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Postcopulatory vocalizations of fallow bucks: who is listening?

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Fallow bucks (*Dama dama*) produce a postcopulatory vocalization (PCV), consisting of an increase in the short-term groaning rate during the first min after mating. In this article, we consider two main hypotheses to assess the possible function of the postcopulatory vocalization. First, the PCV could be directed at females, and used to advertise the current fertility status of the male. Second, the PCV could be directed at males, and used to transmit an intrasexual threat signal. We found that during days when a male gained many matings, his PCVs did not decline, and males with larger intervals between matings did not produce higher PCVs. Lower PCVs were not associated with infertile matings, and for females that mated twice within the same estrus, the PCVs of their first matings were not lower than other PCVs. In addition, higher PCVs were not associated with shorter intervals to a male's next mating. Thus, there was no evidence to suggest that the PCV was involved in transmitting a signal of fertility assurance, either to females that had mated, or to those that were about to mate. We found that PCVs declined as males reached the end of their mating success, therefore suggesting that PCVs are more likely to be involved in transmitting an intrasexual threat signal related to current condition and/or motivation. We suggest that this signal is probably involved in mate guarding. *Key words:* postcopulatory vocalization, fallow deer, *Dama dama,* signal, fertility, body condition, motivation, mate guarding. *[Behav Ecol 12:41–46 (2001)]*

Some male mammals vocalize immediately after mating. Three types of postcopulatory calls have been identified. In some species, the vocalization is phonically different from any other call emitted by the male (Barfield and Geyer, 1972; Grady and Hoogland, 1986; Leger et al., 1984). In others, copulation is followed by a change in the rate of a call that is also produced in other contexts (Cherry, 1989). The third type of postcopulatory call is a vocalization that is used in other contexts, but is also produced after mating (Tamura, 1993, 1995).

Rodents are the main order of mammals for which postcopulatory calling by males has been described and these calls are believed to serve a variety of functions. The brown rat (*Rattus norvegicus*) was the first species for which a postcopulatory call was described, and it reduces the tendency of the mated female to mate with additional males (Barfield and Geyer, 1972). Other postcopulatory calls function in prolonging lordosis of the mated female, attracting other females or deterring males (Cherry, 1989; Grady and Hoogland, 1986; Leger et al., 1984; Tamura, 1993, 1995).

McElligott and Hayden (1999) identified a postcopulatory vocalization produced by fallow bucks. It is the first comprehensive report of a PCV for any male mammal other than rodents, and consists of the highest short-term groaning rate (average 70.7 min) that fallow bucks produce. Postcopulatory roaring has been reported for impala rams (*Aepyceros melampus*), but not described in detail (Jarman, 1979). Socially mature fallow bucks are highly vocal during the breeding season, initiating vocal activity several weeks before the first matings, and also attaining groaning rates of over 3000 per h (McElligott and Hayden, 1999; McElligott et al., 1999).

One of the most important factors related to the mating success of fallow bucks in our study population is their social dominance rank (McElligott et al., 1998; McElligott et al., 1999). This can be assessed after their antlers are fully-grown at the end of August each year, and also before they move to the females' home range and begin vocalizing (Moore et al., 1995). Fallow bucks do not vocalize for approximately 10 months of the year, and high-ranking males are the first to initiate vocal activity in the latter half of September each year. Males that start to vocalize generally continue to do so throughout the breeding season (McElligott et al., 1999).

In assessing the most likely recipients for the signal transmitted by the PCV of fallow bucks, it is first necessary to distinguish the sex differences that are likely to exist in relation to information gathering in this species. The phenotypic condition of socially mature fallow bucks changes greatly during the breeding season, as a large proportion of body weight is lost (Clutton-Brock et al., 1988; McElligott et al., 1999). Current condition therefore does not necessarily represent overall genetic quality and females should be selected to monitor indicators of overall male quality (Kodric-Brown and Brown, 1984; Sullivan, 1990). By contrast, males should be selected to monitor indicators of current condition or motivation to fight, since access to mating opportunities is determined by current competitive ability, in addition to dominance rank (Enquist and Leimar, 1983; McElligott et al., 1998).

