

WILDLIFE BEHAVIOR AND ECOLOGY
George B. Schaller, Editor

RED DEER

*Behavior and Ecology
of Two Sexes*

T. H. Clutton-Brock
F. E. Guinness
S. D. Albon

With original drawings by
Priscilla Barrett

1982

THE UNIVERSITY OF CHICAGO PRESS
Chicago

Continuous Observation of Rutting Groups

During the rut, we also carried out a number of full day watches of stags and hinds. Samples included seven day-watches and five night-watches of mature stags (six years or older) when they were holding harems, seven day-watches of five- and six-year-old stags not holding harems, ten day-watches of anestrus hinds, and four day-watches of hinds in estrus. In addition, the activity of all hinds belonging to the harems of the stags that were watched at night were recorded at 15-min intervals, giving a measure of nighttime activity among hinds.

In connection with detailed studies of the rutting activities of stags (chap. 6), we also carried out shorter periods of continuous observation of individuals. Since in this case we were principally interested in the relative frequency of interactions, we watched only individuals that were standing. These watches varied in length between 10 min and 90 min. In analysis of these data, we combined samples for the same individual, and our sample size is the number of individuals sampled.

Incidental Records

During censuses and continuous watches, certain kinds of data were collected ad libitum. Whenever possible, suckling bouts were recorded and timed using a stopwatch; all threats and interactions were noted, whether or not they involved the target animal; and, during the rut, all approaches, parallel walks, fights, and copulations were recorded and timed. In analyses of fights and threats, we typically combined data from a wide variety of different individuals, since sample sizes for particular animals were too small to provide a reasonable basis for measurement. In analyses of suckling data, data for particular dyads were analyzed separately.

3.4 DEFINITIONS

This section lists definitions of variables used in the rest of the book that are not provided in the relevant chapters. Where development of a nonarbitrary rationale for a particular definition required considerable analysis, this is described in the relevant appendix.

Reproduction in Hinds

Harem: The group of hinds defended by a stag at particular time on a given day during the rut.

Definitions

Harem stability: The proportion of individual hinds seen in the harem of the same stag on successive days.

Turning point: The point at which cumulative sum analysis (see below) revealed an alteration in the rate of change of a process.

Mother's age: The age of a hind in years, assuming she was born on 1 May of her year of birth (i.e., a hind who was born in 1970 and conceived for the first time in 1972, giving birth in the spring of 1973, would be classified as a three-year-old mother). The ages of hinds born after 1968 were known accurately because individual recognition had been maintained since they were calves. Ages of hinds born before 1968 were known to within a year, from maintaining recognition of them since they were yearlings, from ear tags used in a previous study, or from examination of tooth wear.

Fecundity: A hind's fecundity was the proportion of years in which she gave birth to a calf. The fecundity of a category of hinds was the proportion of individuals that produced calves over a given period.

Mother's previous reproductive status: The reproductive status of a hind in the season that preceded the birth of her calf. Five categories of hinds were recognized: first breeders; true yelds (hinds that had given birth before but had not produced a calf in the previous year); summer yelds (hinds that had borne a calf and lost it before the end of September); winter yelds (hinds that had borne a calf and lost it between October and May); and milk hinds (hinds that had successfully reared a calf the previous year). In most comparisons, we combined true yelds and summer yelds (on the basis that, since most summer mortality occurred within a week of birth, summer yelds had not suffered the strains of lactation) and winter yelds and milk hinds (both these categories of mothers had supported calves through the winter, since most winter calf mortality occurs in March and April). We refer to these two categories as "yelds" and "milk hinds."

Mother's subsequent reproductive status: The reproductive status of a hind in the winter following the birth of her calf. Two categories were recognized: pregnant mothers (those that conceived again and gave birth the following year) and barren mothers (those that apparently failed to conceive again and did not give birth the following year).

Mother's home range area: The division of the study area in which the mother's core area...

Kidney fat index (KFI): The total weight of kidneys plus perinephric fat divided by the weight of the kidneys (see Mitchell, McCowan, and Nicholson 1976).

Birth weight: The weight of the calf at birth calculated for calves caught when fourteen days old or younger, assuming a weight gain of 0.4 kg/day (see Guinness, Albon, and Clutton-Brock 1978).

Conception date: The date on which a calf was conceived, estimated by backdating from its birth date by 234 days for female calves and 236 for male calves.

Birth date: Date of calving assessed from daily observations of the hind's udder size and flank distension, the behavior of the mother, and sightings of the calf.

Suckling bout duration: Sucks not separated by more than 15 min were considered a single bout, and the cumulative number of seconds for which an animal sucked was calculated. Isolated bouts of < 1 sec were scored as rejections.

Date of death: The date at which we judged a calf had died, based on observations of its mother, on the shrinkage of her udder, or on the location of the carcass (see Guinness, Clutton-Brock, and Albon 1978).

Reproductive success: The number of calves a mother reared to one year old over a specified period of time.

Lifetime reproductive success: The total number of calves a mother reared to one year old during her lifetime (see Appendix 8).

Reproductive value: The total number of *female* calves an individual of a given age could expect to produce during the rest of her life (see Appendix 9).

Reproduction in Stags

Sparring: When two stags locked antlers and twisted and turned their heads. Stags seldom pushed hard during sparring encounters. Sparring typically occurred between younger stags, and it never involved harem-holders.

Harem size: The total number of hinds one year old or older seen with a particular stag at one time on a given day.

Fighting success: The number of stags an individual beat plus the number that they beat, divided by the number of stags he lost to, plus the number that they lost to (Appendix 10).

Reproductive success: The estimated number of calves fathered by a stag during a given period of time (see Appendix 11).

Lifetime reproductive success: The estimated number of calves *surviving to one year* fathered by a stag during its lifetime (see Appendix 11).

Reproductive value: The number of *female* calves a stag of a given age could expect to father in the future (see Appendix 9).

Peak rut: The period between the turning points of harem stability, defined by cumulative sum analysis (see p. 50). This was closely associated with the conception peak and changed from year to year.

Social Behavior

Party: An aggregation of deer where no individual was more than 50 m from any other animal in the same party (see Appendix 12). The term carries no implication that membership was stable (see Crook 1970).

Party size: The number of animals in a party at a given time (excluding calves).

Matrilineal group: The total number of a hind's known matrilineal relatives.

Association: Two different measures of association between animals were used, though both were based on the frequency of occurrence in the same party. The first of these was the number of occasions on which two animals were seen in the same party, divided by the number of occasions on which either or both were seen in separate parties (coefficient 1). This measure was used in analysis of dyadic association between mothers and their calves and yearlings (sec. 9.3; see Guinness, Hall, and Cockerill 1979). The second measure used (coefficient 2) was essentially the same as the first with the exception that the denominator was the number of times the pair were seen together plus the number of times *each* of the animals was seen separately (Everitt 1974) and consequently gave an absolutely lower figure. This coefficient was used in analyses of association between hinds and their mature daughters as well as between stags (chap. 9, analyses 6, 8, 9, 10, 11, 13; figs. 9.7, 9.8, 9.9).

Nearest neighbor distance: The linear distance between the head of an animal and the head of the animal nearest to it excluding its own calf.

Mother-offspring distance: The linear distance between a mother and her offspring when both were members of the same party.

Range (or core area) overlap: The number of hectare quadrats in an

individual's range (or core area) that also fell in the range (or core area) of another animal, divided by the total number of hectare quadrats in the first animal's range (or core area).

Habitat Use and Feeding Behavior

Season: Some comparisons of feeding behavior and habitat involved only the "central" months of summer and winter. For summer these were May, June, and July; for winter, January, February, and March.

Grazing: When an animal either was actively biting or was chewing recently ingested food in a standing position. Over 95% of grazing records involved standing animals.

Ruminating: When an animal was either chewing or in the process of passing a bolus up to the buccal cavity. Over 95% of ruminating records involved lying animals.

Moving: When an animal was actively locomoting at end of the 1-min period.

Rutting: Included roaring, herding, chasing, or fighting.

Inactive, standing: When an animal was not engaged in any of previous activities and was standing.

Inactive, lying: As above, but lying.

Range: The area enclosed by a boundary set around the total number of sightings of an individual during a specified period (see Appendix 13).

Core area: The smallest number of contiguous hectare quadrats within an animal's range that accounted for 65% of all sightings of that individual (see Appendix 13).

Grazing bout: A period of feeding activity not interrupted by more than 10 successive min of some other activity (Appendix 14).

Day range length: The total number of hectare quadrats an animal entered during a day.

Shelter: Animals were recorded as sheltered if they were not exposed to the direct force of the prevailing wind.

Population Dynamics

Larder weight: The weight of the whole animal less alimentary tract and bleedable blood. This approximates to 73% live weight in stags shot in early autumn, and to 66% and 60% respectively in yeld and milk hinds shot between November and January (Mitchell, Staines, and Welch 1977; Mitchell and Crisp 1981).

Member of the study population: An animal that was seen in at least

10% of surveys of the study area in at least four months of the year.

Population size: The number of animals belonging to the study population (see above).

Cleaning date: The day on which the velvet of a stag's antlers began to fray.

Casting date: The day on which a stag cast its first antler.

Coat change: Animals were scored as changing into winter coats if more than half their summer coats had been shed.

Antler weight: The weight of a single dry antler measured at least six months after casting; only intact antlers were used.

3.5 STATISTICAL ANALYSIS

Selection of Tests

Standard parametric and nonparametric tests were used (Sokal and Rohlf 1969; Siegel 1956): where we used the former, we checked to see that the data were approximately normally distributed. For frequency comparisons, we used *G* tests (Sokal and Rohlf 1969) except where calculations of expected frequencies involved weighting or where the analysis was extracted from earlier papers. An advantage of the *G* test is that, like the analysis of variance, it permits investigation of whether the effects of two independent variables interact (i.e., whether the relationship between two variables differs across the range of a third variable). Where comparisons involved values for individual animals, we used the Mann-Whitney *U* test or, where $k > 2$, the Kruskal-Wallis one-way analysis of variance for independent samples, and the sign test or the Wilcoxon matched-pairs signed-ranks test for related samples (Siegel 1956).

