



Context-related vocalization rates of fallow bucks, *Dama dama*

ALAN G. McELLIGOTT & THOMAS J. HAYDEN

Mammal Research Group, Department of Zoology, University College Dublin

(Received 19 January 1999; initial acceptance 15 March 1999;
final acceptance 7 July 1999; MS. number: 6121R)

We studied the short-term vocalization rates of fallow bucks to determine the primary recipients of the signal conveyed by these rates. We used the contexts in which groans occurred to investigate whether the signal represented an intrasexual threat or an intersexual advertisement. We found that fallow buck groaning rates were highly variable and that this variation was associated with the contexts of groaning. Groaning rates were higher during the rut than during the prerut, and also higher when males were with females than when they were with other males. Males with females groaned at higher rates when other vocal males were nearby. We identified a postcopulation call that consisted of the highest groaning rates that males produced. The presence of a harem did not contribute to the variation in groaning rates, except to a minor extent in postcopulation rates. Our findings suggest that the signal transmitted by short-term vocalization rates is primarily a threat aimed at other males.

© 1999 The Association for the Study of Animal Behaviour

Sexual selection has resulted in the evolution of vocal displays in males of many polygynous mammals, which are important in both intrasexual competition and mate attraction (Andersson 1994). The information encoded in vocalizations may be transmitted through a number of vocal characteristics, for example, phonic structure (Conner 1985), duration (Tyack 1981), loudness (Sekulic 1982) or vocalization rate (McComb 1991). These categories are not necessarily exclusive and individuals may receive information from a combination of these characteristics (Shipley et al. 1981). Nevertheless, many male vocal displays during the breeding season consist of repetitions of the same basic phrase or call (Gibson et al. 1991; McComb 1991; Gerhardt 1994).

The evolution of repetitive display behaviour could have occurred in response to a number of selection pressures. Enquist & Leimar (1983) proposed that repetitive displays evolved in response to inaccuracies in the transmission of information and therefore, by repeating displays, signallers transmit information more accurately to receivers. Payne & Pagel (1996a, 1997) considered that repetitive displays evolved to represent the quality and stamina of the signaller because only high-quality individuals could afford to invest in such displays, particularly if they are expensive. The information that is transmitted through the repetition of a stereotyped display may also be related to the rate at which the display is

performed (Guilford & Dawkins 1991; Endler 1992). For example, Pacific treefrogs, *Hyla regilla*, produce advertisement calls that are attractive to females and emit encounter calls directed at males. These calls differ primarily in the pulse repetition rates within calls (Brenowitz & Rose 1999). In addition, while repetitive calls are often highly redundant, they may be necessary particularly in noisy environments, such as during the fallow deer breeding season, when many males may be vocalizing in close proximity to one another (Jouventin et al. 1999; McElligott et al. 1999).

The vocalizations of fallow bucks consist of stereotyped and repeated groans (Chapman & Chapman 1975). The phonic structure of groans is individually distinct and therefore may act as a vocal signature (Kelly 1998; Reby et al. 1998). Vocal display is important for males because measures of long-term investment in groaning during the breeding season, for example the number of days on which the male is vocal and the proportion of time spent vocalizing, are related to mating success (McElligott et al. 1999).

To date, no studies have specifically addressed the role of short-term vocalization rates in the breeding behaviour of fallow bucks. Several studies have proposed either an intersexual or intrasexual role for groaning without specifying what aspect of the display conveys the signal. For example, groaning may be used as a threat display between males for territory or resource defence (Clutton-Brock et al. 1988; Apollonio et al. 1989, 1990; Komers et al. 1997). Clutton-Brock et al. (1988) also found that average short-term groaning rates were related to mating success. However, the causality in this relationship is

Correspondence and present address: A. McElligott, Institute of Zoology, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland (email: amcellig@zool.unizh.ch). T. J. Hayden is at the Mammal Research Group, Department of Zoology, University College Dublin, Belfield, Dublin 4, Ireland.

unclear, because the groaning rates of fallow bucks could affect mating success either directly by influencing females, or indirectly by influencing other males.

Fallow does may use the information gained from long-term investment in vocal display by males to discriminate between them (McElligott et al. 1999). A possible mechanism for this process is a cumulative receiver assessment rule, as an important factor influencing a female's assessment when using this method of appraisal is the sum of all a male's displays (Payne & Pagel 1996a, 1997). Fallow bucks could also use a cumulative receiver assessment rule when deciding to fight. However, they should do so only over short periods because the current condition or fighting ability of males is more important than their former status (Grafen 1987; McElligott et al. 1998). Thus, when assessing competitors, males need information on the current condition or motivation of competing males. This information could be transmitted by short-term groaning rates, if they represent a male's current ability or motivation to fight.

Studies of mammals with more complex vocal repertoires have used social contexts to interpret the information transmitted by vocalizations (Poole et al. 1988; Weilgart & Whitehead 1990; Janik & Slater 1998). Therefore, for fallow bucks, the relationship between vocalization rates and social contexts might reveal the primary receivers of the signal that is transmitted by short-term groaning rates. In this paper, we describe the contexts associated with the short-term variation in groaning rates of fallow bucks, and test the hypotheses that the signal conveyed by groaning rates is primarily a threat aimed at rival males, or primarily an advertisement for attracting females. Although it is often difficult to separate an intrasexual from an intersexual role for display, the contexts that we use should allow us to identify the primary function of the signal transmitted by short-term vocalization rates.

