

THE LOGICAL STAG: ADAPTIVE ASPECTS OF FIGHTING IN RED DEER (*CERVUS ELAPHUS L.*)

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Abstract. For red deer stags, fighting both has appreciable costs and yields considerable benefits. Up to 6% of rutting stags are permanently injured each year, while fighting success and reproductive success are closely related, within age groups as well as across them. Fighting behaviour is sensitive to changes in the potential benefits of fighting: stags fight most frequently and most intensely where potential benefits are high and tend to avoid fighting with individuals they are unlikely to beat. The relevance of these findings to theoretical models of fighting behaviour is discussed.

Introduction

It has been commonly argued that animals in general, and those possessing dangerous weapons in particular, should tend to avoid fighting, settling disputes by safer methods (Tinbergen 1951; Geist 1971; Wilson 1975). Where fighting does occur, its occurrence and intensity should be affected by the potential costs and benefits to the two contestants (Parker 1974; Maynard Smith & Price 1973; Maynard Smith 1976; Maynard Smith & Parker 1976). Both arguments rely on the assumption that fighting yields considerable benefits and has appreciable costs.

Although it is clear that winners often gain temporary access to limited resources (Wilson 1975) the evidence that consistent individual differences in fighting success confer long term advantages is less well documented. Several studies have shown that social rank among males (which is normally assumed to depend on fighting ability) is related to the frequency of mating (e.g. Suarez & Ackerman 1971; Geist 1971; LeBoeuf 1972, 1974; Grubb 1974; Hausfater 1975; Packer 1977). However, since both rank and reproductive success are commonly age-related (see Rowell 1974; Hausfater 1975) such correlations do not necessarily indicate that rank (or fighting success) affects reproductive success. To our knowledge, no studies of natural vertebrate populations have demonstrated that reproductive success is related to rank when age differences are taken into account, though the fact that not all males achieve high rank at any stage during their lifetime (e.g. Geist 1971; LeBoeuf 1974; Hausfater 1975; Packer 1977) suggests that the two measures are correlated. An additional problem is that even when high rank or fighting success confers advantages

within a particular breeding season, it need not necessarily improve lifetime reproductive success if it is associated with a reduction in the number of years for which high ranking males breed successfully (Geist 1971; Hausfater 1975).

Estimates of the costs of fighting are even more fragmentary. While it has often been shown that fights can lead to permanent injury or death (Geist 1971; Schaller 1972; Sussman & Richard 1974) measurements of the frequency of either are scarce. Most studies (e.g. Darling 1937; Geist 1971) indicate that fights leading to death or serious injury are rare, though a recent survey of musk oxen (Wilkinson & Shank 1977) suggests that 5 to 10% of adult bulls may die each year from rutting injuries, while figures for mule deer (Geist 1974) indicate that up to 10% of males more than 1.5 years of age shown some signs of injury each year.

Finally, there is little firm evidence that the behaviour of individuals in contests is adjusted to variation in the costs and benefits of fighting (see Parker 1974; Clutton-Brock & Harvey 1976; Popp & DeVore 1977). Moreover, this prediction need not necessarily be true since it may be more effective for genes to programme (or, indeed, for an animal to learn) an average fighting strategy which is applied to all contest situations than one which adjusts to the costs and benefits of each fight, particularly where assessment is difficult (Maynard Smith & Price 1973).

In the course of a five-year study of the social behaviour of red deer (*Cervus elaphus L.*) (Plate V, Fig. 1a) on the Isle of Rhum (Inner Hebrides) we have now watched over a hundred rutting fights. Using these data, this paper examines the costs and benefits of fighting and then examines the extent to which individuals adjust their behaviour to variation in costs and benefits.

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In Scottish red deer, the course of the rut is highly predictable from year to year. In mid-September, mature stags (over 5 years old) which have spent the previous 10 months in bachelor groups become intolerant of each other and individuals move to traditional rutting areas (Lincoln et al. 1970; Lincoln & Guinness 1973) where they collect and defend groups of hinds (harems). Younger stags seldom hold harems but attempt to abduct hinds from the harems of older animals. This strategy, known as 'kleptogamy', is apparently usually unsuccessful since young stags are unable to control or defend hinds after they have been abducted (Gibson, in preparation). Hinds are seasonally polyoestrous (Guinness et al. 1971), the majority of the Rhum population conceiving between the second and third weeks of October though some conceptions may occur from late September to early January (Guinness et al., in press). Rutting activities in the stags peak during the same period and decline after October 20, by which time many of the largest stags are exhausted and harems are held by younger animals (Lincoln & Guinness 1973). In the rest of the paper we refer to stags with harems as 'holders' and those without as 'solitaires'.

The course of fights is also predictable (Bützler 1974). One animal approaches another and stands in a visible position, roaring towards him. The approacher responds and the two usually exchange roars for several minutes. If the contest enters a second stage, the approacher advances and the approacher moves to meet him. In the majority of cases, the two stags then enter a parallel walk (see Bützler 1974): 5 to 10 m apart, they walk side by side, usually at right angles to the direction from which the approacher has come. During the walk, either stag may invite contact by turning to face its opponent and lowering its antlers. When invited, the other stag usually turns quickly and the pair lock antlers (Plate V, Fig. 1b). During the ensuing fight, each animal attempts to turn his opponent so that the latter is below him on the slope and fighting stags will circle rapidly. In the course of longer fights, contestants frequently separate for a few seconds at a time, rejoining after one of the pair invites contact again by lowering its antlers. Fights last until one of the pair is pushed rapidly backwards, breaks contact and runs off. Winning stags seldom pursue losers for more than 10 to 20 m: it is evident that there would be little advantage in doing so, antlers being inefficient offensive weapons for a pursuer since,

to use them, the animal must lower its head and lose speed. However, if a stag slips in the course of a fight, its rival will immediately attempt to horn it in the flank, rump or neck and there is no evidence of dangerous attacks being 'inhibited' (Tinbergen 1951) in such situations.

