



Contexts and possible functions of barking in roe deer

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We studied the barking behaviour of free-ranging roe deer, *Capreolus capreolus*, in response to disturbance provoked by a human observer and in response to the playback of recorded barks. Three alternative functions of this behaviour were hypothesized: barking is an alarm call, a pursuit-deterrent call or a territorial call. Our observational data showed that, in the presence of a source of disturbance, solitary individuals barked more frequently than deer in groups, suggesting that barking does not serve to warn conspecifics of potential danger, but rather to inform any potential predator that it has been identified. The frequencies of both barking and counterbarking (barking of a second deer in response to the barks of an initiator) were inversely correlated with ambient luminosity, probably because the assessment of danger is more difficult when visibility is low. Males barked more frequently than females when disturbed. Moreover, when we played back a series of barks from within a buck's territory, this provoked counterbarking or aggressive behaviours rather than flight. Older bucks responded more frequently to playbacks than younger bucks. We suggest that while barking may initially have evolved as a signal to deter predator pursuit, it could play an important, secondary role in the territorial system of this species.

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Species of the family Cervidae make loud, harsh calls when they detect potential danger (Putman 1988). Most Cervinae species bark: red deer, *Cervus elaphus* (Long et al. 1998), fallow deer, *Dama dama* (Alvarez et al. 1975), sika deer, *Cervus nippon* (Long et al. 1998), sambar, *Cervus unicolor* (Schaller 1967), chital, *Axis axis* (Schaller 1967), Chinese water deer, *Hydropotes inermis* (Cooke & Farrell 1998), Indian muntjac, *Muntiacus muntjac* (Wiles & Weeks 1981) and Chinese muntjac, *Muntiacus reevesi* (Yahner 1980); while circumpolar and North and South American Odocoileinae snort: reindeer, *Rangifer tarandus* (Lent 1975), white-tailed deer, *Odocoileus virginianus* (Hirth & McCullough 1977; LaGory 1987), pampas deer, *Ozotoceros bezoarticus* (Jackson 1985) and brocket, *Mazama sp.* (Sarmiento 1988). Two adaptive functions have been discussed for barking or snorting in cervids: Hirth & McCullough (1977) found that snorting in white-tailed deer was more common in groups of probably related individuals ('doe groups') than in groups of unrelated individuals ('buck groups') and suggested that snorts were used to warn nearby kin of potential danger. However, the observations of Yahner (1980) on Chinese muntjac and LaGory (1987) on white-tailed deer did not support this hypothesis, and both authors suggested that

barking signals to the predator that it has been detected, discouraging further pursuit. Indeed, Caro (1994) reached similar conclusions concerning the adaptive significance of snorting in African bovids.

Roe deer, *Capreolus capreolus* (Odocoileinae), make particularly loud, conspicuous barks when they detect a source of disturbance (see Hewison et al. 1998). While barking in roe deer is usually classified as an 'alarm call', it could also play a role in the territorial system of this species (Prior 1995; Danilkin & Hewison 1996). Typically, a disturbed deer heads towards shelter, bounding and making staccato barks, which are comparable to the yapping of a dog. Then, it stops, adopts a stilted gait and barks loudly and repeatedly from a standing position, moving its head up and down and from side to side, occasionally also foot stamping or tree marking. Barks given from a standing position are regularly spaced at a mean rate of 14 barks/min (Hewison et al. 1998). Such series are often interspersed by series of yaps as the deer bounds from one position to another. Neighbouring deer sometimes counterbark antiphonally in response to the bark of the initiator.

Since roe deer are difficult to observe, and because captive animals rarely bark, barking in this species has not yet been studied and its function remains unclear. In this paper, we examine the influence of seasonal and environmental factors on barking in response to the presence of a human observer. We also investigate which

age–sex classes of deer bark and in which social contexts. Specifically, we address the following questions.