Short-term investment in vocalization, in terms of groaning rates, does not necessarily represent overall male quality, since groaning rates are highly variable and low ranking males can produce high rates. Instead, evidence to date suggests that short-term vocalization rates transfer a signal related to current body condition and/or motivation and is mainly involved in intrasexual competition (Komers et al., 1997; McElligott and Hayden, 1999). Long-term investment in vocal display is not related to direct intrasexual competition (McElligott et al., 1999). It probably plays a role in mate choice by allowing females to identify high quality males (McElligott et al., 1999; Wiley and Poston, 1996). Since the phonic structure of groans is individually distinct, and for example, red deer hinds (*Cervus elaphus*) can discriminate between their offspring and

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other calves based on their calls, this remains a viable possibility (Kelly, 1998; Reby et al., 1998; Vanková et al., 1997). The importance of both long-term display by signalers and long-term assessment by receivers, has recently received greater attention in the literature, with evidence also emerging for its existence in other species (Kokko et al., 1999; Payne, 1998).

For species in which the vocal activity of a male changes distinctly when its mate is most fertile, the risks associated with advertising the presence and location of the female must be offset by the benefits (Møller, 1991). Herein, we consider two main hypotheses to assess the possible function of the postcopulatory vocalization of fallow bucks. First, we propose that the PCV is directed at females, and therefore could be used to advertise the current fertility status of the male, that is, the phenotype-linked fertility insurance hypothesis (Sheldon, 1994). Second, we propose that the PCV is directed at males, and could act as an advertisement of current overall body condition and/or motivation. In field-based research that does not involve the manipulation of the study animals, it is often difficult to separate an intersexual from an intrasexual role for display. Nevertheless, our results should allow us to identify the most likely receivers of the signal transmitted by the PCV.

For polygynous mammals such as fallow deer, sperm depletion may occur owing to males mating repeatedly within a short time (Asher et al., 1996; Synnott et al., 1981). Thus, after mating, it could be important to advertise current fertilizing ability, either to reduce the tendency of extra-pair matings by the most recently mated female, or to reassure additional estrous females before they mate. It is unlikely that the PCV signals overall male quality to the mated female, since it occurs after she has mated. In addition, for other females, the long-term investment in vocal activity provides a more reliable signal of overall quality. If the PCV is related to current fertilizing ability, we predict that the PCV would decline due to repeated matings within a short time and, conversely, that the PCV should increase with the time elapsed since the last mating. Mated females should not risk sperm competition from a less attractive male unless it is essential for fertilization (Clutton-Brock and Parker, 1995; Hoogland, 1998). For example, black grouse females (*Tetrao tetrix*) rarely mated more than once unless their first copulation was disturbed (Alatalo et al., 1996). If the PCV advertises fertility to the most recently mated female, we predict that the probability of a female mating twice during the same estrus and also the probability of the female not being fertilized, would be inversely related to the PCV.

The propensity of estrous fallow does to move to males during matings (Clutton-Brock et al., 1988; McComb and Clutton-Brock, 1994), suggests that they could be potential receivers of the signal transmitted by the PCV. Therefore, if the PCV advertises a male's fertility in order to reassure additional estrous females before mating, we predict that they would spend less time before mating with a male, if the PCV accompanying his last mating was high. Thus the interval to a male's next mating should be inversely related to his PCV.

The second possibility is that the PCV advertises current body condition and/or motivation. Since there is evidence for social control of dishonest signals, we consider signals of current condition and motivation to be intrinsically linked (McElligott et al., 1998). While mating, the number of females in the harems of fallow bucks usually increases owing to other females joining, and reaches a maximum shortly after the male ejaculates (Clutton-Brock et al., 1988). Males risk losing their harems if they become involved in fights, regardless of the outcome of the interaction (Apollonio et al., 1989). The PCV may therefore serve as a deterrent to other males at a time when the potential costs of fighting are very high. These costs can be considered in terms of the receptive mated female re-mating immediately, and also the potential for losing a harem containing additional estrous females. Thus, if the PCV acts an indicator of current condition and/or motivation, we predict that some of the variation in the PCV would be explained by factors related to the participation in the rut by males, for example, mating success.