Study Area

All data described were collected on the North Block of the Isle of Rhum, Inner Hebrides. The history and population ecology of the Rhum deer population has already been described elsewhere (Lowe 1966, 1967, 1969; Mitchell 1973) as has our study area and study population (Lincoln & Guinness 1973; Clutton-Brock & Guinness 1975). The study area is regularly used by around 100 hinds 1 year old or more. In the rut, it usually contains 50 to 60 stags more than 1 year old, some of whom are resident there for most of the year: Fig. 2 shows the mean numbers of stags of different age categories found in the study area (see page 214). Since 1972, the number of stags using the study area has remained approximately constant while the

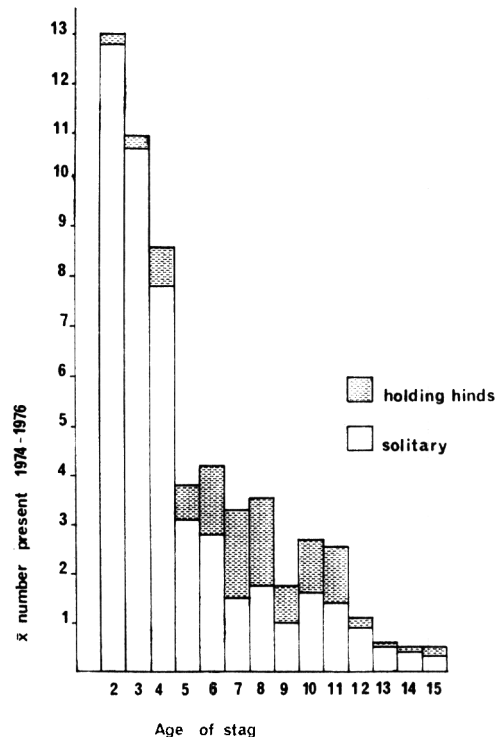


Fig. 2. Mean numbers of stags of different ages (in years) in the study area between 1974 and 1976 (see text).

number of hinds has increased (Guinness et al., in press). The age structure of the population has remained approximately constant.

Methods

Fights were recorded whenever seen. The ideal description of a fight included:

1. The identities and ages (see below) of the contestants.
2. The number of hinds 1 year old or more held by each contestant immediately before the fight (the stag's 'state').
3. The identity of the animal responsible for the initial approach (the 'approacher'). This is usually easy to determine for, in most approaches, one stag moves consistently towards the other. Approaches often involve movements of several hundred metres by the approacher.
4. Whether the fight was preceded by a parallel walk and, if so, its duration.
5. Which stag initiated contact by turning to face the other animal and lowering its antlers (see Bützler 1974).
6. Which stag won the fight: a win was scored where one contestant displaced the other stag or appropriated part of his harem.
7. The number of hinds held by each stag immediately after the fight.

In the analysis, fights were divided into four categories. (In description of fights, the state of the approaching animals is always given first):

These were:

1. Solitary→Solitary: where neither stag held hinds (45% of our sample).
2. Solitary→Holder: where the approaching animal held no hinds before the fight but the approachee held one or more (31% of our sample).
3. Holder→Holder: where both stags held hinds before the fight (22% of our sample).
4. Holder→Solitary: where the approacher but not the approachee held hinds before the fight (2% of our sample).

A total of 107 fights was observed between September 25 and October 25th 1971–1976, involving 72 different stags. Of these, 88% were recorded between 1974 and 1976 and more complete descriptions are available for fights seen in this period. In the majority of cases, the records did not include estimates of all the

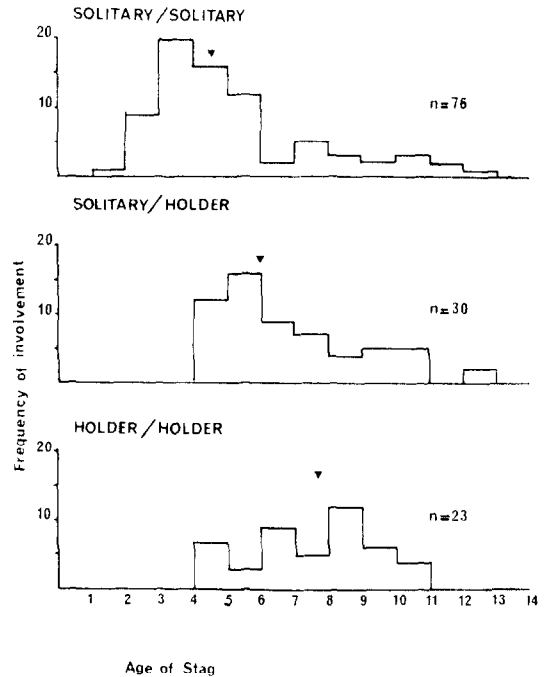


Fig. 3. Frequency of involvement of stags of different ages (in years) in Solitary→Solitary, Solitary→Holder and Holder→Holder fights (data sample 1971–1976 inclusive). Since each fight contributed two involvements, sample size is increased in these plots. ▼ shows the median age of stags involved in each category and in the sample size.

above details and some records had to be omitted in each analysis, with the result that sample sizes vary. In 85 cases, we were able to determine which stag was the challenger. Since young stags of 5 years or less seldom held hinds (see Fig. 2) they tended to be least frequently involved in fights involving hinds and most frequently in fights between solitaires (Fig. 3).

The number of fights in the sample is too small to permit comparison of the behaviour of individuals and, throughout much of the analysis we have lumped data collected on different individuals and in different years. Such a procedure is not ideal, for it assumes that fights are independent of each other whereas, if the behaviour of individuals differs consistently, this will not be the case. However, both because a large number of different stags was involved (no individual stag was involved more than 14 times) and because fights are usually widely separated in time, bias of this kind is unlikely to have an important effect.

The following measures were used in the analysis:

Age. All stags regularly using the study area can be identified individually. The ages of the majority are known to within a year, in most cases from knowledge of the individual since it was a yearling or calf or, in stags which were 3 years old or less when the study began in 1969, from inspection of dental development when the animal was immobilized (see Lowe 1967; Mitchell & Youngson 1968).

Number of antler points. The total number of points on the antler. A point is any extension large enough to hang a pair of binoculars on.

Dressed weight. The weight of a deer carcass, less head, viscera and lower legs.

Antler length. Antler lengths were obtained after the antlers were cast in March (Gibson, 1978). The measure used was the length of the beam from coronet to top, measured along the outside curve.

Availability of stags of different ages. Analysis of the relative frequency with which stags fight partners of particular ages required a measure of the numbers of stags of various ages in the study area. This was calculated from census of the study area: between 1974 and 1976 the whole study area was censused four times each year between September 25th and October 20th and the numbers of stags in different age categories were recorded. For each year, we calculated the mean number of solitary and holding stags in different age categories seen in these censuses. Since (with the minor exception of stags older than 11 years) the age structure of the population was similar in different years, we took the average of these means as our estimate of the availability of individuals of different ages during the study (see Fig. 2).

Reproductive success. Our measure of each individual's reproductive success in each year was the total number of days it held hinds multiplied by the mean number of hinds held on each day (giving a total number of hind/days held per year). Inter-individual differences in this measure are well correlated with more precise measures of reproductive success, including estimates of the number of hinds which conceived when held by each stag (Gibson, 1978).