(1) Is barking an antipredator behaviour? If so, we expect barking to occur in both sexes and all age classes in the presence of a potential source of danger, particularly when low visibility makes identifying the source of disturbance difficult. (a) If barking is an alarm call, it should be given more frequently by individuals within groups and barking should provoke flight in the other group members. If its function is to ensure that nearby kin are aware of any danger (Hirth & McCullough 1977), it should occur mainly in groups of related individuals (i.e. a female with its fawns). We would also expect females to bark more frequently than males as they are more likely to have kin in the vicinity (see Caro 1994), being generally more philopatric than males (Bideau et al. 1993) and forming matrilinear clans (Kurt 1968). (b) If barking is a pursuit-deterrent signal (Tilson & Norton 1981; Caro 1994), we expect that in the presence of potential danger, solitary individuals will be equally likely to bark as individuals in groups.

(2) Is barking a territorial call? If barking has a role in territory maintenance (territory marking), as females and subadult males are not territorial in this species, barking should occur mainly in adult males, particularly during the territorial period. We also expect counterbarking to be given mainly in response to barks of bucks, and barking within an individual's territory to elicit aggressive reactions in territorial bucks.

We also compare the contextual characteristics of barking in roe deer with those observed in some other cervid species, in relation to social system and habitat.

METHODS

Study Species

The roe deer is a small cervid which typically lives in closed, predominantly wooded habitat. It is probably closely related to the common ancestor of the *Odocoileinae* (Putman 1988; Danilkin & Hewison 1996) and its social organization is regarded as primitive (Putman 1988; Hewison et al. 1998). During the winter, roe deer gather in small groups corresponding to family units of a buck, a doe and up to three fawns (Bideau et al. 1983), although larger groups are found in the open plains. In wooded habitat, adult bucks are territorial from mid-March to the end of August, the rut takes place from mid-July to mid-August (Bramley 1970), and most births occur from mid-May to mid-June (Gaillard et al. 1993).

Study Area

We carried out the study in the Fabas forest, near Toulouse, Haute-Garonne, southwest France (43°21'N, 0°51'E) which is situated in a landscape fragmented by agricultural activity. It is a mixed forest of oak, *Quercus* sp., fir, *Abies* sp., pine, *Pinus* sp. and hornbeam, *Carpinus betulus*, covering ca. 600 ha and undulating in altitude between 250 and 300 m in a series of ridges and shallow

valleys. The openness of the habitat is variable: we estimated the average distance at which it would be possible to detect roe deer visually as 35 m in March 1997 (using the Leica Vector 1500 DAE rangefinder binocular, unpublished data), but this varied from a few metres in certain areas with a dense coppice regrowth understorey to more than 100 m in areas of mature pine. An extensive network of roadways and trails afforded excellent penetration, facilitating observation throughout the study site.

Study Population

The roe deer are free ranging and are regularly hunted between September and January. In February 1996 and 1997, we carried out largescale net catches to capture and mark deer. On capture, the deer were processed immediately, without using anaesthetic; no adverse effects of the procedure were noted. Collars were self-extending to allow for growth and seasonal changes in neck girth. We captured and radiocollared three bucks in 1996 and five in 1997. The age classes of the bucks (one yearling, four subadults of 2–3 years, two adults of 4–6 years and one old buck of 7 or more years) were determined by tooth wear (Van Laere et al. 1989). In winter 1997, population density was estimated at 23 deer per 100 ha on a 150-ha sample plot located within the study area using capture–mark–recapture techniques (Reby et al. 1998), giving a total population estimate of about 140 animals in the forest.

Data Collection and Study Periods

Uncontrolled disturbances

We collected observational data when walking four different transects of approximately 4 km each at dawn and dusk (duration 90–150 min). We assessed the daily pattern of barking frequency during a preliminary survey in spring 1995 which indicated that roe deer barked most frequently at dawn and dusk. Roe deer are also most active then (Chapman et al. 1993). We collected data from 1 February to 31 June in 1996 and from 1 February to 15 August in 1997, in order to include the preterritorial period (1 February to 15 March), the territorial period (16 March to 15 July) and the rut (16 July to 15 August). A total of 658 crepuscular transects were walked (preterritoriality: $N=256$; territoriality: $N=356$; rut: $N=46$). On each occasion that we disturbed and observed roe deer, we noted their position on a map. We also noted group size and age–sex composition (fawn: <1 year; yearling: 1–2 years; adult: >2 years). To ensure that the deer had detected our presence, only animals that fled or displayed vigilance behaviours (stilted gait, rapid head movement, foot stamping) were considered. We noted whether the observed animal(s) barked and if other deer in the vicinity responded by counterbarking. When barks from visually unobserved animals were provoked, we noted their approximate location. Finally, we noted separately all barking that was judged to be too distant to be provoked

by the observer's presence, and these data were processed separately.

