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Author(s): T. H. Clutton-Brock and S. D. Albon

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THE ROARING OF RED DEER AND THE EVOLUTION OF HONEST ADVERTISEMENT

by

T. H. CLUTTON-BROCK and S. D. ALBON¹⁾

(King's College Research Centre, University of Cambridge, England)

(With 12 Figures)

(Acc. 31-X-1978)

INTRODUCTION

Many vertebrates expend a considerable amount of time and energy in aggressive displays which often involve either rapid movement of the extremities (SIMPSON, 1968; WILEY, 1970), repeated vocalisations (THORPE, 1961; CHIVERS, 1969; ELLEFSON, 1968), or both. A common functional explanation is that displays serve to intimidate the opponent (HINGSTON, 1933; TINBERGEN, 1951; GUTHRIE, 1971). This argument has the weakness that selection should favour individuals which are not intimidated unnecessarily and which adjust their behaviour only to the probability of winning and the costs and benefits of fighting (MAYNARD SMITH & PRICE, 1973; PARKER, 1974; MAYNARD SMITH & PARKER, 1976). Recent theoretical developments suggest a modification of the original argument: displays may permit individuals to assess their opponents, allowing them to avoid fighting when they are unlikely to win (ZAHAVI, 1975, 1977).

It is frequently stressed that assessment criteria should be closely linked to individual differences in fighting ability since, unless this is the case, selection is likely to favour 'cheating' or 'bluffing' phenotypes which exaggerate their

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real fighting ability with the result that the criterion will no longer provide accurate grounds for assessment and will, presumably, be abandoned. A variety of 'un-fakeable' criteria have been suggested, including antler or horn size in ungulates (GEIST, 1971) and the depth of aggressive calls in birds (MORTON, 1977) (on the grounds that the lowest pitch that an individual can achieve gives a reliable estimate of its body size). For example, a recent study of toads provides direct evidence that the depth of pitch of calls is related to body size and that potential contestants use this cue in deciding whether or not to contest access to receptive females (DAVIES & HALLIDAY, 1978).

While stable criteria such as body size or horn size may be used in assessment procedures, we should be surprised if competitors judged each other on such traits alone. In many vertebrates, fighting ability changes during the course of particular breeding seasons as competing individuals deteriorate in condition and become exhausted (LEUTHOLD, 1966; McCULLOUGH, 1969; LE BOEUF, 1971; LINCOLN & GUINNESS, 1973; GRUBB, 1974). In addition, it often declines in older individuals which are past their prime (CLUTTON-BROCK, ALBON, GIBSON & GUINNESS, 1979; PACKER, 1977). For both reasons, it would be an inefficient assessor which judged its opponents only on traits which were insensitive to temporal changes in fighting ability.

In a wide variety of animals from red grouse to chimpanzees, there is evidence that the frequencies or durations of displays are related to fighting ability or dominance rank (RAND & RAND, 1976; PACKER, 1977; GEIST, 1971; WATSON & MILLER, 1970; BALDWIN, 1968). In addition, several studies have demonstrated that both can change throughout the course of breeding seasons (GEIST, 1971; WATSON, 1970; BALDWIN, 1968; McCULLOUGH, 1969) and vary with age (GEIST, 1971; SAAYMAN, 1971; BYGOTT, 1974). Could it be that competitors often assess their opponents' capabilities on the rates and durations of their displays? If so, this might explain why competitors devote so much time and energy to repetitive, stereotyped movements, aggressive displays or vocalisations.

Our current study of reproductive success in Scottish red deer stags (*Cervus elaphus* L.) allowed us to investigate relationships between display behaviour and fighting ability over four successive breeding seasons (1974-1977). In late September or early October, red deer hinds aggregate in particular areas of their home ranges where they are joined by the stags which have spent the previous ten months in bachelor groups (CLUTTON-BROCK *et al.*, 1979). Stags over 5 years of age collect and defend harems of hinds from which they exclude other stags. Prime stags (aged 7-11) are the first to hold harems, usually defending them for 2-4 weeks. Young stags

of 2-5 years seldom hold harems during the peak period of the rut (though they do so occasionally in areas peripheral to the main rutting grounds). Instead, they hang around the harems of mature stags attempting to abduct hinds when the harem-holder is otherwise occupied (GIBSON, 1978). This strategy, which we refer to as kleptogamy, is apparently largely unsuccessful though it may allow the adolescents to learn the skills necessary for successful handling of hinds.

Harem-holders feed little (<5% of the total 24 hours compared to >50% in the rest of the year) and spend much time collecting and herding hinds and chasing off young stags. They may lose up to 20% of their total body weight (MITCHELL, McCOWAN & NICHOLSON, 1976; MITCHELL, STAINES & WELCH, 1977) and it is probably the effect of declining body condition associated with changes in hormone levels (LINCOLN, 1971; LINCOLN, GUINNESS & SHORT, 1972) which produces a sudden cessation of rutting activity in the second or third week of October. Though the breeding season is well defined, individual stags are not in perfect synchrony and, even within age groups, some animals rut relatively early and others relatively late (CLUTTON-BROCK *et al.*, 1979; GIBSON, 1978).

During the period when they are defending harems, mature stags roar frequently (DARLING, 1937; BUTZLER, 1972). Roars are produced by vibration of the larynx caused by exhaling rapidly. Roaring is facilitated by development of the laryngeal muscles which, like other secondary sexual characteristics evident during the rut, may be controlled by testosterone (LINCOLN, 1971). Several roars (usually 1-3) are typically given on the same exhalation. The rate of roaring can be remarkably high: stags may roar over 8 times per minute for several minutes on end and may average 2 roars per minute throughout the day (see Fig. 3).

The usual functional explanation of roaring is that it serves to scare off other stags (DARLING, 1937). This study explores the possibility that roaring may deter potential challengers from attacking because it allows them to assess the fighting ability of the roarer. Such a trait would have considerable advantage in a species where the costs of fighting are high (MAYNARD SMITH & PRICE, 1973). This is evidently the case among red deer: though fights are uncommon, around 23% of harem-holding stags show some sign of fighting injury each year and approximately 6% are permanently injured (CLUTTON-BROCK *et al.*, 1979). Fighting has the additional disadvantage that kleptogamists frequently disperse harems while their holders are fighting.

We have attempted to answer four main questions. First, do stags have the opportunity to assess each other's roaring capabilities? Second, is roaring

temporally related to fights or to situations where fights are likely to occur? Third, are individual differences and temporal changes in roaring performance related to fighting ability? And finally, is there any evidence to suggest that stags are assessing each other on their roaring performance?

STUDY AREA AND METHODS

All data described were collected in the North Block of the Isle of Rhum (Inner Hebrides) between 1974 and 1977. The history and population ecology of the Rhum deer population has been described elsewhere (LOWE, 1966, 1967, 1969) as has our study area and study population (CLUTTON-BROCK *et al.*, 1979). The study area is regularly used by around 100 hinds ≥ 1 year old. In the rut, it usually contains 50-60 stags >1 year old, some of whom are resident there for most of the year: Fig. 1 shows the mean number of stags of different ages recorded in the study during the rut between 1974 and 1976. Figures are based on census of the study population carried out 5 times in each rut 1974-1976. For each age category, Fig. 1 shows the mean number of animals present in the study area across years.

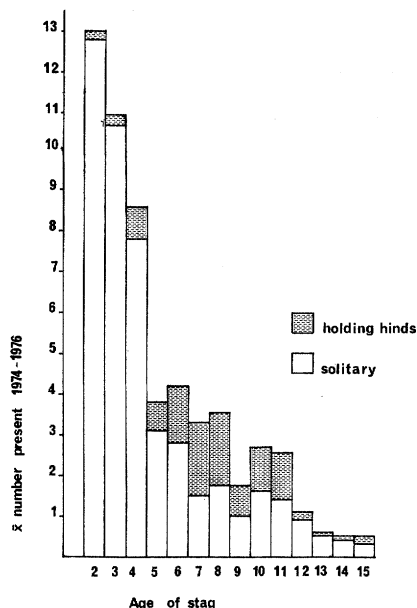


Fig. 1. Mean numbers of stags of different ages present in the study area during October 1974-1976.

All animals using the study area can be recognised individually either by facial characteristics or by ear flashes and/or collars. Ages of animals of ≤ 9 in 1977 are known with full accuracy, individuals of >9 to within a year (GUINNESS, GIBSON & CLUTTON-BROCK, 1978). The animals are habituated to observation and can be watched from <100 m. without disturbance.

Data on different topics were collected in different years and sample sizes consequently differ between analyses. All statistical tests were taken from SIEGEL (1956) and all values of p shown in the text are two-tailed.