Fighting success. Measurement of fighting success poses several problems. Though it is clear that large individual differences exist, it is

not possible to establish a rank order between stags within particular years: not only do many stags never fight each other but dominance changes frequently during the course of the rut as stags exhaust their energy reserves or are wounded. To rank stags on the number of fights won or the number of different individuals beaten (e.g. Brantas 1968) yields unrealistic results since the status of individuals beaten is of obvious importance. One way of solving this problem is to weight an individual's rank according to the ranks of his contestants (see Sade 1972). In this case, for each stag in each year between 1974 and 1976, we calculated the number of stags which it beat (B) plus the total number which they beat excluding the subject (Σb), the number of stags which it lost to (L), plus the total number which they lost to, excluding the subject (Σl). Our index of fighting success was

$$\frac{B + \Sigma b + 1}{L + \Sigma l + 1}$$

the addition of one to each side of the ratio reduces the chance of an anomalous result occurring in cases where individuals were either never observed to beat other animals or never observed to be beaten.

To check that this measure gave as realistic an estimate of social rank as traditional dominance measures (see Brantas 1968; Richards 1974; Syme 1974) we calculated dominance ranks using our method for published data on reindeer (Espmark 1964), horses (Clutton-Brock et al. 1976) and bison (McHugh 1958). We then compared these with the authors' own measures, based either on the technique of minimizing irregularities in the hierarchy (see Brantas 1968) or on the ratio of the number of individuals which each animal dominated to the number which dominated them. In all cases our estimates gave very similar results to the original rank orders ($r_s = 0.929$ (reindeer); 0.980 (Highland ponies); 0.992 (American buffalo); $P < 0.001$).

Like most other measures of dominance, ours assumes that an individual which beats another individual can beat all those animals which the latter can beat: though this is generally true, it is not always the case. It is also likely to have given unrealistic estimates of fighting success for stags which rutted in outlying areas and held few hinds within the study area, as well as for stags which were never seen

either to beat or be beaten and consequently scored the relatively high index of 1. However, such cases should tend only to obscure relationships between fighting success and other variables.

In the analysis of fighting success we included all 25 stags over 5 years old which rutted in the study area between 1974 and 1976 but excluded three animals which rutted on the periphery of the area and were consequently never seen to be involved in fights, and two whose ages were uncertain.

Fight duration. The duration of the period of contact, from first to last contact, including short periods during fights when contestants stood apart. In comparisons of fight duration, we excluded brief clashes of 1 second or less in duration on the grounds that, in such cases, both animals did not appear to commit themselves to the contest.

Because our records of fighting were collected on an ad libitum basis, they provide no estimate of the absolute frequency of fights. However, it is evident that they are not common. In 1976, six mature stags were observed for one full day (approximately 11 h) each during the peak period of rutting activity. During the entire sample, only one fight was observed.

Conception dates. In each year since 1971, the date of birth of the majority of calves born in the area is determined from close observation of hinds at calving time (Guinness et al. in press). For each year, we calculated the percentage of calves born each day then calculated mean percentages per day across years (1971–1976). Assuming a gestation period of 235 days (ibid.), we finally calculated the mean proportion of conceptions occurring on each day of the rut (see Fig. 13).

Results

1. The Costs and Benefits of Fighting

(a) Injury. Between 1974 and 1976 the following injuries have occurred to stags rutting in the study area: permanent blindness of one eye (two cases); temporary blindness of one eye (one case); damaged front leg causing permanent lameness (one case); temporary lameness in one leg (two cases); antler breakage (26 cases). In previous years, injury frequency was not recorded systematically but one broken foreleg, five cases of temporary lameness and five eye wounds were noted. In our total sample of 107 observed fights, two cases of injury occurred.

Between 1974 and 1976, an average of 21 stags of more than 5 years rutted in the study area per year. Excluding minor antler breakage (but including breakage of the main beam), fourteen of these were injured (23% per year) and in four cases (6% per year) injuries had long-lasting effects. Since most stags rut for 3 to 5 years during their lifetime and natural mortality among mature stags is low (Lowe 1969) this suggests that virtually all stags will be slightly injured at some stage and that up to 20–30% will sustain permanent injury during their lifetime. Although injuries occurred throughout the rut, the majority (58%) occurred in the ten days between October 8 and October 18, coinciding closely with the frequency of fights observed (Fig. 13).

Effects of injuries are difficult to assess. In two cases, injuries had an obvious, permanent effect. In 1974, Congal, a seven-year-old stag damaged his right foreleg in a fight with a larger stag. He immediately lost his harem: Fig. 4 compares the size of his harem on seven days prior to his injury with its size on the six days following it. The following year, 1975 (Fig. 4b), he hardly held hinds at all and was still obviously lame. By October 1976, his lameness was less apparent and he successfully held hinds during the latter part of the rut. He died in the spring of 1977, though only 10 years old.

In 1975, Pincer (an 11-year-old stag who had rutted with considerable success in the study area in 1974) was injured in the eye in the course of an unseen fight early in October. On October 16th, he was injured again in the same eye, probably suffering permanent damage. Though he managed to maintain his harem, he died in the course of the following winter (despite being in reasonable body condition) perhaps as a result of internal infection.

Of the other injuries, none had such marked effects. Both lameness and breakage of the antler beam at a low level can have some effect on rutting success (see Lincoln 1972), but our data are inadequate to demonstrate this. Loss of the tops or of one or more points (the majority of cases of antler breakage) apparently has little effect on fighting capacity.

It is important to remember that observable injury is only one of the physical costs of fighting. Costs which we were not able to estimate included short term exhaustion (rendering the stag liable to lose any immediately subsequent

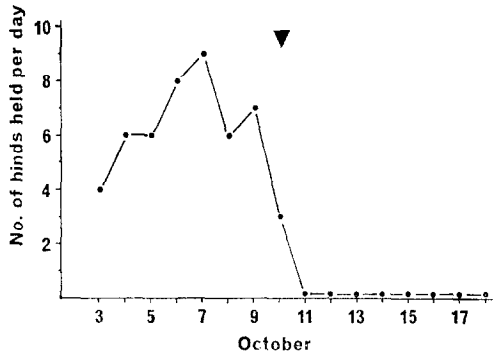


Fig. 4 (a)

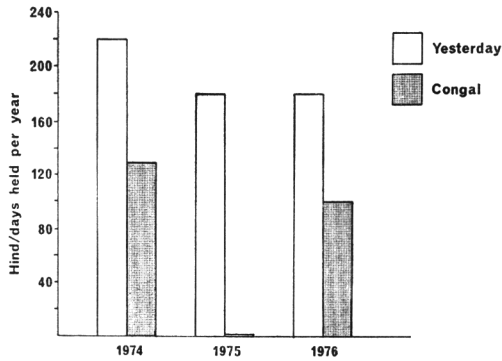


Fig. 4 (b)

Fig. 4. Effects of a leg injury (? a broken ligament) on Congal, a seven-year-old stag. Figure 4a compares the number of hinds held per day by Congal before and after his injury on Oct. 10, 1974 (the record for that day was taken after the injury occurred). Figure 4b compares the number of hind/days held by Congal in 1974, 1975 and 1976 with similar measures for another stag of the same age (yesterday).

fight), depletion of energy reserves and any non-observable injuries.