Individual approaches

During the territorial period of 1997, the eight radiocollared bucks of known age class were regularly and intentionally disturbed to evaluate their individual propensities to bark. For this, the same two observers radiotracked the animal to approach him as close as possible at a slow, steady speed, until the animal fled and/or barked. We used these data only when the animal was alone and counterbarking did not occur. Arbitrarily, we considered a period of 5 min after the flight of the animal before deciding whether he barked or not in response to this disturbance.

Playback experiments

We conducted experiments to assess the effect of broadcasting buck barks within the home range of other bucks. We recorded the vocalizations of seven of the radiocollared males (the eighth, a yearling, never barked, and was excluded from the experiment). From 24 June to 31 July 1997, we broadcast a series of barks of each animal to each of the other six, to compare the propensity of an individual to elicit counterbarking when its barks are played, with its own propensity to counterbark. As all seven marked animals inhabited an area of 150 ha, we assumed that each buck was potentially familiar with the vocalizations of all the others. We recorded barks at between 20 and 50 m from the animals with a Telinga pro-III-S/DAT Mike microphone and a DAT Sony TCD7 recorder (amplitude resolution: 16 bits, sampling rate: 48 kHz). Numerical sound files were imported on a Macintosh Quadra 950 with an Audiomeia 2 sound card and Sound Designer software. A playback sequence, consisting of 11 different barks regularly spaced by 4.75-s intervals of silence (calculated from the observed rate of natural barking; Hewison et al. 1998) was constituted for each individual with Sound Designer software. These were then transferred on to a digital audiotape, and played back from the TCD 7 on an Anchor Liberty MPb 4500 portable sound system providing a flat frequency response between 60 Hz and 16 kHz. We conducted playback experiments at dusk, between 1900 and 2100 hours. We approached the radiocollared buck to ca. 100 m and proceeded with the experiment only if the animal had not detected our presence (i.e. did not flee, bark or display vigilance behaviour). The series of barks was played once. The spatial behaviour (flight or approach) and vocal behaviour (latency and duration of the response) of the focal individual were arbitrarily recorded for the 5-min period after the onset of the playback. All playbacks were carried out from inside the seasonal home range of the focal buck (as estimated from radiotracking data), to simulate a territorial intrusion of the recorded individual.

Statistical Analyses

Depending on the question asked we used different subsets from our data pool. Set A ($N=1642$) included all

observations, while set B ($N=864$) included only those observations for which group size and age-sex composition were also determined. As not all animals were marked, we could not control for the possibility of multiple sampling of the same individuals.

We looked for variation in barking frequency (a binary variable: bark/no bark) between the three periods (pre-territoriality, territoriality, rut), two group sizes (solitary or group) and sexes, using a log-linear analysis (SPSS Logit procedure; Norusis 1994) on data set B (after checking that this variable was approximately binomially distributed). We also looked for variation in counterbarking (neighbours barking in response) between periods and sex of the initiator in the same way (set B).

A third log-linear analysis was performed on data set B to compare barking frequency of solitary females and females accompanied by offspring for the preterritoriality and territoriality periods (not enough data were available for the rut period).

We tested for a correlation between barking frequency (proportion of observed deer that barked) and luminosity using data set A. Sunset and sunrise timetables for the local area were obtained from the Bureau des Longitudes, CNRS. Taking sunrise and sunset as points 0, we defined 13 periods of 15 min each, ranging from -3 (i.e. 45–30 min prior to dawn or after dusk) to $+10$ (i.e. 135–150 min after dawn or prior to dusk). Thus we obtained an index of average luminosity increasing from -3 to $+10$. We then calculated the barking frequency for each of these 15-min periods and looked for a correlation between barking frequency and our luminosity index by using Kendall's correlation test.