METHODS

Study Site, Population and Observations

We observed a herd of European fallow deer in Phoenix Park (53°22'N, 6°21'W), Dublin, Ireland, during the breeding seasons in 1994 and 1995 (McElligott et al. 1999). In 1994 the herd consisted of 105 fawns, 315 females (1 or more years old) and 200 males (1 or more years old). In 1995, there were 136 fawns, 353 females (1 or more years old) and 200 males (1 or more years old). All males used in this study were of known age, had ear tags and were therefore individually recognizable.

We divided the breeding season into two periods; the prerut and rut. The prerut began when all males had cleaned the velvet from their antlers (31 August in 1994, 26 August in 1995), 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 (18 October to 1 November in 1994, 14 October to 1 November in 1995). The first males started vocalizing on 26 and 20 September in 1994 and 1995, respectively (McElligott et al. 1999). The data for the prerut were taken from 17 days in 1994

and 10 days in 1995. The data from the rut were taken from every day during this phase of the breeding season in both years. We began observations at dawn, and from early October observations were carried out from dawn to dusk every day (ca. 11 h) until the rut ended.

The data used in the analysis were obtained from videotape of socially mature males (4 or more years old), which we filmed using a Panasonic NV-MS 4B SVHS video-camera with a $\times 12$ zoom lens, and digital zoom capability of $\times 200$. Data from mature males were used because immature males (up to 3 years old) generally do not groan (McElligott et al. 1999). We used videotape because it allowed us to count groaning rates accurately. The videocamera operator was accompanied by an observer equipped with a telescope (Kowa, $\times 27$ lens magnification). This observer dictated details regarding male identity and presence/absence of females and/or other males on to the videotape soundtrack as filming was carried out.

The data in this paper were collected as part of a long-term study of the mating system of fallow deer in Phoenix Park (Moore et al. 1995; Kelly 1998; McElligott et al. 1998, 1999). During the breeding season, we routinely recorded the locations of mature males hourly each day. Observers were therefore deployed such that any mature male, vocal or silent, if not already under observation, could be located quickly (within ca. 5–10 min). This deployment of observers allowed us to achieve our sampling objective of filming as many mature males in as many situations as possible involving females and/or other males, and also allowed us to avoid any bias towards particular males.

Fallow deer populations show a variety of mating systems but variance in mating success is generally very high (Moore et al. 1995; Clutton-Brock et al. 1988; Apollonio et al. 1989). In Phoenix Park, the males that gain most matings use a low-fidelity territorial/follower strategy, in which access to females is based largely on dominance relationships (Moore et al. 1995). Accordingly, males are not equally likely to be found in certain situations such as consorting with oestrous females or after copulating. Under these circumstances our sampling aims were again to film as many males as possible, giving preference, whenever feasible, to those males that were underrepresented in the data set (Leger & Didrichsons 1994).

Groaning Rates and Contexts

We defined the groaning rate (groans/min) as the number of groans during a continuous 1-min period of vocal activity when a focal male was not engaged in any activity that was incompatible with groaning, for example fighting with antlers in contact. The term 'focal male' refers to the male for which we counted the groaning rate. We extracted 1222 groaning rates that could be unambiguously assigned to the contexts used in the analysis.

All groaning rates were assigned to discrete seasonal and social contexts. The seasonal contexts were the prerut and the rut. These were used to denote whether the

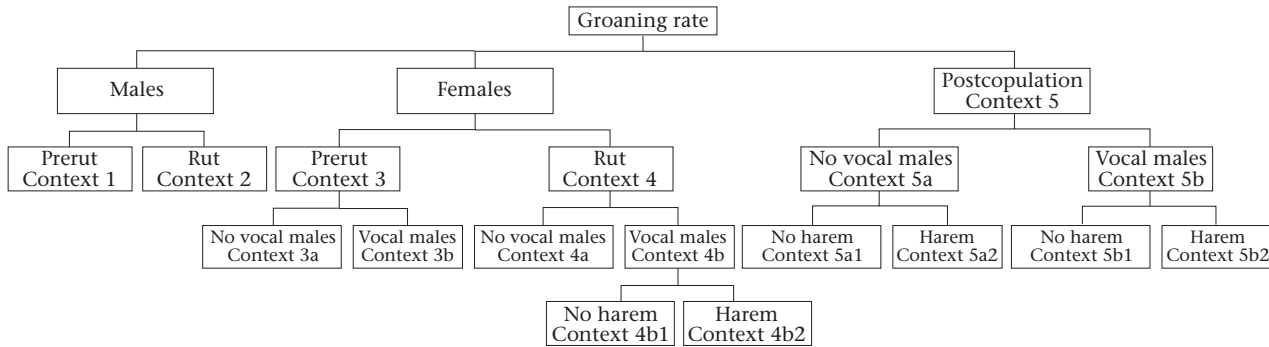


Figure 1. Classification of the main contexts to which groaning rates were assigned. The contexts depended on the stage of the breeding season (prerut, rut), the sex of the focal male's nearest neighbour (males, females), whether the male had just copulated and whether other vocal males or a harem were present.

groaning occurred before or during the period when there were mating opportunities in the population. The groaning rates assigned to the prerut were all recorded after the third week in September, which is the period when the first males became vocal (McElligott et al. 1999). We used three principal social contexts: male, female and postcopulation. Groaning rates were assigned to either male or female social contexts depending on which sex was closer to the vocalizing focal male when the groaning rate was counted. The exact criteria are given in detail below. We noted that groaning rates immediately after copulation were distinctly higher than any other rates of display prior to analysis, and these were therefore assigned to a discrete social context. We subdivided contexts to examine in more detail the factors affecting groaning rates. The criteria used for the classification of contexts are summarized in Fig. 1.