Where we wished to investigate the effects of more than one linear variable at the same time, we used multiple stepwise regression (Snedecor and Cochran 1967), which removes the effects of the most strongly correlated variable, permitting one to examine relationships between other variables and the residual variance. In most cases we restricted such analyses to two independent variables. Where we needed to remove the effects of a nonlinear or categorical variable, we calculated adjusted means using analysis of variance and subsequently related these to other independent variables. Values that were corrected in this way are referred to in the text as "adjusted."

In a number of cases it was necessary to identify the point at

which the rate of a process changed—for example, to identify the peak rut, we needed to locate the date when the proportion of hinds changing harem began to decline. Cumulative sum testing (Woodward and Goldsmith 1964) is suitable for problems of this kind. Briefly, it treats the number of events, from first to last, as the outcome of a process whose rate can vary and calculates the cumulative sum of events that have occurred by each point in time. When the cumulative sum is plotted against position in the sequence, changes in process rate that might otherwise be obscured by short-term variability in the data appear as changes in slope. The locations of such changes (termed “turning points”) were determined visually before testing whether changes in slope were significant (Woodward and Goldsmith 1964).

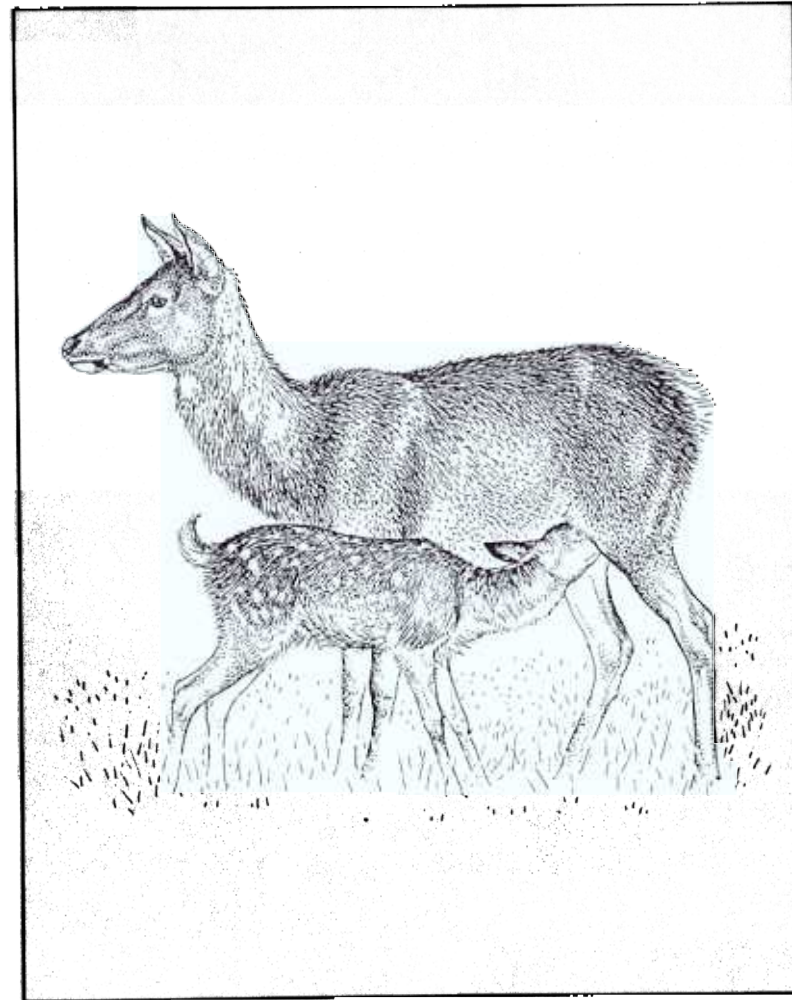
Results of Tests

The statistical tests used are indicated in the text by numbers in square brackets and are listed at the end of each chapter. All probability values are two-tailed unless otherwise specified. Where we state in the text that two samples differ, this indicates a significant difference at the .05 level or at a higher level of significance, while statements that two categories “tend” to differ indicate a nonsignificant result where there were additional grounds for believing that a difference existed. One-tailed probability values were used only when there were firm reasons for predicting the direction of an effect.

3.6 SUMMARY

1. Individual deer were recognized by ear tags, collars, and idiosyncrasies of coloring and shape. After 1971, the population of our study area in the North Block of Rhum increased from 60 hinds and 124 stags to 149 hinds and 135 stags in 1979.
2. The study area was censused five times each month, and the locality, activity, and associations of each animal seen were recorded. Less complete surveys of social relationships between mothers and their offspring were carried out on most other days.
3. Individual deer were also observed for a day (or, in some cases, a day and a night) at a time.
4. Definitions of variables used in the text are listed and our techniques of statistical analysis are described.

4 The Breeding Biology of Hinds



The Male and the Female individual may be compared in various ways with the spermatozoon and ovum. The Male is active and roaming, he hunts for his partner and is an expender of Energy; the Female is passive, sedentary, one who waits for her partner, and is a conserver of Energy.

W. Heape (1913)

4.1 INTRODUCTION

In order to reproduce, a female must select a fertile breeding partner. In practice this seldom presents difficulties, and in most species receptive females can rely on males to find them. It is not yet clear to what extent female mammals can enhance their reproductive success by selecting particular males. Theoretically, they ought to do so either by choosing partners who are able to invest heavily in their joint offspring or by choosing ones that possess superior genotypes (Halliday 1978; Partridge 1980). In red deer, where males play no part in rearing their offspring, the first kind of choice is redundant. Does the second kind of choice occur? In sections 4.2 and 4.3, we describe the mating behavior of red deer hinds and examine evidence for mate selection by hinds.

Since a hind's life span is relatively short, each calf she bears represents a large portion of her reproductive potential, and strong selection pressures will favor mothers that minimize calf mortality. To accomplish this, hinds must minimize the chance that their calves will be caught by predators, at the same time ensuring that they grow rapidly so that they are large and healthy by the onset of the winter. In section 4.4 we describe gestation, birth, and early care, and in the final section we describe the costs of maternal investment and the effects of rearing a calf through the summer on the mother's subsequent condition, reproductive performance, and survival.

4.2 MATING

The first change that was evident in the behavior of hinds at the onset of the rut was a restriction in the size of their ranges, which occurred from early September onward, several weeks before the stags joined the hinds on the rutting grounds. For example, eight hinds whose ranging behavior was monitored in 1975 reduced the total area they used by 45% between 6 September and 26 September, compared with 16 August to 5 September [1] (see fig. 4.1). This change was associated with an increase in the amount of time they spent on the short greens, where they collected in large parties. At approximately the same time, they began to give off a characteristic scent from the region of the vulva that grew in intensity during the following weeks (Guinness, Lincoln, and Short 1971).

Mating

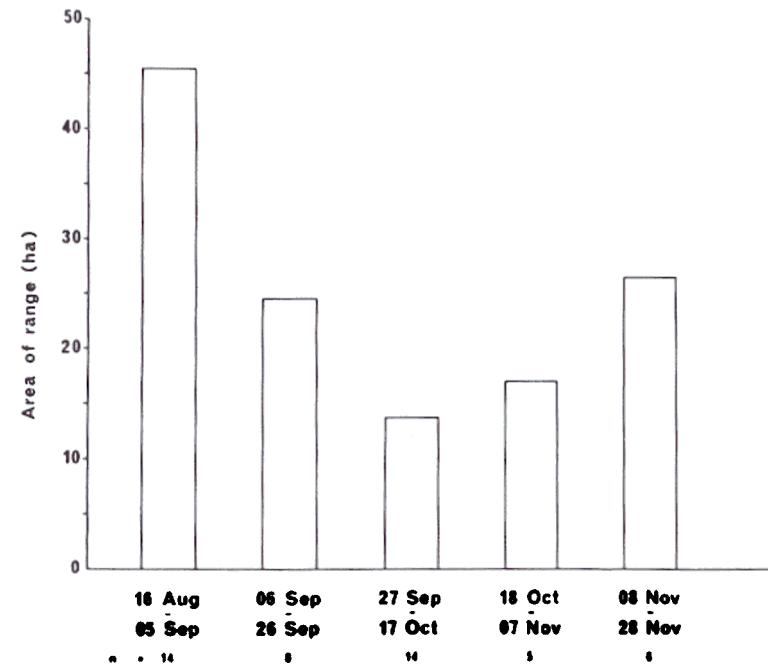


FIG. 4.1. Median range size in hinds during the 1975 breeding season. Samples for each three-week period were based on animals recorded in censuses at least five times during the three weeks. Sample size is shown below each histogram. Range size was determined by the method described in Appendix 13.

Mature stags began to leave their normal ranges in mid-September and usually joined the hinds on the short greens before 1 October, becoming progressively intolerant of each other's presence. At first they showed little interest in the hinds, but by the first few days of October they started to associate more regularly with parties of hinds and became increasingly intolerant of the presence of male yearlings and young stags in the vicinity. As far as possible, they controlled the movement of hinds, preventing individuals from leaving wherever possible by herding them back to the group and driving in extra hinds that approached. The proportion of hinds belonging to harems grew rapidly, and by 5 October only a small proportion of animals were seen outside harems (fig. 4.2). The day range length of hinds decreased from about 2 km per 12-h day to less than 1 km [2], and range size also declined further.

of hinds held in enclosures without stags show that, if still unmated, they continued to cycle as late as April (Guinness, Lincoln, and Short 1971; F. E. Guinness, unpublished data). Mean cycle length in a sample of hinds kept in an enclosure on the island was $18.3 \text{ days} \pm 1.7 \text{ days}$ (Guinness, Lincoln, and Short 1971).