We used Kendall's correlation test on the marked bucks only to look for a relationship between buck age and propensity to bark when disturbed. We used the same test to examine the relationship between an individual's propensity to bark in response to broadcasted barking and the propensity of other bucks to respond to that individual's broadcasted barking. Propensity to bark was defined as the proportion of occasions that a male responded by barking to a disturbance or a broadcast. All tests were two-tailed.

RESULTS

Uncontrolled Disturbances

Of 864 contacts, the majority (75.6%) were solitary individuals, 80.5% of groups were dyads, and the largest observed group comprised four individuals.

All age classes barked to some degree. Solitary yearlings barked on 41.2% of 34 occasions, while barking was even observed twice among 3–4-month-old fawns. In our log-linear analysis on adult deer, the effects of period, group size and sex did not interact significantly in their influence on barking frequency of adult roe deer (chi-square test: group*period*sex: $\chi^2_2=4.92$, $P=0.085$; group*period $\chi^2_2=1.46$, NS; period*sex: $\chi^2_2=3.60$, NS; sex*group: $\chi^2_1=2.81$, NS). Roe deer barked throughout the study period; however, the rate of barking increased significantly across the study periods ($\chi^2_2=41.71$, $P<0.0001$),

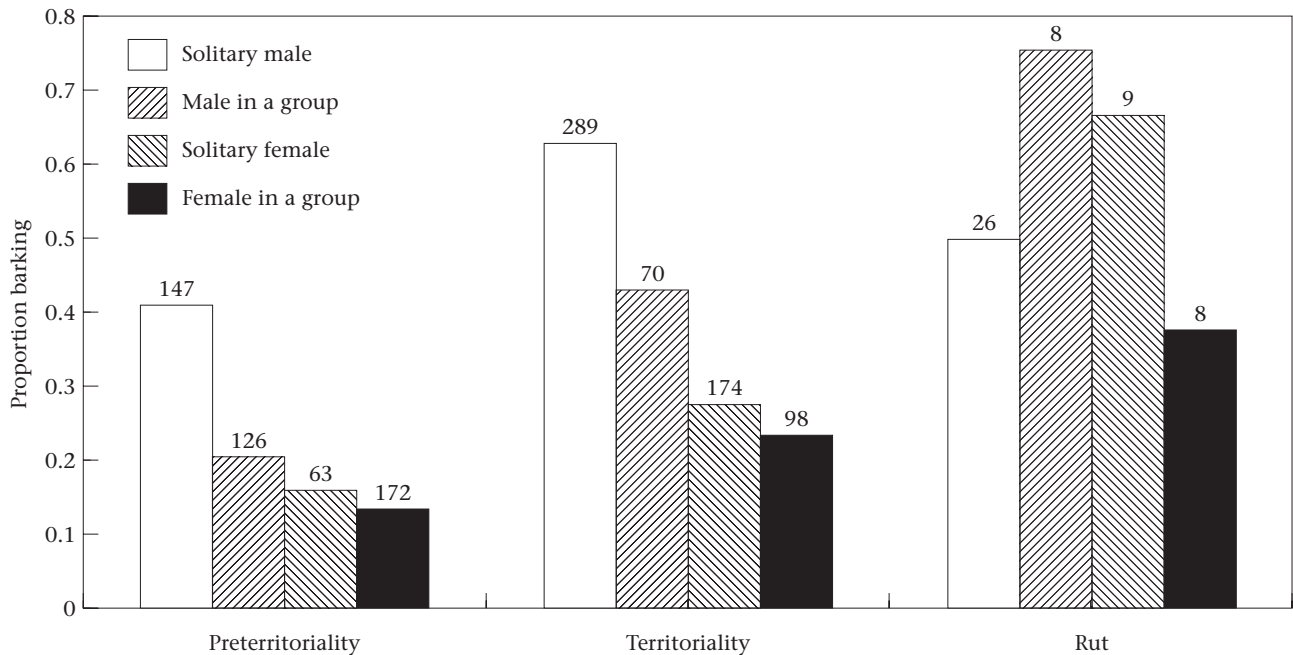


Figure 1. The proportion of adult roe deer that barked in response to a human observer during the study period. The numbers above the bars are the numbers of deer observed in each category.