METHODS

Study site and population

We observed a herd of European fallow deer in Phoenix Park (53°22′ N, 6°21′ W), Dublin, Ireland. The majority of the deer were of known age, tagged, and therefore individually recognizable (McElligott et al., 1999; Moore et al., 1995).

Postcopulatory vocalizations and observation schedule

The PCVs used in the analysis were obtained from videotape of socially mature males that we filmed during the ruts of 1994 and 1995, using a Panasonic NV-MS 4B SVHS videocamera (×12 zoom lens, digital zoom ×200). We used videotape because it allowed us to count groaning rates accurately, particularly since they were high. The rut was the period between the days on which the first and last matings occurred (18 October–1 November 1994, and 14 October–1 November 1995), and we carried out observations from dawn to dusk (ca. 11 h). For additional details of our observations, see McElligott et al. (1999) and McElligott and Hayden (1999). We also conducted observations in November for a period corresponding to 3 weeks after the rut. This is the length of the estrous cycle of females in our study population (O'Connell, 1993). These observations allowed us to identify the small proportion of females that mated again after the rut (11.5%, Farrell ME and Hayden TJ, unpublished data), and thus detect infertile matings that took place during the rut.

In Phoenix Park, the skew in male mating success is high (McElligott et al., 1998, 1999). Thus the number of males contributing data on PCVs will be restricted. In addition, ruts differ in the manner in which the matings are distributed among successful males. For example, the most successful male during the 1994 rut gained 108 (43.4% of total) matings, and also gained those matings throughout the rut. By contrast, in 1995, the top four males gained 41, 34, 30, and 29 matings, respectively (55.6% of total), and none of these males gained matings throughout the rut (McElligott, 1997). Because of these factors, some of the analysis below is limited to a single male for 1994, while data from several males in 1995 were suitable for analysis.

The PCVs were taken from 26 males; 10 in 1994 and 16 in 1995, with five males present in both years. Because of changes in attributes of individual fallow bucks from 1 year to the next regarding age, dominance rank, and investment in vocal activity, we used data from males present in both years, as if they were taken from different males (McElligott et al., 1999). Furthermore, none of the males common to both years contributed large numbers of PCVs in each year. In descending order of the number of PCVs, the males that were common to both years contributed 12, nine, four, two, and one PCV in 1994, while the same males contributed one, one, 17, one and 10 PCVs in 1995, respectively.

Hypothesis 1: The PCV is directed at females and is related to the fertility of the male

We examined the relationship between the PCV and order of matings on 6 days for 4 males. Each of these males gained between seven and 22 matings during a single day and the PCVs for most of these matings were available for analysis. We chose 3 days (23, 24, and 27 October) from 1994 on which

Table 1
Stepwise multiple regression analysis

Variable	Coefficient	t	p
Constant	1.9	—	—
Proportion of the total mating success	−0.1	−5.4	<0.0001
Days since first mating	−0.07	−0.7	0.48

The PCV (log-transformed) is the dependent variable and proportion of the total mating success for each male, and days since first mating for each male (log-transformed), are independent variables.
Multiple $r = .39$ ($r^2 = .15$), $n = 171$, $p < .0001$.

the same male gained 15, 22, and 15 matings, respectively. We also used 3 days from 1995, on which three different males gained nine, seven, and nine matings.

Preliminary analysis revealed that the intervals between matings within days for individual males were bimodal; inter-mating intervals ranged from a few min to several h (McElligott AG, unpublished data). Since any effect of the time elapsed since the previous mating on the PCV would be more likely to be evident in the short-term, we used intervals between matings that were less than 2500 s (42 min) to examine this relationship. This was the obvious cut-off point in these data. We analyzed data for one male between 23 and 27 October 1994, and for five males between 21 and 30 October 1995. We chose these males and periods because they included a large number of inter-mating intervals (43 and 30, respectively).

