking the sanctuary of proximity to a dominant territorial male (Clutton-Brock et al. 1992). While in this non-lekking population also, young males, particularly yearlings, attempt to gain access to perioestrous females, we find little or no association between departures of a doe from a group and the unwelcome attentions of young males. Fewer than 3 % of instances of harassment by yearling males result in a female leaving a group (Harty 2002). Furthermore males show little tendency to attempt to prevent does leaving and when they do, they are largely unsuccessful (Chapman & Chapman 1975; this study). Males of other ungulate species have similarly been reported as being poor at herding females during the breeding season (reindeer *Rangifer tarandus*: Hirotani 1989 and blackbuck *Antilope cervicapra*: Isvaran & Jhala 2000).

The question of costs and benefits associated with these movements by females cannot yet be addressed beyond to suggest that the costs must be low since the distances are well within the range of travel undertaken daily. The magnitude of the distance travelled by does when moving from one buck to another ranged up to 500 m in extent, but most were less than 100 m. In the year when the mating system was more territorial the distances moved between males were correspondingly shorter. Therefore the travel distances involved could not equate to costs of the same order as that of pronghorn females (Byers et al. 2005) or red hinds (Stopher et al. 2011). Furthermore there are no predation risks associated with searching given the lack of predators and the relative rarity of incidences of worrying by uncontrolled domestic dogs. The diurnal rutting area is not traversed by any of the park roadways so no cost accrues from the risk of collision with a motor vehicle. The benefits must be presumed to be indirect since, except in the infrequent mast years, the location of the buck confers no trophic benefit. Even if the costs are truly marginal then slight indirect benefits might be enough to maintain this behaviour. But since models predict that females should search when males are in short supply, then could it be that while males are not a limiting resource, high quality males are? This might explain the frequency of searching behaviour. The extremely high variance in seasonal and lifetime reproductive success of males supports this view. Correlates of male fitness have been reported for this population. Fitter males tend to be larger (McElligott et al. 2001), of higher social rank, fight more, begin vocalisations earlier in the season, vocalise at higher rates and for longer periods (McElligott et al. 1999), and it has been argued that mating males may be of higher quality because they can better assimilate the costs of rutting activities (McElligott & Hayden 2000).

Quality of males encountered by female fallow deer

If the movement patterns reported here represent mate searching by females, it might be expected that female movements should result overall in encounters with males of higher quality (Lieberg et al. 1998, Kokko & Wong 2007, Stopher et al. 2011). In this population we use copulatory success (*a posteriori)* as a proxy for male quality since there is a high correlation between copulatory score and paternity score (Say et al. 2003). Spontaneously moving females were nine times more likely to encounter a successful male than expected from their abundance in the population. Conversely a male who entered a group was no more likely to be successful than expected from their abundance. In other words, incursion is consistent with a mating tactic by males who might otherwise have difficulty in encountering females (Wong & Candolin 2005). Thus although a doe is

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more likely to meet an unsuccessful buck as a result of an incursion (65 % of cases), she will readily mate with an intruder if he is a reproductively-successful buck. Previous studies of this herd have shown a significant relationship between vocal activity and reproductive success (McElligott et al. 1999). It may be that females can distinguish between males based on their vocal signature similar to red deer (Reby et al. 2001) and use this as a cue when switching between bucks. The pattern of movements by females could be a mechanism to avoid inbreeding. If this were so, then given the high skew in mating success of males, there should be a tendency for females to avoid males born in the same year as themselves. This does not appear to be the case. For example, there is no evidence that six or seven year old females avoid mating with males from their own cohort which includes the most successful males (Farrell et al. 2011). Furthermore, does of known paternity were no less likely to mate with a half brother than with a less related buck from the same cohort (unpublished data).

There is no evidence of an ontogenetic effect or age-related searching (prediction 6 and 7). There is no particular tendency for does of a certain age preferentially to exhibit either class of behaviour. Does of all ages were equally likely to be recorded in multiple encounters as not. This is not necessarily unexpected since although does may live to be over 20 years, a buck rarely ruts successfully in more than three years and thus does are obliged to mate with several bucks over their lifetime. Of the 176 does seen to mate in two or more years, only 30 (17 %) mated with the same buck in two years and one female mated with the same buck in three years. For the five years analysed, about 50 % of females can be identified in multiple encounters. This is probably a minimum value. But there remains a sizeable proportion of does that do not show apparent searching behaviour over the three hours prior to mating and some for even longer. This suggests, if all does search, either that (i) they differ in the amount of information they have accumulated prior to the day on which they mate or (ii) searching is a conditional strategy although the factors on which it depends have yet to be established. We have previously suggested that the fact that bucks enter the doe range and begin rutting activity, particularly vocalisation, some four weeks before the first does come into oestrus provides does with the possibility to employ cumulative assessment or simultaneous comparison of potential mates (McElligott et al. 1999). Thus by the time they come into estrus a mate may already be selected and therefore on the day of mating they are recorded in the presence of that buck and no other. If this is true it may be argued that about 50 % of does have chosen a mate based almost entirely on information gathered prior to the day on which they mate. The remainder, who although they may also have some prior information, may be considered to be insufficient to make a final choice without some further input.

If particular does consistently follow one approach or the other then the argument for searching as a conditional strategy would be untenable. Examination of those females who appeared more than once in the 5-year dataset indicated that there was no relationship between the category to which a doe was assigned in year one and the category in which she appeared in a subsequent year. The mating system of fallow deer is highly variable across populations. Nevertheless in several different populations, movements of females between males have been reported, in some cases to avoid harassment by young males and in others apparently spontaneously (Langbein & Thirgood 1989, Clutton-Brock et al. 1989). In lek systems moving females may consort with on average 3.7 bucks per hour during oestrus (Clutton-Brock et al. 1988). Thus using a combination of doe sightings and movements, together with information on the context of these moves we have shown that doe behaviour is not random and is consistent with predictions of mate-searching. If so it may be a condition-dependent tactic as has been suggested for roe deer (Lovari et al. 2008). We cannot quantify the residual extent to which male-male competition influences female choice (Clutton-Brock & McAuliffe 2009, Stopher et al. 2011). Nevertheless, in this population the potential obscuring effect of spatial constraint by males does not apply and behaviour consistent with mate searching is clear.

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