

**The influence of the quality of the habitat
on sexual selection in red deer:**

a comparison between Rhum (Scotland) and Jægersborg deerpark (Denmark)



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student report

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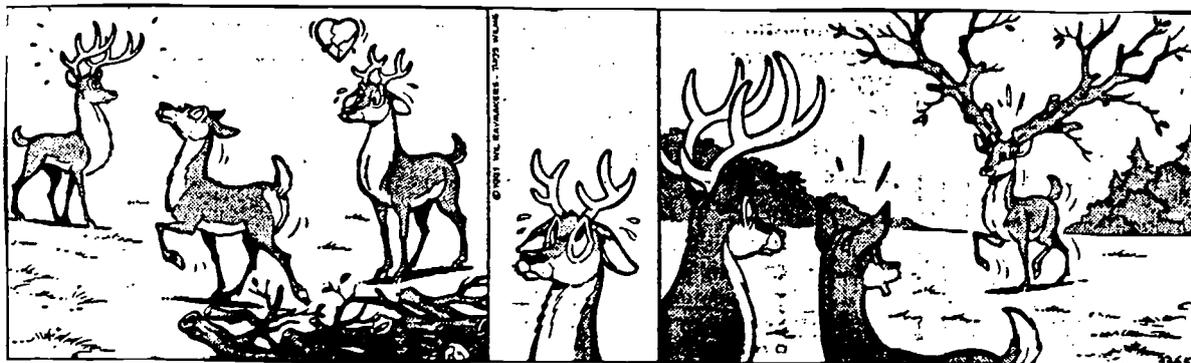
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Cover: Juletræet, a promising young stag of six year old in Jægersborg deerpark (26-9-1990)



(Thanks to Geja)

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INTRODUCTION

It is generally accepted that the size, weight and physical condition of conspecific deer living in different areas tend to reflect the quality and quantity of food offered by the habitat (e.g. Geist 1978, Langbein 1990). In a study about the effects of density and age on body condition, reproductive performance, behaviour and survival of fallow deer (*Dama dama*), Langbein (1990) found a high variability in winter live weights between parks in England, population means ranging from for example 19.5 to 32.3 kg for male fawns and 12.1 to 42.6 kg for yearling females. In a poor habitat (whether the result of poor resources, a harsh climate or high population densities) the secondary sexual characters of males are particularly affected, because these characters have low growth priorities (Geist 1978, Clutton-Brock *et al.* 1982).

Most secondary sexual characters have a direct or indirect effect on the reproductive success of the owner. It is generally believed that they evolved to their present form by sexual selection (Darwin 1871). Sexual selection can work in two ways: by favouring the ability of one sex (usually males) to compete directly with one another for fertilizations, for example by fighting (intra-sexual selection), or by favouring the ability to attract a member of the other sex (inter-sexual selection). Presumably the two kinds of selection act simultaneously (Krebs & Davies 1987). The most direct test whether sexual selection is operating is to investigate whether differences in phenotype affect mating rate or mate quality (Clutton-Brock 1988b). This means that the partial regression of mating success on a character, holding all other characters constant, has to be determined. This regression coefficient is called the (sexual) selection gradient (Arnold & Wade 1984a). If differences in phenotype do affect mating success, sexual selection is occurring, however small the observed variance in mating success. If not, it will seldom be possible to be sure that sexual selection is occurring, however large the variance in mating success (Clutton-Brock 1988b). The variance in mating success is called the opportunity for (sexual) selection (Arnold & Wade 1984a).

Competition between males can affect many traits that are not regarded as secondary sexual characters, for example lung size. Inter-male competition may also affect female characteristics. Because of this it is usually more useful to attempt to relate traits that are more developed in one sex to differences in selection pressures operating on males and females than to try to distinguish between differences that are a consequence of natural selection and those that have been produced by sexual selection (Clutton-Brock *et al.* 1982, Zahavi 1991).