Our data included the PCVs for the first mating of 17 females that mated twice during the same estrus, herein defined as "double-mating" females. We then compared these with the PCVs of matings of females that mated once. In addition, we compared the PCVs of the first and second matings of 10 double-mating females. We also had the PCVs that accompanied the rut matings of 22 females that mated again 20–23 days later during November. We then compared these PCVs, with the PCVs accompanying the matings of females that did not mate again.

To examine any effect of the PCV on the subsequent inter-mating interval, we again only considered intervals between copulations that were less than 2500 s (see above). In this analysis, we also used data for one male from 23 to 27 October 1994, and for five males between 21 and 30 October 1995.

Hypothesis 2: The PCV is directed at males and is related to current body condition

From the results of the analysis on the PCV for one male on 3 days in 1994, aimed at determining if PCVs declined within days when males gained many matings, it was apparent that the PCV might indicate a long term loss of condition (23, 24, and 27 October, see mean PCVs for male one below). Therefore we examined the variation in PCV on these 3 days. We could not carry out this analysis for other males in 1994 or for males in 1995, because they did not gain large numbers of matings on days that were several days apart.

To further examine a possible link between the PCV and current body condition, we adopted an approach that allowed us to include a larger number of males for each year. Fallow bucks do not begin to participate in the breeding season simultaneously, and as stated earlier, the skew in mating success is also high (McElligott et al., 1998, 1999). Therefore, we assigned two variables to each PCV, as proxy indicators of male participation in the rut; the number of days since a male's first mating and the proportion of his total mating success. The PCV for each mating was assigned, post hoc, a value expressed as a proportion of the breeding season's total mating success for that male. It serves as an indicator, in retrospect, of how close the male was to the end of his mating success. Therefore the first variable normalizes the males for the start of their mating success, and the second normalizes the total mating success of each male to one. We used data from six males in 1994 and five males in 1995 for this analysis.

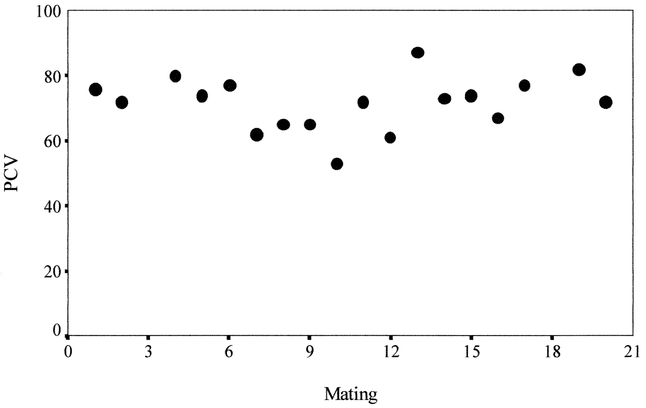

Figure 1
Relationship between the PCV and the daily order of matings on 24 October 1994, when male one gained 22 matings ($r = .09$, $p = .36$, $n = 18$, mean PCV = 71.6 ± 2.0).

Statistical analysis

We carried out statistical tests using SPSS. We log-transformed two of the data sets (indicated in Table 1) in the stepwise multiple regression and partial correlation analyses to improve the normality of their distributions (Kolmogorov-Smirnov test). This was not necessary with any of the other data. We used multiple regression analysis to determine the variation (r^2) in PCV explained by the two variables used as indicators of male investment in the rut. However, because of collinearity between these variables, we used partial correlations to check our result. For all analyses in which we made a priori predictions regarding the direction of results (Hypothesis 1), p values are one-tailed. Means are given with standard errors.

