



# Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*

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We carried out behavioural observations to investigate the function of long-term investment in vocal display by fallow bucks during the breeding season. The measures of long-term investment used were the date of initiation of vocal activity, the number of days vocal during the breeding season, and the proportion of time spent vocalizing. We analysed data from 3 years (1993–1995) to assess the relationship between the date of initiation of vocal activity, and the number of days vocal, and age, dominance rank and mating success. Observations from a sample of focal males in 1996 were used to determine the effect of the proportion of time vocal during the breeding season on dominance rank and mating success. The majority of socially immature males ( $\leq 3$  years old) did not vocalize; among socially mature males ( $\geq 4$  years old), dominance rank was more important than age in explaining variation in vocal activity. The onset of vocal activity by fallow bucks was not a direct consequence of the presence of mating opportunities since the first males became vocal more than 3 weeks before any matings occurred. Long-term investment in vocal activity did not alter the dominance relationships that had been established between males before they became vocal. When we considered all mature males from 3 years of observations, the majority of matings were achieved by those that had high rank, initiated vocal activity early during the breeding season and remained vocal on most days. For the 1-year sample of mature males, the factor most highly correlated with mating success was the proportion of time that males spent vocalizing during the rut. Thus we have shown a strong relationship between the time invested in vocal display by fallow bucks and their mating success.

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Vocal display by males is a common feature of the mating system of many species (Andersson 1994). However, it is not always clear how the information encoded in vocalizations is interpreted in intrasexual or intersexual communication. Vocalizations may be an important component of the agonistic interactions between males (Davies & Halliday 1978; Clutton-Brock & Albon 1979). Females might use vocalizations both to discriminate between potential mates and to assist in mate selection (McComb 1991; Jennions & Petrie 1997). Therefore, a male's investment in display may affect mating success either by influencing other males, or through effects, direct or indirect, on females (Wiley 1991). If vocalizations are an indicator of male quality, they should be expensive to produce, in terms of time, energy or risk, since cheating by low-quality males might otherwise be a

viable strategy (Johnstone & Grafen 1993; Payne & Pagel 1996). Although the energetic costs of vocalizations have not been directly measured in mammals, it is known that they are expensive among other animals such as birds, frogs and insects (Halliday 1987; Vehrencamp et al. 1989).

Although vocal displays may offer clues to the quality of an advertiser, a distinction may be made between current condition (e.g. phenotype) and overall quality (e.g. genotype). This is because the appearance and condition of males may change during the breeding season while their genetic characteristics and therefore overall quality do not (Halliday 1987). The current condition of a competitor is important for a male contemplating a challenge because access to mating opportunities in many species is related to fighting success (Gosling 1986; Gross 1996). By contrast, females may be selected to monitor current condition and/or other characteristics of males that indicate overall 'quality' (Kodric-Brown & Brown 1984). It should therefore be important for females to monitor males over a longer period of time for an accurate assessment of their overall quality (Sullivan 1990; Byers et al. 1994). Thus repetitive display behaviour

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may have evolved to inflate the cost such that high-quality individuals may be discriminated from those of lower merit (Payne & Pagel 1997). Recent models of display behaviour show that receivers could evaluate overall signaller quality based on the cumulative receiver assessment rule (Payne & Pagel 1996, 1997). This assessment rule is one of three models advanced to explain the evolution of repetitive display (Enquist & Leimar 1983; Payne & Pagel 1997). When animals evaluate potential adversaries or mates based on the cumulative receiver assessment rule, the most important criterion is the cumulative sum of all displays. An additional feature of this assessment rule is that the display should be costly, represent the stamina of the individual displaying, and thus be an honest advertisement of male quality (Clutton-Brock & Albon 1979; Payne & Pagel 1997).

Fallow bucks are highly vocal for a limited period each year during the breeding season (Chapman & Chapman 1975). Their vocalizations consist of stereotyped and repetitive groans. The phonic structure of groans is individually distinct and therefore may act as a vocal signature (Kelly 1998; Reby et al. 1998). Males begin groaning several weeks before the first mating opportunities are available (Moore et al. 1995a), and they are also capable of sustaining high and variable groaning rates over prolonged periods. For example, Birkett (1994) recorded one fallow buck vocalizing almost continually for 33.4 h, producing 60 323 groans during this time. Fallow deer exhibit a wide range of mating systems in different populations (Langbein & Thirgood 1989), but common to all is a relationship between dominance status and mating success (Clutton-Brock et al. 1988; Festa-Bianchet et al. 1990; Moore et al. 1995a). Dominance rank is evident soon after males regrow their antlers each year and is well established before the rut (McElligott et al. 1998). If rank is an indicator of quality (Ellis 1995), then a link between it and long-term investment in repetitive vocal display might be expected in fallow deer.

In this study, we describe the seasonal onset of vocal activity in fallow bucks in relation to age and dominance status. We examine the scheduling of vocalization and investigate whether the signal conveyed by long-term investment in vocal display (as opposed to short-term rates) is directed primarily at other males, or primarily at females. If the long-term investment in vocal activity is directed at other males, we predict that it would alter dominance status. We therefore compared the dominance ranks of males before and after they began to vocalize. We also examined the relationship between changes in the proportion of time vocal and changes in dominance rank during the breeding season. By contrast, if long-term investment in vocalization is directed at females, we hypothesize that it should explain variation in male mating success beyond that due to dominance rank.

## METHODS

### Study Site, Population and Observations

We observed a herd of European fallow deer in Phoenix Park (709 ha, 20% woodland, 80% pasture; 53°22'N,

**Table 1.** Population size of the fallow deer herd in Phoenix Park during the present study

Year	Fawns	Females (≥1 year old)	Males (≥1 year old)	Total
1993	105	265	190	560
1994	105	315	200	620
1995	136	353	200	689
1996	142	390	147	679

The numbers refer to those present during the breeding season.