Fallow deer harems were described by Clutton-Brock et al. (1988), in their study of a lekking population, as the females in a male's territory. Since only a minority of males in Phoenix Park are intermittently territorial and the majority of matings do not take place on territories (Moore et al. 1995; McElligott 1997), this definition was not appropriate for our study. Therefore, we defined a harem as a group of perioestrous females (usually more than two) adjacent to the focal male that were defended by the focal male against other males. The degree of herding of the females by the male in the harem is generally low and females are usually free to move away from the male (Chapman & Chapman 1975). Perioestrous females could be identified when the focal male began to mount one of them, and/or as a result of their characteristic female–female mounting activity (Fraser 1968).

Statistical Analysis

We assigned groaning rates to contexts and planned the comparisons between contexts before carrying out any analyses (see Fig. 1). Therefore the appropriate statistical approach to detect any variation in groaning rates between contexts was to use planned or a priori comparisons, also known as contrast analysis. In addition, contrast analysis is the most appropriate method for the

analysis of variance when the numerator degrees of freedom are greater than one (Rosenthal & Rosnow 1984, 1989). Available software allows up to 10 comparisons in any single analysis. Therefore we designed the analysis to gain the greatest amount of information using as few contrasts as possible, thereby minimizing the possibility of type I errors. We used Levene's test for homogeneity of variance to determine whether pooled or separate variance estimates were to be used for paired comparison (Zar 1974). The data in Table 1 were log transformed to improve the normality of the distribution (Kolmogorov–Smirnov test). This was not necessary with any of the remaining data sets. All tests are two tailed. Levels of significance were Bonferroni adjusted (Rice 1989). Groaning rates are given as $\bar{X} \pm SE$. We carried out all statistical tests using SPSS, version 6.1.2.

The groaning rates were taken from 69 males: 32 in 1994 and 37 in 1995, with 19 males present in both years. Fallow bucks do not vocalize for ca. 10 months between each breeding season. In addition, since measures of long-term investment in vocal activity and other factors such as age and dominance ranks of males change from one breeding season to the next, we used data from males present in both years, as if they were taken from different males (McElligott et al. 1999).

We carried out preliminary analyses to check for an effect of year, male identity, age, dominance rank and time of day on groaning rates, prior to pooling data in each context. In contexts 3, 4 and 5, some males contributed multiple observations to the data set, raising the question of how their data should be treated. The answer depends on whether intrasubject variance exceeds between-subject variance (Leger & Didrichsons 1994). To examine this, we randomly selected 10 rates per individual from males that contributed 10 or more points to data sets for contexts 3, 4 and 5 ($N=3, 6, 7$ males, respectively). Intrasubject variance was high relative to between-subject variance, and in those contexts where there were substantial numbers of males, none of the intermale differences in groaning rate was significant on post hoc pairwise comparisons (Scheffé tests). In view of this, given that males that contributed multiple observations represented a small proportion of the males sampled in each context, we pooled the data (Leger & Didrichsons 1994).

Stage of Breeding Season and Sex of Neighbours

We used the following contexts to determine if groaning rates differed depending on the stage of the breeding season and the sex of the focal males' closest neighbours.

Context 1: males present within 30 m of the focal male and closer than any females if these were also present, during the prerut (abbreviated in Table 1 as: prerut, males). This context includes groaning rates when the focal males were involved in agonistic interactions, such as fights (McElligott *et al.* 1998). During fights, we counted groaning rates only when intervals between bouts of antler clashing lasted at least 1 min. Context 1 also includes groaning rates when the other males were not interacting in an obvious manner with the focal male. A preliminary comparison (A. G. McElligott, unpublished data) showed that the groaning rates in these two situations did not differ and therefore they were pooled. The data were taken from 10 males contributing 27 rates in 1994 and 20 males contributing 45 rates in 1995.

Context 2: males present within 30 m of the focal male and closer than any females if these were also present, during the rut (abbreviated in Table 1 as: rut, males). The data were taken from 13 males contributing 17 rates in 1994 and 11 males contributing 15 rates in 1995.

Context 3: females present within 30 m of the focal male and closer than any other males if they were also present within 30 m, during the prerut (abbreviated in Table 1 as: prerut, females). In some cases, the focal male was monitoring females for signs of oestrus by sniffing or licking them, during the minute when the groaning rate was counted. A preliminary comparison (A. G. McElligott, unpublished data) showed that the groaning rates in these two situations did not differ and therefore they were pooled. The data were taken from 27 males contributing 119 rates in 1994 and 16 males contributing 42 rates in 1995.

Context 4: females present within 30 m of the focal male and closer than any other males if they were also present within 30 m, during the rut (abbreviated in Table 1 as: rut, females). In this context, we used the groaning rates only when the focal male was not engaged in any monitoring activity, since it significantly reduced the groaning rate (see Monitoring behaviour and vocal males). The data were taken from 15 males contributing 189 rates in 1994 and 17 males contributing 112 rates in 1995.

Context 5: first minute after copulation (abbreviated in Table 1 as: postcopulation). Copulations were clearly identifiable because the males mounted the females and jumped forwards as they ejaculated, with both hind legs usually leaving the ground. The data were taken from 10 males contributing 110 rates in 1994 and 16 males contributing 93 rates in 1995.