The following definitions of the activities of stags were used:

Approach: any instance where a harem-holding stag moved consistently towards another stag who was in his direct line of sight and came within 100 m. of him.

Roar: a single vocalisation audible to the observer. Each roar is usually clearly separated from the next.

Roar bout: a number of roars < 5 secs apart, usually given in the course of a single exhalation.

Roar rate: the mean number of roars per minute calculated for times when the stag was standing (stags roared little when lying down). Rates are divided into *contest rates* (rates during times when stags were regularly exchanging roars and at least one of the pair was roaring at > 2.0 roars per minute), *basal rates* (when an individual was not exchanging roars with a rival) and *overall rates* (where no distinction was made). In the analysis we use both *mean roar rates* (means calculated across all days for which that stag was recorded) and *maximum roar rates* (the highest rate recorded in any observation period for that subject). Roar rates were measured only during the main rutting period (Oct. 1-20) and exhausted stags were excluded.

Answer: any roar bout which followed within 10 secs of an opponent's roar bout.

Roar direction: stags were recorded as roaring towards each other if they were facing within 45° either side of their opponent.

Parallel walk: after one stag approaches another, the two may enter a parallel walk, walking tensely up and down 3-15 m. apart, usually at right angles to the direction from which the approacher came.

Initiation of contact: when a stag lowers its head 'inviting' its rival to lock antlers (see CLUTTON-BROCK *et al.*, 1979).

Fight duration: the entire period of contact between two stags, including short periods when contestants stood apart before re-locking antlers.

Fighting ability: our measure of fighting ability is described and justified in detail elsewhere (CLUTTON-BROCK *et al.*, 1979). It is the number of individuals which a stag beat plus the combined number which they beat (excluding the subject) plus one, divided by the number of individuals it lost to plus the number that they lost to plus one. In this analysis, an individual was regarded as having beaten another if the two had fought and the latter had withdrawn or if one stag had been displaced by another.

This rather elaborate index was necessary because stags avoided fighting with obviously superior individuals and the number of fights in which each individual was involved was small. When we compared results obtained by this method with traditional indices of dominance in samples of published interaction data it gave very similar results (*ibid.*). The rank of stags on this measure was closely related to their ranks on reproductive success.

Equal fighting ability: contestants were arbitrarily defined as 'equals' if they differed from each other by ≤ 3 ranks (based on our measure of fighting ability) and as 'inequals' if they differed by ≥ 4 ranks.

Data were recorded onto pocket tape recorders and (usually) transcribed the same day. Accuracy of counting was checked by filming stags with a Sony videorecorder and comparing results with observers' counts.

Fights, parallel walks and roar contests were recorded opportunistically. Unfortunately, we were seldom able to collect data covering the entire duration of a challenge since escalated contests were rare. We were usually made aware of a contest by hearing two stags roaring at each other and seldom arrived in time to document the full course of roaring contests which preceded fights. Basal roaring rates in different rutting stags were recorded in approximate rotation. Since records were terminated when stags lay down, the duration of samples varied from 5-60 minutes, with a mean value of 30 mins. Where two samples were collected on the same stag on the same day, rates were averaged and included as a single figure when mean rates were calculated for each stag.

RESULTS

Roaring contests?

Roaring is largely restricted to harem-holding stags during the period when they are holding hinds (approx. September 25-October 25). Before and after this, stags roar little while, during the rut, mature stags without harems (solitaries) roar less frequently than harem-holders (Fig. 2). And in our sample of mature stags, individuals roared most on days when they were holding large harems (>6 hinds) than on days when they were holding smaller ones (Wilcoxon Matched Pairs Signed Rank Test, $n = 8$, $T = 1$, $p < .02$).

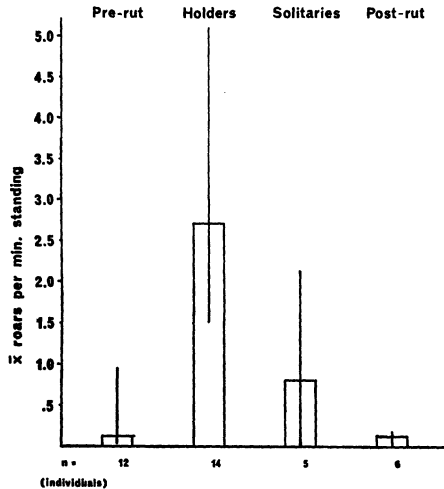
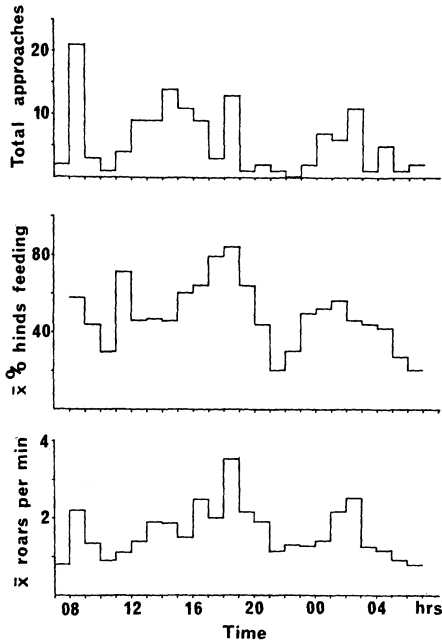


Fig. 2. Overall roaring rate (per minute standing time) in mature red deer stags before the rut (September 15-25); in harem-holding stags during the rut (September 25-October 25); in mature stags which were not holding harems during the same period; and in mature stags after they had finished defending harems (October 20-30). Analysis was based on 1974 data and restricted to stags of ≥ 6 years old. The number of individuals sampled (n) is shown beneath each histogram. Extending lines show inter-quartile ranges.

Stags roared most in situations where they were likely to be challenged. They roared most on days when the nearest holding stag was closer to them than average than on days when it was more distant (Wilcoxon Matched Pairs Signed Ranks Test, $n = 8$, $T = 1$, $p < .02$) and at times of day when they were most likely to be approached by other stags. In 1976, ten stags were observed for 1 day between dawn and dusk and in 1977, a further five from dusk to dawn using infra-red viewing equipment. Mean roar rates were calculated for each hour of the day and were significantly correlated both

a



b

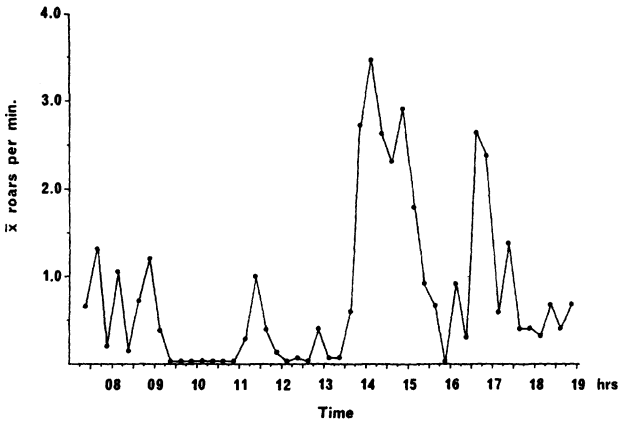


Fig. 3. (a) Mean number of roars per min calculated across hours of the day for ten haremholding stags observed during daylight in 1976 and five observed during the night in 1977. The mean percentage of hinds in the stag's harem which were feeding in each hour (based on census' made every five mins) and the total number of approaches to within 100 m of the harem by males of ≥ 1 year old are also shown. Night data were collected by a team of observers taking 4-hour watches and using infra-red viewing equipment. (b) Number of roars given per quarter hour through the day by one haremholding stag (Saggie) in October 1976.

with the total number of approaches by stags ≥ 1 year old per hour ($r_s = 0.553$, d.f. = $p < .001$) and with the proportion of hinds in the harem that were feeding ($r_s = .676$, d.f. = 21, $p < .001$) (see Fig. 3a). The latter relationship probably existed because harems were most widely dispersed when hinds were feeding and harem dispersion affected both the roaring rate of the holder and the probability of other stags approaching the harem.

Though roaring showed consistent diurnal patterning, its distribution throughout the day was extremely variable. Fig. 3b shows the number of roars per quarter hour given by one 11 year old (Saggie) during the course of one day. As can be seen, periods of frequent roaring alternated with intervals of little activity. The latter coincided with times when the stag was lying or interacting with his hinds: in this particular sample, the overall rate of roaring during minutes when the stag was standing was 0.99 while it fell to 0.11 roars per minute when he was lying.