Selection causes observable changes within a generation in the means, variances and covariances of distributions of phenotypic traits. Thus selection can be described in purely phenotypic terms without recourse to the inheritance of characters. In contrast, evolutionary response to selection, for example the change in phenotypic mean from one generation to the next, certainly does depend on inheritance (Arnold & Wade 1984a).

This pilot study investigates the influence of habitat quality on the elaboration of a secondary sexual character in two red deer (*Cervus elaphus*) populations, which are living in different habitats. The breeding system of red deer is a classical example of temporary harem polygyny (Darling 1937). After the

summer (approximately September until December) stag groups fragment as individuals move towards traditional rutting sites where they try to collect and defend harems, which consist of unstable groups of females of two to thirty or more individuals (Clutton-Brock *et al.* 1988). Only stags that have reached full adult weight are able to hold large harems during the period of peak conceptions, though young (< 5 years) and old (> 11 years) stags hold harems before and after this date. Fights between rutting stags occur regularly and the size of a stag his harem is closely related to his success in fights. Fighting ability and reproductive success were related to body size and condition. Among stags over five years old on Rhum (Inner Hebrides, Scotland), neither fighting success nor reproductive success is related to antler length. Both measures are related to antler weight, but the most likely explanation is that both fighting success and antler weight are related to differences in body size and weight (condition) (Clutton-Brock *et al.* 1982).

Antler weights provide a useful measure to study the question whether there are differences in variance between two populations living in habitats of different quality. On the one hand, the data are relatively easy to obtain since the stags always shed their antlers at the end of the winter and the antlers can easily be recognized individually. On the other hand, the positive correlation between antler weight and mating success (Clutton-Brock *et al.* 1988) suggests that antler weight is an important measure for mating success. The distribution of mating success over stags in the two habitats and the importance of antler weights for the determination of mating success are also compared.

Two study populations were chosen which live in habitats of different quality. The population on the island of Rhum was used for a population in a poor habitat. Quantitative data on reproductive success of individual animals of this population have been gathered for more than twenty years by the Large Animal Research Group of the University of Cambridge. The red deer population of Jægersborg deerpark, near Copenhagen in Denmark, was used for a population living in a rich habitat. The data of this population were gathered during the rutting season of 1990.

MATERIAL & METHODS

Stags and hinds are defined as being individuals over a year old, while reproductive stags are defined as stags of at least six years of age. A reproductive hind is in Jægersborg at least one and a half year old and on Rhum at least two and a half year. A rutting stag is defined as a reproductive stag with a harem.

1 Rhum

On Rhum original deer stocks went extinct by the end of the eighteenth century, but the island was restocked in 1845 and the population rose to about 1600 individuals by 1958. By culling, numbers have ranged from 1175 to 1842 between 1959 and 1980. For culling purposes, the island is divided into five blocks that are culled in proportion to the number of deer counted in them during the spring counts. The red deer population on the North Block of Rhum (an unfenced area of about 12 km²) has been studied intensively by the Large Animal Research Group. Since 1973, culling of both hinds and stags in the North Block has been completely suspended for research purposes (Clutton-Brock *et al.* 1982). The number of individuals resident in the study area rose from 57 hinds and 116 stags to 166 hinds in 1983 and 155 stags in 1978, which then declined to 86 by 1983 (Clutton-Brock *et al.* 1988). An individual was defined as resident in the study area if it was seen in at least 10% of censuses in at least four months of the year.

Rhum is largely covered by *Calluna*- and *Molinia*-dominated moorland. Small areas of *Agrostis* and *Festuca* grassland are widely distributed and heavily used by the deer (Clutton-Brock *et al.* 1982).

2 Jægersborg

Jægersborg deerpark was established in 1669 by fencing a natural forest. The original population of deer in the forest and surroundings was gathered before the fence was closed. The park has been fenced ever since, but not always in the same size as today. Today the park is almost 1000 ha, of which 800 ha is accessible to the deer. At present there are about 2100 deer in the park of which about 250 are red deer (Waage Sørensen: pers.comm.). Annually about 600 deer are shot by a few professional hunters. This number corresponds closely to the number of calves produced per year (National Forest and Nature Agency 1979).