(b) Hinds gained and lost. In two-thirds of our total sample of 107 fights, one of the two stags was holding hinds. Of a total of 22 cases where approachers beat holding stags, they increased their harem size in 77% of cases (17), taking over all or a part of the losers' harems.

To estimate the benefits of fighting in different situations, we divided fights involving holding stags into four kinds. (As elsewhere, the approaching animal is listed first.) (1) Solitary \rightarrow holder fights where the approacher won, (2) solitary \rightarrow holder fights where the approacher lost, (3) holder \rightarrow holder fights where the approacher won, (4) holder \rightarrow holder fights where

the approacher lost. (The two cases where holders approached and fought solitaires were excluded from this analysis.)

The potential gains of fighting to solitary approachers are considerable. In 13 solitary \rightarrow holder fights where the (solitary) approacher won, winners gained an average (mean) of 4.3 hinds (see Fig. 5). In the 11 cases where solitary approachers lost, they risked injury but obviously lost no hinds. Holding approachers are apparently likely to gain less and lose more: in nine fights where holding approachers won, they gained fewer hinds per fight (mean gain = 1.7) than winning solitaires ($U = 29$, $n_1 = 13$, $n_2 = 9$, $P \approx 0.05$). This was not due to any difference either in the sizes of the harems approached, which did not differ significantly in size (means 4.8 and 5.6 respectively), or in the number of hinds that losers managed to retain (in both cases the latter lost most of their harems). The explanation of the difference is that holder \rightarrow holder fights are longer (see Fig. 6) and are more likely to attract kleptogamists (see Fig. 7) who chase off a proportion of the hinds involved: when all holder \rightarrow holder fights are considered (see Fig. 8) a significantly larger proportion of the total number of hinds involved are lost to both contestants than in solitary \rightarrow holder fights (U test, $Z = 3.1$, $n_1 = 23$, $n_2 = 16$, $P < 0.002$). Holding approachers also risk more: in the seven cases where they were beaten they lost an average of 1.0 hinds (or 31% of their harems).

Stags that successfully beat challengers apparently seldom gain from fights and can lose a considerable proportion of their hinds. Holding

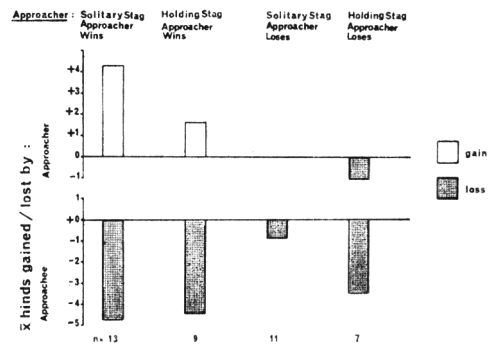


Fig. 5. Mean gains and losses of hinds to the approacher and the approachee in fights involving holding stags which had different outcomes. Excluded from this analysis were cases where an approacher displaced a holding stag without a fight (4); inconclusive fights (3) and cases where holding stags approached stags without hinds (2).

stags which fought and beat solitary approachers only lost hinds in one case out of 10, giving an average loss of 0.7 hinds per fight. In contrast, holding stags which won fights initiated by holding challengers, lost hinds in five cases out of seven (Fisher Exact Probability Test, $P < 0.05$), giving an average loss of 3.4 hinds per fight. This difference, too, was probably a result of the increased opportunity for depredation by kleptogamists in holder/holder fights. After fights in which a holding stag beat a holding approacher, the latter usually quickly withdrew to his own harem. Surprisingly, successful defenders seldom follow (apparently preferring to round up their remaining hinds and chase off kleptogamists), with the effect that holders which approached and lost usually retained the bulk of their harems (see Fig. 5). This may be the case because an attempt to take over the harem of a defeated approacher would require them to leave their own harem open to depredation by kleptogamists, which tends to intensify during long fights (see Fig. 7).

The apparent tendency for holding stags which approach other holders and are beaten to lose fewer hinds than those which are approached by other holders and win (Fig. 5) is a product of a (non-significant) difference in mean harem size between holders which approach other holders ($\bar{x} = 4.2$ hinds) and holders which are approach-

ed by other holders ($\bar{x} = 8.3$ hinds). Percentage losses are similar in both cases.

Though the numbers of hinds gained and lost provide some measure of the costs and benefits of fighting, several other considerations must be taken into account. Hinds are not of equal value. For example, it may be advantageous for a stag to abandon several anoestrous hinds in order to capture a single hind in oestrus. Second, harems are not stable and hinds captured from a neighbouring stag may subsequently escape from his harem, while temporary loss of hinds may be offset by the advantages of capturing (or defending) a good rutting area. Hinds abducted by kleptogamists frequently return to their previous rutting areas and it is evident that possession of particular areas enhances a stag's opportunities for collecting a large harem (Gibson, 1978). Finally, it is possible that, by fighting, stags may enhance their

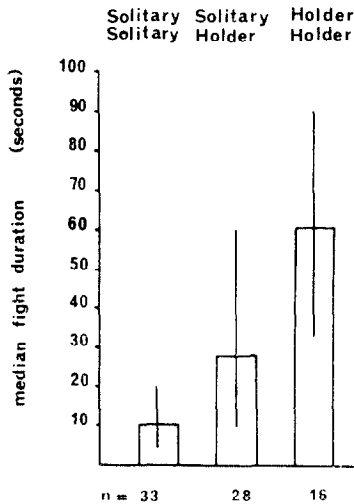


Fig. 6. Fight duration (in seconds) in Solitary→Solitary, Solitary→Holder and Holder→Holder fights. Histograms show median values, extending lines the interquartile ranges. The analysis excludes short clashes of ≤ 1 s duration.

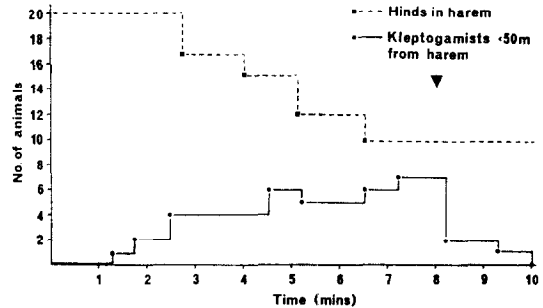


Fig. 7. Numbers of kleptogamists within 50 m of the harem of a 7-year-old holding stag which engaged in an 8 min fight with another holding stag. The numbers of hinds left in the harem are also shown. ▼ shows the point at which the fight ended and the holding stag returned to the harem.