High roaring rate was associated with the activities of neighbouring stags: an approach by a neighbouring stag or a series of roars directed at the subject usually increased his roaring rate. A typical example is shown in Fig. 4. In this case, two stags with neighbouring harems (Boss and Pincer) started roaring at each other and were joined by the third stag in the area (Fingal). Both the number of roar-bouts and the number of roars given by the three stags per 4-minute period were correlated with each other ($r_s = 0.71-0.89$, d.f. = 8, $p < .05-.01$). Periods of reciprocal roaring activity (which we shall refer to as 'contests') rarely involve two stags and in most cases the majority of stags within earshot join in to some extent. Where one stag approaches another, the rate of roaring tends to increase as they get progressively closer.

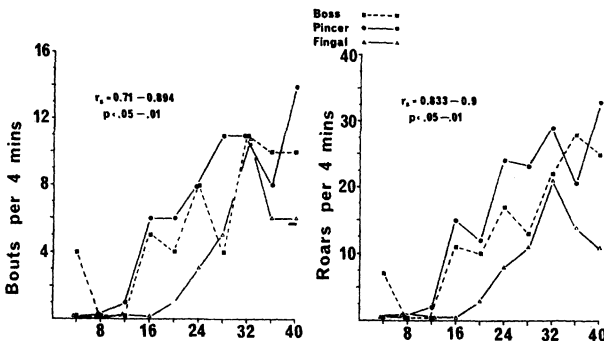


Fig. 4. Frequency of roars per 4-minute period given by three harem-holding stags (Boss, Cecil, Starn) during a 40-minute contest in 1975.



Fig. 5. A harem-holding stag replying to our artificial stag. (The equipment shown in this photograph was that used in experimental series III and IV). In most cases, this apparatus was set up further from the stag and was better hidden than in this photograph.

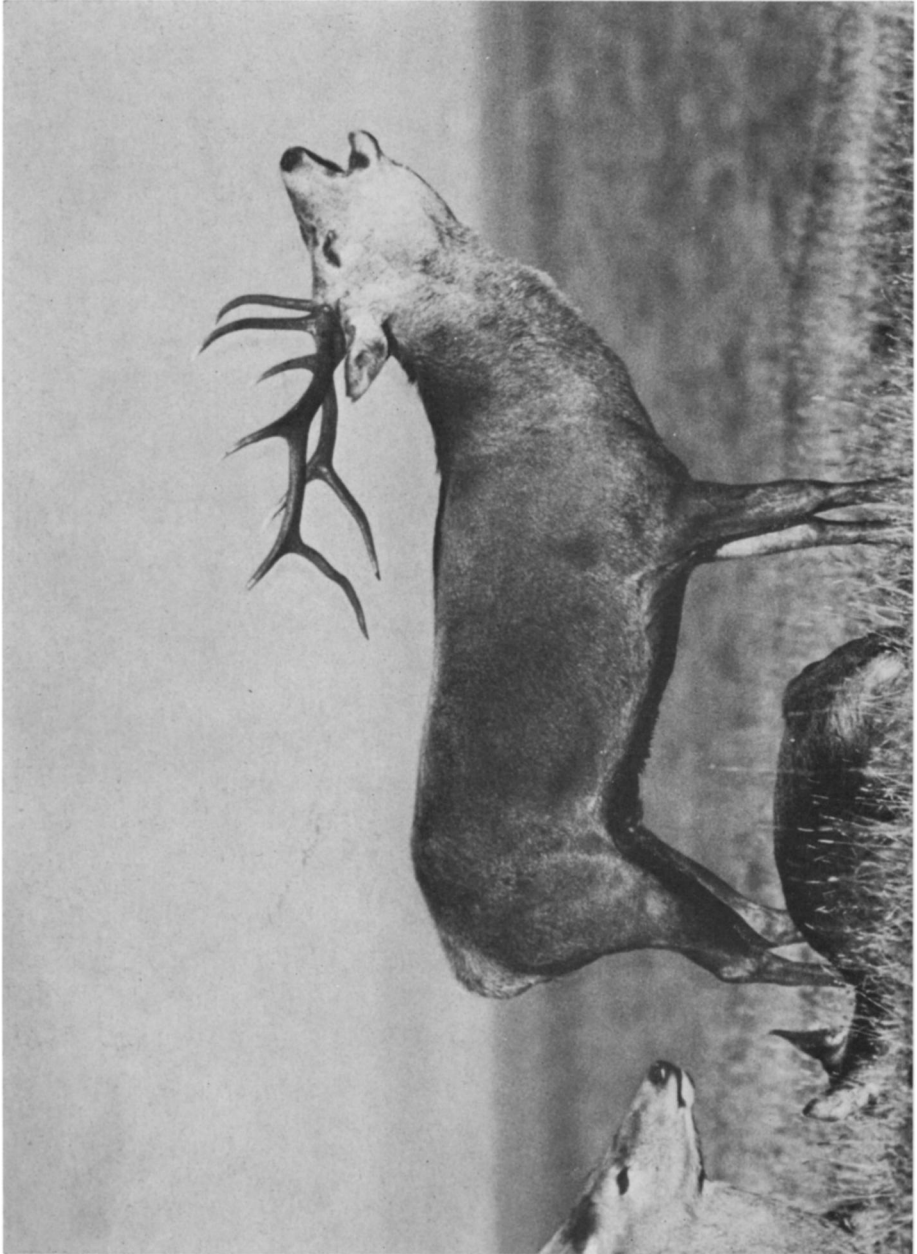


Fig. 8a. A harem-holding stag roars at an intruder.

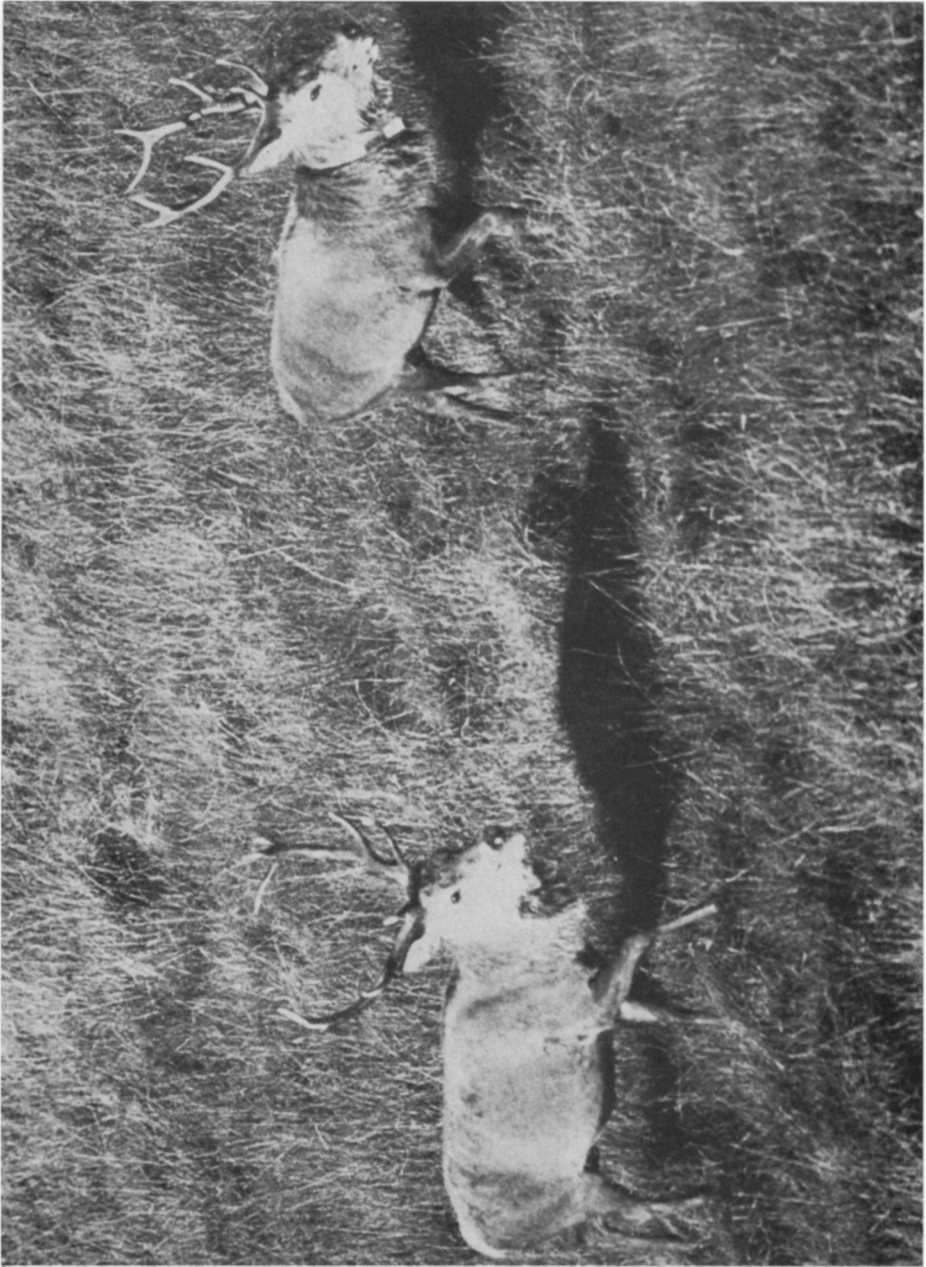


Fig. 8b. A harem-holding stag and a challenger parallel walk. (Note the open mouths and lolling tongues).

