Red Deer (Cervus elaphus) Hinds Discriminate Between the Roars of Their Current Harem-Holder Stag and Those of Neighbouring Stags

David Reby, Mark Hewison, Marta Izquierdo & Dominique Pépin


Abstract

During the period of reproduction red deer stags gather harems and roar loudly and repeatedly, both toward competing stags and toward the hinds that they actively herd. It has been proposed that red deer hinds may actively choose their mate on the basis of a comparison of the roaring rate of competing stags. Hinds may also choose to mate with the male that is most familiar to them, i.e. that male who spent most time and effort in retaining them within his harem and in roaring at them. Such a mechanism of female choice implies that females are able to discriminate individual characteristics in the stags' roars. We investigated this possibility by conducting playback experiments based on the habituation–discrimination paradigm. Our results show that hinds are able to discriminate between the roars of their current harem-holder stag and those of other neighbouring stags and suggest that this ability, a necessity for individual recognition, may be important in female mate choice in red deer.

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Introduction

Red deer stags call loudly and repeatedly during the period of reproduction. The period of vocal activity lasts approximately 4–5 wks during which the roaring rate of an individual is highly variable, with periods of low roaring activity (2 roars per min) and more intensive phases generally corresponding to
male–male contests (Clutton-Brock & Albon 1979). Roaring repeatedly may be costly (in terms of energy expenditure and probability of detection by predators) and could therefore constitute an honest predictor of stag body condition (body weight and roaring ability decline over the course of a breeding season). Clutton-Brock & Albon (1979) found evidence that red deer stags use roaring contests to assess each other’s fighting ability, thereby avoiding potentially costly confrontation. McComb (1988, 1991) hypothesized that roaring in red deer stags also serves to attract females. While the pitch of the roar was found to be a poor predictor of male body condition (and fighting success), playback experiments suggested that females may instead rely simply on roaring rate to choose a partner for reproduction. Indeed, females were preferentially attracted to males with high roaring rates, but were indifferent to variations in roar pitch (McComb 1991). As red deer hinds regularly enter and leave the harems of reproductive stags (Clutton-Brock et al. 1982), it was proposed that they may choose which harem to join on the basis of roaring rate, a potentially reliable indicator of stag quality. Such a schema implies that females make an active choice on the basis of their assessment of the roaring rates of competing males.

Over the course of the breeding period, hinds may become progressively and passively familiarized to the vocalizations of the stag by which they are most herded. Thus, while absolute roaring rate (a purely quantitative concept) is certainly of great importance to hinds’ mate choice, familiarity, resulting from a combination of the duration of exposure, the rate, the loudness (harem holders’ roars will be received at a higher level of amplitude), and the context of the exposure (combined with tactile, visual and olfactory interactions specific to the harem-holder stag) may also be of great importance. The subsequent ‘familiarity’ of that stag may be a reliable indicator of male quality as it represents both the stag’s ability to roar at a high rate, but also its ability to retain the female within its harem. Therefore, females could be selected for choosing to mate with males that are most familiar to them. This ‘mate-investment hypothesis’ through familiarization has been proposed for other mammal species (spotted hyena Crocota crocuta: East & Hofer 1991; mouse lemur Microcebus murinus: Zimmerman & Lerch 1993). Such a mechanism requires that three conditions are met:

1 Stags possess vocalizations that are individually distinct.
2 These individual vocal cues are salient for, and distinguishable by, females.
3 ‘Familiarity’ actually influences hinds’ mate choice.

Potential features for individual vocal recognition exist in the acoustic structure of loud calls emitted during the reproduction period by males of polygynous deer species (fallow deer Dama dama: Reby et al. 1998; red deer: McComb 1988; Reby 1998). In this paper, our purpose is to test the second of the above conditions, that females are able to discriminate between their current harem holder and neighbouring stags on the basis of their vocalizations.
Methods

Experimental Site and Animals

The study was carried out at the Institut National de la Recherche Agronomique experimental red deer farm at Redon which is located near Theix, Puy de Dome (France), from early Sep. until the middle of Oct. 1996. Four adult stags and 24 adult hinds were used in the experiment. Stag 1 and Stag 2 were 5 and 8 yr old, with respective body weights of 210 and 230 kg. They were kept into two adjacent paddocks and each was given a group of 12 adult hinds, with ages ranging from 3 to 8 yr. Thus, these stags represented the harem holder for each of the tested groups and were considered ‘very familiar’ to them. Two other adult stags (Stag 3 and Stag 4, both 6 yr old, with respective body weights of 210 and 215 kg) were kept in two other neighbouring enclosures, each with a group of hinds which were not considered in this study. Therefore, the two groups of tested females were considered to be only ‘familiar’ with the two latter stags, as only visual and auditory contact could occur.