Vocal Males

We used the following contexts to determine if groaning rates differed depending on the presence of vocal males. We subdivided contexts 3 and 4, based on the absence (context 3a, abbreviated in Table 2 as: prerut,

females, no vocal males) or presence (context 3b, abbreviated in Table 2 as: prerut, females, vocal males) of other vocal males. The data were taken from 13 males contributing 33 rates in 1994 and 12 males contributing 20 rates in 1995 for context 3a and 24 males contributing 86 rates in 1994 and 12 males contributing 22 rates in 1995 for context 3b. Similarly, contexts 4a (abbreviated in Table 2 as: rut, females, no vocal males) and 4b (abbreviated in Table 2 as: rut, females, vocal males) refer, respectively, to focal males with females in the absence or presence of other vocal males. The data were taken from six males contributing 27 rates in 1994 and six males contributing 16 rates in 1995 for context 4a and 13 males contributing 162 rates in 1994 and 14 males contributing 96 rates in 1995 for context 4b. We also included postcopulation groaning rates (context 5) in this comparison.

Vocal Males and Harems I

We used the following contexts to determine if groaning rates differed depending on the presence of vocal males and harems. We subdivided postcopulation groaning rates on the basis of absence (context 5a, abbreviated in Table 3 as: postcopulation, no vocal males) or presence (context 5b, abbreviated in Table 3 as: postcopulation, vocal males) of other vocal males. Context 4b was also included in this comparison but was subdivided based on the absence (context 4b1 abbreviated in Table 3 as: rut, females not in harem, vocal males) or presence (context 4b2, abbreviated in Table 3 as: rut, females in harem, vocal males) of a harem. For context 4b1, 12 males contributed 65 rates in 1994 and 13 males 37 rates in 1995. For context 4b2, six males contributed 96 rates in 1994 and seven males 60 rates in 1995. For context 5a, seven males contributed 33 rates in 1994 and seven males 28 rates in 1995. For context 5b, nine males contributed 77 rates in 1994 and 15 males 65 rates in 1995.

Vocal Males and Harems II

We used the following contexts to determine if postcopulatory groaning rates differed depending on the presence of vocal males and harems. We subdivided the postcopulation groaning rates based on the absence or presence of vocal males, and the absence or presence of harems. Therefore, context 5a1 refers to the postcopulation groaning rates when neither vocal males nor harems were present (abbreviated in Table 4 as: postcopulation, no vocal males, no harem). Context 5a2 is as context 5a1, except that a harem was present (abbreviated in Table 4 as: postcopulation, no vocal males, harem). Context 5b1 refers to postcopulation groaning rates when vocal males were present and a harem was absent (abbreviated in Table 4 as: postcopulation, vocal males, no harem). In context 5b2 both vocal males and a harem were present (abbreviated in Table 4 as: postcopulation, vocal males, harem). For context 5a1, six males contributed 25 rates in 1994 and seven males 20 rates in 1995. For context 5a2, three males contributed eight rates in 1994 and three males eight rates in 1995. For context 5b1, eight males contributed 30 rates in 1994 and 14 males

39 rates in 1995. For context 5b2, five males contributed 47 rates in 1994 and six males 26 rates in 1995.

Monitoring Behaviour and Vocal Males

When males were with females, their vocalizations were often interrupted by interactions with those females, such as sniffing, licking, or touching them with any part of their head or antlers. During this time, the males were silent. Here, we define this activity as monitoring; it could be carried out with one or more females during the minute when the number of groans was counted. In addition, when males were involved in mating sequences with oestrous females, we often observed the same activities during the intervals between mounts. We considered that a male was involved in a mating sequence if it had mounted a female at least once, and the female involved did not attempt to avoid the attention of the male. Therefore, we defined a mating sequence as the period between the first mount of a male with a receptive oestrous female and the final mount and ejaculation, or until the male and female separated. The groaning rates during mating sequences were recorded only when the intervals between the acts of mounting lasted at least 1 min. This avoided the reduction of groaning rate owing to the mounting action, when males did not groan.

A preliminary contrast (A. G. McElligott, unpublished data) showed that the mean number of groans per min was significantly lower if the minute included an episode of monitoring a female ($\bar{X} \pm SE = 44.9 \pm 0.6$, $N = 453$), than if it did not (53.3 ± 0.7 , $N = 301$; context 4). However, we considered that this resulted from the monitoring activities, which were incompatible with groaning. Therefore, a random sample of the minutes from which these rates were recorded was used to estimate the percentage of time that males spent involved in monitoring activities ($N = 40$ min, $N = 15$ males). We found that males, on average, spent $16.9 \pm 2.2\%$ of these minutes engaged in activities not compatible with groaning. Therefore, we adjusted the rates to take account of these periods and calculated the true groaning rates. The analysis in Table 5 was carried out based on these adjusted rates, to determine whether the groaning rates when males were monitoring females differed from those when males were with females without engaging in this activity. Contexts 6a and 6b refer to the adjusted groaning rates when males were monitoring one or more females; vocal males absent or present, respectively. These were abbreviated in Table 5 as follows: 6a, rut, monitoring females, no vocal males (adjusted), 6b, rut, monitoring females, vocal males (adjusted).