6°21'W), Dublin, Ireland. Approximately 80% of the park's area is available to the deer. The majority of the deer were of known age and individually recognizable. Approximately two-thirds of each cohort were tagged as fawns. The entire herd was captured in 1991 and unmarked individuals were tagged and aged (Moore et al. 1995b). The population size and sex structure is given in Table 1. Males were divided into two age categories, socially immature ( $\leq 3$  years old) and socially mature ( $\geq 4$  years old). This classification is based on the distinct behavioural differences of males in these age classes (Komers et al. 1997; McElligott et al. 1998).

We divided the breeding season into two main periods according to the state of development of the males' antlers, and the availability of mating opportunities. The prerut began when all males had cleaned the velvet from their antlers (late August or early September), and ended on the day before the first mating. The rut was the period between the days on which the first and last matings occurred (mid-October to early November).

We conducted observations throughout the prerut and the rut (1993–1996). Initially two to four observers were in the field while the males were still in an aggregated bachelor herd on their summer range. From late September onwards, the males began to move on to the females' range and became more dispersed (Moore et al. 1995a). During this period, 6–11 observers were in the field each day. Observations usually began at dawn. From early October, we carried out observations every day from dawn to dusk (ca. 11 h), until the rut ended. Observers were in radio contact and deployed to maximize coverage of all animals. The deer were under observation for a total of 1710 h (1993–1996).

In addition to the observations outlined above, we investigated the proportion of time that mature males spent vocalizing during the 1996 breeding season. We selected 19 males as focal animals based on their age and dominance status. They ranged in age from 5 to 8 years old and included the top 10 ranked males and nine others distributed among the lower-ranking individuals. We observed these males from 2 October to 4 November. The rut in 1996 began on 16 October and finished on 4 November. We observed the focal males for one or two 1-h periods each day, noting at 2-min intervals the behaviour of the focal individual. We chose observation periods so that each male was observed at different times of the day throughout the study. On average, each male

was observed for  $29.6 \pm 2.4$  h ( $\bar{X} \pm SD$ ). The total number of focal 1-h observations was 562.

### Data Recorded

We carried out all-event recording of agonistic interactions and matings, and also noted each day whether males were vocal. We used the results of agonistic interactions to calculate an index of dominance for each mature male according to Clutton-Brock et al. (1979). The dominance rank of each male was estimated as follows:

$$I = (B + \Sigma b + 1) / (L + \Sigma l + 1)$$

where  $B$  is the number of males defeated by the focal male,  $\Sigma b$  is the total number of males (excluding the focal male) defeated by the losers,  $L$  is the number of males that defeated the focal male and  $\Sigma l$  is the total number of males that defeated them, excluding the focal male. A male was classified as a winner relative to another if he won the majority of their interactions. The dominance rank of each male is based not only on the number of his subordinates, but also on the relative dominance of these subordinates together with the relative dominance of animals superior to each male. Dominance rank here refers to the rank that was calculated using all decisive agonistic interactions, involving clear threats and retreats among mature males recorded during the prerut. The male with the highest index value ( $I$ ) in each year was assigned the rank of 1 and all other males were ranked accordingly. The number of males for which dominance rank could be calculated differed in each year: 50, 70, 77 and 66, 1993–1996, respectively. We also calculated rut dominance ranks for males in 1996. Immature males were not included in the calculation of the dominance hierarchies owing to their low frequency of interactions with mature males. A small number of mature males were also excluded from the calculation of dominance rank because they did not associate with the other males during the prerut, and therefore a valid rank could not be assigned to them (McElligott et al. 1998). The numbers of matings in each year were 179, 249, 241 and 327, 1993–1996, respectively.

For every male, the date of first vocalization in each rut was recorded (1993–1996). We then expressed each date as the number of days since the first male became vocal in that particular rut. Therefore, the date of first vocalization is a relative measure, where the date of the first vocal male is 1, and the initiation of vocal activity by all other males is measured in relation to this date. We refer to it in the Results as the 'latent period of initiation of vocal activity'. The number of days vocal is defined as the total number of days in each rut on which each male was observed groaning. Using this daily measure of vocal activity, a single bout of groaning was sufficient to denote a male as vocal on a particular day. The average number of days on which males of each cohort were vocal was calculated only for those that became vocal.

We used the focal observations in 1996 to examine the relationship between the percentage of time vocalizing and mating success. However, the causality in a

relationship between aspects of display such as the percentage of time vocalizing and mating success is often unclear (Wiley 1991), and could arise in our study in two ways. First, males that spend more time vocal could be more likely to attract and mate with more females. Alternatively, males that attract and mate with more females could spend more time vocalizing as a consequence. Thus prior to analysis, we removed data for any hour during which a focal male achieved a mating ( $N=3$  h).

### Statistical Analysis

We carried out statistical tests using SPSS (Version 6.1.2) and used parametric statistics when possible (Sokal & Rohlf 1981). We checked variables for collinearity prior to regression analysis. Partial correlation analysis was used when collinearity between some variables was unacceptably high (Bryman & Cramer 1994). Mating skew was calculated according to Kokko & Lindström (1997). Using this measure of skew,  $\lambda_{\min} > 0$ , indicates nonrandom mating. We considered results significant at the  $P < 0.05$  level (all two-tailed). Some variables were transformed to improve the normality of their distributions (Kolmogorov–Smirnov test). We log-transformed age, date of first vocalization, number of days vocal and mating success ( $x+1$ ). We arcsine square-root transformed the percentage of time vocal during the prerut and rut (Zar 1974).