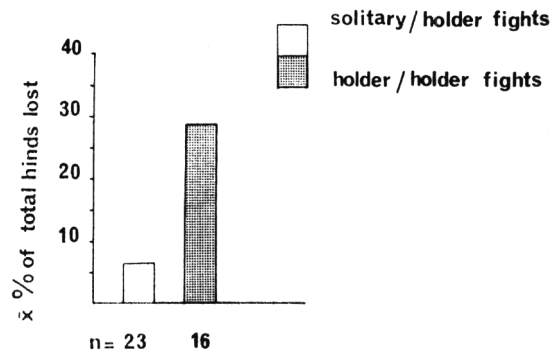


Fig. 8. Mean percentage of total hinds lost by holding stags during solitary/holder and holder/holder fights.

competitive abilities in the future, either through the acquisition of dominance rank or by increasing skill in the complex manoeuvring which occurs during fights. Unfortunately, such factors are difficult to measure.

(c) Fighting success and reproductive success.

Reproductive success is closely related to fighting success, both peaking in animals of 7 to 10 years old: Fig. 9 shows the median indices of fighting success (see page 214) for all stages of 5 to 14 years which rutted in the study area between 1974 and 1976 (with the exceptions described on page 214). For each age class, we also calculated the median number of hind/days held per year (see page 214). The two measures are closely correlated ($r_s = 0.891$, $df = 8$, $P < 0.001$). To test whether differences in reproductive success were related to variation in fighting ability within age classes, we allocated all stags which rutted in the study area in 1974–1976 to four age categories: 5 to 6, 7 to 8, 9 to 10, and 11 years or more. Where individuals occurred twice in the same age category (for example as 5 and then as 6 year-olds) we took the mean of the two estimates as their score for that category. Where individuals occurred in different age categories they were recorded as independent data points.

Examination of the scores on fighting success and reproductive success shows that the two are related among prime stags (7 to 8 year olds $r_s = 0.786$, $n = 7$, $P < 0.05$; 9 to 10 year olds $r_s = 0.708$, $n = 8$, $0.1 > P > 0.5$) but that the

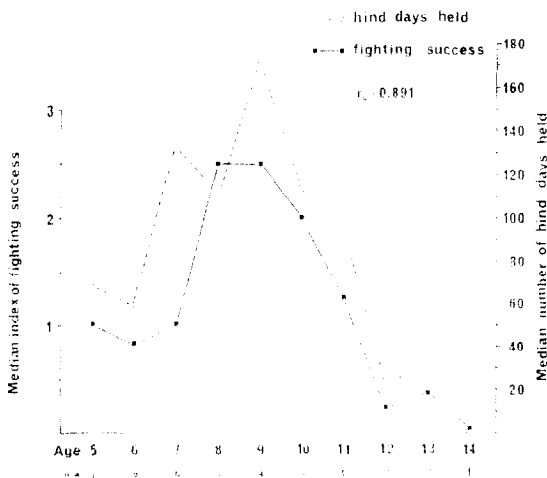


Fig. 9. Fighting success and reproductive success in relation to age in stags ≤ 5 years old. (See text.)

relationship disappears in young stags (5 to 6 year olds $r_s = 0.17$, $n = 11$, $P > 0.1$) and old stags (11 year olds or older $r_s = 0.537$, $n = 7$, $P > 0.1$). However, even here, coefficients are high enough to show that an overall trend is present when all four groups are considered (Kraemer Test, $\zeta = 0.551$, $z = 3.05$, $P < 0.0022$; see Kraemer 1975). Most of the individual cases are where indices of fighting ability for prime stags do not match measures of reproductive success. They are obviously the product of unrealistic estimates of one of the two measures, occurring either because the stag rutted in a part of the study area where fights were less likely to be seen or because it usually held its harem outside the study area, occasionally pursuing hinds inside (with the result that its score on reproductive success was artificially low).

The duration of the study is, as yet, inadequate to compare breeding life-span between individuals differing in fighting ability. However, successful fighters show no marked reduction in the number of seasons in which they rut and it is clear that, if any differences of this kind exist, they are too small to remove the advantages of fighting ability. Other factors affecting reproductive success in stags will be described in detail elsewhere (Gibson, 1978).

(d) Determinants of fighting ability. Although they are fertile as yearlings (Mitchell 1973), stags seldom hold hinds before they are five years old. This suggests that body weight may affect fighting ability: before the age of 6 years, stags gain body weight each year whereas, after this, weight is approximately stable until around 11 years, when it begins to decline (Mitchell et al. 1976; Mitchell et al. 1977). As would be expected, age differences are related to the outcome of fights between animals of 5 years or less and older individuals: of 31 fights involving one stag of 2 to 5 years and an animal at least 1 year older, the latter won in 25 cases ($\chi^2 = 11.6$, $df = 1$, $P < 0.001$) (see Fig. 10.) In comparison, of 46 fights between animals of 6 to 11, the older animal won in only 21 cases, a significant difference from the first sample ($\chi^2 = 7.72$, $df = 1$, $P < 0.01$).

In stags of more than 5 years it is evident that body size still has some effect on fighting ability: all the most successful stags we have known have been of large body size. However, many behavioural factors apparently affect an individual's chance of winning. Some stags fight skilfully, taking advantage of ground surface, slope and

their opponent's behaviour, while others do not. Some are determined fighters, tenaciously holding their ground even after they have been pushed back several times by a larger stag, whereas others give up easily: similar conclusions were reached by Gossow (1971).

Several authors have suggested that the size of antlers or horns is related to fighting ability (Beninde 1937; Geist 1971) though none have been able to control for age variation. In red deer, both antler length and the number of points increase rapidly until the age of five years and subsequently continue to show slight increases each year (Mitchell et al. 1977). To examine relationships between rutting success and antler size, we restricted ourselves to stags of 7 to 10 years on the grounds that this is the period of peak rutting performance while age variation in antler size within this category is small. In the sample of eight stags for which we were able to collect the relevant measures between 1974 and 1976, there was no relationship between antler length and either fighting success ($r_s = -0.15$, $n = 8$, NS) or the total number of hind/days held ($r_s = -0.03$, $n = 8$, NS). The number of points was weakly correlated with fighting ability ($r_s = 0.466$, $n = 13$, $P \approx 0.1$) though more closely with the number of hind/days held ($r_s = 0.738$, $n = 13$, $P < 0.01$).