RESULTS

Figure 2 illustrates the continual and variable nature of the groaning activity of fallow bucks. Similar groaning records were obtained for other males. We calculated, using a sample of 10 of these 1-h groaning records for eight different males during the rut, that males could groan, on average, 3164 ± 112 times per h. The minimum

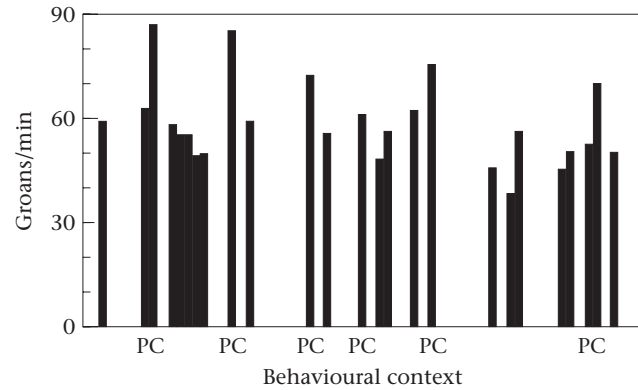


Figure 2. An example of groaning rates, recorded for a male over 1 h (0834–0933 hours, 27 October 1994). The male was active and continually vocal during this time. The groaning rates after copulation are indicated (PC). All other groaning rates were recorded while the focal male was with females; other vocal males were also present. The gaps in the groaning record represent periods when the groaning rates could not be counted over a continuous period of 1 min, but the male was vocal during these times.

number of groaning rate counts used in calculating this estimate was 20 (or 33.3% of their total groans).

Groaning rates were generally higher during the rut than during the prerut (Table 1). In addition, males groaned at higher rates when with females than when they were with other males (Table 1). The highest groaning rates were recorded immediately after copulation. All except one of the comparisons in this part of the analysis were significant; the groaning rates of males with other males during the rut did not differ from those of males with females during the prerut (Table 1).

During both the prerut and rut, males with females groaned at higher rates when other vocal males were present (Table 2). The postcopulation groaning rates were again higher than the rates in other contexts. All comparisons carried out in this part of the analysis were significant (Table 2).

Postcopulation groaning rates were significantly higher when other vocal males were present (Table 3). The groaning rates after copulation when no other vocal males were present were also significantly higher than the next highest rates (contexts 4b1 and 4b2). There was no difference between the groaning rates of males in harems and those of males with females that were not in harems (Table 3). In both situations considered, other vocal males were present.

Postcopulation groaning rates were highest when other vocal males and a harem were present (Table 4). The main differences in the comparison were associated with the presence of other vocal males; the presence of a harem contributed less of the variation in postcopulation groaning rates (Table 4). No safe results can be drawn from the comparisons involving context 5a2 owing to the small sample size. This sample size indicates the rarity of harems that do not have other vocal males present, in addition to the focal male.

The groaning rates of males that were monitoring females did not differ from those of males that were with

Table 1. Contrast analysis of the effects of the stage of the breeding season and sex of closest neighbours on groaning rates of males

	1, Prerut, males	2, Rut, males	3, Prerut, females	4, Rut, females	5, Postcopulation
Groaning rate (groans/min)	16.8±1.6 (72)	23.5±2.1 (32)	24.3±1.1 (161)	53.3±0.7 (301)	70.7±0.8 (203)
1, Prerut, males	—	$P=0.01†§$	*†	*†	*†
2, Rut, males	—	—	NS†	*†	*†
3, Prerut, females	—	—	—	*‡	*‡
4, Rut, females	—	—	—	—	*†

Means are given±SE. Sample size in parentheses. See Fig. 1 for classification of contexts. $F_{4,764}=475.2$, $P<0.0001$.

†Contrast based on pooled variance estimate.

‡Contrast based on separate variance estimate.

§NS after Bonferroni adjustment.

* $P<0.001$.

Table 2. Contrast analysis of the effects of vocal males on groaning rates of males with females

	3a, Prerut, females, no vocal males	3b, Prerut, females, vocal males	4a, Rut, females, no vocal males	4b, Rut, females, vocal males	5, Postcopulation
Groaning rate (groans/min)	20.9±1.7 (53)	26.0±1.4 (108)	44.0±2.2 (43)	54.8±0.7 (258)	70.6±0.8 (203)
3a, Prerut, females, no vocal males	—	$P=0.01†§$	*†	*‡	*†
3b, Prerut, females, vocal males	—	—	*†	*‡	*†
4a, Rut, females, no vocal males	—	—	—	*‡	*†
4b, Rut, females, vocal males	—	—	—	—	*†

Means are given±SE. Sample size in parentheses. See Fig. 1 for classification of contexts. $F_{4,660}=345.8$, $P<0.0001$.

†Contrast based on pooled variance estimate.

‡Contrast based on separate variance estimate.

§NS after Bonferroni adjustment.

* $P<0.001$.

Table 3. Contrast analysis of the effects of vocal males and harems on groaning rates of males

	4b1, Rut, females not in harem, vocal males	4b2, Rut, females in harem, vocal males	5a, Postcopulation, no vocal males	5b, Postcopulation, vocal males
Groaning rate (groans/min)	53.6±1.4 (101)	55.6±0.6 (157)	67.0±1.6 (61)	72.2±0.9 (142)
4b1, Rut, females not in harem, vocal males	—	NS‡	**†	**‡
4b2, Rut, females in harem, vocal males	—	—	**‡	**‡
5a, Postcopulation, no vocal males	—	—	—	*†

Means are given±SE. Sample size in parentheses. See Fig. 1 for classification of contexts. $F_{4,764}=475.2$, $P<0.0001$.

†Contrast based on pooled variance estimate.

‡Contrast based on separate variance estimate.

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

females, but not engaged in any monitoring activities (Table 5). However, the effect of the presence of other vocal males (detected in contrast 2), was also apparent in this analysis. The groaning rates of males that were monitoring females in the presence of other vocal males were significantly higher than the rates when no other males were vocal.