In the park are many old trees over 200 years of age, mostly beech and oak. A large part is covered with grasslands. From November to April the deer are additionally fed with clover-hay, oat and barley leaves, sugar beets and maize (National Forest and Nature Agency 1979).

3 Estimated parameters

The reproductive performance of a population gives an indication of the quality of the habitat (Mitchell *et al.* 1977). As a measure of the reproductive performance the calf/hind ratio in autumn and the mean antler weight, corrected for the age of the stag, are used. For the calf/hind ratio only reproductive hinds are used.

The weight of the shed antlers was recorded on Rhum and in Jægersborg deerpark. Antler weights from the rutting seasons of 1987 to 1990 have been used from Jægersborg and from the rutting seasons of 1985 to 1989 from Rhum. The sum of the weight of the left and right antler of an individual reproductive stag was calculated. When one of the antlers was missing twice the weight of the available antler was taken. No correction for broken antlers was made to try to estimate the weight of the complete antlers. The correlation between antler weight and reproductive success was only estimated for reproductive stags, because only under stags of these age classes a substantial proportion of individuals did hold harems. The age at which stags started to hold harems slightly preceded the point at which they reached full adult weight. This is usually reached at the age of six (Clutton-Brock *et al.* 1982).

The harem size of each rutting stag on Rhum is determined by daily censuses of all ground below 120 m during the rut. In this census area virtually all rutting groups in the study area were present (Clutton-Brock *et al.* 1982). Data are used from one rutting season: 14 September until 13 December 1989. During this rutting season 171 hinds and 136 stags were resident in the study area. All animals could be individually recognized by coloured plastic ear tags/ashes or physical idiosyncracies. Ages of the majority of animals were known to within a year either from observations of individuals as calves or yearlings or from inspection of tooth eruption and wear after immobilization (Clutton-Brock *et al.* 1982). In Jægersborg only the reproductive stags could be individually recognized and the harem size of each rutting stag was determined between 13 September and 5 October 1990 by daily censuses. During this period 84 stags and 123 hinds were in the park (Christiansen: pers.comm.). The age of all reproductive stags in Jægersborg is known.

Data of roaring frequencies and number of chivies of several reproductive stags on Rhum are available from some rutting seasons. Chivying is the chasing of hinds by stags over short distances. During these chases the stag trots after the hind with neck outstretched, sometimes extending his tongue (Clutton-Brock *et al.* 1982). Frequencies of both chivying and roaring can be used to estimate the intensity of the rut (Albon: pers.comm.). These frequencies were obtained during continuous observations of several hours. In Jægersborg these data were gathered from about ten reproductive stags, who were observed on several evenings during the rut for about 20 minutes per evening. The number of reproductive hinds in his harem and the presence or absence of another reproductive stag in the neighbourhood was also taken into account. Each observed copulation or fight was also noted.

3 ESTIMATION OF MATING SUCCESS

3.1 Rhum

For the estimation of the mating success of reproductive stags on Rhum two methods were used:

- A method based on the frequency distribution of the estimated date of conception of each calf born in the study area from the rut of 1969 up to and including 1989. This method is referred to as UK-field.
- The method used in Clutton-Brock *et al.* (1988), corrected for the results of a DNA fingerprinting study (Pemberton *et al.* 1992). This method is referred to as UK-DNA.

3.1.1 UK-field

The date of conception of each calf born in the study area was estimated by backdating from its birth date by 236 days for males and 234 days for females (Clutton-Brock *et al.* 1988). For each year between 1969 and 1989 the frequency distribution of the estimated date of conception, compared to the median estimated date of conception of that year, was determined. Figure 1 shows the summary statistics for the whole time period and it contains 1315 of the 1322 calves born.