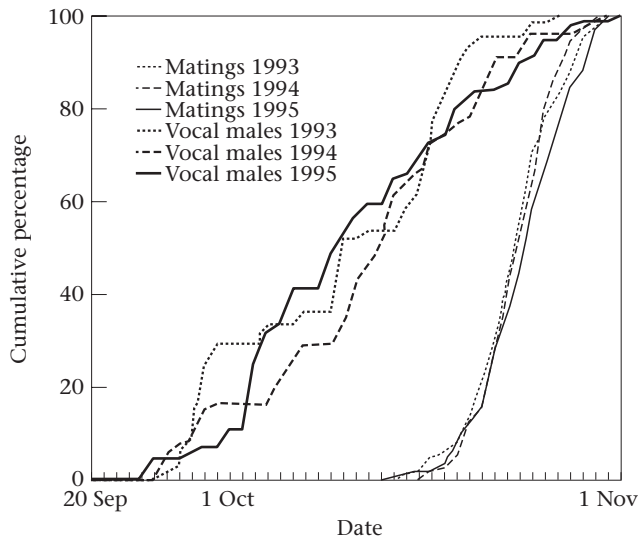
We included the data for all males in each year, to determine the relationships between age, dominance rank, the date of first vocalization, the number of days vocal and mating success across 3 years (1993–1995). Some males were present for more than 1 year, but preliminary analysis (A. G. McElligott, unpublished data) showed that the measures of vocal activity and the dominance ranks of males in this study did not persist from one year to the next. Therefore it was appropriate to pool the data (Leger & Didrichsons 1994). The sample sizes differ slightly in the analyses because not all variables were available for all males in each year. Means are given  $\pm$  SE, and medians with range.

In our study population the relationship between age and mating success is curvilinear; 6-year-old males are more successful than any others (Moore et al. 1995a; McElligott 1997). Furthermore, few males survive beyond 8 years (Hayden et al. 1992; McElligott et al. 1998). Thus to improve linearity prior to multiple regression or partial correlation analysis, we assigned to each male a new age variable. This consisted of the absolute difference in years between the age of each male and 6 years (the age of the most successful cohort).

## RESULTS

### Onset of Vocal Activity

The dates on which the first male became vocal were similar in 1993, 1994 and 1995 (23, 26 and 20 September, respectively; Fig. 1). When matings started, the mean



**Figure 1.** Cumulative percentage of vocal males and matings. A male was classified as vocal on the day when he was first heard to groan. The first male was vocal on 23, 26 and 20 September in 1993, 1994 and 1995, respectively. Matings occurred from 15 to 31 October in 1993, 18 October to 1 November in 1994, and 14 October to 1 November in 1995.

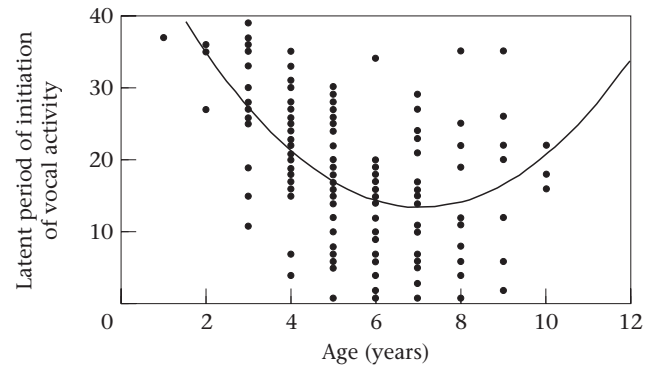
**Table 2.** Age, the proportion of males vocal in each age class and the mean number of days on which males were vocal

Age (years)	No. of tagged males in age class (1993–1995)	% Age class vocal	Number of days vocal ( $\bar{X} \pm SE$ )
$\geq 9$	14	92.9	11.2 $\pm$ 2.4
8	15	100	14.8 $\pm$ 3.0
7	26	100	17.5 $\pm$ 1.7
6	32	93.8	18.2 $\pm$ 1.9
5	54	96.3	13.9 $\pm$ 1.0
4	64	78.1	6.4 $\pm$ 0.7
3	62	41.9	2.4 $\pm$ 0.4
2	69	4.3	1.6 $\pm$ 0.3
1	77	1.3	—

proportion of all males that were vocal in each of 3 years was  $65.8 \pm 4.6\%$ ,  $N=220$ . Matings usually began during the third week of October (Fig. 1), and most occurred during the fourth week ( $70.5 \pm 3.4\%$ ,  $N=475$ , 1993–1995). The number of males vocalizing on each day during the rut was correlated with the number of matings on those days, in 2 of the 3 years examined (1993 and 1994; Pearson correlation:  $r=0.53$ ,  $N=17$  and  $r=0.56$ ,  $N=15$ ,  $P<0.05$ , respectively). The relationship for 1995 was not significant (Pearson correlation:  $r=0.16$ ,  $N=19$ , NS).

### Age and the Proportion of a Cohort Vocal

Males of different age classes were not equally likely to groan ( $G$  test:  $G_8=171.7$ ,  $P<0.001$ ; Table 2). The majority of immature males were not vocal, whereas the majority of mature males were vocal. Only one yearling male was recorded as vocal, and on only one occasion.



**Figure 2.** Relationship between age and date of first vocalization for all males (1993–1995). The latent period of initiation of vocal activity for each male is the number of days between his first vocalization and that of the earliest vocal male for that breeding season. The date of the first vocal male is day 1 and all others are measured in relation to this date. Equation of the regression:  $Y=51.6-69.0X+30.0X^2$ ,  $N=214$ ,  $F_{2,211}=13.5$ ,  $P<0.0001$ ,  $r=0.52$ ,  $R^2=0.27$ .