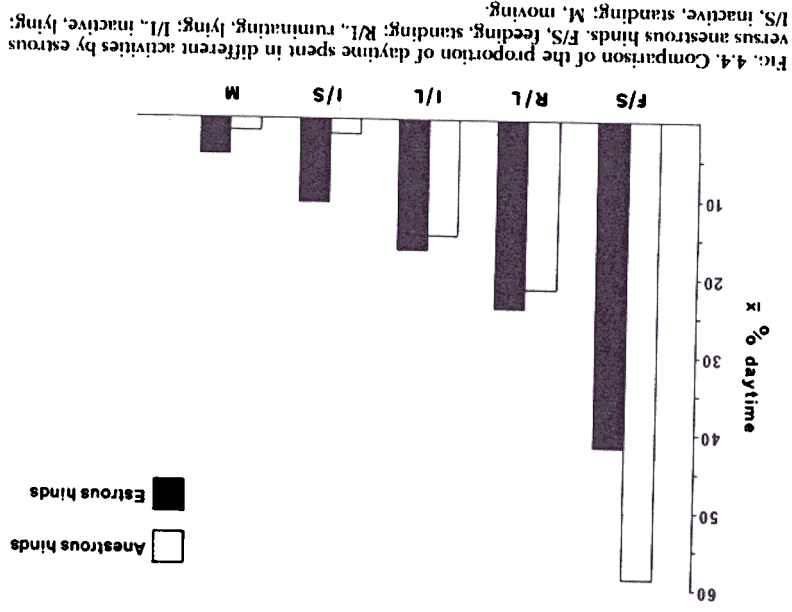


FIG. 4.4. Comparison of the proportion of daytime spent in different activities by estrous versus anestrous hinds. F/S, feeding; standing; R/L, ruminating; lying; I/L, inactive; lying; I/S, inactive; standing; M, moving.

4.3 HAREM MEMBERSHIP AND MATE SELECTION

The stability of harem membership gradually increased during the early weeks of the rut, peaking at the same time as the frequency of conceptions among hinds (see figs. 4.3, 4.6). However, even when harems were most stable, changes in harem membership were common, though they were often temporary. The causes of harem changing were diverse. Hinds often left a harem to feed elsewhere and were subsequently gathered up by a neighboring stag. When family groups had been split up as a result of conflicts between stags, individuals often left the harem they were in to rejoin their relatives in another rutting group. And, in cases where the harem-holding stag persistently threatened a hind's calf or yearling, the mother often left the harem. The activities of competing stags were also important in influencing harem membership. Young stags that infiltrated



FIG. 4.5. An estrous hind stands with back slight arched, allowing the stag to press his chin on her back (a) and finally to mount her (b) and (c).

harems often chased out hinds when the harem-holder was otherwise occupied, and fights between harem-holders were often associated with changes in harem membership among the hinds.

knew the birth date of the calf gave a figure of 236.1 ± 4.75 days for gestation of male calves and 234.2 ± 5.04 for females. Other studies indicate that, although gestation length may be influenced by environmental variables, such effects are not pronounced and represent a small percentage of the total length (see Verme 1965; McEwan and Whitehead 1972; Clegg 1959; Alexander 1956).

Both resorption and fetal loss appear to be uncommon in red deer (Blaxter et al. 1974; Mitchell, Staines, and Welch 1977), and evidence for other cervids suggests that the rate of fetal loss usually lies between 10% and 15% (Robinette, Gashwiler, Jones, and Crane 1955; Teer, Thomas, and Walker 1968; Ransom 1967; Nellis 1968; Markgren 1969). In a small number of cases, hinds weaned a calf but failed to give birth the following season, and it seems likely that these animals may have aborted or resorbed the embryo. However, where hinds did not give birth, we believe they usually had failed to conceive in the previous autumn.

Birth

The first sign that a hind is about to calve is a marked swelling of the udder, usually 1–2 days before parturition (see Blaxter et al. 1974). A few hours before birth, the perineal area becomes red and slightly swollen (see Hall 1978). During labor, which usually lasts 30–120 min (Arman 1974; Hall 1978; Arman, Hamilton, and Sharman 1978), the hind becomes more and more restless, frequently nuzzling or grooming her flanks, udder, and perineal area. During the days before and after parturition, hinds sometimes bellow, raising their noses in the air and giving a loud deep moan similar to a stag's roar but softer in tone, a behavior that may be promoted by the high levels of estrogen characteristic of the perinatal period. In the later stages of labor hinds normally lie on their sides, straining as the fetus begins to emerge. Once it is partly exposed, they frequently stand, allowing it to fall out (see fig. 4.8a).

Immediately after the birth, the mother licks the calf clean, then eats the membranes, licking up the amniotic fluid from the ground (fig. 4.8b). Calves are usually able to stand within half an hour of birth, and the first suckling bout typically occurs within 40 min of the end of labor (Arman, Hamilton, and Sharman 1978). The placenta is expelled 1–1½ h after birth and is immediately eaten by the hind; the ground where it fell is cleaned and any



FIG. 4.8. (a) A hind, who has been lying during labor, stands as the fetus emerges, allowing it to fall out and (b) cleans her newly born calf. (Photographs by Marion Hall.)

stained grass is eaten (see Hall 1978). After cleaning their calves, hinds commonly rest close to them for a short period. Subsequently, another bout of licking and sucking occurs, and at the end of this the mother normally moves slowly away from the place of birth, encouraging the calf to follow her. At some stage during this movement (which seldom exceeds 300 m) the calf leaves the mother, adopting a characteristic hunched posture with head held low, and eventually lies down, typically curling up in a patch of deep grass or heather. During the next few hours the mother grazes or rests within sight of the calf but rarely approaches it

closely. After a further 2–3 h she usually visits the calf, and a third bout of licking and sucking occurs—the mother eats the calf's feces and urine as the calf sucks (fig. 4.9). Subsequently the calf again lies down, and the mother moves farther away.



FIG. 4.9. A hind suckles her week-old calf. The mother is licking beneath the tail to stimulate the calf to defecate.

Early Care

Though many red deer populations live in areas where predators are uncommon, this is a comparatively recent circumstance, and studies of populations living where substantial numbers of mammalian predators still exist show that predation can have important effects on recruitment (e.g., McCullough 1969). Since each calf represents a large fraction of a hind's lifetime reproductive success, strong selection pressures should favor mothers that take care not to reveal the position of their calves.

Hinds about to calve typically move away from their matrilineal groups and their usual home ranges (Clutton-Brock and Guinness 1975) and keep their calves on high ground. Isolation of nursing mothers from their usual social groups and separation of the calf from the mother throughout most of the day probably help to make both of them inconspicuous to predators hunting by visual

or olfactory cues (see Lent 1974; Geist 1982): across ungulate species, separation of mothers and offspring during the days following birth is associated with cryptic coloration of the young and with ingestion of their feces by the mother (Walther 1965, 1968, 1969).

When their calves were standing (and therefore visible), hinds were intensely vigilant. Before calving, most individuals alerted (raised the head and gazed around) during approximately 20% of minutes in which they were seen feeding (see fig. 4.10); after calving, the percentage increased to about 70% when they were accompanied by standing calves under twenty-one days old. If hinds with young calves were suddenly disturbed when the calf was visible, the hind commonly barked, and the calf quickly hid (see also Bubenik 1965). The hiding response was uncommon among calves over a week old, though evidence suggests that it may continue for up to three weeks in elk (Altmann 1963). On Rhum, hinds with calves over a week old quickly fled when disturbed. Their flight distance was considerably greater when they were accompanied by standing calves less than two weeks old than either before calving or after calving when the calf was lying, though this distance decreased rapidly with increasing calf age (see fig. 4.11).

As calves grew older, both their own behavior and their mother's behavior changed rapidly. During their first three weeks, calves spent over 80% of the time their mothers were with them within 3 m of the hind. However, they rarely lay down close to their mothers and usually moved at least 20 m away before doing so (Clutton-Brock and Guinness 1975). This appeared to represent a preference for lying away from the mother, since they frequently ignored lying places close to her that were apparently suitable. After the third week of life, though calves spent less time close to their mothers, they more often lay down closer to them.

Calves selected their lying sites carefully. They usually lay in long vegetation, in sites raised above the surrounding ground and sheltered from sight on at least one side (see fig. 4.12). In many cases sites were within a gully or a dip in the hill's face. This aspect of site selection appeared to be reinforced by the mother's behavior: mothers with standing calves tended to avoid moving out of dead ground, and they traveled swiftly when on the open face of the hill. As they grew older, calves more frequently lay on the

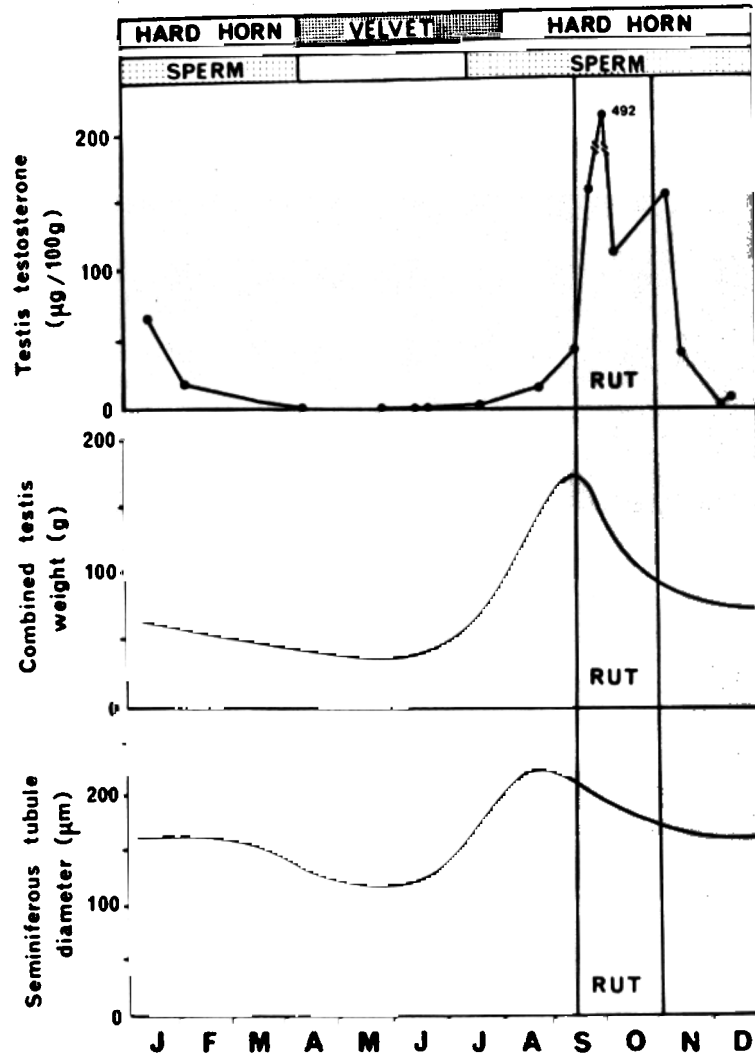


FIG. 6.1. Seasonal changes in the weight, testosterone concentration, and seminiferous tubule diameter of the testes of stags (redrawn from Lincoln 1971a).