There was no significant difference (independent samples t test: $t_{30}=1.4$, NS), between the groaning rate when the focal male was with other males, none of whom was vocal ($\bar{X} \pm SE=26.4 \pm 2.7$, $N=16$), and the groaning rate when other males present were vocal (20.7 ± 3.2 , $N=16$). This relationship was examined only for the rut, because during the prerut males were intermittently

Table 4. Contrast analysis of the effects of vocal males and harems on groaning rates of males after copulation

	5a1, Postcopulation, no vocal males, no harem	5a2, Postcopulation, no vocal males, harem	5b1, Postcopulation, vocal males, no harem	5b2, Postcopulation, vocal males, harem
Groaning rate (groans/min)	66.0±1.9 (45)	69.8±3.0 (16)	70.1±1.4 (69)	74.2±1.1 (73)
5a1, Postcopulation, no vocal males, no harem	—	NS†	P=0.06†	*‡
5a2, Postcopulation, no vocal males, harem	—	—	NS†	NS†
5b1, Postcopulation, vocal males, no harem	—	—	—	P=0.02‡§

Means are given±SE. Sample size in parentheses. See Fig. 1 for classification of contexts. $F_{3,199}=5.2$, $P<0.01$.

†Contrast based on pooled variance estimate.

‡Contrast based on separate variance estimate.

§NS after Bonferroni adjustment.

* $P<0.001$.

Table 5. Contrast analysis of the effects of monitoring behaviour and vocal males on groaning rates of males

	4a, Rut, females, no vocal males	4b, Rut, females, vocal males	6a, Rut, monitoring females, no vocal males (adjusted)	6b, Rut, monitoring females, vocal males (adjusted)
Groaning rate (groans/min)	44.0±2.2 (43)	54.8±0.7 (258)	47.2±1.6 (137)	56.0±0.8 (316)
4a, Rut, females, no vocal males	—	*‡	NS‡	*‡
4b, Rut, females, vocal males	—	—	*‡	NS‡
6a, Rut, monitoring females, no vocal males (adjusted)	—	—	—	*‡

Means are given±SE. Sample size in parentheses. See Fig. 1 and Methods for classification of contexts. $F_{3,750}=19.5$, $P<0.0001$.

†Contrast based on pooled variance estimate.

‡Contrast based on separate variance estimate.

* $P<0.001$.

vocal. As a result, most of the rates available were in situations when there were no other vocal males present (16.8 ± 1.6 , $N=72$).

DISCUSSION

Our results show that the groaning rates of fallow bucks are highly variable and that this variation is associated with the context of groaning. Males invested considerable effort in groaning, producing more than 3000 groans/h when continually vocal during the rut. We found that the groaning rates of males with females during the prerut (context 3) were higher than the groaning rates of males with other males during the prerut (context 1). Similarly, during the rut, groaning rates of males with females were higher than for males with other males (context 4 versus context 2). However, it is important to emphasize that even when males were with females, there were almost always other males nearby (within 30 m). The groaning rates of males with females during the rut represent a large increase in the rates in the same situation during the prerut (context 4 versus context 3). The magnitude of the difference between the prerut and rut groaning rates in male contexts was far less (context 2 versus context 1). The presence of vocal males was associated with higher

groaning rates in all but one context: when males were with other males during the rut. The presence of a harem did not contribute any variation in groaning rates, except to a minor extent in postcopulation rates and these were the highest that males produced (context 5).

Our results suggest that the signal transmitted by the groaning rates of fallow bucks was not primarily directed at attracting females, since the highest rates were produced by males in the presence of females. The signal may instead act to retain females with which males are consorting. Since groaning rates of males with and without harems did not differ, however, either the signal conveyed by groaning rates was also not primarily directed at retaining females, or males do not discriminate between perioestrous and other females. The latter explanation is unlikely, as, in our study population during the rut, the rate of fighting between males each day is closely related to the number of mating opportunities that are available (McElligott et al. 1998). Moreover, oestrous fallow does tend to join other groups of females, largely independently of the behaviour of males (Clutton-Brock & McComb 1993; McComb & Clutton-Brock 1994). This is in contrast to the findings for red deer, *Cervus elaphus*, in which hinds are attracted by high roaring rates (McComb 1991). In our study, the increased groaning rates associated with the presence of other vocal

males in all contexts involving females suggest that the signal conveyed by groaning rates was primarily a threat display directed at rival males. This display was produced in response to the presence of any males, but its intensity increased when other vocal, and therefore actively rutting, males (Moore et al. 1995) were also present.

If the signal that a fallow buck conveys by groaning rates is primarily directed at other males, we suggest that it serves to protect a male's resources by preventing fights. This is consistent with the view that overt fights are often replaced with signals that are used for assessment when the costs of fighting are high (Clutton-Brock & Albon 1979; Dawkins & Guilford 1991; Enquist et al. 1998). In our study population, the numbers of matings and fights each day are closely related (McElligott et al. 1998), demonstrating that males are more likely to fight when the potential to gain access to mating opportunities is greater. However, males may incur a variety of costs as a result of fighting. In addition to the temporal and energetic costs (Riechert 1988), there are a number of others, such as injury or death (A. G. McElligott, personal observation), loss of dominance status, or loss of females. Although serious injuries may result from fights, they are not inevitable, however. Furthermore, status is not always lost as a result of fighting and, even if it is, a decline in status may not be permanent. Many fights are also inconclusive, and the majority of males win at least some of their fights (Festa-Bianchet et al. 1990; McElligott et al. 1998). One consequence of fighting that is almost certain to occur is the loss of females, provided that a male is already with females. This is usually caused by intrusions from other males after a fight has begun, and happens regardless of whether the male that was accompanying females wins or loses the interaction (Clutton-Brock et al. 1988; Apollonio et al. 1989). Therefore, the loss of females could be considered one of the most serious consequences of fighting for fallow deer, because males that have gained access to females also have the potential to achieve matings.