Vocalizations of immature males consisted of bouts of groans which were audibly different to those of mature males. Since immature males rarely vocalized, they were not included in most of the analysis below.

### Dominance Rank and Vocal Activity

The dominance rank of mature males was established before they became vocal. It was closely related to that which pertained when the majority had initiated vocal activity, but before any matings occurred. The relationship was similar in the 2 years examined (Pearson correlation:  $r=0.85$ ,  $N=65$  and  $r=0.90$ ,  $N=69$ ,  $P<0.001$ , 1994 and 1995, respectively). The number of decisive agonistic interactions recorded during the prerut in 1993 was not sufficient to allow this relationship to be examined.

In 1996, the dominance ranks of the focal males during the prerut and the rut were highly correlated (Pearson correlation:  $r=0.89$ ,  $N=19$ ,  $P<0.001$ ). The minor changes in dominance rank between these two periods were not related to the change in the proportion of time that males spent vocalizing from the prerut to the rut (Spearman rank correlation:  $r_s=0.16$ ,  $N=19$ , NS).

### Age, Dominance and Vocal Activity

When all males were considered, age affected both the date of initiation of vocal activity (Fig. 2), and the number of days on which they were vocal (regression:  $Y=-0.94+3.9X+1.8X^2$ ,  $N=212$ ,  $F_{2,209}=49.6$ ,  $P<0.0001$ ,  $R^2=0.32$ ; Table 2). The relative effects of age and dominance rank on vocal activity among males of all ages were not assessed because it was inappropriate to calculate ranks for males aged 1–3 years old (see Methods). Among mature males, when age and dominance rank were examined together, rank affected the date of initiation of vocal activity and the number of days on which they were vocal; age was not a significant additional factor (Tables 3 and 4). Mature males of higher rank became vocal earlier

**Table 3.** Stepwise multiple regression analysis of the initiation of vocal activity by mature males, with the date of first vocalization as the dependent variable and dominance rank and age as independent variables (1993–1995)

Variable	Coefficient	SE	<i>t</i>	<i>P</i>
Dominance rank	0.01	0.001	8.4	<0.0001
Age	0.04	—	0.6	NS
Constant	0.86	0.04	21.5	

$F_{1,177}=70.5$ ,  $P<0.0001$ , multiple  $r=0.53$ ,  $R^2=0.28$ ,  $N=179$ ,  $SE=0.27$ .

**Table 4.** Stepwise multiple regression analysis of the number of days on which mature males were vocal; dominance rank and age are independent variables

Variable	Coefficient	SE	<i>t</i>	<i>P</i>
Dominance rank	-0.01	0.001	-13.3	<0.0001
Age	-0.08	—	-1.5	NS
Constant	1.4	0.04	35.9	—

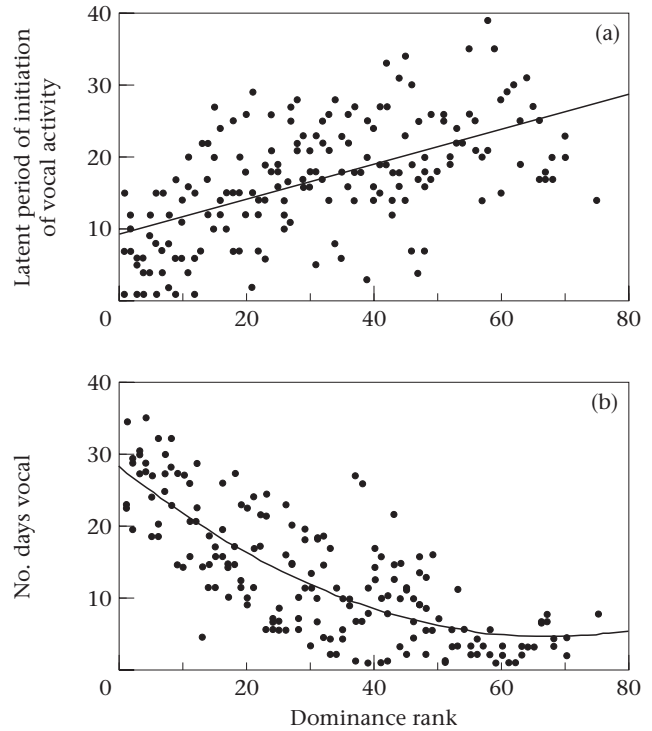
$F_{1,173}=175.9$ ,  $P<0.0001$ , multiple  $r=0.71$ ,  $R^2=0.50$ ,  $N=175$ ,  $SE=0.27$ .

and were vocal on more days during the breeding season, than those ranked lower than them (Fig. 3).

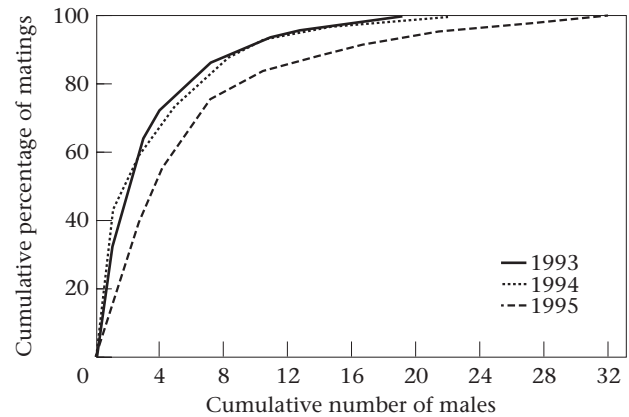
**Dominance, Mating Success and Vocal Activity**