One explanation of this relationship is that the heaviest stags may be both most likely to

win fights and to grow most antler points. To test this possibility, we examined the relationship between point number and dressed carcass weight (see page 214) in a sample of 139 stags of 7 to 10 years shot on Rhum. Point number for stags allocated to eight point categories ($\leq 5 - \geq 12$) was closely correlated with mean carcass weight ($r_s = 0.857$, $n = 8$, $P < 0.02$).

2. Adaptive Aspects of Fighting Behaviour

Investigation of the costs and benefits of fighting yields four trends of importance in interpreting the adaptive significance of fighting behaviour: the potential costs of fighting in terms of injury are appreciable; successful fights allow approaching stags to increase their harem size but the gains to holding stags are lower than the gains of solitaires; stags which defend their harems successfully never gain and can lose a large proportion of their hinds, especially if the contestant previously held hinds; and fighting ability is age-related, particularly in stags of 5 years or less.

If, as models of fighting strategies predict, the behaviour of individuals in contests is adapted to maximize the benefits and minimize the costs of fighting, the following predictions should be confirmed:

(a) **Assessment.** To avoid taking unnecessary risks, stags should assess each other carefully before fighting.

The high success rates of approaching stags and especially of individuals which approached stags holding fewer hinds than themselves (see (g)) suggests that potential contestants assess each other before fighting. The topic is discussed at length elsewhere (Clutton-Brock & Albon, in press). Both roaring contests and parallel walks may allow stags to judge their opponents.

(b) **Age differentials between contestants.** Individuals should avoid fighting when their chances of winning are low. Since, among stags of 5 years or less, age differentials will be related to differentials in body size and hence to fighting ability (see above), we should expect to find individuals of this age fighting mostly with animals of similar age to themselves. Among stags 6 years old or more, greater age differentials between opponents should be expected since age is no longer closely related to differences in body size or fighting ability. In this case, stags should either show a weaker trend towards fighting with individuals of similar age or, since

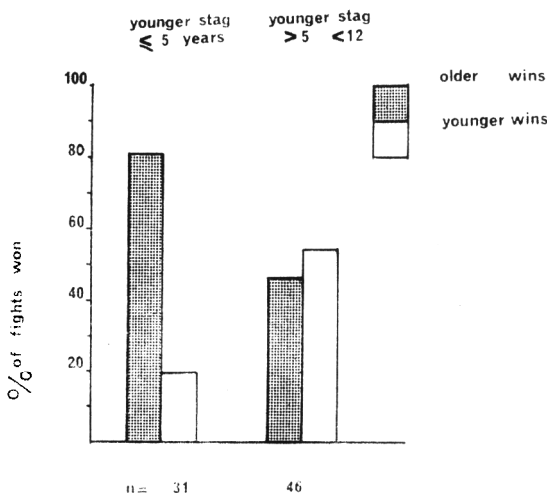


Fig. 10. Frequency with which older versus younger stags won in fights (a) involving a stag of ≥ 5 years and an older animal, (b) two stags of 6 to 11 years.

the declining abilities of stags more than 11 would lead to a proportion of cases where younger animals would be expected to win, no trend at all. (This argument assumes that the costs to young stags of fighting with stags considerably older than themselves are as great as those suffered when fighting with like-aged partners. That this is likely to be the case, is suggested by the absence of any difference in fight duration between fights where the contestants were less than 2 years apart in age and those where they were 2 years or more apart.)

Both predictions are confirmed (see Fig. 11). Stags 5 years old or less fight more often with individuals whose ages are within a year of their own than with animals which differ from them by two or more years ($\chi^2 = 17.5$, $df = 1$, $P < 0.001$). Stags of more than 5 years show no such trend ($\chi^2 = 1.40$, $df = 1$, N.S.). (Expected frequencies were calculated from the numbers of stags of different age classes in the study area, taking into account differences in the

frequency that members of each age class were involved in fights.) This difference between the two age categories was highly significant ($\chi^2 = 11.59$, $df = 1$, $P < 0.001$). It was not a product of any obvious tendency for animals of similar age to associate with each other since rutting stags apparently move independently of each other.

(c) **Fight duration.** Assuming that the costs of fights increase with their duration, fights should be longest and most intense when the potential gains are greatest. They should therefore be longer when hinds are involved than when they are not and longer when the likelihood that hinds will conceive is greatest.

Both predictions are confirmed (see Figs. 6 and 12). Fights between solitaires were significantly shorter than fights where hinds were involved (Median Test, $n = 77$, $P < 0.001$). Fights involving hinds were significantly longer in the 12-day period of peak conception (October 6 to 18) than in the preceding and succeeding 12 days (Fig. 13; Median Test: $n = 51$, $P < 0.05$).

Fight intensity could not be measured. However, the frequency of rutting injuries (Fig. 13) peaks at the time when most hinds conceive.

(d) **Timing of fights.** Assuming that the benefits of fighting are greatest during the period when most hinds conceive and that temporal variation in fight duration (see above) is insufficient to

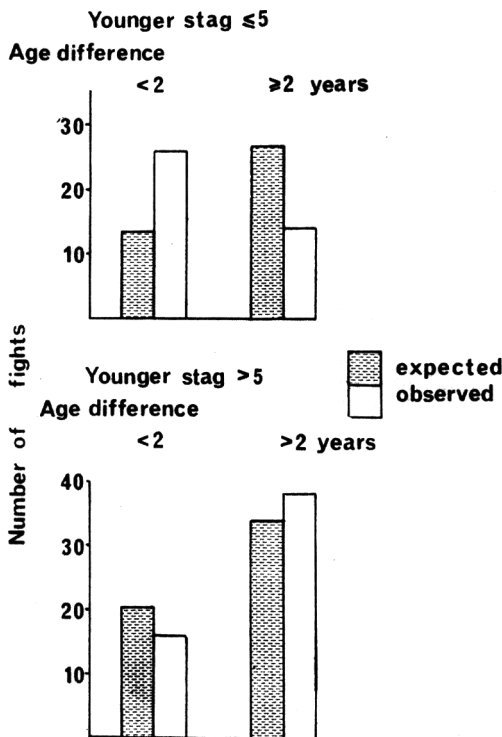


Fig. 11. Observed and expected frequencies of age differentials in rutting fights between stags of > 5 years in fights between stags of ≤ 5 years.