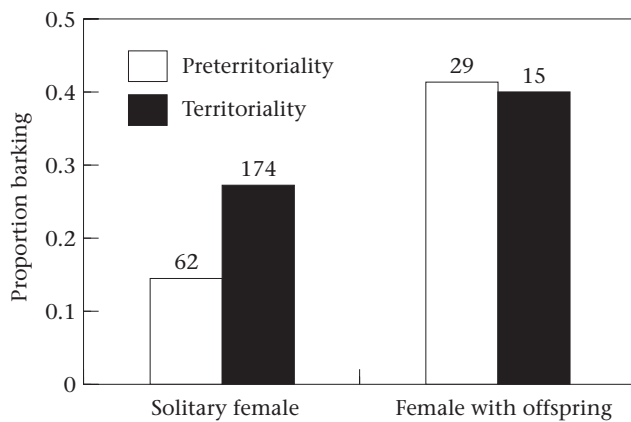


Figure 2. The proportion of solitary adult females and females with offspring that barked in response to a human observer. The numbers above the bars are the numbers of deer observed in each category.

reaching a peak during the rut (Fig. 1). Males barked significantly more than females ($\chi^2_1=68.32$, $P<0.0001$), and solitary individuals barked significantly more than individuals in groups ($\chi^2_1=15.66$, $P<0.001$), although solitary males barked rather less during the rut than expected. Solitary females barked significantly less than females with offspring, independently of the period considered (log-linear analysis; offspring*period: $\chi^2_1=1.31$, NS; presence of offspring: $\chi^2_1=7.29$, $P<0.01$; period: $\chi^2_1=3.3$, $P=0.069$; Fig. 2).

In 11.6% of cases, barking provoked counterbarking in neighbouring animals. Such reciprocal barking sessions included up to five deer from distinct localizations (average 2.4 deer). The frequency of counterbarking did not vary across the study period and buck barks did not elicit more reciprocal barking than female barks (log-linear

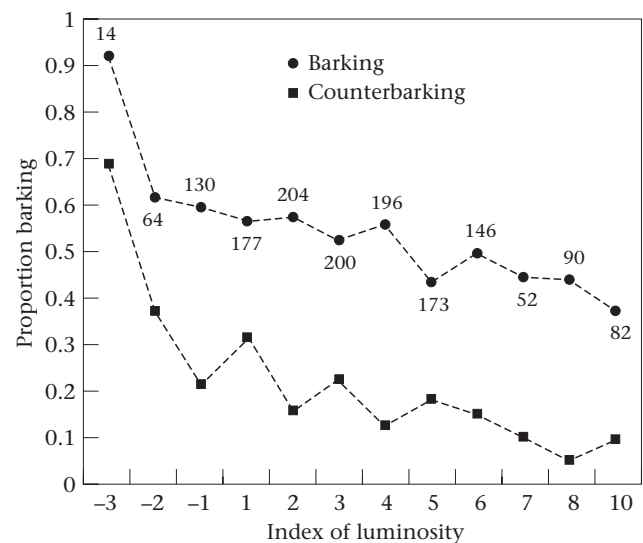


Figure 3. The proportion of roe deer that barked and counterbarked in response to a human observer as a function of ambient brightness (see text for details). Sample sizes are given for each point and indicate the numbers of deer observed.

analysis: sex*period: $\chi^2_2=0.23$, NS; period: $\chi^2_2=0.49$, NS; sex: $\chi^2_1=0.42$, NS).

Both the proportion of visually observed roe deer that barked (Kendall $\tau=-0.879$, $N=12$, $P=0.0001$) and the proportion of barking deer that elicited counterbarking from neighbouring deer (Kendall $\tau=-0.788$, $N=12$, $P=0.0004$) were significantly negatively correlated with our index of luminosity over the crepuscular period (Fig. 3). Thus, as brightness decreased, the propensity to bark increased.