The mating success across 3 years (1993–1995) was significantly skewed ( $\lambda_{med}=0.17$ , confidence intervals 0.16–0.18). The top eight males in terms of mating success gained 88.3, 86.7 and 78.4% of matings, from 1993 to 1995, respectively (Fig. 4). The median dates of first vocalization by mature males in each of the corresponding years were 10 October (range 1–33), 12 October (range 1–35) and 7 October (range 1–39). The majority of matings were achieved by the males that began to vocalize before the median groaning dates (96.6%,  $N=621$  matings). By the time matings commenced, the mean proportion of mature males that had commenced vocal activity was  $78.5 \pm 6.3\%$ ,  $N=186$ . Mating success was also related to the number of days on which males were vocal. During the 1993 breeding season, the males ( $N=23$ ) that were vocal on more than the median number of days (14.4, range 1–29) achieved 98.9% of the matings ( $N=176$ ). The relationship in the 2 subsequent years was similar when such males achieved 99.6 and 96.2% of matings (31 males and 243 matings in 1994; 32 males and 228 matings in 1995), respectively.

The relationship between age and dominance rank was curvilinear (regression:  $Y=160.3-39.3X+2.7X^2$ ,  $N=179$ ,  $F_{2,176}=37.2$ ,  $P<0.0001$ ,  $R^2=0.30$ ); 6- and 7-year-old males were dominant to all others. Mating success was significantly correlated with age, dominance rank, the date of first vocalization and the number of days vocal, when all variables were considered independently (Table 5). When dominance rank was controlled, age was no longer significant and therefore excluded from further analyses.



**Figure 3.** Relationship between rank and (a) the date of first vocalization and (b) the number of days vocal for mature males (1993–1995). The latent period of initiation of vocal activity for each male is the number of days between his first vocalization and that of the earliest vocal male for that breeding season. The date of the first vocal male is day 1 and all others are measured in relation to this date.



**Figure 4.** Distribution of matings among successful males during the 1993–1995 ruts. The number of males in each year that gained matings was 19, 22 and 32, respectively.

Dominance rank and both measures of long-term investment in vocal activity were correlated with mating success to a similar extent.

In 1996, males increased the proportion of time vocalizing from 2–15 October to the rut (16 October to 4 November) ( $\bar{X}=4.3 \pm 1.0\%$ , range 0–15.4% and  $11.9 \pm 2.2\%$ , range 0–33.7%, respectively; paired  $t$  test:  $t_{18}=3.8$ ,  $P<0.01$ ). The relationship between the

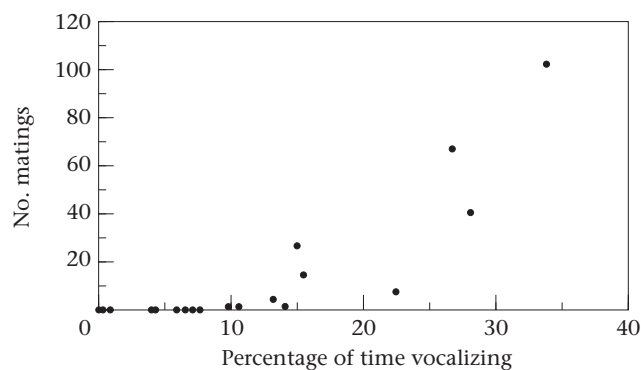
**Table 5.** Pearson correlation coefficients for mature males (1993–1995) with mating success as the dependent variable ( $N=173$ )

	Mating success						
	Simple $r$	Partial $r$ Rank	Partial $r$ Days vocal†	Partial $r$ Date†	Partial $r$ Rank/days vocal†	Partial $r$ Rank/date†	Partial $r$ Date/days vocal†
Age	-0.28***	-0.02	—	—	—	—	—
Dominance rank	-0.57***	—	-0.31***	-0.42***	—	—	-0.27***
Date of first vocalization	-0.49***	-0.26**	-0.24**	—	-0.19*	—	—
No. days vocal	0.55***	0.25**	—	0.37***	—	0.17*	—

Rank: Controlled for dominance rank; days vocal: controlled for no. of days vocal; date: controlled for date of first vocalization; rank/days vocal: controlled for dominance rank and no. of days vocal; rank/date: controlled for dominance rank and date of first vocalization; date/days vocal: controlled for date of first vocalization and no. of days vocal.

†Age excluded.

\* $P<0.05$ ; \*\* $P<0.01$ ; \*\*\* $P<0.001$ .

**Figure 5.** Relationship between the percentage of time vocalizing during the rut and mating success of focal males (1996).**Table 6.** Pearson correlation coefficients for mature males (1996), with mating success as the dependent variable ( $N=19$ )

	Mating success		
	Simple $r$	Partial $r$ Time vocal‡	Partial $r$ Days vocal‡
Age	-0.50*	-0.12	-0.40
Dominance rank	-0.54*	-0.16	-0.35
Date of first vocalization	-0.21	—	—
No. days vocal	0.45†	0.58*	—
% Time vocal prerut	0.28	—	—
% Time vocal rut	0.87**	—	0.90**

Time vocal: Controlled for % time vocal in rut; days vocal: controlled for no. of days vocal.

‡Date of first vocalization and % time vocal prerut excluded.

† $P=0.06$ ; \* $P<0.05$ ; \*\* $P<0.001$ .

proportion of time that individual males spent vocal during early October and during the rut was marginally significant (Pearson correlation:  $r=0.44$ ,  $N=19$ ,  $P=0.06$ ). When all variables were considered independently, the proportion of time vocal during the rut was the factor that was most highly correlated with mating success (Fig. 5, Table 6). In addition, the number of days vocal, age and the dominance rank of the males were correlated with mating success (Table 6). When the proportion of time vocal during the rut was controlled, mating success

remained significantly correlated with the number of days vocal, but the relationship between mating success and both age and dominance rank was no longer significant (Table 6). Similarly, when the number of days vocal was controlled, mating success was correlated with the proportion of time vocal during the rut, but not with age or dominance rank.