RESULTS

Hypothesis 1: The PCV is directed at females and is related to the fertility of the male

PCVs did not decrease as males gained matings during the day (see e.g., Figure 1). Similarly, the relationship for the same male on two additional days, and three different males, was also not significant (male 1, 23 October, $r = .44$, $p = .08$, $n = 12$, mean PCV = 79.1 ± 2.2; male 1, 27 October, $r = .33$, $p = .19$, $n = 9$, mean PCV = 51.2 ± 3.9; male 2, $r = -.38$, $p = .23$, $n = 6$, mean PCV = 73.5 ± 1.4; male 3, $r = -.19$, $p = .36$, $n = 6$, mean PCV = 77.7 ± 2.1; male 4, $r = .03$, $p = .49$, $n = 7$, mean PCV = 72.7 ± 1.4). PCVs did not increase as the time elapsed since the previous mating increased (Figures 2 and 3). Similarly, there was no effect of time since last mating on the PCV when data for some days in 1994 were considered singly (23 October, $y = 76.7 + 0.002\,x$, $n = 10$, $r = .12$, $p = .75$, $r^2 = .40$; 24 October, $y = 61.9 + 0.008\,x$, $n = 17$, $r = .36$, $p = .15$, $r^2 = .23$; 27 October, $y = 42.3 + 0.008\,x$, $n = 8$, $r = .48$, $p = .23$, $r^2 = .16$).

For double-mating females, the PCVs of their first matings (mean = 72.6 ± 2.2, $n = 17$), did not differ from the PCVs following the matings of females that mated once (mean = 71.5 ± 1.0, $n = 124$; $t = 0.38$, df = 139, $p = .70$). Further-

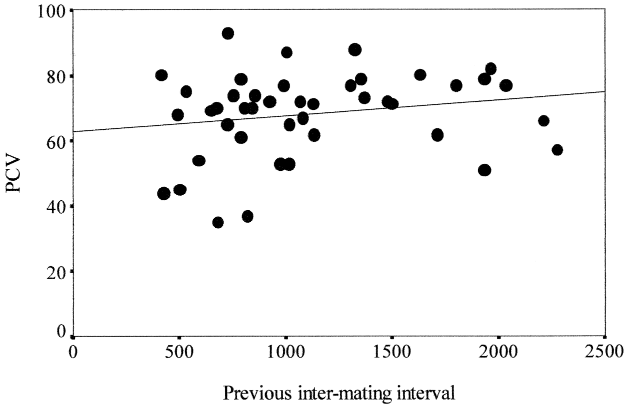

Figure 2
Relationship between previous inter-mating interval and the PCV for one male, 23–27 October 1994. Equation of the regression: $y = 62.7 + 0.005$ x, $n = 43$, $r = .19$, $p = .2$, $r^2 = .04$.

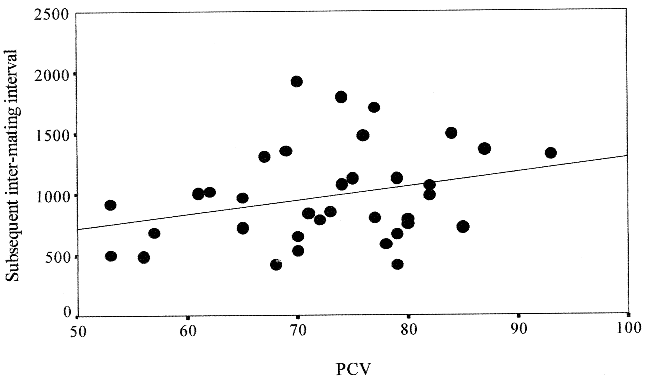

Figure 4
Relationship between the PCV and subsequent inter-mating interval for one male, 23–27 October 1994. Equation of the regression: $y = 147 + 11.5$ x, $n = 35$, $r = .28$, $p = .1$, $r^2 = .08$.

more, for double-mating females for which we had the PCVs accompanying both matings, the PCVs of the first mating (mean = 72.7 ± 2.8, $n = 10$), were not lower than those of the second mating (mean = 67.9 ± 3.6, $n = 10$). In fact, the reverse was the case (paired t test, $t = 2.8$, df = 9, $p = .02$).

The PCVs of infertile matings (mean = 71.9 ± 2.7, $n = 22$), that is, the females that mated again in November, did not differ from the PCVs following the matings of females that mated once (mean = 71.5 ± 1.0, $n = 124$; $t = 0.14$, df = 144, $p = .89$).