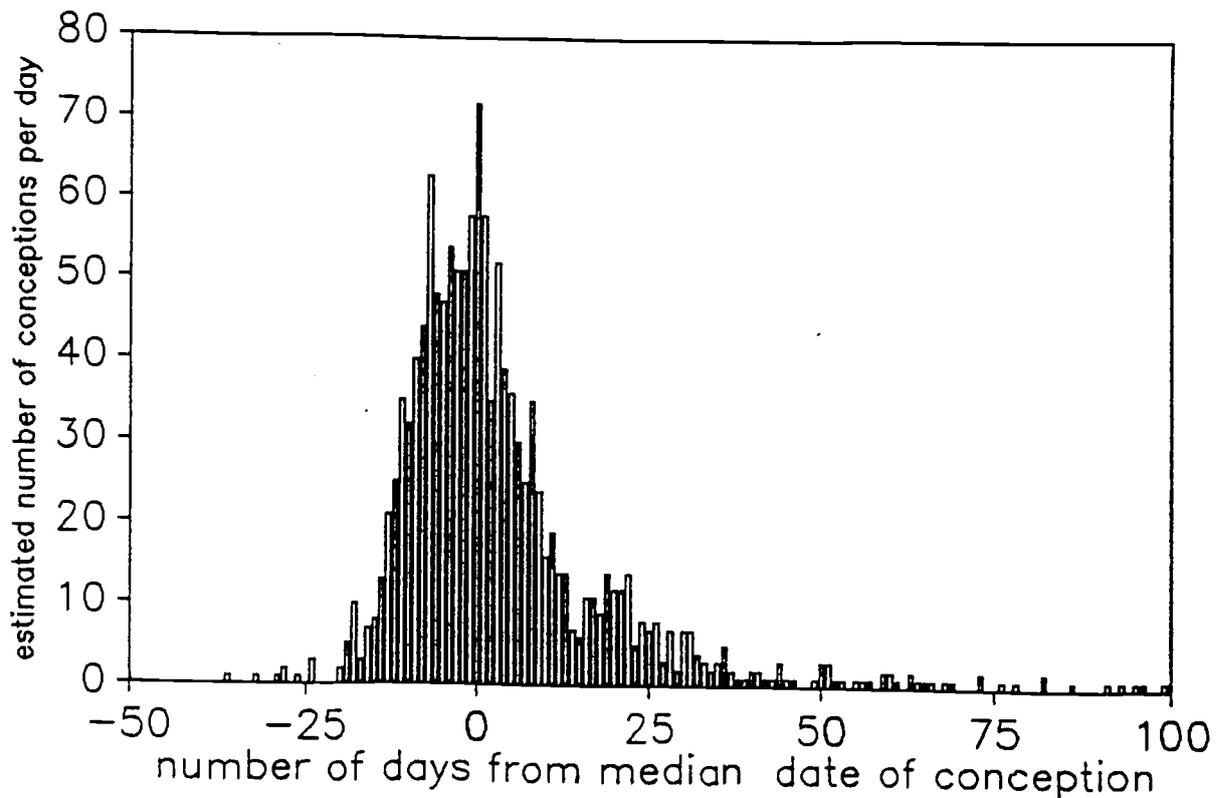


Figure 1. Estimated number of conceptions per day compared to the median date of conception (see text for details).

A straightforward method for estimating reproductive success of stags would be to multiply his harem size of each day with the estimated number of conceptions for that day. However, because the stags were not seen every day, it is necessary to divide the distribution of the estimated number of conceptions into several periods. Four periods were determined by eye, with as little variation as possible in the estimated number of conceptions within each period. The four periods, with the mean estimated fraction of the number of reproductive hinds served per period, are given in table 1. The data obtained for a male were only considered reliable when he was seen at least a minimum number of times. If stags were observed less than this arbitrary value, they were not considered as rutting stags during that period. Because most hinds are served during the second period, the ad hoc value for this period is higher than for the other periods. If they were observed at least this minimum number of times, the mean harem sizes of the individual reproductive stags was multiplied with the estimated fraction of reproductive hinds served during that period. Summed over all four periods, this gives an estimation of the number of calves sired during the rut for each reproductive stag.