1973). However, other hormones are also involved (Fletcher and Short 1974), and the timing of rutting behavior is affected by environmental factors including photoperiod (Jaczewski 1954; Goss 1969a,b), odor from the hinds, and past experience of rutting (Lincoln, Guinness, and Short 1972).



FIG. 6.2. A six-year-old stag with his harem at Kilmory in 1974.

Displays and Interactions

As mature stags spend more of their time associating with hind groups, they move less and less, remaining with their harems in one particular area of the rutting grounds (Lincoln and Guinness 1973) and moving only as their harems move to new feeding areas or to sheltered positions (see fig. 6.2). They begin to display regularly and frequently interact with their hinds. The displays and interaction patterns of stags have already been described in detail (Struhsaker 1967; Bützler 1974; Geist 1982). In our study we used a simplified typology of displays and interactions to make quantification easier. The displays and interactions we examined were as follows.

- Roaring:** A deep guttural roar (see Clutton-Brock and Albon 1979). Roars are aggregated into bouts of one to ten that are often given on the same exhalation. Roaring rate was the mean number of roars given per minute (see fig. 6.3).
- Barking:** A series of short barks typically directed at young stags after they have been chased away.
- Thrashing:** The stag rakes the ground and vegetation with his antlers, often spraying the area he is thrashing with urine and subsequently rolling on it (see fig. 6.4).
- Wiping:** Harem-holding stags commonly rub their chins, antler pedicles, or preorbital glands on outstanding "landmarks," including posts and rocks (fig. 6.5).

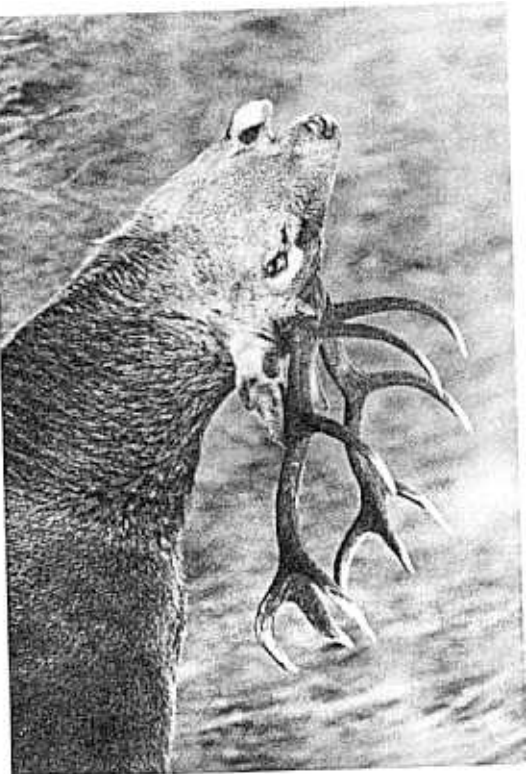


FIG. 6.3. A nine-year-old stag roars at an intruder



FIG. 6.4. A seven-year-old stag thrashes in Juneau marsh



FIG. 6.5. A seven-year-old stag marks on a log at Kilnory.



FIG. 6.6. A five-year-old stag wallows during mid-September



FIG. 6.7. A four-year-old stag on the edge of a harem, showing flehmen.

Wallowing: The stag wallows in a pool or peat bog, often also urinating into it and wiping his antorbital glands and antlers on nearby vegetation (fig. 6.6).

Flehmen: After sniffing a hind or the place where a hind has urinated, stags sometimes show flehmen, raising their heads and curling back their upper lips (fig. 6.7).

Sniffing and licking: Stags frequently approach lying hinds and lick the back of their heads and necks, gradually working over the head toward the preorbital region (fig. 6.8). This may be followed by an attempt to sniff and lick around the base of the tail. Bouts of sniffing and licking, which may last several minutes, are usually terminated by the hind's getting to her feet and moving away. After this, the stag commonly sniffs and licks the grass where the hind has rested. Hinds often urinate while lying, and this may permit the stag to scent pheromones released in the urine.

Herding: Stags often head off hinds that are attempting to leave their harems by walking outside them, head held high, with a stiff, prancing gait (see fig. 6.9). The stag's head is typically at an angle to the direction of movement with eyes half closed. If the hind persists in attempts to leave the harem, the stag may

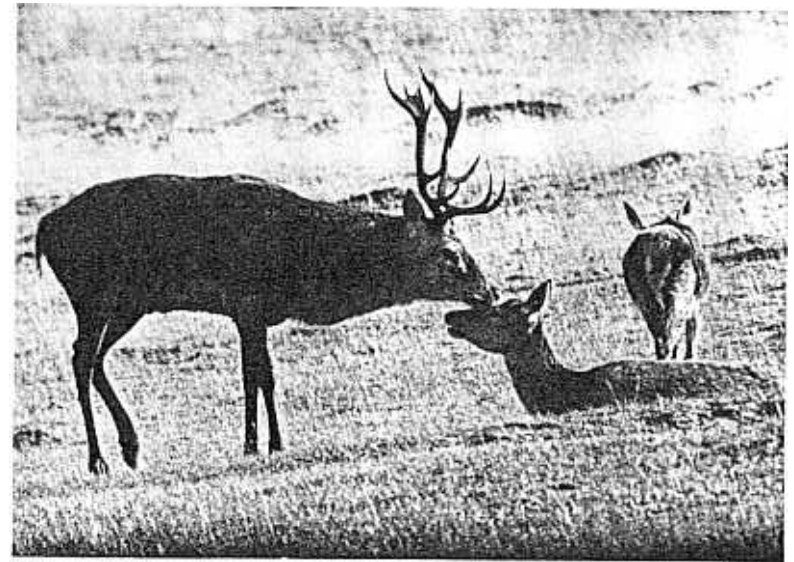


FIG. 6.8. A stag licks the face and orbital area of a lying hind.

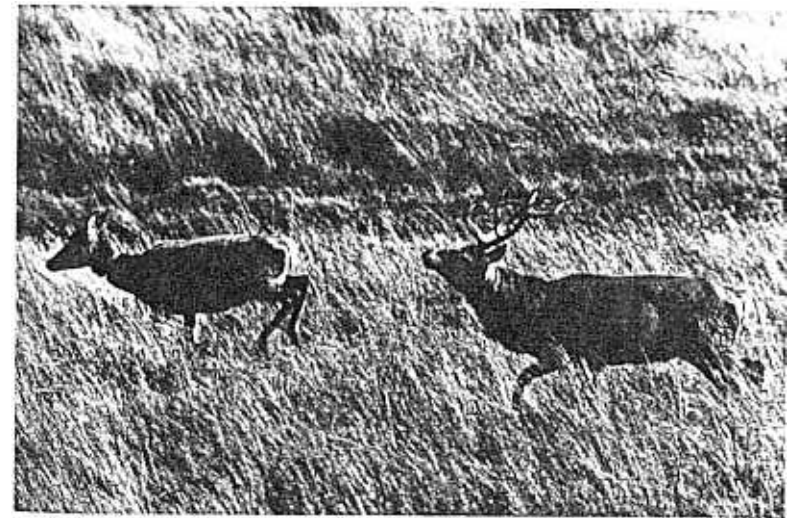


FIG. 6.9. Driving in an outlying hind. The stag's nose is lifted, and he looks sideways at the hind.



FIG. 6.10. A nine-year-old stag chivying a mature hind.

threaten her with lowered antlers or by giving a brief scissors kick with his front legs and may bark at her. Hinds that are herded are almost always on the periphery of the harem. In over 90% of observed cases, hinds moved back toward the center of the harem when herded.

Chivying: Stags frequently chase hinds over short distances within their harems (fig. 6.10). During these chases the stag trots after the hind with neck outstretched, sometimes extending his tongue. Chivies end when the stag stops, apparently losing interest, and they are often followed by a bout of roaring.