Both groups of tested hinds were randomly subdivided into four experimental subgroups of three hinds each (Stag 1 group: 1a, 1b, 1c, 1d; Stag 2 group: 2a, 2b, 2c, 2d). Because the hormonal status of hinds may influence their reaction to stag vocalizations, we controlled and synchronized hind ovulation during the experiment. For this purpose, we used intravaginal sponges providing a continuous release of progesterone for a period of 12–15 d (Thimonier & Sempéré 1989) to inhibit the normal hormone cycle associated with oestrus (Kelly et al. 1982). The date of introduction and removal of intravaginal sponges for each hind subgroup are given in Table 1. Immediately after the removal of the intravaginal sponges, an injection of 400 UI of PMSG (pregnant mare serum gonadotrophin) was given to induce oestrus and ovulation 48 h later. We performed our playback experiment just before intravaginal sponge removal (i.e. 48 h before oestrus), the period when the choice of harem by females may have the greatest importance for reproduction of both sexes. In order to examine possible variation in hind discrimination abilities in relation to hormonal status, we also repeated the experiment during oestrus and 6–8 d after oestrus. However, probably due to a pronounced

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<th>Hind subgroups</th>
<th>Intravaginal sponges</th>
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<td>Date of insertion</td>
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<tr>
<td>Stag 1</td>
<td>9th Sep.</td>
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<td>1a &amp; 1b</td>
<td>11th Sep.</td>
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<td>Stag 2</td>
<td>16th Sep.</td>
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<td>2a &amp; 2b</td>
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Table 1: Experimental protocol to control hormonal status of hinds at the Redon red deer farm. The playback tests were carried out just before the removal of intravaginal sponges.
habituation to the experimental design, hinds reacted very rarely to the playbacks conducted during the oestrus and the post-oestrus periods. Therefore, only the results concerning the pre-oestrus period were analysed and are considered and discussed in this paper.

**Vocalization Recording**

Two weeks before the playback trials, all four stags began to roar and herd their hinds. In the week preceding the start of playback experiments, we recorded roars from the four stags using a Telinga pro-III-S/(DAT) Mike microphone (Telinga, Tobo, Sweden) and a DAT Sony TCD-D7 recorder (amplitude resolution: 16 bits, sampling rate: 48 kHz). Stags were recorded at distances ranging between 2 and 10 m. Recorded vocalizations were directly transferred via an Audiomedia II (Digidesign, Palo Alto, CA) soundcard to a Macintosh Quadra 950 computer with Sound Designer software (input: digital, 16 bits, 48 kHz). Sound amplitude was then adjusted in order to ensure that all stimuli have standardized sound pressure level.

**Playback Trials**

Red deer emit bouts of 1–10 roars (McComb 1988; Reby 1998). In order to standardize the experimental protocol, only single roar bouts of comparable duration were used to constitute the playback series. We used the habituation–discrimination paradigm to evaluate the ability of hinds to discriminate between vocalizations of different individual stags (see Cheney & Seyfarth 1988; Johnston & Jernigan 1994; Hauser 1996; Rendall et al. 1996; Hare 1998). The ability of a subject to discriminate between two individuals on the basis of their vocalizations is inferred from the subjects’ reaction to a change in stimulus. First, the subject is habituated to type-A stimulus through repeated exposure. Then type-B stimulus is provided (dishabituation) and discrimination is inferred if the subject shows a renewal in the level of response. Finally, the subject is re-exposed to type-A stimulus again (rehabilitation). Consequently, our playback series were composed of 12 different single roars of comparable length and structure, separated by 20-s intervals of silence. The first 10 roars and the twelfth roar in the series were all from different bouts of the same individual (stag ‘A’), whereas the eleventh came from a different one (stag ‘B’, Fig. 1). Thus, we aimed to provoke habituation to the roars of stag ‘A’ (roars 1–10), and then, by playing a vocalization from a different individual (stag ‘B’, roar 11), to test if the hind detects changes in the roar’s features. If so, we expect the hind to show a heightened level of reaction to the eleventh roar (stag ‘B’), equivalent to that observed for the first vocalization of the series. The twelfth vocalization in the series was from stag ‘A’, and is played to test if the observed rebound for roar 11 was not merely chance; thus, if the female remains habituated to the initial caller, we expect the level of reaction to fall again. To ensure a symmetric experimental design (Hauser 1996), hinds were alternatively habituated with roars from their
harem holder then dishabituated with roars from one of the three other (familiar) stags, or vice versa.