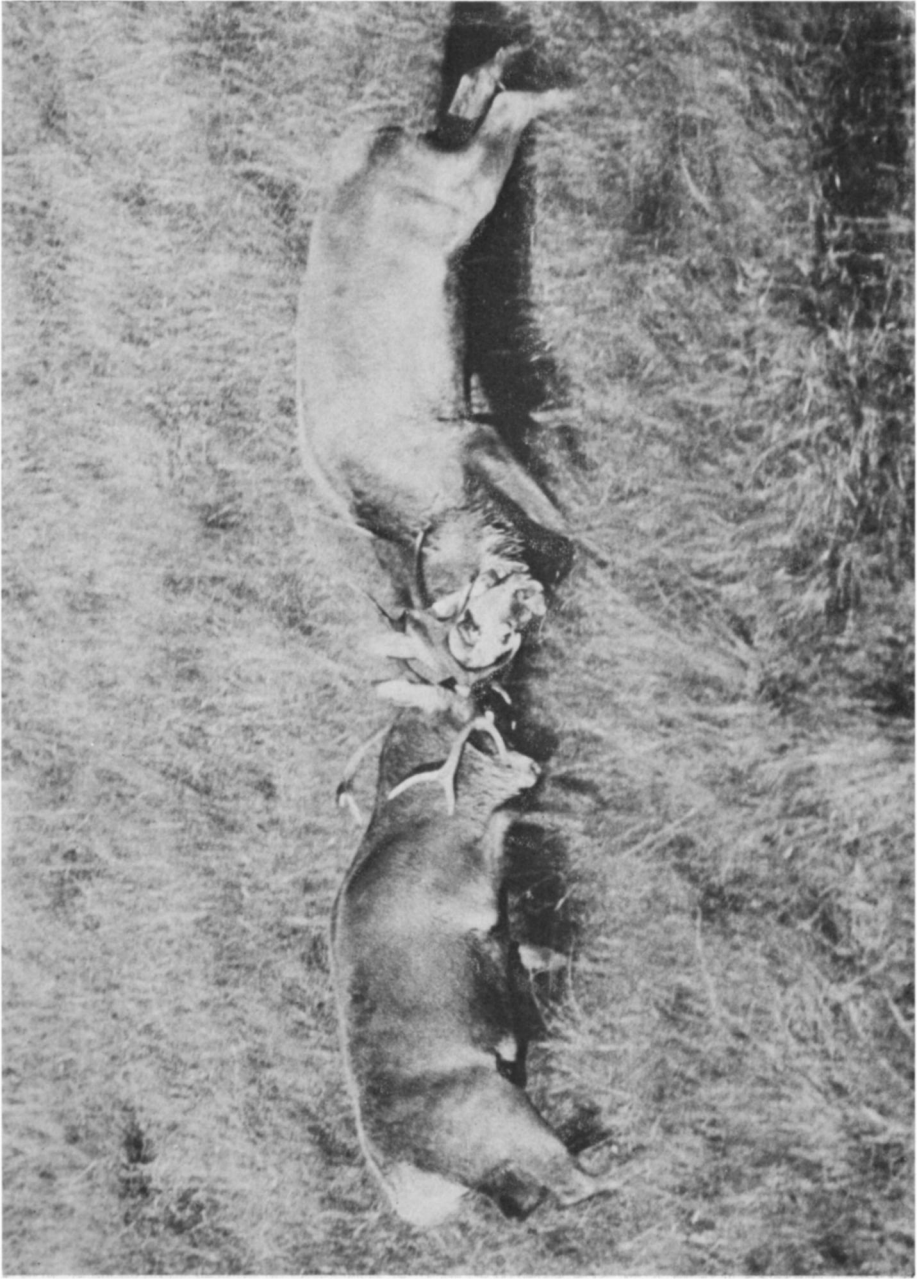


Fig. 8c. The latter two stags fight.

Experimental Series I.

To confirm that roaring provoked other stags to reply, we tape-recorded the most dominant stag in the study area and played five minutes of his roars (at a mean rate of 5 roars per minute) to six different stags, comparing their roaring behaviour in the five minutes during the playback with the preceding and succeeding five minutes (see Fig. 5). This series of experiments was carried out in October 1975, using an Eagle 10 watt public address amplifier, a 15-watt public address speaker and a Philips cassette tape recorder. The play-back equipment was set up around 100 m from the stag but out of sight and started at a time when he was not engaged in a roaring contest. During the experiments, the observer related a running commentary of the stag's roaring behaviour into a pocket tape recorder.

As Fig. 6 shows, the playback caused most individuals to increase their overall rate of roaring by increasing both the number of bouts that they gave

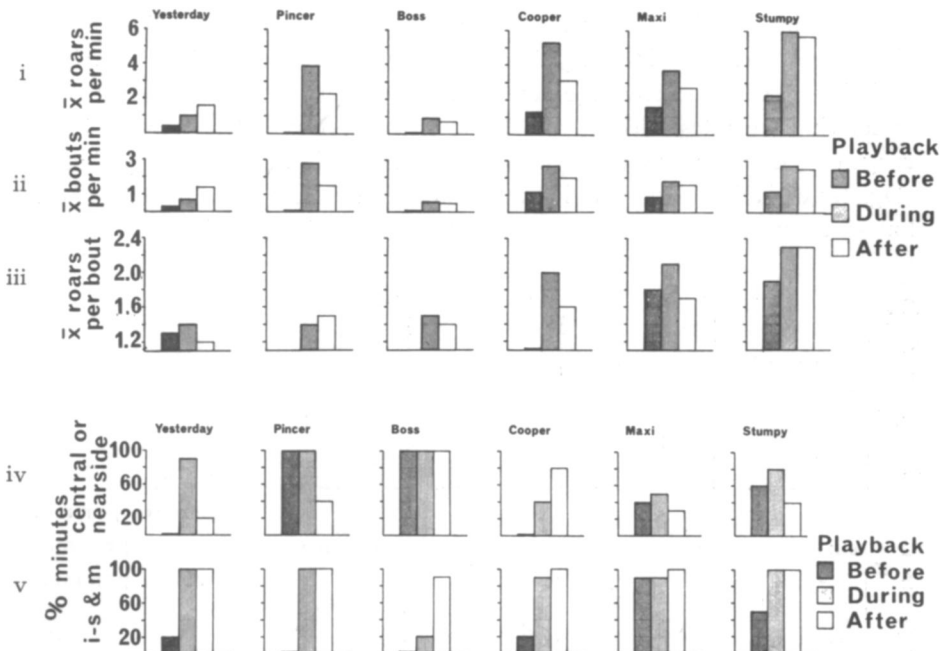


Fig. 6. *Experimental Series I*. Five minutes of pre-recorded roars at an average rate of 5 roars per minute were played to six harem-holding stags, 6-12 years old. Histograms compare the behaviour of subjects before, during and after the playback, showing: (i) mean number of roars given per minute; (ii) mean number of roar-bouts given per minute; (iii) mean number of roars per bout; (iv) % of minutes spent on the side of the harem nearest the playback; (v) % of minutes inactive, standing or moving (versus feeding or lying).

and the number of roars per bout. During and after the playback, the subjects gave a larger proportion of bouts towards the playback and the majority spent more time on the side of the harem closest to the playback, less time feeding and lying and more time inactive, standing or moving. The effects of the playback usually continued during the succeeding five minutes.

Experimental Series II.

Moreover, the frequency with which a stag roars is related to the frequency of roars it hears. In a second series of experiments, we played seven mature harem-holding stags three periods of roars at average rates of 2.5, 5.0 and 10.0 roars per min. This series was carried out in 1976. Roars were recorded, using a Sennheiser directional microphone and a Uher Report tape recorder, from the 3 most dominant stags in the area (Saggie, Maxi and Boss). Tapes were edited to remove answering roars and to give different rates of roaring. The mean number of roars per bout was held approximately constant in the three playback periods. A 30-watt horn speaker, the Eagle amplifier and the Uher Report were used to relay the playback to the subjects and each playback period was separated from the next by five minutes of silence. The rationale underlying the rates selected was that 2.5 roars per minute lay in the lower range of roaring frequencies, 5 roars a minute lay in the upper range but all stags tested had been observed to attain at least this rate while none had been known to sustain ten roars per minute over a five minute period.