Mounting: Only hinds in estrus allow the stag to mount. Mating sequences usually involve several mountings over a period of up to an hour or more (see Morrison 1960; McCullough 1969) (fig. 6.11). Ejaculation can be easily identified by a sudden thrust

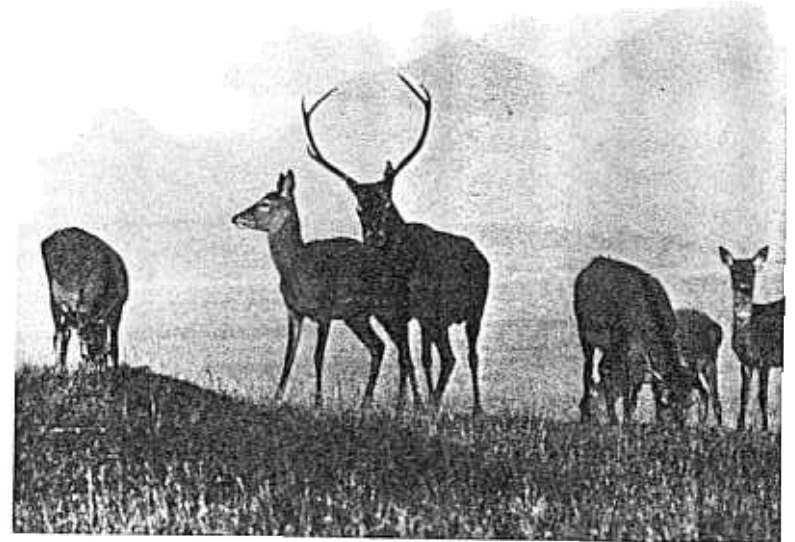


FIG. 6.11. Preparing to mount. An estrous hind stands with her back legs splayed as the stag licks her rump.

that jerks the stag's body upright, often throwing the hind forward several paces (fig. 6.12).

Displacing: Stags displace young stags or rivals that approach their harems by walking steadily toward them. We defined displacements as cases where the harem-holding stag approached another stag and the latter retreated.

Approaching: Where one stag moves to within 100 m of another.

Parallel walk: After one stag has approached another, the pair may move into a tense walk in which they move parallel to each other, typically 5–20 m apart (fig. 6.13). At this stage their hair is often raised, and their gait is slow, regular, and stiff. The duration of parallel walks was the total duration of an interaction involving parallel walking, and it usually included several circuits.

Initiating: One stag lowers his antlers, inviting contact. Antler joining often follows so quickly that identifying the initiator of a fight is impossible (fig. 6.14).

Fighting: The two stags lock their antlers and push to and fro, occasionally disengaging, until one individual is driven rapidly backwards (figs. 6.15, 6.16). Fight duration was the period from first antler contact to last contact, including short intervals when stags disengaged before locking antlers again.



FIG. 6.12. A leaping stag at the moment of ejaculation when the stag leaps clear of the ground.

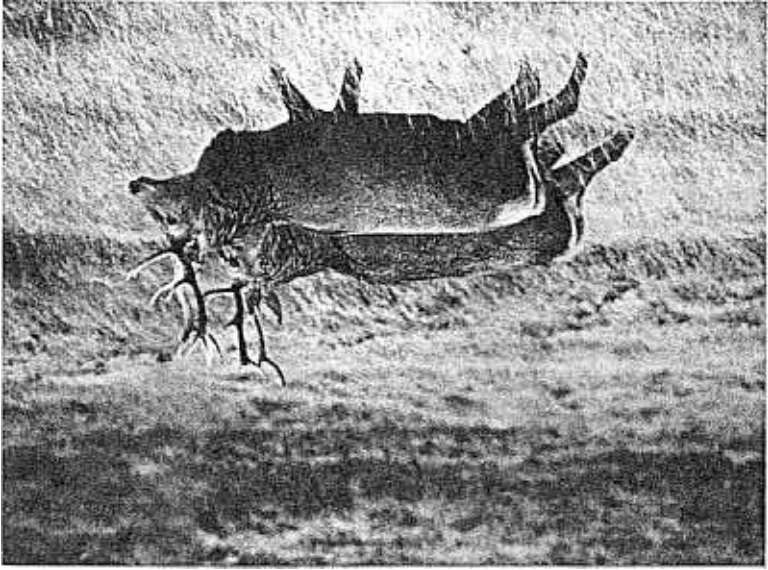


FIG. 6.13. Two mature stags parallel walk during the latter part of the rut.

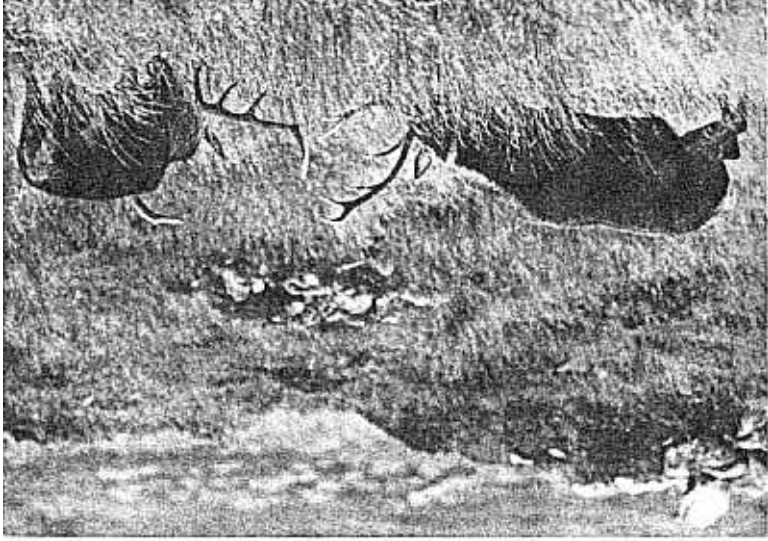


FIG. 6.14. After parallel walking, two stags simultaneously lower their antlers, initiating contact.

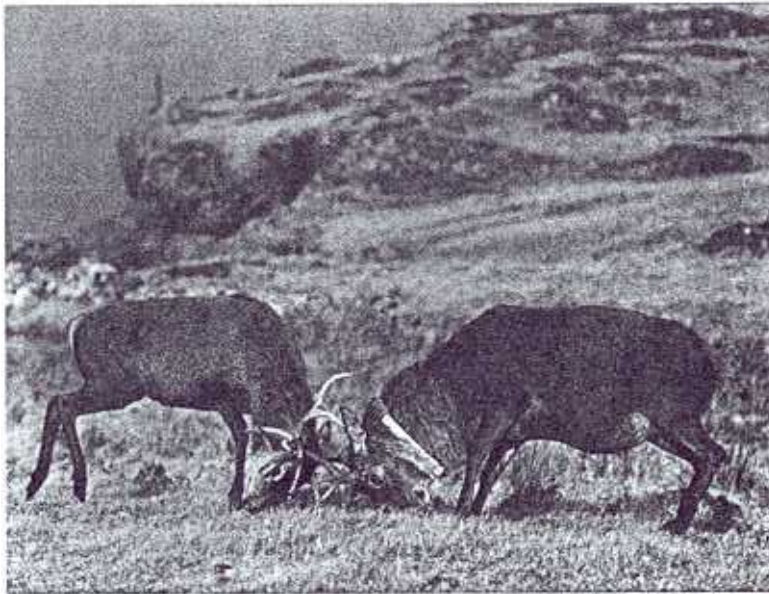


FIG. 6.15. Two mature stags fight during the late rut

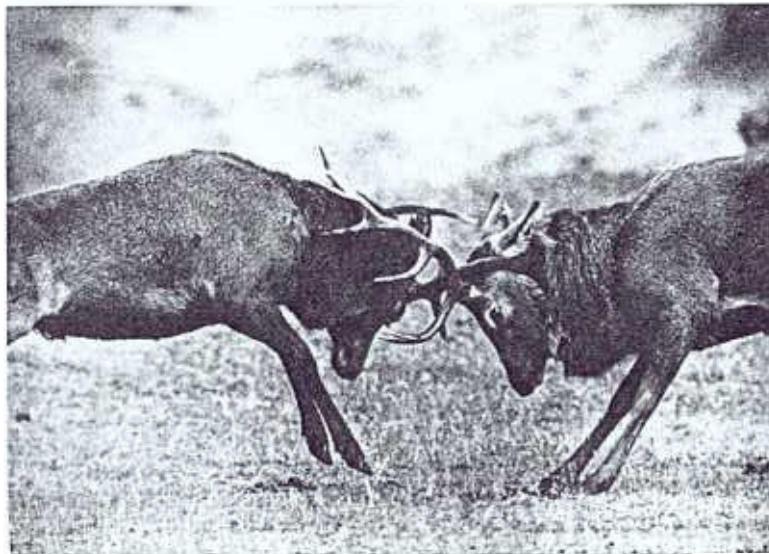


FIG. 6.16. A stag leaps up and forward in an attempt to dislodge his opponent



FIG. 6.17. A harem-holder chases a yearling male from the harem.

Chasing: Stags chase yearlings or young stags away from their harems by running directly at them, often pursuing them till they are more than 100 m from the harem (fig. 6.17). Chases terminate when the harem-holder stops and turns back to his harem. Stags often end a chase with a scissors kick of the forelegs followed by a bout of roaring. On some occasions stags also chase calves and even yearling females out of the harem, and particular stags do so regularly. Removal of calves from the harem must be of dubious advantage to the stag, since their mothers often follow them when they leave.

Rutting Activities and Age

Only among mature stags five years old or more did a substantial proportion of individuals hold harems: figure 6.19 shows the mean number of stags of different ages that were seen holding hinds in the study area between 25 September and 25 October. The age at which stags started to hold harems slightly preceded the point at which they reached full adult weight (see fig. 2.4), though their breeding success did not peak till they were eight (see below). Studies of other populations indicate that breeding is

largely confined to stags of similar ages (Gossow 1971; Mitchell, Staines, and Welch 1977).



FIG. 6.18. At the height of the rut, a group of two- to five-year-old stags collects close to the harem of SAGY on the Kilmory greens.

Stags of two to four years old rarely held harems and spent much of their time on the periphery of the larger harems, frequently attempting to infiltrate or disperse them (see fig. 6.18). Though we never saw such stags mount a hind successfully during the peak of the rut, their depredations could lead to rapid reductions in harem size. Their success in penetrating the harem depended on the position of the harem-holding stag: they were consistently more successful in entering harems if the holder was on the far side of the harem, and they typically approached from the "blind" side (Gibson 1978). A common technique used by young stags was to run through the harem giving alarm barks and thus causing the hinds to scatter. However, in less than 10% of attempts made when harem-holding stags were present did young stags manage to extract hinds successfully, though when the stag was absent they generally did so.