Table 1. Number of reproductive hinds served divided into four periods with the corresponding fraction. The minimum number of observations of a reproductive stag with harem, required for regarding him as sexually active during that period, is also given.

Number of period	Date compared to median	Fraction served	Min. number of obs.
1	[-30, -11]	136/1279 \approx 0.11	3
2	[-10, 10]	910/1279 \approx 0.71	5
3	[11, 30]	190/1279 \approx 0.15	3
4	[31, 50]	43/1279 \approx 0.03	3

For the rutting season of 1989 the harem sizes were determined on the basis of the number of hinds who indeed gave birth to a calf in the next spring (the operational harem size). The median estimated date of conception was 11 October. In this way 39 different reproductive stags, of whom 15 did not succeed to father any calf, were involved with an estimated total number of 55 calves sired (Fig. 2a), while there were 74 calves born in the spring of 1990. The coefficient of variation (the ratio of standard deviation to mean) for this distribution is 1.18.

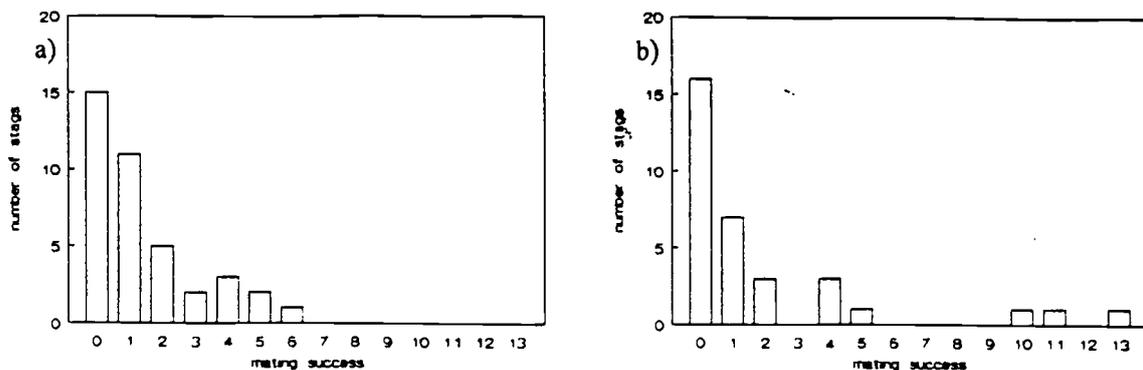


Figure 2. Estimated number of calves sired per reproductive stag for UK-field (a) and UK-DNA (b).

3.1.2 UK-DNA

The estimated date of conception was determined in the same way as described in 3.1.1. For five days before and after the estimated conception date (the standard deviation of gestation length) the stag in whose harem the mother was seen was identified, awarding each stag a fraction of the calf corresponding to the fraction of the eleven day period in which the mother was in his harem (Clutton-Brock *et al.* 1988). These fractions were summed for all the calves born in the spring of 1990 for each individual reproductive stag. With DNA fingerprinting analysis of 80 calves, most of them born in 1982 and 1983 on Rhum, and their potential parents, it was found that the probability that a male fathers a calf is closely related to the number of days he holds the female in his harem, increasing from 0.12 for 1 day to 1.0 for six days or more. This method accurately identifies the relative success of individual males but is a poor predictor of absolute success: the behavioural method underestimates the true success of successful males and overestimates the success of many males who in fact fail to father any calves (Fig. 3) (Pemberton *et al.* 1992). The estimated number of calves sired during the rut of 1989 was corrected for each reproductive stag with the regression line of figure 3. In this way 33 different reproductive stags, of whom 16 did not succeed in fathering any calf, were involved with an estimated total number of 64 calves sired (Fig. 2b), while of 58 calves at least one rutting stag was keeping the mother in his harem in the period of eleven days around the estimated date of conception of the mother. The coefficient of variation for this distribution is 1.72.