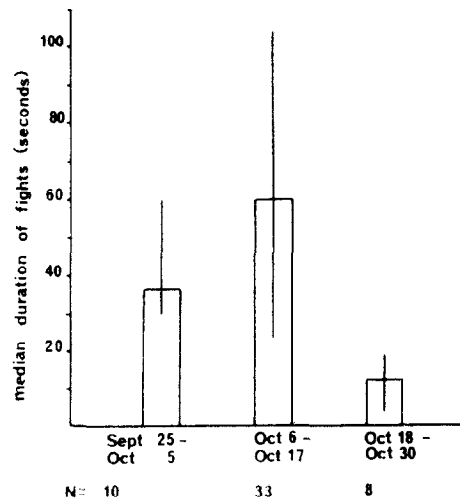


Fig. 12. Median duration of fights involving hinds during different periods of the rut (excluding fights ≤ 1 s in length). Histograms show median values and extending lines the interquartile ranges of each sample.

offset major differences in benefits, we should expect most fights to occur during the period when most hinds conceive.

This proves to be the case. Fights involving hinds show a marked peak between October 6th and October 18th (see Fig. 13) and the number seen per 4-day period is correlated with the number of hinds conceiving during that time ($r_s = 0.66$, $df = 9$, $P < 0.05$). Since fights were recorded ad libitum (see page 214), it is possible that part of this effect could be the product of differences in the amount of observer time spent in the field. However, approximately similar amounts of time were spent in observation between October 1st and 25th, yet the numbers of fights seen varied considerably.

(e) Age differences in the frequency of fighting. Among red deer stags on Rhum, life expectancy is approximately constant from the age of one year until 7 to 8 years and then declines rapidly (Lowe 1969). Since there is no indication that fights involving at least one animal of 5 years or less were shorter than those involving two older stags (Median Test, $P > 0.1$), younger stags might be expected to fight less both because they risk a greater proportion of their reproductive potential by fighting (Parker 1974; Clutton-Brock & Harvey 1976) and because their potential gains are lower (see Figs. 2 and 9).

This proved not to be the case. To calculate the relative frequency of involvement of different age classes, we divided the numbers of fights involving individuals of each age class by the

number usually present in the study area (see page 212). Stags of 6 to 9 years were most frequently involved in fights (Fig. 14), a result which parallels observations of mountain sheep where rams fight most frequently soon after they have attained maturity (Geist 1971).

(f) Fighting frequency and contestants' states. Since we must assume that solitary stags are generally inferior in fighting ability to holders, it is difficult to make firm predictions concerning the relative frequency of fighting. However, because they stand to gain little or nothing from fighting, it is reasonable to predict that holding stags should rarely approach and fight solitaires.

Figure 15 compares the frequencies of solitary \rightarrow solitary, solitary \rightarrow holder, holder \rightarrow solitary and holder \rightarrow holder fights with expected frequencies, calculated on the assumption that stags fought each other at random, irrespective of state. As predicted, holder \rightarrow solitary fights are considerably less common than would be expected by chance. Solitaires also tended to fight holders relatively more often than they fought each other. There was a weak tendency for holders to fight other holders with larger harems than their own.

(g) Fighting success. Unfortunately, it is not possible to predict the level of success which approaching stags should tolerate without a precise measure of the costs and benefits of fighting: it might, for example, always be advantageous for an approacher to fight (even

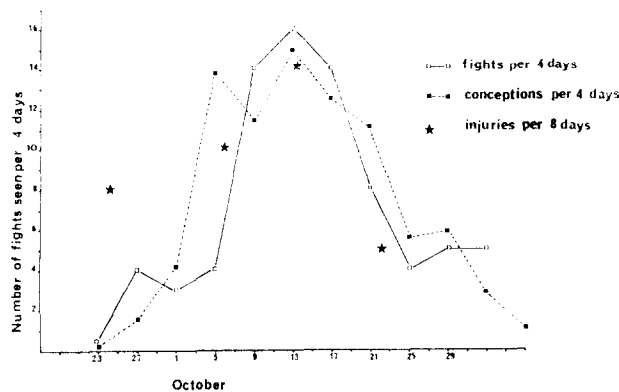


Fig. 13. Distribution of fights during the rut. The figure compares the number of fights per 4-day period with the number of calves conceived in each period, calculated by backdating from calf birth dates, assuming a gestation length of 235 days.

when his chances of winning are low) if the costs of fighting are very low or the benefits very high (see Clutton-Brock & Harvey 1976). However, it is reasonable to predict that stags which are particularly unlikely to gain by fighting should only approach and challenge other individuals where their chances of winning are very high. On these grounds, we predicted that holding stags which approached solitaires or holders with harems smaller than their own should show a higher success rate than stags approaching animals with harems larger than their own.

In the sample as a whole, approaching animals won in 54% of cases. Holding stags which approached animals with fewer hinds than themselves won in a larger proportion of cases (92%) than solitaires approaching solitaires ($\chi^2 = 4.09$, $df = 1$, $P < 0.05$), solitaires approaching holders ($\chi^2 = 6.02$, $df = 1$, $P < 0.02$) or holders approaching holders with more hinds than themselves (Fisher Exact Probability Test, $P < 0.05$; see Fig. 16). However, an alternative explanation of these results is that the stags holding the largest harems are most likely to be successful.

(h) Initiation of contact and contestants' states. Many approaches are terminated by a withdrawal on the part of the approacher (Clutton-Brock & Albon, in press). In

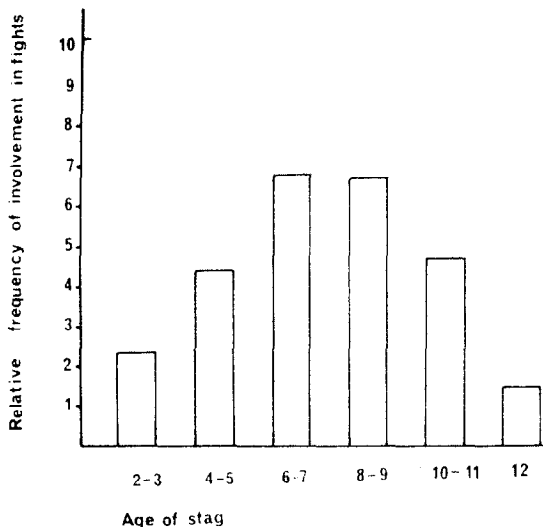


Fig. 14. Relative frequency of involvement of stags of different ages in fights of all kinds. Relative frequency was calculated by dividing the number of cases where an animal in each age grade was involved by the mean number of animals of that age grade present in the study area 1974-1976 (see Fig. 3).

Since approachees rarely or never gain from fights and may lose a considerable proportion of their harems, they should be reluctant to initiate contact unless this confers an important strategic advantage.

In 82% of the 27 fights where we were able to determine which stag initiated contact, it was the approaching animal ($\chi^2 = 10.7$, $df = 1$, $P < 0.01$).