Most stags over eleven failed to hold harems and reverted to

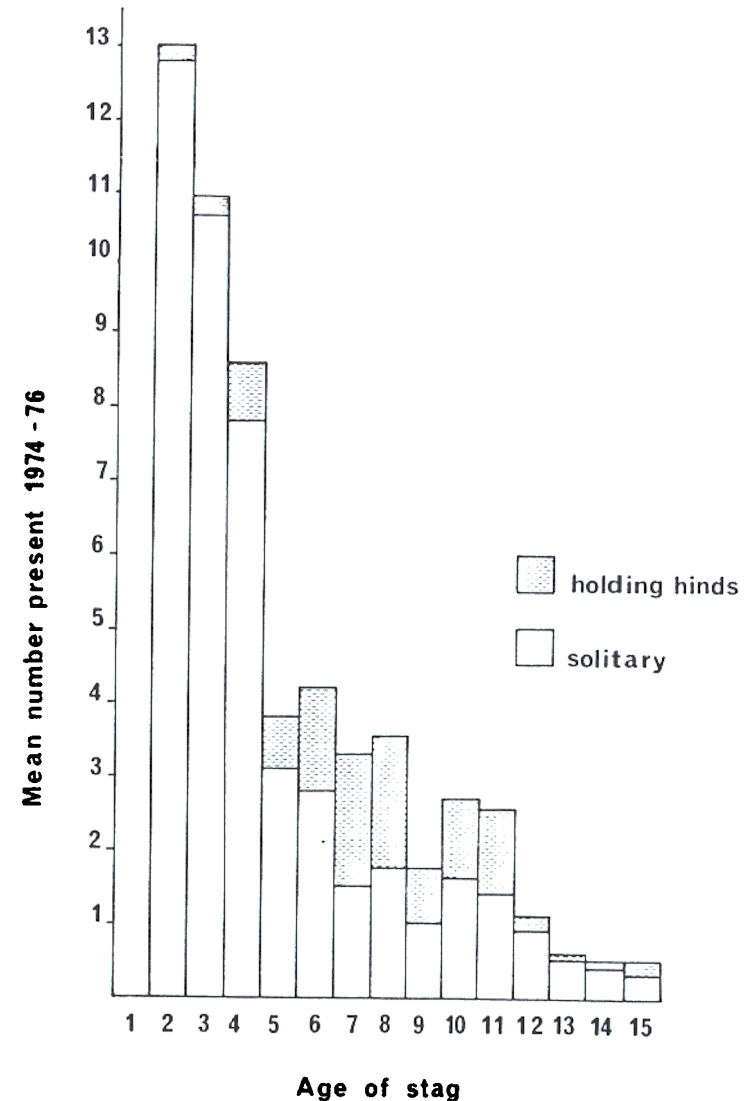


FIG. 6.19. Mean numbers of stags of different ages (in years) in the study area between 1974 and 1976 during the rut.

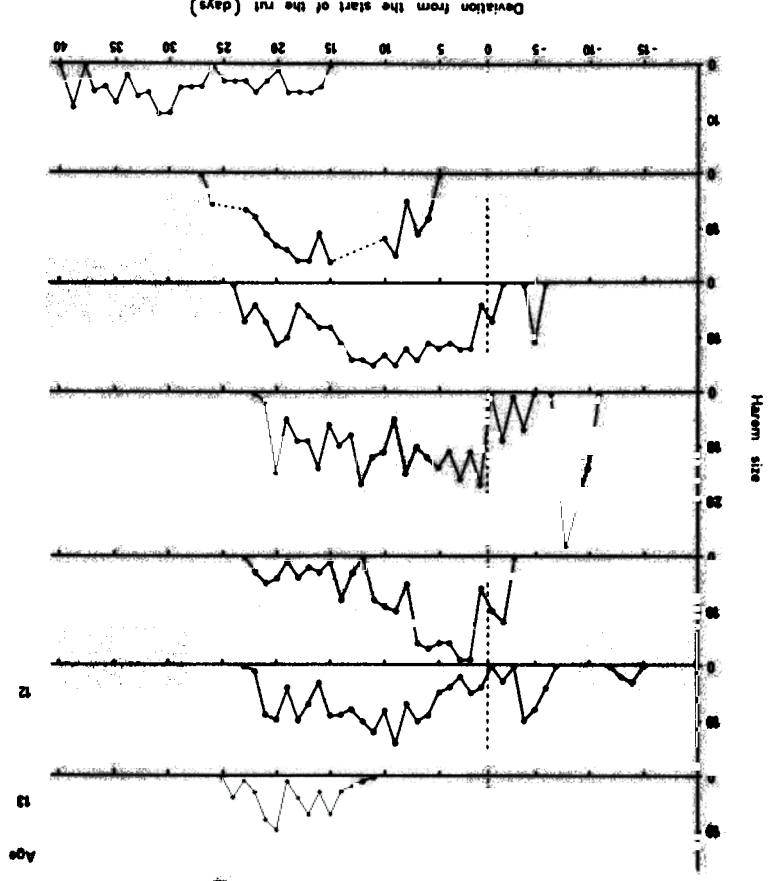


FIG. 6.20. Number of hinds held per day in each of seven years by a successful stag (SAGY). The distribution of harem-holding in each year was standardized around the onset of the peak period of rutting in the population, defined as the first turning point in harem stability.

wandering around the harems of prime stags, abducting an occasional hind. Other studies have shown that both condition and weight typically start to decline at about this age (Mitchell, Staines, and Welch 1977), and most old stags in our study area were in obviously poor condition. Studies of other populations of red deer and elk have shown similar variations in rutting activity between males of different ages (McCullough 1969; Gottschlich 1968). The timing of harem-holding also varied with the stag's age and prowess. Young and old stags held harems later than those in their prime. For example, figure 6.20 shows the number of hinds

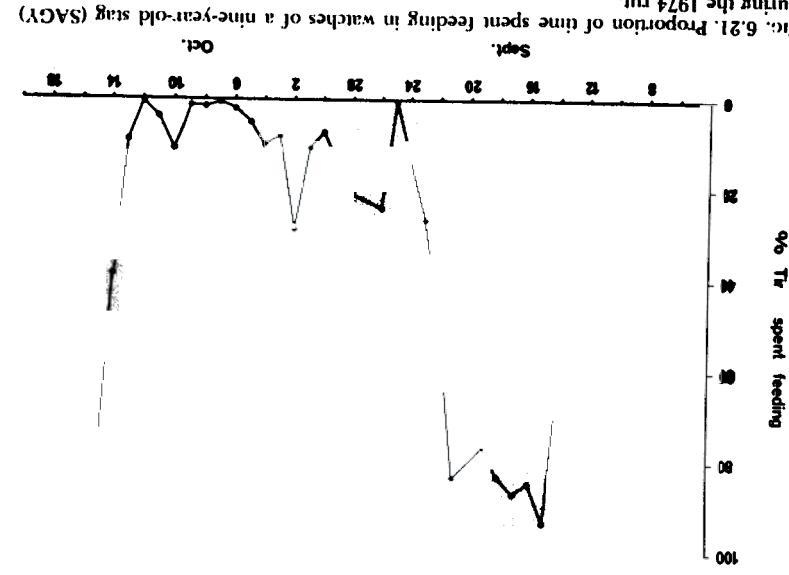


FIG. 6.21. Proportion of time spent feeding in watches of a nine-year-old stag (SAGY) during the 1974 rut.

held per day in each of seven years by a very successful stag (SAGY). As SAGY matured, he held harems progressively earlier relative to the onset of the peak rutting period, and as he aged his rutting period again became later. These changes in the timing of harem-holding were probably partly a direct consequence of changes in condition and partly a result of the fact that less successful fighters were more likely to retain harems when the intensity of competition was reduced.

Activity Budgets of Harem-Holders

When they started to hold harems, the activity budgets of harem-holders showed dramatic changes (see fig. 6.21). The proportion of daytime spent grazing fell from 44% during the summer to less than 5% in the rut, while the proportion of time spent moving and standing inactive increased from 3% and 4% to 15% and 33% respectively (see table 6.1). Nighttime budgets showed similar changes. Young stags and stags without harems did not show as marked a decline in grazing time, though they grazed less than at other times of year. The decline in grazing associated with harem-holding was quickly reversed when the stag ceased to hold a harem, and it increased from a low level to at least as high as at other times of year within 24 h (see fig. 6.21).

TABLE 6.1 Proportion of Time Spent in Different Activities during the Rut (25 September–25 October)

	Day	Lying				Moving	Rutting ^a
		Grazing	Ruminating	Inactive	Standing Inactive		
<i>Day</i>							
Harem-holders ≥ 6 years old	7	4.0	<1.0	36.8	33.1	15.5	
2-5-year-olds		35.5	18.0	26.2	9.5	6.8	
Estrous hinds	4	41.8	24.1	16.7	10.7	4.6	
Anestrous hinds	10	58.8	21.5	14.8	1.9	1.6	
<i>Night</i>							
Harem-holders > 6 years old	5	5.6		40.5	41.8	10.7	
Anestrous hinds	Scan data	37.5		56.0	4.4	1.3	

^a Times when the stag was engaged in any of the rutting activities listed on p. 00 but was not moving.

Similar changes in the activity patterns of rutting stags have previously been described in elk (Struhsaker 1967; McCullough 1969). Physiological studies indicate that they are probably controlled by hormonal mechanisms, for penned animals maintained on a natural cycle of lighting but kept separate from hinds show a decline in appetite and body weight at the time of the rut (Simpson 1976; Kay 1978; Magruder, French, McEwan, and Swift 1957).