The variation in groaning rates in different contexts indicates that fallow bucks did not always groan at the maximum attainable level. Instead, groaning rates appeared to represent the value of the resources that males were protecting and therefore the cost to males of losing those resources by becoming involved in fights (Enquist & Leimar 1987; Enquist et al. 1998). For example, the lowest groaning rates were by males that were with other males during the prerut (context 1). At this time, there were no mating opportunities in the population and the risks associated with fighting, such as injury or loss of dominance status, far outweigh the benefits that might accrue to either participant. In addition, males would probably already be capable of recognizing each other using a range of other visual and olfactory cues, from the period they associated together in bachelor groups before they became vocal (Guilford & Dawkins 1991; Moore et al. 1995).

Our findings suggest that fallow bucks adjusted their groaning rates in relation to the motivation of their competitors. Increased motivation of rival males was evident from their vocal activity, which has previously

been used as a measure of minimum participation in the rut (Moore et al. 1995). At the very least, the presence of vocal males near another male that is vocalizing indicates to that male that there are other socially mature males nearby, since immature males generally do not vocalize (McElligott et al. 1999). Therefore the potential threat was far greater than if only immature males were present, since immature males almost never fight with mature males (McElligott et al. 1998). This effect of the presence of competitors on breeding displays has been found in a diverse array of species. For example, in bison, *Bison bison*, male bellowing is primarily an intrasexual display, with bellowing rates affected by the number of other males present when a male consorts with a female (Berger & Cunningham 1991). Galeotti et al. (1997) found that the phonic structure of songs of male barn swallows, *Hirundo rustica*, differs in relation to the competitiveness of social contexts and competitiveness also depends on the number of other males present. Similarly, in smooth newts, *Triturus vulgaris*, male courtship intensity increases in response to the presence of other males (Verrell 1984). During the rut, we found that the groaning rates of fallow bucks that were not with females did not increase in response to the presence of vocal males. This indicates that the motivation levels of both signallers and receivers were lower in this context, because access to females was not at risk.

One of the cues that fallow does may use to discriminate between potential mates is the cumulative long-term investment in vocal display by males during the breeding season (Payne & Pagel 1997; McElligott et al. 1999). However, if females do not have sufficient information on mate quality after deciding to associate with particular males (Sullivan 1990, 1994), females could also use short-term rates of display before deciding to mate. For example, Clutton-Brock et al. (1988) found that fallow does avoid males with low display rates. In other species, females often use more than a single cue when choosing mates (Berglund et al. 1996; Jennions & Petrie 1997). Our study does not allow us to exclude a role for short-term groaning rates in intersexual advertisement, but our results suggest that it is not the primary function of the display. Recent evidence also suggests that the groaning of fallow bucks is not involved in the advancement of oestrus in females (Komers et al. 1999), in contrast to the roaring of red deer stags (McComb 1987).

We have identified a distinct escalation in fallow buck groaning rates after copulation (Fig. 2). Here we use the term 'escalation' to indicate an increase in action intensity within one display form, consistent with Payne & Pagel's (1996a) definition of intraphase escalation. To our knowledge, this is the first postcopulation call reported for any male ungulate. To resolve the paradox of a male revealing the presence of a female in oestrus, we propose that the high postcopulation groaning rates could serve to reduce the possibility of extrapair matings, either by deterring potentially kleptogamous males or retaining the mated females. In our study population, 16% of females mate more than once (McElligott 1997), and therefore sperm competition by other males represents a threat to the reproductive success of a male that has just mated.

Postcopulation groaning rates were higher when other vocal males were present, thus providing additional evidence that the postcopulation groaning rates serve either to deter competing males or to retain a female in oestrus. The fact that postcopulation groaning rates were high in the absence of vocal males is indicative of the potential risk from males that were formerly not active or vocal. For example, immature males are physically capable of mating, but rarely vocalize (Chaplin & White 1972; McElligott et al. 1999). The infrequency and brevity of groaning rates produced at the level of the postcopulation rate are consistent with a 'best-so-far' model of repetitive display behaviour (Payne & Pagel 1996b, 1997).

In conclusion, our findings suggest that the signal conveyed by the short-term groaning rates of fallow bucks is primarily an intrasexual threat. It may represent a signal of motivation related to the resources of the vocalizing male and also to the potential of rival males to compete for those resources by fighting (Maynard Smith & Harper 1988; Enquist et al. 1998).

Acknowledgments

We thank Dúchas The Heritage Service, J. McCullen, Park Superintendent, and the Rangers and other staff of Phoenix Park. We are grateful to the following for field assistance: C. Carlin, J. Collins, S. Elliot, M. Gammell, S. Kenny, J. Meehan, K. Nevin, D. O'Brien, D. Paini, C. Reynolds, N. Reynolds, S. Rooney, F. Saunders and E. Teeling. We thank Dr J. Connolly (Department of Statistics, UCD) and Dr T. Bolger (Department of Zoology, UCD) for statistical advice. We thank M. Apollonio and three anonymous referees for comments on the manuscript. We acknowledge the financial support of Dúchas The Heritage Service, the Department of Education and Enterprise Ireland (A.G.M.).