## DISCUSSION

We found that the first fallow bucks became vocal more than 3 weeks before any oestrous females were present (range 22–24 days, 1993–1995). Our results therefore show that the onset of vocal activity by males was not a direct consequence of the presence of mating opportunities. The majority of socially mature males ( $\geq 4$  years old) vocalized and the majority of socially immature males ( $\leq 3$  years old) did not. Among mature males, long-term investment in vocal activity was more related to dominance rank than age. The dominance relationships between mature males were clearly evident before any began vocalizing and rank order remained largely unchanged between the onset of vocalization and the first matings. In addition, there was no relationship between the minor changes in rank order that occurred from the prerut to the rut and the simultaneous changes in the percentage of time vocal. Over 3 years of observations, the majority of matings were achieved by mature males of high rank that began vocalizing early during the breeding season and remained vocal on most days. When a subset of mature males was used as focal animals in 1 year, the variables most related to mating success were the proportion of time that males spent vocalizing during the rut and the number of days vocal during the breeding season. Thus we have shown a strong relationship between the time invested in vocal display and mating success of fallow bucks.

Display is generally considered to be expensive (Halliday 1987). The relationship between vocal activity and age in our study is consistent with this view. Immature fallow bucks invest in growth rather than display, until they are old enough to compete more effectively with other males (Birgersson & Ekvall 1997; Pélabon 1997). The majority of immature males were not

vocal in the presence of mature males. The increased vocal activity at 4 years old represents a switch between conditional strategies in response to an increase in competitive ability; an example of status-dependent selection (Gross 1996). This alteration in behaviour probably results from age-related increases in body size and plasma testosterone concentrations (Rolf & Fischer 1990; Moore 1993). In support of our findings, Komers et al. (1997) found that immature fallow bucks (2–3 years old), which were vocal in the absence of mature males, decreased their rate of groaning in response to playbacks of groans from mature males. In the same study, mature males increased their rates of groaning in response to playbacks.

The dominance ranks of fallow bucks are established largely by noncontact agonistic interactions prior to the rut, and rank is one of the most important attributes of males related to mating success during the rut (Moore et al. 1995a; McElligott et al. 1998; this study). Long-term investment in vocal activity, although strongly related to dominance rank, is unlikely to have had a major role in intrasexual communication. This is because the ranks evident while males were silent (early and mid-September) were almost identical to the ones determined when a large proportion of males had begun to vocalize, and rank changes from the prerut to the rut were also unrelated to simultaneous changes in the proportion of time that males spent vocalizing. Furthermore, for males the current condition of an opponent is one of the most important factors influencing the decision to fight, and therefore males should rely on indicators of current condition rather than phenotypical correlates of overall quality or fitness (Enquist & Leimar 1983; McElligott et al. 1998). Reliance on long-term investment in vocal activity as an indicator of current condition might be misleading since males lose weight during the rut (Clutton-Brock et al. 1988; Apollonio et al. 1989). If long-term investment in vocal display formed part of the intrasexual assessment by males, then fights between mismatched opponents should be less likely late in the rut when the accumulated differences in vocal investment between males would still be increasing. In fact the reverse is the case. Fights are more likely to occur between formerly mismatched opponents late in the rut (McElligott et al. 1998). However, we are not suggesting that all aspects of the vocal activity of fallow bucks are unrelated to intrasexual competition. While males do not engage in vocal contests in a similar manner to red deer, *Cervus elaphus*, stags (Clutton-Brock & Albon 1979), they may still use short-term groaning rates to assess current competitive asymmetries with rivals, as suggested by the playback experiments of Komers et al. (1997). In addition, Clutton-Brock et al. (1988) found that mating success of males was related to short-term groaning rates.

The dominance status of fallow bucks, an indicator of overall quality and competitive ability (Ellis 1995), was evident before males became vocal. Thus long-term investment in vocal activity later during the breeding season also represents the overall quality of mature males, since it was closely related to mating success and dominance rank, and unrelated to age. The high quality of the

males is further demonstrated because they can afford to invest in display. There are clearly at least two direct or intrinsic costs as a result of this display: the time allocated to vocalizations and the energy used to produce sound. We found that mature fallow bucks spend up to 34% of their time vocalizing during the rut. The metabolic cost to a male of producing a groan, arising from muscular activity of the thoracic and cervical muscles, has not been measured, but given the time costs, it may account for a substantial proportion of the weight loss ( $22 \pm 0.6\%$  of body weight; T. J. Hayden, unpublished data) during the rut.

For the focal males in the 1996 breeding season, mating success was related to the proportion of time vocal during the rut, the number of days vocal during the breeding season and dominance rank (Table 6). However, when either the proportion of time vocal during the rut or the number of days vocal was controlled, dominance rank was no longer related to mating success. The males used in this part of the study included the 10 most highly ranked individuals out of 66 ranked males in that year. Therefore, our results show the importance to fallow bucks of maintaining their vocal display after attaining high rank.

The evolution of animal signals is influenced by the learning and memory of those signals by receivers (Guilford & Dawkins 1991; Endler & Basolo 1998). The groans of fallow bucks are sufficiently distinct to act as a vocal signature (Kelly 1998; Reby et al. 1998). Therefore, we suggest that females encountering vocal males in the weeks leading up to the rut could learn to recognize individual males, and then discriminate between them based on their long-term investment in vocal display during the breeding season. The behaviour of females during the weeks leading up to and during the rut is consistent with a scenario in which females could assess males based on their long-term vocal effort. During these periods females both visit territorial males and are also relatively free to move between males (Alvarez et al. 1990; Festa-Bianchet et al. 1990; McElligott 1997).