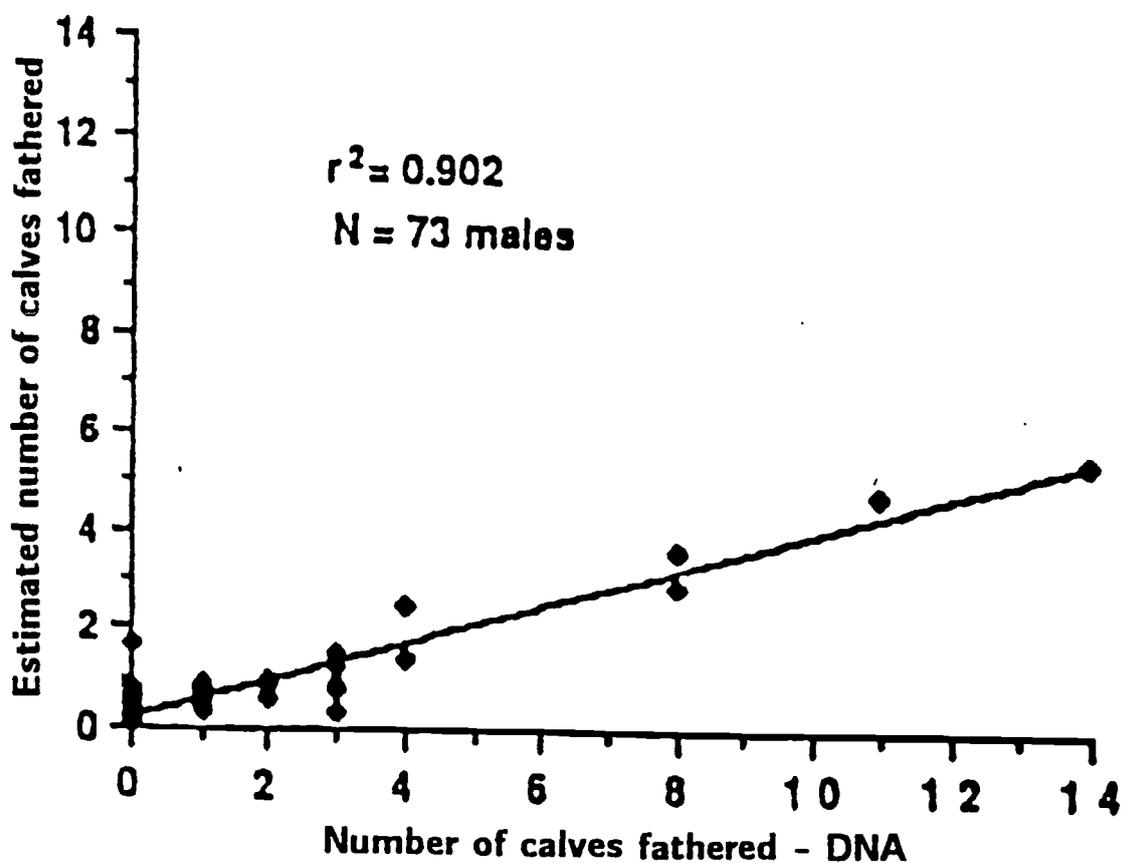


Figure 3. Estimated number of calves fathered, for the method described in the text, plotted against true number of calves fathered, as determined with DNA-fingerprinting (from Pemberton *et al.* 1992).

3.2 Jægersborg

For Jægersborg the birth date of the calves are unknown, because the calves are usually not seen in the first week of their lives (Christiansen: pers.comm.). Therefore, an ad hoc approach had to be taken, which is based on the following considerations:

- On the basis of first observations of young calves in Jægersborg, it is likely that the majority of births is concentrated in a shorter time period than on Rhum (Christiansen: pers.comm.), so it is likely that the hinds are more synchronously served in Jægersborg than on Rhum.
- There are far fewer births after the main period of births in Jægersborg than on Rhum (Christiansen: pers.comm.), so it is likely that the distribution of the number of hinds served is more symmetric in Jægersborg than on Rhum.