As a result of the high energy costs of rutting and reduced food intake, the body weight and condition of rutting stags shows a rapid decline in September and October (see fig. 6.22), and some individuals lose as much as 20% of their body weight over this period. It is presumably declining condition and associated changes in hormone levels that cause stags to terminate their rutting activities. This typically occurred suddenly, and stags could switch from a high level of activity one day to an almost total cessation of rutting activities combined with intense feeding on the subsequent day (see fig. 6.21). There was apparently a relationship between the body condition of the stag at the beginning of the rut and the number of days he rutted—stags that entered the rut in poor condition sometimes ceased rutting as early as 7 October, several days before the main peak of conceptions.

Quantitative Aspects of Displays and Interactions

Though the rut gave the impression of frantic activity, it was less disorganized than it appeared, and the frequency of most displays and interactions was closely related to variation in the benefits of performing them. Harem-holders displayed and interacted more frequently than animals of the same age that were not defending harems (table 6.2), and their behavior changed rapidly if they lost their harems. A natural experiment occurred when a successfully rutting six-year-old stag ruptured a ligament in his leg in the course of a fight and consequently lost his harem. By the following day he had almost ceased to rut and was feeding intensely (table 6.3).

Among harem-holders, the frequency of most displays and interactions peaked during the first two weeks of October, when the majority of hinds conceived, and varied in relation to the "value" of the harem. For example, harem-holders observed in 1974 roared more frequently on days when their harems were

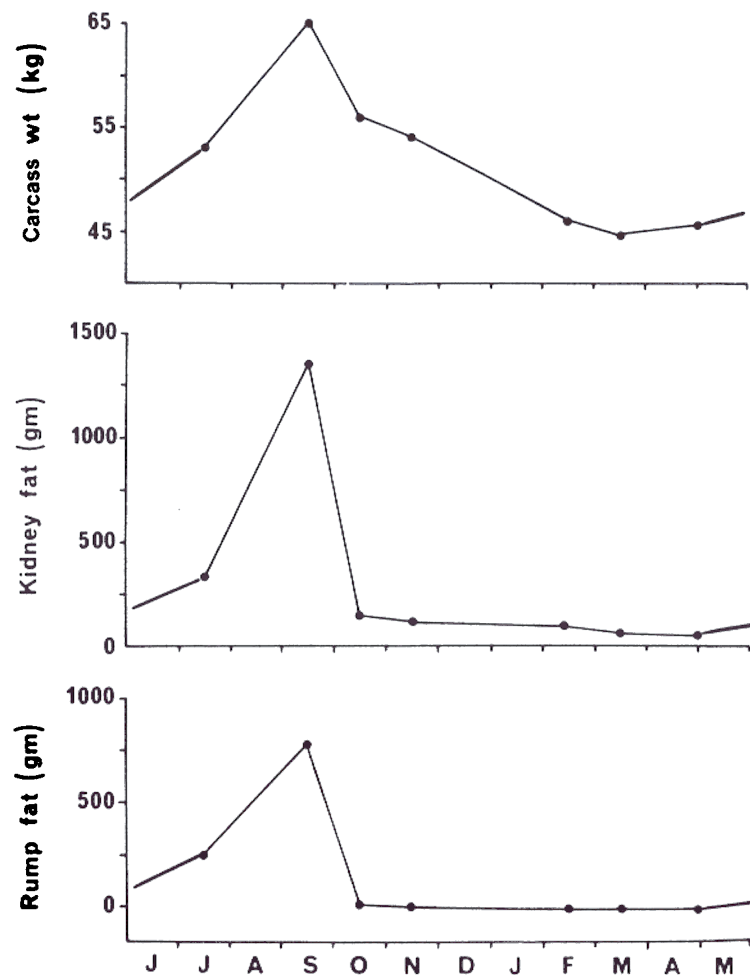


FIG. 6.22. Seasonal changes in body weight and condition of five- to ten-year-old stags shot on Rhum (from Mitchell, McCowan, and Nicholson 1976).

larger than usual than on days when they were smaller [1]. They also tended to roar more, spent less time feeding, and stayed closer to their harems on days when there was an estrous hind in their harem.

The frequency of displays was also related to the probability that the harem-holder would be approached or attacked by other stags. Harem-holders roared more [2] and tended to spend less

TABLE 6.2 Mean Frequencies of Some Common Rutting Activities Matur Stags (over Five Years)

	Time Period			
	2	3	4	
Sample size (individuals)	12	14	5	6
Percentage of time spent grazing	84.5	12.0	52.5	82.7
Roars/min	0.1	2.7	0.8	<0.1
Thrashes/h	1.1	1.39	1.0	<0.1
Chivies/h	0.2	7.0	0.2	<0.1
Displacement and chases/h	1.3	2.7	0.7	<1
Nearest-neighbor changes/h	5.3	18.2	7.2	4.5

Note: (1) before the rut (10 September–20 September) (2) during the rut (20 September–20 October); (3) during the rut when solitary; (4) after the rut (after 20 October).

Results are expressed as mean frequencies per minute when the stag was standing. Data from the 1974 rut.

TABLE 6.3 Effects of Leg Injury on the Rutting Behavior of a Six-Year-Old Stag

	Before ^a	After ^b
Hinds in harem	7.4	0
Percentage of standing time spent grazing	12.0	65.0
Roars/min	2.8	0.6
Modal distance to nearest male over a year old (m)	150	5
Chivies/h	2.7	0
Herds/h	4.7	0

Note: The injury was probably a ruptured ligament.

^aMean frequencies of different activities across the six days before the stag's injury.

^bMean frequencies of different activities across the two days after the stag's injury.

TABLE 6.4 Frequency with Which a Successful Nine-Year-Old Stag Chased Stags That Approached His Harem in 1974

Age of Approaching Stag	Period of Rut			
	14 Sept.– 21 Sept.	22 Sept.– 30 Sept.	1 Oct.– 7 Oct.	8 Oct.– 16 Oct.
2-3	0.25 ^a	2.6	0.4	0.8
4-5	0.40	3.7	5.4	1.6
	0.80	1.7	1.0	0.1

^aChases per hour

harem, and the frequency with which they licked and chivied them was higher than average. Stags holding larger harems did not compensate by chivying hinds more often, and the frequency with which individual hinds were chivied or licked was negatively related to harem size [7]. However, on days when particular stags held large harems, they tended to stay closer to them and spent less time feeding.

When a hind was in estrus, the harem-holder directed most of his attentions toward her, interacting more frequently with her than with other hinds. Stags typically mounted hinds in estrus several times before ejaculating and remained close to them afterward, subsequently showing progressively more interest in other hinds. Several sequences of mounting sometimes occurred with the same hind, particularly late in the season when the estrous behavior of hinds was more pronounced.

As we described in chapter 4, the stability of harems varied throughout the rut and was highest during the period of peak conception when the stags were rutting most intensively.

6.4 INTERACTIONS BETWEEN HAREM-HOLDERS AND YOUNG STAGS

During the early stages of the rut, harem-holding stags chased the male yearlings out of their harems. The latter hung around, attempting to get back to their mothers, and were regularly threatened by the harem-holders until they learned to keep their distance. The extent to which harem-holders tolerated yearling males within the vicinity of a harem appeared to depend on the development of the yearling's secondary sexual characteristics: in cases where two or more yearling males were within 50 m of a harem and the stag moved out to chase or displace them, the harem-holder first chased the one with the longest knobs or spikes on over 90% of occasions. These interactions were common features of the rut, and during the early rut they occurred as often as five times per hour on average (see table 6.4).

The reaction of a harem-holder to an approacher depended on the latter's age. Whereas yearlings were often allowed within 25 m of the harems, harem-holders usually reacted to an approach by a four- or five-year-old when he was over 100 m from their harem (fig. 6.24). In addition, harem-holders displaced or chased older approachers farther from their harems than younger stags, and, when a harem-holder was approached by several young males at

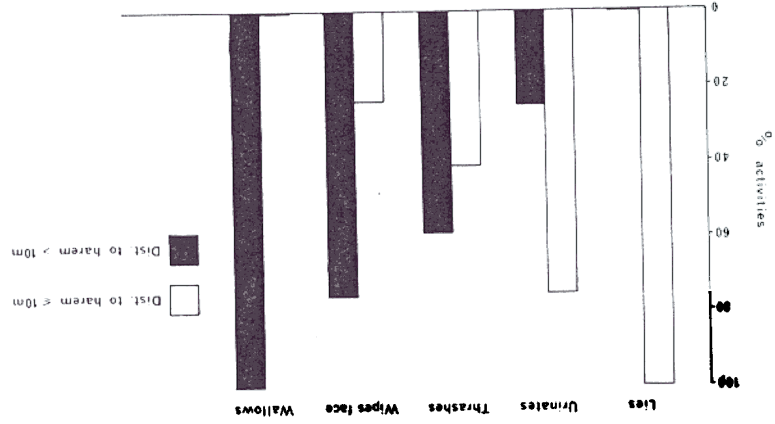


FIG. 6.23. Percentage of different activities by one nine-year-old stag that were performed within 10 m of the edge of the harem versus beyond this distance (1974 data).

time feeding [3] on days when the nearest rutting stag was closer than average. They also roared more frequently and spent more time standing at times of day when their hinds were feeding [4], when the harem was consequently more dispersed and more liable to infiltration by young stags than when their hinds were lying. This was probably related to the fact that other stags were more likely to approach the harem when a high proportion of hinds were feeding [5] (Clutton-Brock and Albon 1979).

The frequency of most rutting activities also had a characteristic spatial distribution. Stags roared infrequently when they were distant from their harems [6], perhaps avoiding advertising that their harems were unprotected. Both lying and urinating tended to occur close to the harem, whereas thrashing, rubbing, and wallowing usually occurred beyond the periphery of the harem (fig. 6.23).