**Playback Equipment and Timing**

Playback experiments were conducted directly from the Quadra 950 computer connected to a Liberty Sound System (Anchor Audio, Torrance, CA) by a 25-m coaxial cable. We used the Sound Designer software to play the sound files. Sound level settings of the software and of the Liberty speaker were constant during all the playback experiments. The playback tests were conducted in the morning (07:00–09:30 h) in a separate paddock, apart from their stag, but in which the hinds were regularly kept. Because red deer hinds are gregarious, we could not test them individually. Tests were therefore conducted on subgroups of three individuals. Five minutes before the start of the experiment the hinds were introduced into the paddock and fed with some wheat at 20 m from the speaker. Then, the behaviour of females was videotaped from 2 min prior to the playback experiment period until 2 min after it. Two cameras were used, the first one was focused on the hinds at the feeding area and the second had a wide-angle lens in order to record the behaviour of the females all over the paddock.

**Behavioural Analyses**

Videotapes were time coded and analysed with Observer VTA for Windows Software (Noldus, Wageningen, Netherlands). Sequences were played frame by frame and duration of a given behaviour was noted to the nearest 0.04 s. All time measurements were checked twice by two separate observers. Behaviours of each hind were classified into three distinct categories: attention oriented toward the speakers (orienting ears toward the source or looking in the direction of the source); attention not oriented toward speakers; and ‘others’ (interactions, feeding, grooming, etc.). We considered that a hind responded to the playback whenever it modified its current behaviour in a way that increased its level of attention directed toward the source (speakers). We quantified the reactivity of hinds with two behavioural parameters: response latency and response duration. Response latency is defined as the time lapse between the onset of the roar playback and the onset of the behavioural response. Response duration is the length of the response, and does not exceed the interval between two roars in the playback series (20 s + the considered roar duration). In order to limit the amount of variation in the behavioural data caused by individual hinds that displayed stress-related behaviours distracting them from the vocalization broadcast, we decided to apply a preselected criterion for each individual hind to enter the statistical analyses: we eliminated those hinds that reacted less than 3 times out of 10 in the habituation series. Because the behaviour of each individual in the subgroup may be influenced by the behaviour of the others, analyses of hind responses were not considered independently. Therefore, the
behavioural response of the three individuals was averaged to characterize the group response.

**Statistical Tests**

In order to test whether habituation occurred, we looked for significant differences in latency and duration between roar 1 (R1) and roar 10 (R10). Similarly, we tested whether dishabituation occurred by looking for differences between R10 and R11, and whether rehabituation occurred by looking for differences between R11 and R12. For all tests, we conducted one-tailed ‘permutation tests for paired samples’ (Siegel & Castellan 1988). Thus, we tested the following hypotheses: Duration (R1) > Duration (R10), Duration (R10) < Duration (R11), Duration (R11) > Duration (R12), Latency (R1) < Latency (R10), Latency (R10) > Latency (R11), Latency (R11) < Latency (R12).

**Results**

Seventeen of the 21 hinds from 7 subgroups responded to the playback trial. The subgroup 1c was eliminated from the analysis because hinds were stressed and moved continuously inside the paddock, without paying attention to any of the broadcast vocalizations. Four other hinds that displayed similar behaviour were also rejected because they failed to meet our criterion of reacting to more than 3 roars out of 10 in the habituation series.

Between the first playback (R1) and the last playback (R10) in the habituation series, response duration decreased significantly (p = 0.039, n = 7) and response latency increased significantly (p = 0.016, n = 7), showing that the hinds had become habituated to the broadcasting of different roars from a single individual (Fig. 1). The unexpected increase of attention toward the loudspeakers, which occurs between R5 and R8 of the habituation series, and which is characterized by a temporary increase in response duration and decrease in response latency, was due to a decrease in the feeding activity of some of the hinds, and suggests that our habituation series was longer than necessary.