Evidence for female mate preferences based on phenotypic characteristics of fallow bucks remains controversial (Carbone & Taborsky 1996; Clutton-Brock et al. 1996). Most studies of mating success, have dealt with territorial males on leks (Clutton-Brock et al. 1988, 1989; Apollonio et al. 1989, 1990, 1992; Festa-Bianchet et al. 1990). In studies of ungulates that did not involve lekking males, for example red deer (McComb 1991; Carranza 1995) and pronghorn, *Antilocapra americana* (Byers et al. 1994; Min 1997), female choice of mates was influenced by a number of distinctly different cues such as behaviour, morphology or location. By contrast, in lek mating systems it is often difficult to separate the factors that result in differential mating success of males (Höglund & Alatalo 1995).

Attributes of dominance are related to the mating success of fallow bucks in both lekking and non-lekking populations (Clutton-Brock et al. 1988; Festa-Bianchet et al. 1990; McElligott et al. 1998). However, the mechanism by which dominance rank translates to mating success is not clear. For example in one lekking population,

a key factor related to the mating success of males is their ability to protect oestrous females from the attentions of nonterritorial males (Clutton-Brock et al. 1988, 1993). On the other hand, in a second lekking population, the main factor influencing male mating success is the territory they occupy (Apollonio et al. 1989), and protection from harassment is not important (Apollonio et al. 1998). In Phoenix Park, males do not lek, and even among the few males that hold territories, the majority of their matings take place elsewhere (Moore et al. 1995a; Kelly 1998).

Does the long-term investment in vocal display by fallow bucks play a role in mate choice? Since the variation in long-term vocal investment explains a significant proportion of the variance in mating success, it may be argued that it restricts the female's set of potential mates. This is the minimum requirement for the existence of mate choice (Halliday 1983). For females to show preferences for particular males, that is, direct mate choice sensu Wiley & Poston (1996), they must be capable of discriminating between males based, in our study, on their long-term vocal display evaluated through the cumulative receiver assessment rule. The vocalizations of fallow bucks are probably sufficiently distinct to represent a vocal signature (Kelly 1998; Reby et al. 1998), although playback experiments to demonstrate that females will recognize a particular male remain to be carried out. Furthermore, Vinnedge & Verrell (1998) suggested that a result such as ours, showing a relationship between long-term investment in vocalization and mating success, provides evidence that male displays may have evolved through female choice. Even though in our field-based study we could not control for a possible confounding influence of intrasexual communication on mating success, our results suggest that long-term investment in vocalization is probably not involved in competition among males. Instead, our findings point to a relationship between differential mating success among males and long-term investment in vocalization which may act by influencing females.

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### References

- Alvarez, F., Braza, F. & San José, C. 1990. Coexistence of territoriality and harem defense in a rutting fallow deer population. *Journal of Mammalogy*, **71**, 692–695.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Apollonio, M., Festa-Bianchet, M. & Mari, F. 1989. Correlates of copulatory success in a fallow deer lek. *Behavioral Ecology and Sociobiology*, **25**, 89–97.
- Apollonio, M., Festa-Bianchet, M., Mari, F. & Riva, M. 1990. Site-specific asymmetries in male copulatory success in a fallow deer lek. *Animal Behaviour*, **39**, 205–212.
- Apollonio, M., Festa-Bianchet, M., Mari, F., Mattioli, S. & Sarno, B. 1992. To lek or not to lek: mating strategies of male fallow deer. *Behavioral Ecology*, **3**, 25–31.
- Apollonio, M., Festa-Bianchet, M., Mari, F., Bruno, E. & Locati, M. 1998. Habitat manipulation modifies lek use of fallow deer. *Ethology*, **104**, 603–612.
- Birgersson, B. & Ekvall, K. 1997. Early growth in male and female fallow deer fawns. *Behavioral Ecology*, **8**, 493–499.
- Birkett, A. 1994. Reproductive behaviour and mating strategies of fallow deer in an enclosed deer park. Ph.D. thesis, Manchester Metropolitan University.
- Bryman, A. & Cramer, D. 1994. *Quantitative Data Analysis for Social Scientists*. London: Routledge.
- Byers, J. A., Moodie, J. D. & Hall, N. 1994. Pronghorn females choose vigorous mates. *Animal Behaviour*, **47**, 33–43.
- Carbone, C. & Taborsky, M. 1996. Mate choice or harassment avoidance? A question of female control at the lek. *Behavioral Ecology*, **7**, 370–373.
- Carranza, J. 1995. Female attraction by males versus sites in territorial red deer. *Animal Behaviour*, **50**, 445–453.
- Chapman, D. I. & Chapman, N. G. 1975. *Fallow Deer: their History, Distribution and Biology*. Lavenham, Suffolk: Terence Dalton Ltd.
- Clutton-Brock, T. H. & Albon, S. D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour*, **69**, 145–170.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour*, **27**, 211–225.
- Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M. & Albon, S. D. 1988. Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology*, **23**, 281–296.
- Clutton-Brock, T. H., Hiraiwa-Hasegawa, M. & Robertson, A. 1989. Mate choice on fallow deer leks. *Nature*, **340**, 463–465.
- Clutton-Brock, T. H., Deutsch, J. C. & Nefdt, R. J. C. 1993. The evolution of ungulate leks. *Animal Behaviour*, **46**, 1121–1138.
- Clutton-Brock, T. H., McComb, K. E. & Deutsch, J. C. 1996. Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder to Carbone and Taborsky. *Behavioral Ecology*, **7**, 373–378.
- Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.
- Ellis, L. 1995. Dominance and reproductive success among non-human animals: a cross-species comparison. *Ethology and Sociobiology*, **16**, 257–333.
- Endler, J. A. & Basolo, A. L. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*, **13**, 415–420.
- Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Festa-Bianchet, M., Apollonio, M., Mari, F. & Rasola, G. 1990. Aggression among lekking male fallow deer (*Dama dama*): territory effects and relationship with copulatory success. *Ethology*, **85**, 236–246.