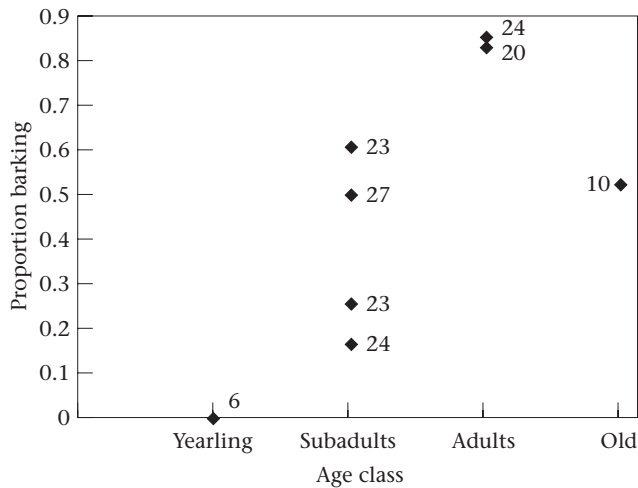


Figure 4. Barking frequency of individually marked bucks, in relation to their age class, when provoked by a human observer. Sample sizes are the number of individual approaches by the observer for each buck.

Individual Approaches

The propensity of an individual deer to bark when disturbed increased significantly with age (Kendall τ corrected for tied observations: $\tau=0.619$, $N=8$, $P=0.032$; Fig. 4). Barking frequency peaked for the two adult bucks (4–6 years).

Playback Experiments

Of 38 playback experiments, the focal individual counterbarked in 13 cases. The response was provoked on average \pm SE 82.0 ± 13.5 s after the onset of the playback and lasted 151 ± 28.2 s. Bucks counterbarked from their initial position ($N=6$) or approached the speaker ($N=6$), but rarely fled ($N=1$). In one case, the barking deer ran aggressively towards the speaker, and in two further cases the focal individual displayed aggressive behaviours, pawing the ground and marking tree trunks. During these experiments, the propensity of an individual to elicit counterbarking was negatively correlated with that individual's propensity to counterbark (Kendall τ corrected for tied observations: $\tau = -0.8$, $N=6$, $P=0.024$; Fig. 5).

DISCUSSION

The overall percentage of observed roe deer that barked in response to our disturbance is much higher than those reported by Danilkin & Hewison (1996) for European roe deer in the Belgorod and Kursk area (7%), and for the Siberian roe deer, *Capreolus capreolus pygargus* (24.5%).

Is Barking an Antipredator Behaviour?

Generally, roe deer bark in response to seeing or hearing a disturbance, and barking is then associated with postures that are characteristic of a state of alarm in cervidae: flared target (erect caudal hair), jumps, stilted

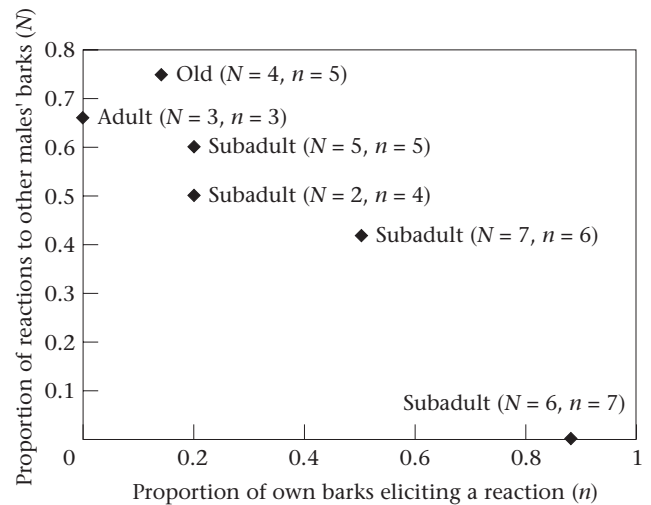


Figure 5. The proportion of occasions (N) on which six male roe deer of various age classes reacted by barking when the barks of other males were broadcast plotted against the proportion of occasions (n) on which their own broadcast barks elicited barking by other males.

gait, and brusque vertical head movements, indicating that barking is strongly associated with disturbance (Hewison et al. 1998; personal observations). However, roe deer are also liable to bark spontaneously or in the context of agonistic interactions (Danilkin & Hewison 1996; this study).