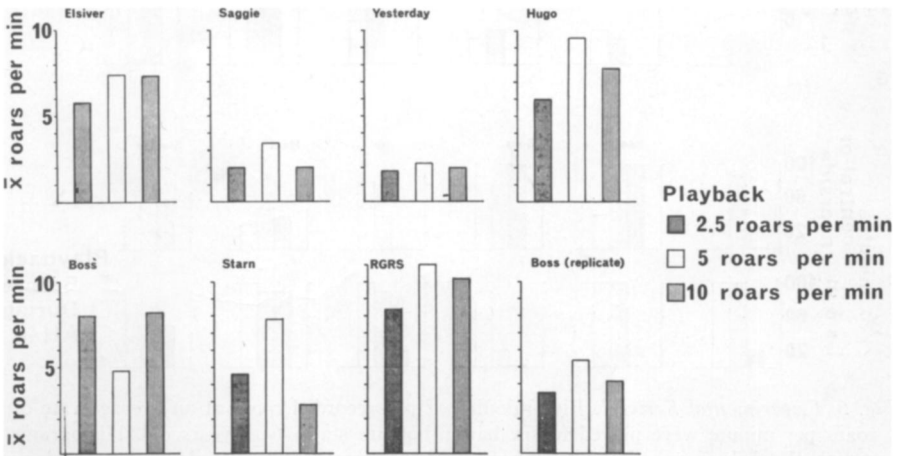


Fig. 7. *Experimental Series II.* Three five-minute sequences of pre-recorded roars (at mean rates of 2.5, 5.0 and 10.0 roars per minute), separated by five-minute silent periods were played to six harem-holding stags 6-12 years old. Histograms show the mean number of roars per minute during the three playbacks.

As can be seen (Fig. 7) six out of seven stags responded more to the 5 r.p.m. playback than the 2.5 r.p.m., and the exception (Boss) also did so when tested a second time. In contrast, only one out of seven responded more to the 10 r.p.m. playback than the 5 r.p.m. This was apparently not the result of habituation: to check this point, we reversed the order of the playback series in two experiments in 1977. The situation was unnatural because roaring contests seldom start at a high rate of roaring and de-escalate and, for this reason, might have been expected to give unpredictable results. In both cases, the subjects responded least to the 10 r.p.m. playback. Mean roaring rates in these two experiments were 3.5 and 0.9 (to the 10.00 r.p.m. playback), 4.8 and 4.2 (to the 5.00 r.p.m.) and 6.5 and 3.2 r.p.m. (to the 2.5 r.p.m.).

Perhaps the most likely explanation of the decline in response to the 10 r.p.m. playback is that stags tended to avoid roaring while their opponents were doing so, usually waiting for 5-10 seconds before answering. In the 10 r.p.m. playback roar bouts followed each other in such quick succession that stags had little time to reply.

The frequency with which stags roar in natural contests might have been inter-correlated either through (general) mutual stimulation or because they replied to each other's roars. The evidence suggested a reply system:

(1) Stags tend to roar alternately. After a stag has roared, it usually pauses for several seconds. If the opponent responds, it will typically wait until he has completed at least one bout of roars before roaring again. As a result, contests usually consist of alternate bouts of roars given by the two or more stags that are involved. Stags appear to avoid roaring when another animal is doing so even if this is not the individual they are exchanging bouts with, and if they are interrupted when they have just started a bout, will sometimes terminate the bout and wait until the other stag has ceased.

(2) Stags usually roar facing towards their opponents: For six conversations percentages of bouts directed towards opponents were 65, 76, 87, 72, 100 and 67%.

(3) Roar bouts directed away from an opponent were less likely to be answered than those directed towards him. Only in three of the above conversations sufficient numbers of bouts were directed away to permit comparison of answering rates. In these three, 76, 70 and 85% of bouts towards were answered, only 53, 43 and 40% of bouts away and these results are typical of other conversations.

Roaring contests and fights.

Roaring contests usually occur in situations where fights are likely. Though fights involving harem-holding stags are not common, most harem-holders have to defend their harems once every 4-6 days (CLUTTON-BROCK *et al.*, 1979). The typical course of events is that a challenging stag approaches to within approximately 200 m-300 m of a harem-holder, the two roar at each other for several minutes after which the approacher usually withdraws. Alternatively, he may continue to approach in which case the two stags often enter a parallel walk, moving tensely up and down at right angles to the direction from which the approacher came. For a sample of 50 cases where an approaching stag came to within 100 m of its opponent, Fig. 9 shows the number that led to roaring contests, parallel walks and fights. As the figure shows, once an approacher has come within 100 m, the contest is likely to escalate in around 50% of cases.

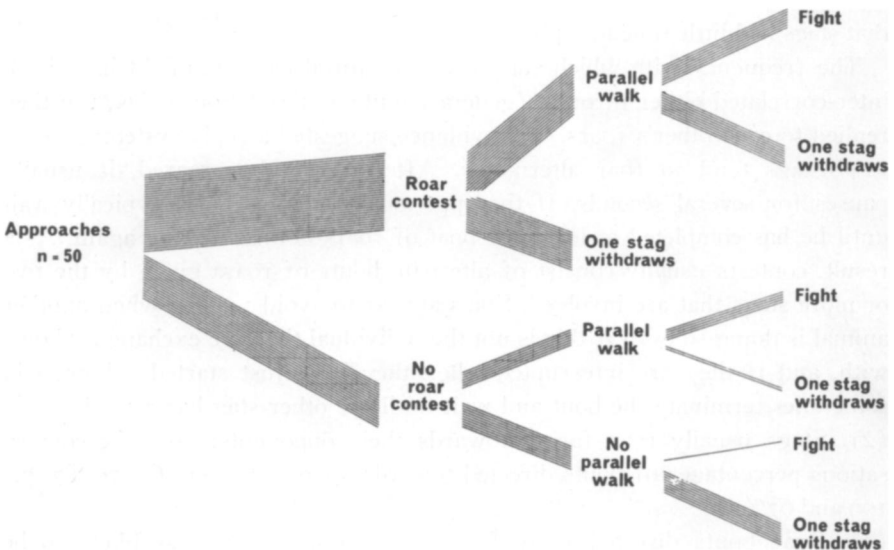


Fig. 9. Number of approaches to within 100 m involving two stags of ≥ 6 years which led to roaring contests, parallel walks and fights, in a sample of 50 observed in 1977. Each parallel line represents one case.

At any stage during a parallel walk, one stag may lower its head, inviting contact: in the majority of cases it is the approaching stag which initiates (*ibid.*). Such invitations are generally accepted and the two then lock antlers and push until one of the pair is driven rapidly backwards. Where one stag withdraws without fighting, it is usually the approacher: it is very rare for

harem-holding stags to abandon their harems without a fight, whatever the odds. In the few cases where this has been observed, the harem-holder had generally usurped the harem of the approacher while the latter was absent fighting or gathering hinds and relinquished it on his return.

In a sample of 50 approaches where both opponents were ≥ 6 years, Fig. 9 shows the proportion of approaches which led to roaring conversations, parallel walks and fights. As can be seen, most fights are most commonly preceded both by roaring conversations and parallel walks and only one out of 14 was preceded by neither. Fights not immediately preceded by roaring contests tend to occur either where a stag has occupied another's harem during the latter's temporary absence and is challenged without preliminaries by the returning owner; or where there is an obvious inequality in the fighting abilities of the two contestants (see p. 149).

Roaring and fighting ability.

(a) *Differences between individuals.*

These results suggested that roaring contests provided an opportunity for individuals to assess each others' roaring ability. If roaring is used in assessment some aspect of roaring performance should be correlated with fighting ability.

Several aspects of roaring behaviour were related to individual differences in fighting ability. In 10 stags of 7-12 years¹⁾ holding harems in the study area in October 1977, mean and maximum rates of roaring were calculated across all samples collected between October 1 and October 20 1977, excluding those collected after individuals had started to decline in rutting performance and were feeding regularly. Sample number varied between stags from 2-10 with a mean of 5 and was not correlated with fighting ability ($r_s = 0.38$, d.f. = 8, $p > .1$). Mean rates of contest roaring varied between stags from 1.76 to 5.62, maximum rates from 2.70 to 8.60. Mean and maximum roaring rates during contest were significantly correlated with our measure of fighting ability ($r_s = 0.800, 0.761$; $t = 3.77, 3.32$; d.f. = 8; $p < .01, < .02$ respectively).

Mean and maximum numbers of roars per bout were also calculated for each sample: the maximum number of roars per bout for an individual was the highest mean value recorded in any sample for that animal and was also significantly correlated with fighting ability ($r_s = 0.745$, $t = 3.16$, d.f. = 8,

1) This sample of stags included all mature stags which held hinds regularly in the two main rutting areas in the 1977 rut but excluded five stags which held hinds irregularly or in peripheral areas.