- Gosling, L. M. 1986. The evolution of mating strategies in male antelopes. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 244–281. Princeton, New Jersey: Princeton University Press.
- Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution*, **11**, 92–98.
- Guilford, T. & Dawkins, M. S. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour*, **42**, 1–14.
- Halliday, T. R. 1983. The study of mate choice. In: *Mate Choice* (Ed. by P. P. G. Bateson), pp. 3–32. Cambridge: Cambridge University Press.
- Halliday, T. R. 1987. Physiological constraints on sexual selection. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 247–264. Chichester: J. Wiley.
- Hayden, T. J., Moore, N. P. & Kelly, P. F. 1992. The fallow deer of Phoenix Park: an evolving management plan. In: *Management, Welfare and Conservation of Park Deer, Proceedings of the Second Deer Park Symposium* (Ed. by D. J. Bullock & C. R. Goldspink), pp. 27–45. Potters Bar: UFAW.
- Höglund, J. & Alatalo, R. V. 1995. *Leks*. Princeton, New Jersey: Princeton University Press.
- Jennions, M. D. & Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews*, **72**, 283–327.
- Johnstone, R. A. & Grafen, A. 1993. Dishonesty and the handicap principle. *Animal Behaviour*, **46**, 759–764.
- Kelly, P. F. 1998. Mating success of male fallow deer (*Dama dama* L.): mating strategy, antler geometry and vocal characteristics. Ph.D. thesis, University College Dublin, National University of Ireland.
- Kodric-Brown, A. & Brown, J. H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist*, **124**, 309–323.
- Kokko, H. & Lindström, J. 1997. Measuring the mating skew. *American Naturalist*, **149**, 794–799.
- Komers, P. E., Pélabon, C. & Stenström, D. 1997. Age at first reproduction in male fallow deer: age-specific versus dominance-specific behaviors. *Behavioral Ecology*, **8**, 456–462.
- Langbein, J. & Thirgood, S. J. 1989. Variation in mating system of fallow deer (*Dama dama*) in relation to ecology. *Ethology*, **83**, 195–214.
- Leger, D. W. & Didrichsons, I. A. 1994. An assessment of data pooling and some alternatives. *Animal Behaviour*, **48**, 823–832.
- McComb, K. E. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour*, **41**, 79–88.
- McElligott, A. G. 1997. Fighting, vocal activity, annual mating success and lifetime mating success of fallow bucks (*Dama dama* L.): short-term investment and long-term cost. Ph.D. thesis, University College Dublin, National University of Ireland.
- McElligott, A. G., Mattiangeli, V., Mattiello, S., Verga, M., Reynolds, C. A. & Hayden, T. J. 1998. Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. *Ethology*, **104**, 789–803.
- Min, S. E. 1997. The effect of variation in male sexually dimorphic traits on female behaviour in pronghorn (*Antilocapra americana*). *Ethology*, **103**, 732–743.
- Moore, N. P. 1993. Mating success in fallow (*Dama dama*, Linnaeus 1758) bucks in Phoenix Park, Ireland. Ph.D. thesis, University College Dublin, National University of Ireland.
- Moore, N. P., Kelly, P. F., Cahill, J. P. & Hayden, T. J. 1995a. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behavioral Ecology and Sociobiology*, **36**, 91–100.
- Moore, N. P., Cahill, J. P., Kelly, P. F. & Hayden, T. J. 1995b. An assessment of five methods of age determination in an enclosed population of fallow deer (*Dama dama*). *Biology and Environment*, **95B**, 27–34.
- Payne, R. J. H. & Pagel, M. 1996. Escalation and time costs in displays of endurance. *Journal of Theoretical Biology*, **183**, 185–193.
- Payne, R. J. H. & Pagel, M. 1997. Why do animals repeat displays? *Animal Behaviour*, **54**, 109–119.
- Pélabon, C. 1997. Is weight at birth a good predictor of weight in winter for fallow deer? *Journal of Mammalogy*, **78**, 48–54.
- Reby, D., Joachim, J., Lauga, J., Lek, S. & Aulagnier, S. 1998. Individuality in the groans of fallow deer (*Dama dama*) bucks. *Journal of Zoology*, **245**, 79–84.
- Rolf, H. J. & Fischer, K. 1990. Serum testosterone (T) and 5- $\alpha$ -Dihydrotestosterone (DHT) in male fallow deer (*Dama dama* L.): seasonality and age dependence. *Comparative Biochemistry and Physiology*, **95A**, 445–452.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. San Francisco: W. H. Freeman.
- Sullivan, M. S. 1990. Assessing female choice for mates when the males' characters vary during the sampling period. *Animal Behaviour*, **40**, 780–782.
- Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989. The energetic cost of display in male sage grouse. *Animal Behaviour*, **38**, 885–896.
- Vinnedge, B. & Verrell, P. 1998. Variance in male mating success and female choice for persuasive courtship displays. *Animal Behaviour*, **56**, 443–448.
- Wiley, R. H. 1991. Lekking in birds and mammals: behavioral and evolutionary issues. *Advances in the Study of Behaviour*, **20**, 201–291.
- Wiley, R. H. & Poston, J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution*, **50**, 1371–1381.
- Zar, J. H. 1974. *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice-Hall.