With this information three instead of four periods have been used for the method DK-field, which are half as long as the periods of UK-field (Table 2). In this table the distribution of the number of hinds served from Rhum is used, with the exception that the distribution is made symmetric by making the numbers after the median equal to those before the median: the part after the median equals the part before the median.

Table 2. Number of reproductive hinds served divided into three periods for Jægersborg, derived from the distribution of Rhum, with the corresponding fraction. The minimum number of observations of a reproductive stag with harem, required for regarding him as sexually active during that period, is also given.

Number of period	Date compared to median	Fraction served	Min. number of obs.
1	[-15, -6]	136/1320 \approx 0.1	3
2	[- 5, 5]	1048/1320 \approx 0.8	5
3	[6, 15]	136/1320 \approx 0.1	3

Because the birth date of the calves are unknown in Jægersborg, the median estimated date of conception is also not known. There are several possibilities to estimate this date:

- A) personal interpretations of the rutting behaviour of the deer;
- B) total number of reproductive hinds in harems of all rutting stags during the rut;
- C) number of roars per unit time;
- D) number of chivies per unit time;
- E) number of fights and copulations.

These points are handled in detail below. The results are summarized in table 3.

- A) With the help of several observers it is concluded that the peak of "excitement and rumour" was at about 23 September.

Table 3. Results of the five different methods used for estimating the median date of conception in Jægersborg. "Corrected" means adjusted for the observed differences on Rhum between the date found by the used method and the median estimated date of conception (see text for details).

Method	Date
A) Peak of excitement	23 September
B) Peak in harem size	25 September
corrected	27 September
C) Peak in roaring frequencies	27 September
corrected	29 September
D) Peak in chivying frequencies	-
E) Peak in number of fights and copulations	-

B) On Rhum the estimated median date of conception in the rutting season of 1989 was 11 October. The peak in the number of hinds (only expectant mothers) in harems is difficult to determine (Fig. 4a), so the running mean over a period of nine days was calculated (Fig. 4b). On the basis of this figure, the peak in the number of hinds in harems on Rhum is estimated at 6 or 7 October.

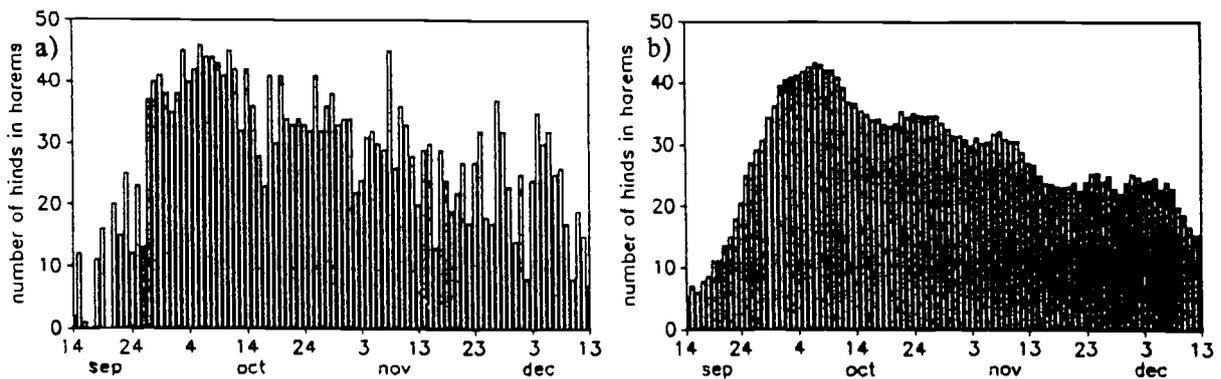


Figure 4. Data from Rhum of a) Number of hinds (expectant mothers) in harems of rutting stags; b) The number of hinds as running mean over a period of nine days.