$p < .02$) though the mean number of roars per bout calculated across all contest samples in each individual was not ($r_s = 0.46$, d.f. = 8, $p > .1$).

Both fighting behaviour and roaring performance declined in stags over 11 years old which rarely equalled younger stags either in contest rate or in overall rate. A decline in roaring rate with increasing age was particularly evident in our most successful stag (Saggie) whose performance was monitored between the ages of 9 and 12.

The relationship between roaring performance and fighting ability meant that it was generally possible for a human observer to predict which of two contestants would win by comparison of their roaring rates. Fights were more commonly preceded by contests where the approacher roared more frequently than the approachee than *vice versa* and prospective winners roared more in the five minutes before the fight than prospective losers (Wilcoxon Matched Pairs Signed Ranks Test, $T = 5$, $n = 14$, $p < 0.01$). In six cases where a challenger roared *less* than the haremholder he had approached but went on to fight him, the challenger never won, whereas in our total sample of contests, challengers won in around 50% of cases (CLUTTON-BROCK *et al.*, 1979).

(b) *Temporal changes in roaring rate.*

Roaring rates changed throughout the course of the rut. In most individuals, they increased during the early weeks and showed a sharp decline at some point between October 10 and 20 (see Fig. 10) which was invariably associated with a decline in other measures of rutting activity and with an

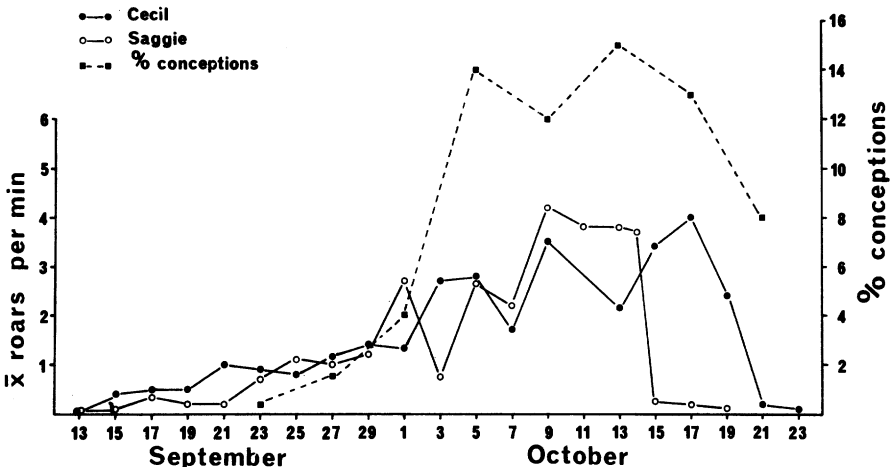


Fig. 10. Mean number of roars given per minute standing time by two mature stags throughout the rut.

increase in time spent feeding (CLUTTON-BROCK, unpublished data). Changes in rutting activity were not closely synchronised across individuals: as Fig. 10 shows, though the two stags started rutting at the same time, the older stag who was aged 12 finished earlier than the younger one who was aged 9 apparently because of a faster deterioration in body condition. During the latter stages of a stag's rut, fighting ability clearly declines. At this stage, mature stags tend to avoid fighting, they tolerate the presence of younger males close to their harems and, on several occasions, were observed to lose fights with individuals they had previously beaten.

Experimental Series III.

To check that the decline in roaring frequency at the end of the rut was not a product of a reduction in the number of roars to be answered by stags, we played 5 minutes of roars recorded from mature stags to six mature harem-holders during their rutting peak and again towards the end of their rut when basal roaring rates had declined and they had begun to feed consistently. This series of experiments was carried out in October 1977, using equipment with improved low frequency response, a Tannoy APT-60 30-watt amplifier with 100 volt line transformer, a Wharfdale E70 cabinet speaker and the Uher tape recorder. Otherwise the procedure was the same as in Experimental Series II. All six stags responded little to the later playbacks (Fig. 11).

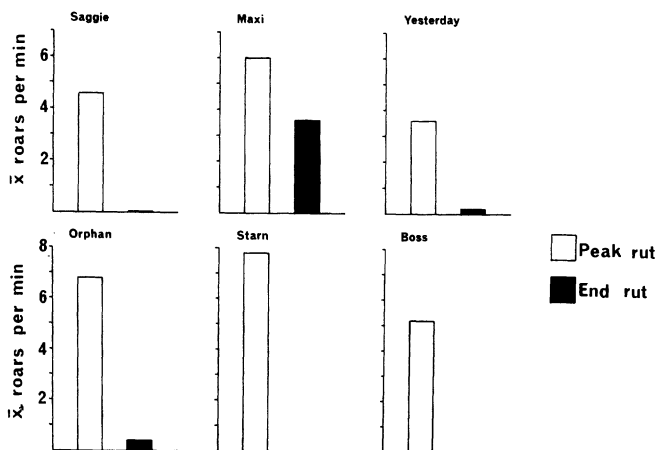


Fig. 11. *Experimental Series III*. Five minute periods of roars, at an average rate of 5 roars per minute, were played to six rutting stags of 7-12 years (a) during their period of peak rutting activity; (b) during the terminal stages of their rut when body condition was obviously poor and they had started to feed again.

The rapid decline in roaring suggested that it might be caused by changing hormone levels associated with declining body condition. Rutting behaviour of red deer stags has been shown to be affected by testosterone levels (LINCOLN & GUINNESS, 1973; LINCOLN, GUINNESS & SHORT, 1972) which are probably affected by body condition in many species (SADLEIR, 1969).

Roaring and assessment.

While the relationship between roaring rates and fighting ability indicated that stags could have assessed each other in roaring contests, it did not show that they actually did so. Circumstantial evidence strongly suggests that this was the case. It is clear that some form of assessment preceded fights: Only a small proportion of all approaches terminated in fights, the majority ending in the withdrawal of the approacher. While approaches involved stags of very different fighting ability, fights usually occurred between well-matched stags and fights between 'equals' (stags ≤ 3 ranks apart) were commoner than would have been expected by chance (One-sample χ^2 test, $n = 26$, d.f. = 1, $p < .001$). Finally, the distribution of roaring contests suggested that they were associated with assessment.

(1) Roaring contests seldom occurred where there was a visible discrepancy in fighting ability between two potential contestants. Examination of the outcomes of fights showed that stags of ≤ 5 years rarely won when fighting older individuals (CLUTTON-BROCK *et al.*, 1979). Approaches by young stags of ≤ 5 years to mature harem-holders were seldom followed by either roaring conversations or parallel walks: of 36 approaches to within 100 m by 5 year old males to stags of ≥ 6 years, none was followed by roaring contests, only two by parallel walks and only one of these by a fight. In all other cases, the 5 year old withdrew. Presumably, in these cases, the relative fighting abilities of both contestants were obvious and no further assessment was necessary. The situation contrasts with approaches involving two mature stags where of 50 approaches to within 100 m, 33 were followed by roaring contests.

Mature stags commonly ignored the roars of 4-5 year olds which had approached them. The roars of stags ≤ 5 are conspicuously higher in pitch than those of mature animals.

Experimental Series IV.

To test whether mature stags differentiated between the roars of young stags and those of mature animals we recorded 5 minutes of roars of a 5 year old (at an average frequency of 2.5 roars per minute) and paired this with five minutes of roars of a mature animal at the same rate. These

experiments were carried out in 1977 using the same equipment as in Series III, and as in Series I and II, the playback periods were separated by five minutes of silence. To ensure that differences in reaction could not be confused with any effects of habituation, we played the roars of the 5-year old before those of the mature stag. The rate of roaring was reduced from 5.0 r.p.m. to 2.5 r.p.m. in these experiments because young stags rarely roar more frequently than this. As Fig. 12 shows, the harem-holders roared less frequently at the roars of the young stags than at those of the mature stags.

(2) Roaring contests occurred more frequently between mature stags of equal fighting ability (*i.e.* differing from each other by ≤ 3 ranks in fighting success) than between inequals. Seventeen fights for which roaring data were available were observed in 1977. Of these, seven were between equals (≤ 3 ranks apart) and ten were between inequals (≥ 4 ranks apart). All seven equal fights were preceded by roaring contests but only three unequal fights (Fisher Exact Probability Test, $p < .02$).