We found that barking frequency was negatively correlated with visibility. Barking increased from February to August (Fig. 1), which could be due to the growth of the vegetation understorey, leading to a marked reduction of visibility (but see below for the influence of territoriality). A potentially confounding variable here is the distance at which animals were disturbed. As disturbance distance is likely to increase with visibility and as visibility decreased with period we might expect barking to decrease with period. Our results, in fact, suggest the opposite, so that this is not a problem. Indeed, over the crepuscular period, barking was negatively correlated with ambient brightness (Fig. 3). Higher frequency of barking at dawn and dusk was also found in muntjac (Barrette 1977; Yahner 1980; Wiles & Weeks 1981). This relationship may occur because, when luminosity is low, it is more difficult to assess the threat of a given detected disturbance. In these conditions, it could be more costly not to bark when danger is present than to bark unnecessarily when there is actually no danger. Counterbarking was also negatively correlated with visibility (Fig. 3). On many occasions, during the daytime, we observed individual deer that did not react to the barks of a remote conspecific, probably because they could see the threat themselves.

Is Barking an Alarm Call?

Females accompanied by their offspring barked more frequently than solitary females, supporting the hypothesis that barking in female roe deer serves to warn kin of danger (Fig. 2). However, the fact that solitary individuals

of both sexes barked more often than individuals in groups suggests that the presence of other individuals in the vicinity is not necessary to elicit barking. As [Tilson & Norton \(1981\)](#) pointed out for alarm duetting in klip-springer, *Oreotragus oreotragus*, barking in roe deer is louder and repeated more than need be to warn immediate group members (mean repetition rate of 14 barks/min; [Hewison et al. 1998](#)). Moreover, roe females and fawns make clear, high-pitched contact squeaks ([Prior 1995](#); [Danilkin & Hewison 1996](#)), which are inconspicuous and better adapted to short-range communication. If barking is an alarm call, we would expect females to bark more frequently than males as they are more likely to have kin nearby (see Introduction). However, we found that females barked less than males. Overall, therefore, these results do not support the hypothesis that, in this species, barking is an alarm call specifically designed to warn conspecifics of imminent danger.

Is Barking a Pursuit-deterrent Call?

Solitary individuals barked more often than individuals within groups, suggesting that barks are directed towards the source of disturbance. Some authors have proposed that barking in muntjac ([Yahner 1980](#)) and snorting in white-tailed deer ([LaGory 1987](#)) are antipredator behaviours by which the predator is informed that it has been detected and that further stalking is useless. Indeed, while roe deer that were surprised at close quarters fled immediately without barking (very close visual contact mostly provoked immediate and silent escape; [Hewison et al. 1998](#)), deer standing at a distance from the observer barked repeatedly as if to inform a potential predator that the deer was aware of its presence. Similarly, counterbarking may also act as a pursuit-deterrent call or, alternatively, barking and counterbarking sequences of several individuals from different locations may confuse the potential predator ([Oli & Jacobson 1995](#)). Furthermore, this may explain why females with fawns may bark more frequently than single females, as predator deterrence should benefit both the mother and her young, thereby increasing the mother's inclusive fitness. Thus, although we could not address these questions directly because of the absence of natural predators in our area, the results from our observational transects are consistent with the hypothesis that barking in roe deer acts as a pursuit-deterrent signal.

Is Barking a Territorial Call?

Although in our population roe deer barked throughout the study period, barking frequency varied between sexes, age classes and seasons. Bucks barked more than females and barking increased from preterritoriality to the rut ([Fig. 1](#)). However, although the three-way interaction was not quite significant ($P=0.085$), solitary males tended to bark most during the territoriality period ([Fig. 1](#)), when there is both increasing intolerance between males and intensive marking activity ([Johansson et al. 1995](#)). Indeed, the observed tendency for less

frequent barking during the rut in bucks coincides with reduced marking activity ([Johansson et al. 1995](#)), suggesting that barking in roe deer is linked to the expression of territoriality among bucks.