(i) Initiation tactics. Stags would be expected to initiate contact when they are at a tactical advantage. Two adaptive aspects of initiation tactics are obvious though no formal quantification was attempted.

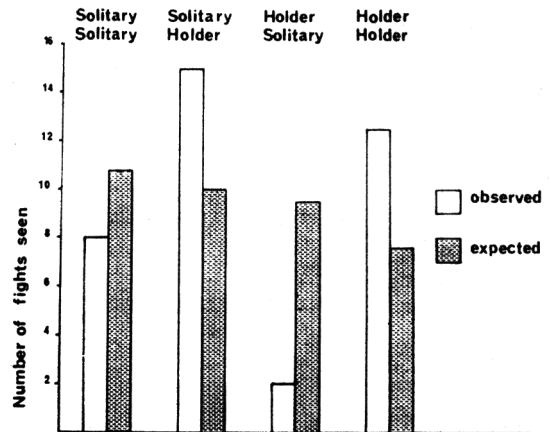


Fig. 15. Observed and expected frequencies of fights between holding stags and solitaires of > 5 years ($n = 36$). Expected frequencies were calculated on the assumption that stags fought each other at random, irrespective of state.

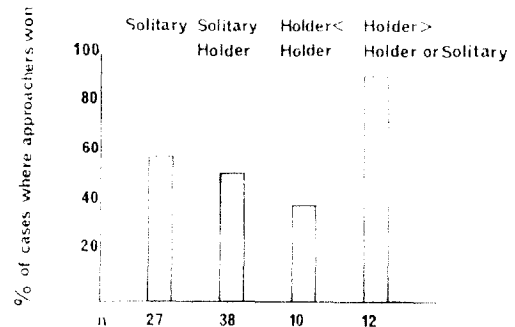


Fig. 16. Proportion of cases where approaching stags won in contests between (a) solitaires ($n = 27$), (b) solitaires and holders where the solitary approached ($n = 38$), (c) holders and holders where a holder approached a holder with more hinds than himself ($n = 10$) and (d) holders who approached other holders with fewer hinds than themselves ($n = 10$) or solitaires ($n = 2$).

For a fighting stag, being above its opponent on the slope confers an important advantage: stags circle rapidly while fighting, attempting to twist their opponents into a down-slope position and then to push them down the hill. During a parallel walk, stags will frequently invite contact (by turning to face their opponents and lowering their antlers) when they are above their opponents on the slope. Such invitations are almost always refused while invitations by animals standing on the level are generally accepted, the opponent then locking antlers with the initiator.

Fighting is clearly exhausting: after fights, stags are often panting heavily and may rest for an extended period. On six occasions we have observed young or subordinate stags to initiate a fight with a dominant animal immediately after the latter has fought another stag. Two of these, the young stag was successful and replaced the dominant though, in both cases, the former was displaced again soon afterwards.

Discussion

The analysis shows that, in red deer, fighting evidently involves appreciable costs. If, for example, we assume that rutting stags fight once every five days (see page 215), that they hold hinds for 20 days per year for five years during their life (Gibson, in preparation) and that one in a hundred fights leads to permanent injury or death (see page 215), we should expect 20% of individuals to be permanently injured at some time during their lifespan. These estimates are probably conservative both because the frequency of fights may be greater than one per five days (see Clutton-Brock & Albon, in press), and because injuries may occur which are invisible (e.g. abdominal puncture). In fact, the frequency of observed injuries is apparently slightly higher than these estimates (6% per year: see page 215). In addition, in an environment where predators (either human or animal) are present, the costs of both temporary and permanent injuries may be much greater: studies of African carnivores show that a large proportion of ungulates killed are ill or infirm (Schaller 1972; Kruuk 1972) and a rutting injury would probably result in a marked increase in the individual's liability to predation.

The benefits of fighting are also large. By fighting, winners can gain control of up to a dozen hinds (see page 216). Although winners

who already possess a harem gain few hinds (owing to losses to kleptogamists), they may extend or improve the area which they control, gaining increased access to hinds in the future both because hinds tend to collect in the same areas and because individuals which have been chased away by kleptogamists frequently return (or can be herded) back to their original location.

Long-term benefits of fighting ability are also important. Both fighting success and reproductive success are closely related to age, peaking in stags of 7 to 10 years. (The apparent increase in reproductive success among 7-year-olds (see Fig. 9) is almost certainly the product of small sample size.) Differences in reproductive success within age groups are also correlated with variation in fighting success, indicating that reproductive success depends on fighting success. There is no evidence to suggest that the advantages of fighting ability are offset by any marked reduction in breeding lifespan (see Geist 1971) and it seems likely that fighting success will prove to be closely related to lifetime breeding success.

The data show that the number of antler points that an individual carries is weakly related to fighting success and more strongly to the number of hind/days held. The difference in the strength of the relationship may be due to the fact that our measures of fighting success are often inaccurate due to small sample size: the number of hind/days held may, in practice, provide a more sensitive measure of fighting success. It seems likely that the correlation between point number and fighting success/reproductive success is the product of an association between point number and body weight and between weight and fighting ability. Although points permit stags to 'hold' their opponents and thus to gain firm purchase when pushing, variance in point numbers is largely the result of differences in the number of crown points which are seldom used in fights.

The study provides evidence that both the frequency and the intensity of aggression in red deer are affected by variation in the benefits of fighting: stags fought most frequently and most intensely at times when most hinds were likely to conceive. They also tended to avoid fighting with individuals they were unlikely to beat: additional data (Clutton-Brock & Albon, in preparation) suggested that ritualized behaviour preceding fights allowed individuals to assess their opponents' fighting ability. Fighting behaviour was not obviously sensitive to variation in the costs of fighting: there was no tendency for

young animals to fight less than old ones nor for harem holders (who stand to lose a proportion of their hinds if they are beaten) to fight less than solitaries. However, this could be a product of our rudimentary measure of variation in fighting costs.

These results are of importance in relation to theoretical investigations of fighting behaviour (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Maynard Smith 1976). Fights are asymmetric contests where the contestants' resource holding potential varies widely and their behaviour is adjusted to differences in pay-off. While stags probably assess each other carefully before fighting (Clutton-Brock & Albon, in press), it is clear that they cannot do so with great accuracy and frequently have to resort to escalation to clarify the situation. Excluding young stags, which adopt kleptogamous tactics (Gibson, 1978), there is no evidence for the existence of mixed strategies. Fights themselves fit the paradigm of the 'war of attrition' model (Maynard Smith & Parker 1976) in which costs mount with the duration of the contest, with the additional possibility that a false move may lead to injury in either contestant at any stage after the two animals have locked antlers.

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