We found that the subsequent inter-mating intervals were not shorter when PCVs were high (Figures 4 and 5), indicating that the time to a male's next mating was not influenced by his PCV.

Hypothesis 2: The PCV is directed at males and is related to current body condition

There was significant variation in the PCV for male one on the 3 days examined ($F_{2,36} = 26.4$, $n = 39$, $p < .0001$), with the mean PCV on 23 and 24 October significantly higher than on 27 October (Scheffé test at $p < .05$).

We found that as males approached the end of their matings, their PCVs declined; the proportion of total mating success influenced the PCV, although the variation explained was low (Table 1). The number of days since a male achieved its first mating had no additional effect. Partial correlation analysis confirmed this result. When the relationship between the proportion of total mating success and PCV was controlled, the number of days since a male achieved its first mating was not significantly related to the PCV ($p = .49$). Conversely, when the relationship between the number of days since a male achieved its first mating and the PCV was controlled, the relationship between the proportion of total mating success and PCV remained significant ($p < .001$).

DISCUSSION

We found no evidence to suggest that the PCV was involved in transmitting a signal of fertility assurance, either to females that had mated, or to those that were about to mate. PCVs did not decline during days when a male gained many matings, and males did not produce higher PCVs when they had larger intervals between matings. Lower PCVs were not associated with infertile matings, and for females that mated twice within the same estrus, the PCVs of their first matings were not lower than other PCVs. In addition, higher PCVs were not associated with shorter intervals to a male's next mating. Since PCVs declined as males reached the end of their mating success, it suggests that they may be involved in transmitting an intrasexual threat signal related to current male condition and/or motivation. McElligott and Hayden (1999) found that

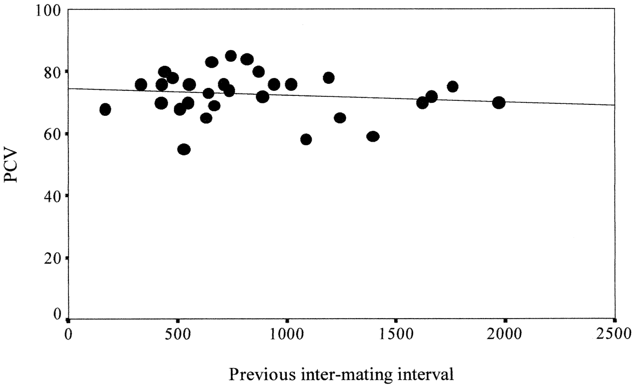

Figure 3
Relationship between previous inter-mating interval and the PCV for five males, 21–30 October 1995. Equation of the regression: $y = 74.5–0.002$ x, $n = 30$, $r = .14$, $p = .47$, $r^2 = .02$.

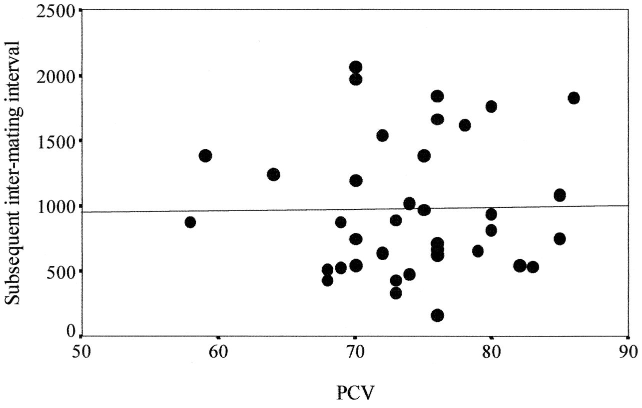

Figure 5
Relationship between the PCV and subsequent inter-mating interval for the five most successful males, 21–30 October 1995. Equation of the regression: $y = 880.4 + 1.4$ x, $n = 37$, $r = .02$, $p = .9$, $r^2 = .0003$.

PCVs are highest when the potential threat from other males is greatest, thereby providing additional support for this hypothesis.