6.3 INTERACTIONS BETWEEN HAREM-HOLDERS AND HINDS

From the first week of October onward, harem-holding stags interacted regularly with the hinds—sniffing, licking, chivying, and herding them (see Appendix 17). On the whole, stags distributed their attentions evenly among the mature members of their harem, though they interacted with calves, yearlings, and two-year-olds less frequently than with adult hinds. Stags also paid particular attention to hinds that had recently joined their

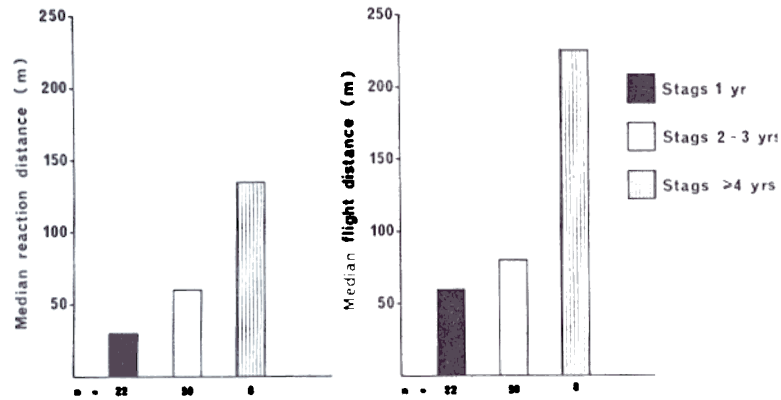


FIG. 6.24. Median distance of approaching stag to harem when the holder began the chase or displacement (reaction distance) and when he ended the interaction (flight distance). The number of interactions in the sample is shown below each histogram.

the same time, he almost invariably chased the oldest or best-developed one first.

The age of the approacher was also related to the type of interaction that followed. When approached by stags of two to three years (which were appreciably smaller than older animals), the defending stag usually ran directly at them and chased them away. In contrast, when approached by stags of over four years, harem-holders usually walked toward them and rarely ran at them immediately (fig. 6.25). The advantage of this behavior was presumably that it gave stags the opportunity to impress the rival with their size and strength, giving him time to assess them and avoiding the chance that he would precipitate an unnecessary fight.

6.5 INTERACTIONS BETWEEN MATURE STAGS

The Form of Contests

Relationships between harem-holding stags were almost invariably hostile, and fights were common. Continuous watches of individual stags suggested that most mature stags fought at least once every five days during the rut and were usually involved in about five fights during each breeding season (Clutton-Brock et al. 1979). During the peak rutting period, most fights involved mature stags (see fig. 6.26), of which at least one was in possession of a harem, though young stags sometimes fought each other and

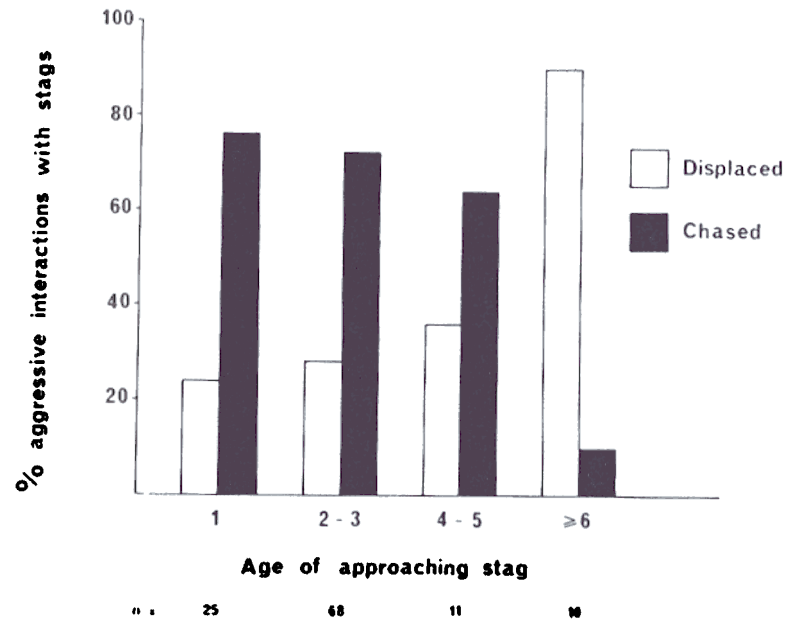


FIG. 6.25. Proportion of aggressive interactions involving harem-holding stags and approaching stags of different ages in which the approacher was chased versus displaced (see text) by the harem-holder.

occasionally challenged harem-holders, especially in the later stages of the rut.

Between 1971 and 1976, we observed 107 fights involving 72 different stags (Clutton-Brock et al. 1979). The typical course of events was that a challenging stag approached to within approximately 200 m to 300 m of a harem-holder and the two roared at each other for several minutes, after which the approacher usually withdrew. If the approaching stag came within 100 m of his opponent, the contest was more likely to escalate first to a further exchange of roars and then, in the majority of cases, to a parallel walk, with the two contestants moving tensely up and down, typically at right angles to the direction from which the approacher came. At any moment during a parallel walk, either stag might invite contact by turning to face his opponent and lowering his antlers. Opponents almost always accepted this invitation, turned quickly, and locked antlers. Both animals would then push vigorously, attempting to twist the opponent to gain the advantage of

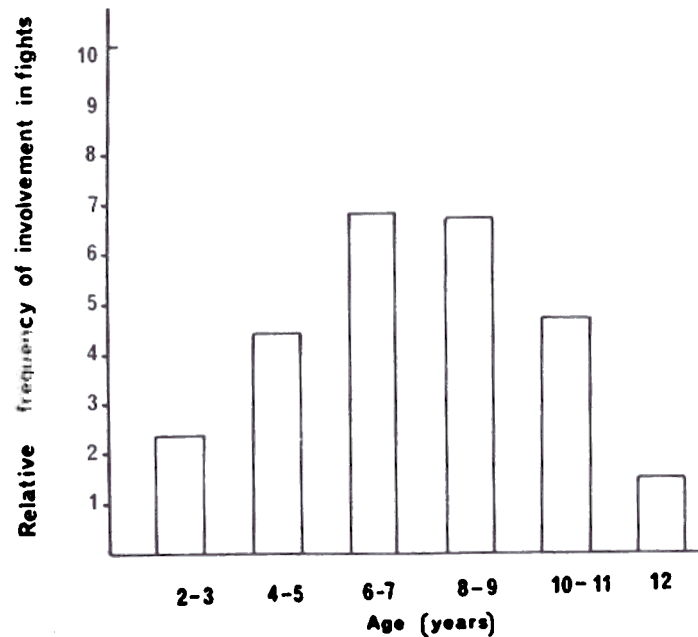


FIG. 6.26. Relative frequency of involvement of stags of different ages in fights during the rut. Relative frequency was calculated by dividing the number of cases where an animal in each age grade was involved by the mean number of animals of that age grade present in the study area (1974-76).

any slope. In the course of longer fights, contestants frequently separated for a few seconds at a time, rejoining after one of the pair invited contact again by lowering his antlers. Fights lasted until one of the pair was pushed rapidly backward, broke contact, and ran off. Winning stags seldom pursued losers for more than 10 to 20 m, though if a stag slipped in the course of a fight his rival would immediately attempt to horn him in the flank, rump, or neck, and there was no evidence of dangerous attacks being inhibited in such situations.

For a sample of fifty cases where an approaching stag came to within 100 m of his opponent, figure 6.27 shows the number that led to roaring contests, parallel walks, and fights. Fights that were not preceded by roaring contests or parallel walks mostly occurred either where there was an obvious inequality in fighting ability between the contestants or where an intruding stag had

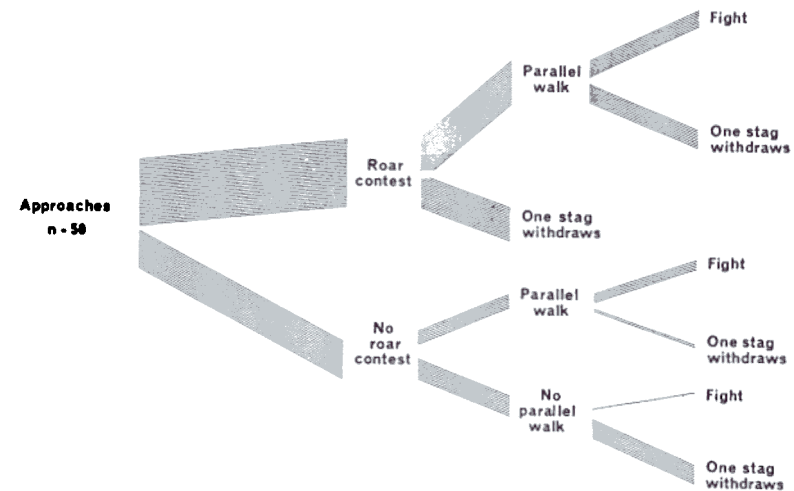


FIG. 6.27. Number of approaches to within 100 m involving two stags six years old or older that led to roaring contests, parallel walks, and fights, in a sample of fifty observed in 1977. Each line represents one case.

usurped a harem in the temporary absence of its holder and was discovered on the latter's return. In such cases the previous holder almost invariably challenged the intruder without preliminary displays.

Fighting Success

Analysis showed a close relationship between fighting success and age (see fig. 6.28): fighting success peaked between the ages of seven and ten years and declined rapidly in stags of over eleven. There was thus a close relationship between age changes in fighting success and those in body weight (see chap. 2), which peaked over the same period.

The association between age, weight, and fighting success was supported by examination of the outcome of fights between individuals of different ages. Before the age of five, substantial increments in body weight occurred each year, whereas after this growth rates were slower. Consequently, when a stag of five years or less fought an older individual, there was usually a substantial discrepancy in weight between them. This was not necessarily the case when stags more than five years old fought. As would be expected if body weight played an important part in fighting