For the dishabituation playback (R11), response duration abruptly increased (p = 0.008, n = 7), and latency abruptly decreased (p = 0.016, n = 7). For both parameters, the levels of response to R11 were comparable to the response level for the first playback (R1) in the habituation series. Lastly, in the rehabilitation playback (R12), response duration decreased (p = 0.008, n = 7) and latency increased (p = 0.039, n = 7) relative to R11, returning as expected to the levels of response observed at the end of the habituation series (R10).

**Discussion**

In this experiment, hinds showed a significant rebound in reaction to the dishabituation test. The rehabilitation control (R12) indicates that this rebound
was not a spontaneous recovery of response level. Following Rendall et al. (1996), we used 10 different roars from a single individual in a given habituation series in order to ensure that hinds became habituated to the individual content of different calls, and not to the repetition of a single call. However, as Hare (1998) points out, dishabituation may result from the fact that the call of the individual used for dishabituation (R11) is dissimilar to those used in the habituation series (R1–R10) from a single individual. In other words, hinds do not respond to the change of caller identity, but rather to a change in the similarity of consecutive calls. However, if this was the case in our experiment, we would expect the level of reaction to R12 to remain high, as R12 is presumably equally dissimilar to R11. In fact, we observed a subsequent decrease of reaction level in the rehabituation playback (R12), which argues

Fig. 1: Response duration (a) and latency (b) of red deer hind groups (groups: n = 7, individuals: n = 17) to the playback of stag roars. R1–R10: habituation series (Stag ‘A’); R11: dishabituation playback (Stag ‘B’); R12: rehabituation playback (Stag ‘A’).
against this hypothesis, and strongly suggests that habituation occurred to the vocalizations of stag ‘A’, rather than to a series of similar stimuli. Therefore, we conclude that these female red deer are capable of discriminating between roars of two different individuals, which, in our experiment were their harem-holder vs. neighbouring stags. Although these results do not imply the existence of an individual recognition mechanism, they suggest that hinds have the ability to discriminate between roars from individuals differing by their degrees of familiarity. It should be noted that our small sample size (only 2 harem holders were involved in the experiment) may affect the generalization of our results. However, the fact that we used roars from adult stags of comparable body weight significantly reduces the size-related acoustic variation potentially occurring between senders in a natural environment and should therefore reduce this problem.

In mammals, most individual vocal recognition studies have concerned mother–young relationships (e.g. reindeer Rangifer tarandus: Epsmark 1971, 1975; red deer: Vankova et al. 1997), contact calling (Rhesus monkeys Macaca mulatta: Rendall et al. 1996) or alarm calling (Richardson’s ground squirrel Spermophilus richardsonii: Hare 1998). To our knowledge, this is the first demonstration for a mammalian species that females discriminate between the mating calls of individual males.

As in this experiment, the call rate, the playback loudness and the roar length were controlled and constant, discrimination was not due to any of these potentially confounding factors. It has been proposed that call rate or signal amplitude directly influence female attraction in vertebrates’ polygynous species where males call loudly during the breeding season (Gerhardt 1991; McComb 1988; McComb 1991). In a species such as red deer, where unstable harems are formed, and where males invest time and energy in gathering females and roaring repeatedly at them, we propose that the familiarization of females to a certain male may also influence their choice. Indeed, cumulative display intensity (short-term roaring rate combined with time spent roaring and herding) may be a reliable cue of male genetic quality. This may particularly be the case where an individual’s roaring rate is highly variable over the course of the breeding season (as is the case for red deer, Clutton-Brock & Albon 1979) and therefore more likely to reflect current body condition or fighting ability rather than genetic quality.

Though we have demonstrated in this study that individuality in the acoustic structure of stags’ roars is salient for hinds, we do not have any evidence that these individual cues (alone or together with olfactory and visual cues) actually influence females’ mate choice in the wild. Thus, the next step to understanding the role of individuality in the roars of red deer stags during the rut will therefore require playback experiments to elucidate the ‘choice’ behaviour of hinds in response to roars from individual stags of varying degrees of familiarity.
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