If the PCV is directed at males, its main role is probably in mate guarding, and also possibly maintaining the integrity of a harem, if present. The intensity of the display may be necessary if the possibility exists for the receptive estrous female to re-mate immediately, and also if the mated male undergoes a refractory period after copulation (Fraser, 1968). In our study population, 16% of females mate more than once within the same estrus (McElligott, 1997), and therefore sperm competition could affect the reproductive success of a male that has mated. The PCV clearly announces to other males the presence of an estrous female. At first this might seem risky, but if males can detect the presence of an estrous female anyway (by observation or olfaction), then it might be a viable strategy for the mated male to give an indication of his current vigor. Møller (1988, 1991) suggested a similar hypothesis to explain why male yellowhammers (*Emberiza citrinella*) and other male birds sing most during the most fertile period of their mates. A difficulty with this idea is that for the fallow bucks competing for matings, indications as to the declining condition of the consort male are only available after he has successfully mated. Their interests would have been better served if they could have obtained the information regarding the consort male before he mated. Nevertheless, the PCV could provide information that other males could use at the next mating opportunity. Since estrous females have a tendency to join a male when he is mating (Clutton-Brock et al., 1988), it is likely that other estrous females and therefore additional mating opportunities, would also be present.

Recent research suggests that fallow does in non-lekking populations may choose their mates based on male quality (Komers et al., 1999; McElligott et al., 1999). If mate copying was also involved in the mating success of fallow bucks, then the PCV could be a factor, by announcing that a male had mated. However, of course, this could not be considered copying in the strict sense of the term (Pruett-Jones, 1992). Although there is currently no evidence to suggest that copying plays a role in the mating success of fallow bucks, it may be useful to explore this through further research. Moreover, our results do not provide any support for copying linked to the PCV, since the intervals to a male's next mating were not shorter if his PCV was high.

Fallow bucks groan at variable rates that seem to represent the value of their current resources and also the potential threat from other males (McElligott and Hayden, 1999). Since the PCV is the highest groaning rate that fallow bucks attain, it could be considered the only truly honest advertisement of current male condition or motivation that is transmitted by short-term vocalization rates (Clutton-Brock and Albon, 1979; Payne and Pagel, 1996). Although it is currently not feasible to measure the cost of producing the PCV, there are a number of factors that suggest that it may be expensive. The magnitude of the display, in terms of groaning rate, is very high (see Figures 1–3) and also cannot be maintained for long at this level (McElligott and Hayden, 1999). In addition, the proportion of males in the population that produce groaning rates at this level each year is very low, since it is only those that gain matings, and mating success is highly skewed (McElligott et al., 1998, 1999). Thus changes in the PCV of a fallow buck may indicate to opponents the shifting nature of the asymmetry in their competitiveness (Enquist and Leimar, 1983). Late in the rut, the difference in dominance ranks between males that fight increases (McElligott et al., 1998). This indicates that fallow bucks monitor changes in the condition of other males, although the exact manner in which this information is obtained is not yet clear.

A change in vocal activity associated with the possibility of sperm competition has also been found, for example, in Grevy's zebra (*Equus grevyi*). In this species, males vocalized more when mating with promiscuous females and the increased level of vocal activity acts in a mate guarding capacity (Ginsberg and Rubenstein, 1990). In bison (*Bison bison*), male bellowing is also involved in mate-guarding. However, after mating, the rate of vocalization drops to 16% of its precopulatory level (Berger and Cunningham, 1991). Sika deer stags (*Cervus nippon*) also engage in mate guarding when females have a tendency for extra-pair matings (Endo et al., 1997), although their vocalizations do not appear to be involved.

In conclusion, the available evidence suggests that PCV functions primarily as an intrasexual threat. This threat display is likely to be directed at any number of competing males, and could therefore be considered to be an example of signaling in a communication network (McGregor and Dabelsteen, 1996). Although the variation in PCV explained by male investment in the rut was not very high (15%), we suggest that this probably results from PCVs becoming less frequent as males approach the end of their mating success. Moreover as soon as the body condition declines, the likelihood that males are replaced by competitors that then gain the available matings increases (McElligott et al., 1998).

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