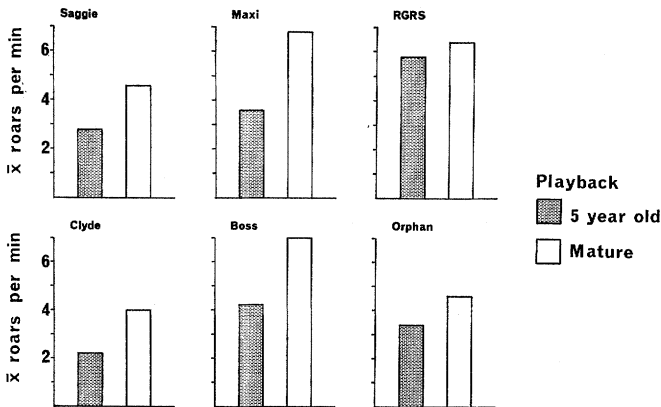


Fig. 12. *Experimental Series IV*. Two five minute sequences of pre-recorded roars at an average frequency of 2.5 roars per minute, one recorded from a 5 year old stag, the other from a mature stag, were played to six harem-holding stags of 6-12 years. Histograms show the mean number of roars per minute given by the subjects during the two playbacks.

(3) Fights were more frequently preceded by roaring contests where the approacher roared more frequently than the approachee than by ones when the approachee roared more frequently than the approacher (2-sample χ^2 test, $n = 20$, $\chi^2 = 3.81$, d.f. = 1, $p \approx .05$).

(4) In a number of particular cases, the roaring frequency of an approachee appeared to determine whether it was attacked or not. On October 13th, 1977 we watched a seven year old stag (Clyde) enter the Shamnan Insir rutting grounds for the first time that year. He approached the stag

with the largest harem in the area (Boss) and engaged in a 20-minute roaring contest in which he roared at a mean rate of 4.8 r.p.m., while Boss roared at a mean rate of 8.5 r.p.m. At the end of this, he withdrew and approached another mature stag with a similar sized harem (RGRS). The two exchanged roars over a three-minute period, Clyde roaring at a rate of 5.2 r.p.m., RGRS at 1.5 r.p.m. At the end of this, Clyde approached and the two fought. He was evidently the stronger stag, but lost the fight by allowing himself to be pushed against the side of a bank. Leaving RGRS, Clyde then moved to an 8-year-old stag with a small harem of 2 hinds. The two exchanged roars over a 30-minute period, Clyde roaring at an average rate of 7.1 r.p.m., the eight-year-old at 10.0 r.p.m. They parallel-walked briefly, then Clyde withdrew.

To roar or not to roar and the problem of basal roaring.

Our investigation of roaring in contest situations indicated that rutting stags probably used roaring as a means of assessment. However harem-holders also roar intermittently throughout the day (see Fig. 3). 'Basal' roaring may represent a statement to potential contestants by the harem-holder that his harem is occupied by a mature stag in rutting condition. Young stags of 5-6 years seldom roar when they are holding harems: in 1977, we measured basal roaring rates in six 5-year-old animals while they were holding harems. Average rates varied from 0.3 to 1.53 roars per minute between individuals, with a mean of 0.73. Average numbers of roars per bout varied from 1.0-2.35 roars with a mean of 1.41. This contrasted with basal samples from our sample of 10 mature stags of 7-12 years which gave average rates per minute of 2.24 (range 1.2-3.01) and per bout of 2.21 (range 1.89-2.70). Differences between the two groups were significant (Mann-Whitney U test, $U = 3$, $n = 6$, 10; $p < .002$; $U = 6$, $n = 6$, 10; $p < .02$).

Young stags are clearly able to roar more frequently since they often do so when not holding harems. They may roar little when they are holding harems because it is to their advantage to avoid attracting the attention of older and larger stags which are likely to displace them. This is supported by observations on two mature stags. Congal, a seven-year-old stag in 1974, permanently damaged his right fore-leg in a fight with a larger stag. In the 1975 rut, he was almost totally unsuccessful while in 1976, he held a harem intermittently throughout the rut. Though a large and powerful stag, his injury prevented him from fighting successfully and he could be displaced by considerably smaller individuals. In contrast to his behaviour before being injured in 1974, he roared little when he was holding a harem though roaring at least as frequently as most other stags of his age when not doing so.

Stumpy, a 9-year-old stag in 1977, showed a similar pattern of behaviour, roaring more often when he was not holding a harem than when he was holding. Though not obviously injured, he was the lowest ranking stag in that year and was defeated, on several occasions, by younger and smaller stags. When, in 1976 and 1977 respectively, we played two 5-minute records of roars to Congal and Stumpy (at average rates of 2.5 and 5.0 roars per minute) both reacted less than any of the other mature stags we had tested: mean rates of roaring during 2.5 r.p.m. playback 1.2, 0.2; mean rates during 5.0 r.p.m. playback 0.2, 0.2 r.p.m. Both may have learned that they were unlikely to win any fight and may consequently have avoided advertising the position of their harems.

Among mature stags, basal roaring levels may provide more subtle information than whether or not the harem is occupied. Basal roaring rates for the topranking five stags in the sample of 10 observed in 1977 were significantly higher than in the bottom-ranking five stags (Mann-Whitney U test; $U = 3$, $n_1, n_2 = 5$, $p < .028$) though mean basal rates were not significantly correlated with fighting success ($r_s = 0.479$, d.f. = 8, $p > .1$), largely because one 12-year-old stag who was declining in fighting success roared relatively seldom but continued to hold a large harem.

A contributory cause of reduced basal roaring rates in lower ranking animals may be their tendency to show low rates after they have been recently defeated. Immediately after decisive fights, losers showed reduced roar frequency and differentials in rate between winners and losers increased (1976 data, Wilcoxon Matched Pairs Signed Ranks Test comparing differentials in overall roaring rate between winners and losers in the five minutes before and after fights where the outcome was clear, $T = 10$, $n = 11$, $p < .05$). This was not the case in indecisive fights, even if they had been of long duration and the animals were obviously tired (1976 data, Mann-Whitney U Test comparing differentials in roar rates after decisive encounters ($n = 17$) and indecisive ones ($n = 4$): $U = 1$, $p < .002$). Reductions in roaring rate among losers usually lasted for several hours.

Parallel walks and assessment.

The majority of fights are preceded by a parallel walk between the two contestants (Fig. 9) which may be as short as 5 seconds or as long as 30 minutes. Like roaring contests, only a proportion of parallel walks are followed by fights and they often end with the withdrawal of the approaching animal.

The distribution of parallel walks suggests that they, too, may allow competing stags to assess each other:

(1) They occur more frequently between well-matched opponents than between individuals which obviously differ in fighting ability: of 50 approaches involving two stags of ≥ 7 years, 24 led to parallel walks while of 36 approaches by 5-6 year olds to mature animals only 2 did so. (1977 data, sample sizes 50, 36. 2-sample χ^2 test, $\chi^2 = 17.94$, d.f. = 1, $p < .001$).

(2) The duration of parallel walks is related to the occurrence and duration of subsequent fights. Longer parallel walks are less likely to be followed by fights (Mann-Whitney U test comparing durations of parallel walks not followed by fights with those followed by fights $n = 25, 29$, $z = 2.29$, $p < .03$), and in cases where stags parallel walked and subsequently fought the duration of the parallel walk was positively correlated with the duration of the subsequent fight ($r_s = .498$, d.f. = 22, $p < .02$).

(3) The occurrence of parallel walks is related to the resources at stake. The costs of fighting to harem-holding stags are likely to be highest, both because fights are longest and because both stags may lose their harems as a result of the depredation of young stags. Fights between harem-holders are more commonly preceded by parallel walks than either fights between solitary stags (2-sample χ^2 test, $n = 18, 21$, $\chi^2 = 9.1$, d.f. = 1, $p < .01$) or fights between solitary stags and harem-holders (2 sample χ^2 test $n = 19, 18$, $\chi^2 = 3.83$, d.f. = 1, $p \approx .05$).

DISCUSSION

The evidence supports the hypothesis that roaring may permit competing stags to assess each other's fighting abilities. Harem holding stags regularly engage in periods of reciprocal roaring with challengers. Both individual differences and temporal changes in contest roaring rates are correlated with differences in fighting ability. And challengers seldom press home attacks against individuals which have out-roared them and rarely win if they do so. It may be advantageous to a holding stag to roar regularly outside contest situations in order to inform competitors that his harem is occupied by a mature animal in rutting condition, thus deterring potential approachers. When approached, it may be to his advantage to roar as frequently as he can in order to inform the challenger of his fighting ability and condition and to 'convince' him that any subsequent fight will be long and costly. It is less obvious why a challenging stag should roar since holding stags rarely relinquish their harems without a fight. One possible explanation is that it may be necessary in order to provoke the approacher into displaying his potential, thus allowing the challenger to estimate the costs of escalating. Exactly what aspect of roaring is used as the basis for assessment is not clear: stags could be judging on mean roaring rate, maximum rate over a

given period, average roars per bout or the duration for which peak rates can be maintained. It seems likely more than one cue may be involved. Regular roaring outside contest situations is probably confined to mature harem-holders because small stags would be unlikely to beat a challenger and consequently cannot afford to announce their presence.