The positive correlation between the propensity to bark when disturbed during the territorial period and the age of the buck is consistent with roe deer bucks being more likely to hold a territory as they get older (although very old animals may lose their territory). Moreover, our playback experiments showed that adult bucks did not flee in reaction to barking from within their home ranges, but rather approached the loudspeaker and/or displayed aggressive behaviours. We observed interindividual variations in propensity to counterbark: older bucks tended to counterbark more than subadults (although not statistically tested because of small sample sizes), particularly in response to the barks of subadults. This is consistent with the possibility that subadults in search of a territory may pose a bigger threat than other adult bucks to territorial bucks, as adults probably have an established territory elsewhere ([Wahlström 1994](#)). More generally, our results may indicate individual differences in propensity to bark that are related to dominance (which in turn may be partially related to age). Under this scenario, more dominant/territorial males would be more likely to bark in response to a playback, and their barks would be less likely to elicit a barking response in others.

During observational transects, individuals barked in response to the observer's presence from their current home ranges. Thus, they were not considered as 'intruders' by potential counterbarkers, which could explain why counterbarking in response to these barks did not vary across study periods, and was not affected by the sex of the initiator. On many occasions deer that were far enough away not to have detected our presence barked (0.52 spontaneous barking series/h, $N=627$). Although we could not identify the stimulus that had elicited the barking, given the absence of natural predators and other humans in our study area, these barking series were certainly either spontaneous or a result of intraspecific interactions. [Danilkin & Hewison \(1996\)](#) reported that strongly excited bucks sometimes bark while they mark their territory, and we also observed on four occasions that, after a combat between males, one or both opponents barked repeatedly.

Our study suggests that, although barking is not strictly a territorial behaviour and may have initially evolved as an antipredator strategy; it plays a secondary role in territory maintenance for bucks during the territorial period. Whereas visual and chemical cues (scraping and rubbing; [Johansson et al. 1995](#)) are long-term marks, barking signals the immediate presence of the barker to neighbouring individuals. The acoustic structure of the vocalization potentially carries information on the sex, and probably on the age and the identity, of the barker ([Hewison et al. 1998](#); D. Reby, B. Cargnelutti, J. Joachim & S. Aulagnier, unpublished data). Consequently, barking may enable roe deer to identify and locate each other, and perhaps to assess dominance status, particularly during barking/counterbarking sessions involving several animals. This function has also been suggested in territorial Arctic foxes,

Alopex lagopus, where barking occurs in similar contexts (Frommolt et al. 1997). Further playback experiments, involving a larger set of animals of both sexes and of known age, spatial and dominance status are needed to assess the potential meaning of individual information encoded in roe deer barks.

Both the acoustic structure and the context of barking are surprisingly similar in roe deer (Hewison et al. 1998), Indian and Chinese muntjac (Barrette 1977; Yahner 1980; Wiles & Weeks 1981; Oli & Jacobson 1995) and Chinese water deer (Cooke & Farrell 1998; personal observation). This, and the fact that roe deer, muntjac and Chinese water deer live in closed habitat, may suggest that barking in these species represents a case of evolutionary convergence. However, roe deer are considered the most primitive living Odocoileinae (Putman 1988), and is the only species in this subfamily that barks, as all other species snort in response to disturbance, including small, forest-living South American brockets, *Mazama* sp., whose ancestral-like characteristics are considered to be secondarily acquired (Eisenberg 1987). Barking in roe deer and primitive Cervinae (muntjacs, Chinese water deer) might therefore be considered as an ancestral characteristic. In less primitive species that are gregarious and live in more open habitat, such as fallow deer and red deer, barking is almost exclusively by adult females, either when solitary or with offspring (Alvarez et al. 1975; personal observation), and provokes alarm and flight behaviours in other group members. This suggests that the function of barking in cervids has evolved in relation to the social habits of the different species.

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