References

- 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.
- Berger, J. & Cunningham, C. 1991. Bellows, copulations, and sexual selection in bison (*Bison bison*). *Behavioral Ecology*, **2**, 1–6.
- Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, **58**, 385–399.
- Brenowitz, E. A. & Rose, G. J. 1999. Female choice and plasticity of male calling behaviour in the Pacific treefrog. *Animal Behaviour*, **57**, 1337–1342.
- Chaplin, R. E. & White, R. W. G. 1972. The influence of age and season on the activity of the testes and epididymides of the fallow deer, *Dama dama*. *Journal of Reproduction and Fertility*, **30**, 361–369.
- Chapman, D. I. & Chapman, N. G. 1975. *Fallow Deer: Their History, Distribution and Biology*. Lavenham, Suffolk: Terence Dalton.
- 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. & McComb, K. E. 1993. Experimental tests of copying and mate choice in fallow deer (*Dama dama*). *Behavioral Ecology*, **4**, 191–193.
- 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.
- Conner, D. A. 1985. Analysis of the vocal repertoire of adult pikas: ecological and evolutionary perspectives. *Animal Behaviour*, **33**, 124–134.
- Dawkins, M. S. & Guilford, T. 1991. The corruption of honest signalling. *Animal Behaviour*, **41**, 865–873.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist*, **139**, S125–S153.
- Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Enquist, M. & Leimar, O. 1987. Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology*, **127**, 187–205.
- Enquist, M., Ghirlanda, S. & Hurd, P. L. 1998. Discrete conventional signalling of a continuous variable. *Animal Behaviour*, **56**, 749–754.
- 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.
- Fraser, A. F. 1968. *Reproductive Behaviour in Ungulates*. London: Academic Press.
- Galeotti, P., Saino, N., Sacchi, R. & Møller, A. P. 1997. Song correlates with social context, testosterone and body condition in male barn swallows. *Animal Behaviour*, **53**, 687–700.
- Gerhardt, H. C. 1994. The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics*, **25**, 293–324.
- Gibson, R. M., Bradbury, J. W. & Vehrencamp, S. L. 1991. Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behavioral Ecology*, **2**, 165–180.
- Grafen, A. 1987. The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Animal Behaviour*, **35**, 462–467.
- Guilford, T. & Dawkins, M. S. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour*, **42**, 1–14.
- Janik, V. M. & Slater, P. J. B. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, **56**, 829–838.
- Jennions, M. D. & Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews*, **72**, 283–327.
- Jouventin, P., Aubin, T. & Lengagne, T. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Animal Behaviour*, **57**, 1175–1183.
- 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.
- 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.
- Komers, P. E., Birgersson, B. & Ekvall, K. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. *American Naturalist*, **153**, 431–436.

- Leger, D. W. & Didrichsons, I. A. 1994. An assessment of data pooling and some alternatives. *Animal Behaviour*, **48**, 823–832.
- McComb, K. E. 1987. Roaring by red deer stags advances the date of oestrous in hinds. *Nature*, **330**, 648–649.
- McComb, K. E. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour*, **41**, 79–88.
- McComb, K. E. & Clutton-Brock, T. H. 1994. Is mate choice copying or aggregation responsible for skewed distributions of females on leks? *Proceedings of the Royal Society of London, Series B*, **255**, 13–19.
- 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.
- McElligott, A. G., O'Neill, K. P. & Hayden, T. J. 1999. Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. *Animal Behaviour*, **57**, 1159–1167.
- Maynard Smith, J. & Harper, D. 1988. The evolution of aggression: can selection generate variability? *Philosophical Transactions of the Royal Society of London, Series B*, **319**, 557–570.
- Moore, N. P., Kelly, P. F., Cahill, J. P. & Hayden, T. J. 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behavioral Ecology and Sociobiology*, **36**, 91–100.
- Payne, R. J. H. & Pagel, M. 1996a. Escalation and time costs in displays of endurance. *Journal of Theoretical Biology*, **183**, 185–193.
- Payne, R. J. H. & Pagel, M. 1996b. When is false modesty a false economy? An optimality model of escalating signals? *Proceedings of the Royal Society of London, Series B*, **263**, 1545–1550.
- Payne, R. J. H. & Pagel, M. 1997. Why do animals repeat displays? *Animal Behaviour*, **54**, 109–119.
- Poole, J. H., Payne, K. B., Langbauer, W. R., Jr & Moss, C. J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology*, **22**, 385–392.
- 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.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Riechert, S. E. 1988. The energetic costs of fighting. *American Zoologist*, **28**, 877–884.
- Rosenthal, J. & Rosnow, R. 1984. *Essentials of Behavioral Research: Methods and Data Analysis*. New York: McGraw-Hill.
- Rosenthal, J. & Rosnow, R. 1989. *Contrast Analysis: Focused Comparisons in the Analysis of Variance*. Cambridge: Cambridge University Press.
- Sekulic, R. 1982. The function of howling in red howler monkeys (*Alouatta seniculus*). *Behaviour*, **81**, 38–54.
- Shipley, C., Hines, M. & Buchwald, J. S. 1981. Individual differences in threat calls of Northern elephant seal bulls. *Animal Behaviour*, **29**, 12–19.
- Sullivan, M. S. 1990. Assessing female choice for mates when the males' characters vary during the sampling period. *Animal Behaviour*, **40**, 780–782.
- Sullivan, M. S. 1994. Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Animal Behaviour*, **47**, 141–151.
- Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology*, **8**, 105–116.
- Verrell, P. A. 1984. Sexual interference and sexual defense in the smooth newt, *Triturus vulgaris* (Amphibia, Urodela, Salamandridae). *Zeitschrift für Tierpsychologie*, **66**, 242–254.
- Weilgart, L. S. & Whitehead, H. 1990. Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioural contexts. *Behavioral Ecology and Sociobiology*, **26**, 399–402.
- Zar, J. H. 1974. *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice Hall.