At least two different mechanisms could explain the relationship between roaring and fighting ability within mature stags. Both fighting and roaring use much of the same thoracic musculature and it is conceivable that roaring may be tiring (after roaring contests, stags are sometimes visibly short of breath and lie down) and a stag's ability to maintain a high roaring rate may indicate that it would tire slowly in a fight. If we assume that selection could not produce a mutant which was able to roar more frequently without increasing its strength or stamina in fights, this argument satisfies the requirement that an assessment criterion should be closely linked to fighting ability (PARKER, 1974; MAYNARD SMITH & PARKER, 1976; ZAHAVI, 1977). However, it has the weakness that, if roaring is tiring, it would be advantageous for neighbouring stags to challenge competitors which had recently engaged in roaring contests (DAWKINS, pers. comm.) — though this need not necessarily be the case either if (i) the usual preliminaries to fighting were sufficiently drawn out to permit recovery (ii) the tiring effects were specific to the muscles involved in roaring but the condition of these was inevitably related to overall body condition or (iii) stags which took such a temporary advantage were likely to be quickly ousted and to gain little. The first and last of these possibilities are likely to be the case while current knowledge of cervid physiology is inadequate to allow us to evaluate the second.

Alternatively, both roaring rate and fighting ability may be related to hormonal levels which depend on body condition. While this is probably the case (SADLEIR, 1969), it does not provide a convincing reason why roaring should be a reliable assessment criterion since we might expect selection to have favoured bluffers whose roaring performance was not related to their hormonal level. However, in the absence of any knowledge of the evolutionary flexibility or hormonal control systems, it is difficult to assess the validity of this argument.

The distribution of parallel walking indicates that stags may continue to assess each other during subsequent phases of the contest. We can suggest two possible criteria which they could be using in such cases: parallel walks sometimes continue long enough to be tiring: note the lolling tongues in the stags in Fig. 8. Alternatively, it is conceivable that a challenger's best guide to whether he will win or not is his rival's estimate of the situation. A tense and protracted interaction at close range may allow him to assess his op-

ponent's confidence and to decide whether he will escalate or withdraw. Though this situation might lead to selection for individuals able to maintain a "poker face" and to disguise their internal states, it seems possible that perfect concealment would be difficult to achieve.

The growing literature on assessment techniques suggests that honest advertisement may be a common phenomenon in animal societies. In several species, displays (or the structures associated with them) are related to body size and thus to fighting ability. For example, in anurans, large individuals have larger larynxes and give deeper calls than smaller ones. Recent experiment with toads (DAVIES & HALLIDAY, 1978) provide convincing evidence that males use these calls in deciding whether or not to attack each other. Similarly, MORTON (1977) suggests that aggressive calls in birds and mammals tend to be deep in pitch because this provides a reliable indicator of body size. Among ungulates, differences in horn and antler size are commonly related to body size and may be used in assessment (GEIST, 1971) for this reason, while our data suggest that gross differences in the pitch of roars are involved in the assessment procedures of red deer (see p. 160).

In red deer, it would be surprising if individuals assessed their opponents on the pitch of their roars alone since their fighting ability varies during the rut and declines with age (CLUTTON-BROCK *et al.*, 1979) while the pitch of their roars appears to remain approximately constant after they attain full body size. While our data suggest that they may use some aspect of the rate of roaring, this obviously does not indicate that other cues are not involved as well. It seems very likely that during the preliminary stages of contests, stags use a wide variety of cues to assess each other, perhaps including visual estimates of body condition, carriage and deportment as well as olfactory cues (see McCULLOUGH, 1969). In a number of other animal species, the frequency or type of aggressive displays is closely related to temporal changes in body condition and, probably, to fighting ability. Among nesting female iguanas (*Iguana iguana*) there is intense competition for burrows which are energetically costly to dig. A detailed study of contests (RAND & RAND, 1976) shows that the amount of energy which females are able to invest in contests changes throughout their breeding cycle, and that displays which are energetically costly are more likely to displace opponents than those which are not. Among red grouse (*Lagopus scoticus*) cocks take up territories during winter which they defend against rivals by displays involving song flights and by fighting. Individual differences in the frequency of song flights are correlated with dominance rank and territory size and may be related to hormonal variation (WATSON, 1970; WATSON & MILLER, 1971; MILLER & WATSON, 1978). Lastly, *anubis* baboons provide an example of age-related

changes in fighting ability which are reflected in displays. Among adult males, fighting ability is related to canine wear (PACKER, 1977) and competing males perform open-mouth yawns which reveal their canines to their opponents. As would be expected if such displays permit assessment, individuals with long sharp canines yawn more frequently than those with worn or broken ones while DARWIN (1850) reports a case of a captive baboon which no longer yawned after its canines had been sawn off.

Olfactory cues, too, may be important. For example, male squirrel monkeys (*Saimiri sciureus*) show a dominance display which involves penile erection and urination at or near the recipient's face (BALDWIN, 1968, 1970). Castration experiments indicate that the display is related to hormonal levels (PLOOG, BLITZ & PLOOG, 1963; GREEN, WHALEN, RUTLEY & BATTIE, 1972) and at least one observer (BALDWIN, 1968, 1970) has suggested that olfactory stimuli in the urine may inform the recipient of the physical state of the signaller. In addition, many physical characteristics involved in displays may be related to changes in body condition, and thus to fighting ability. Possible examples include colouration in several fishes (*e.g.* VAN IERSEL, 1958) and distinctive fat deposits in many mammals (C. POND, pers comm.).

We predict that further investigation of other species of large animals will reveal relationships between temporal variation in fighting ability and many different aspects of display behaviour, perhaps including rates of movement or vocalisation, duration of displays, and latencies or amplitudes. If, as we suggest, the frequency and form of many displays is related to fighting ability as a result of a common dependence on body condition, the potential evolution of 'cheating' or 'bluffing' phenotypes (MAYNARD SMITH & PARKER, 1976) may be restricted. ZAHAVI (1977) has recently suggested that only signals which reduce the signaller's fitness cannot be faked and argues the selection will favour the evolution of 'costly'¹ signals for this reason. While any signal must presumably have some energetic cost the advantages of developing elaborately costly signals will be reduced if many aspects of signalling ability are closely linked to fighting potential. Contrary to ZAHAVI, we should expect selection to have favoured individuals which honestly advertised their real potential by the cheapest possible means.

SUMMARY

In many large animals, changes in fighting ability within breeding seasons or across the lifetime of individuals are related to changes in body condition but not to obvious changes in size. In situations where a conflict of interests is likely to lead to a fight, we might consequently expect opponents to assess each other on traits which are related to variation in body condition. This appears to be the case among red deer stags. Competing

1) Cost being measured in terms of reproductive potential (ZAHAVI, 1977).

stags engage in roaring 'contests' in situations where fights are likely. Observation combined with playback experiments showed that stags answered each others' roars and that their roaring rate was related to that of their opponent. Both individual differences and temporal changes in roaring rates were correlated with changes in fighting ability and roaring contests usually occurred only where there was no obvious size discrepancy between opponents. The study suggested that assessment procedures probably continued during the parallel walks which commonly succeed roaring contests.

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ZUSAMMENFASSUNG

Bei vielen großen Tieren stehen Schwankungen der Kampffähigkeit während der Paarungszeit oder im Laufe der individuellen Lebenszeit mit Veränderungen im körperlichen Zustand im Zusammenhang, nicht aber mit offensichtlichen Veränderungen in der Größe. In Situationen, wo ein Interessenkonflikt wahrscheinlich zu einem Kampf führen wird, dürfen wir folglich erwarten, daß die Gegner einander nach Merkmalen abschätzen, die sich auf Unterschiede im körperlichen Zustand beziehen. Das scheint bei Rothirschen der Fall zu sein. In Situationen, wo ein Kampf wahrscheinlich ist, röhren konkurrierende Hirsche um die Wette. Beobachtungen zusammen mit Playbackexperimenten zeigten, daß die Hirsche das Röhren des Gegners einschätzen, und daß die Frequenz ihres Röhrens der des Gegners entsprach. Sowohl individuelle Unterschiede als auch zeitliche Schwankungen in der Röhrfrequenz hingen mit Schwankungen der Kampffähigkeit zusammen, und Wettröhren fand normalerweise nur dann statt, wenn kein auffallender Größenunterschied zwischen den Gegnern bestand. Die Untersuchung deutete an, daß der Abschätzungsprozeß wahrscheinlich noch während des Parallelschreitens weiterging, das oft auf Wettröhren folgte.