In Jægersborg the peak in the number of reproductive hinds in harems was observed on 25 September. The data from Rhum show that this does not necessarily correspond with the estimated median date of conception. When the difference between the median date of conception and the peak in the number of reproductive hinds in harems on Rhum is used to estimate the median date of conception in Jægersborg, taking for granted that the rutting season is twice as short in Jægersborg than on Rhum, this is estimated at 27 September.

C) According to McComb (1987) roaring in red deer advances the date of ovulation and harem holders can improve their mating success by regular calling. Clutton-Brock *et al.* (1982) found that harem holders roared more when their harems were larger than usual, when there was an oestrus hind in their harem and when the nearest rutting stag was closer than average.

There are data of roaring frequencies from Rhum available on several reproductive stags from the rutting season of 1980, 1981 and 1982. These data were standardized to the median estimated date of conception of 1980. With the use of regression roaring frequencies are related to date and $(\text{date})^2$,

corrected for the harem size. Date, (date)² and harem size had all a significant influence on the roaring frequencies, but only 32% of the observed variance was explained. The estimated peak in roaring frequencies was at 18 or 19 October, while the estimated median date of conception was on 22 October.

The peak in roaring frequencies in Jægersborg, estimated with the use of regression with the independent variables harem size, date and (date)², was at 27 September. When the difference between the median date of conception and the peak in roaring frequencies on Rhum is used to estimate the median date of conception in Jægersborg, taking for granted that the rutting season is twice as short in Jægersborg than on Rhum, this is estimated at 29 September.

- D) According to Clutton-Brock *et al.* (1982) stags paid particular attention to hinds that had recently joined their harems and the frequency with which they licked and chivied 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. Although it is expected that the number of chivies is dependent on the number of hinds in oestrus, it was not possible to detect any relationship between the number of chivies and date or (date)² for the data of Jægersborg. Because of this it is not possible to estimate the median date of conception for Jægersborg with the use of the number of chivies.
- E) The number of fights between stags shows a very close relationship with the number of conceptions on Rhum. Continuous observations of individual stags suggest that most mature stags fight at least once every five days and are usually involved in about five fights during the rut (Clutton-Brock *et al.* 1982). Unfortunately fights and copulations in Jægersborg were rarely seen (Table 4). Because of this there are too few data to estimate the median date of conception in Jægersborg on the basis of the number of fights and copulations.

Table 4. Frequency of observed fights and copulations during the rutting season of 1990 in Jægersborg.

Date	Number of fights	Number of copulations
23 September	0	3*
24 September	2	0
25 September	0	0
26 September	0	0
27 September	1	0
28 September	2	0
29 September	1	1
30 September	1	0
1 October	1	0

* all three copulations by one stag

The estimated median date of conception in Jægersborg, calculated with the use of the different methods described above, is not very reliable. An estimated median date of conception at 27 September (B) or 29 September (C) is too late: several strong stags who had very big harems until these dates for several weeks, would shortly after these dates leave their rutting areas. At these dates also several young males tried

to hold incoherent harems, so it is very likely that the median date of conception was before 27 September. It is not surprising that roaring frequencies (C) and the number of chivies (D) are not very reliable, because of the low fraction of variance explained in the regression models. It is very likely that roaring frequencies and the number of chivies depend on a lot of factors which cannot be corrected for with the use of regression. The number of hinds in harems is probably also not a very reliable estimate for the number of hinds served, because young and old stags try to hold harems (before and) after the period of peak conceptions (Clutton-Brock *et al.* 1982), although they will not gain many copulations at that time. There is also a difference in visibility of the harems between Rhum and Jægersborg and it is possible that the difference in quality of the habitat has a lot of influence on the stability and size of the harems (see chapter 5.3.3). The number of fights and copulations are probably a reliable estimation for the number of hinds served, but these are rarely observed in Jægersborg.

Because of the problems with estimating the median date of conception in Jægersborg, three different situations are used for calculation of the estimated number of hinds served:

-DK-field1: median date is 23 September;

-DK-field2: median date is 27 September;

-DK-field3: the chance of fertilizing a hind is not dependent on the date during the rut.

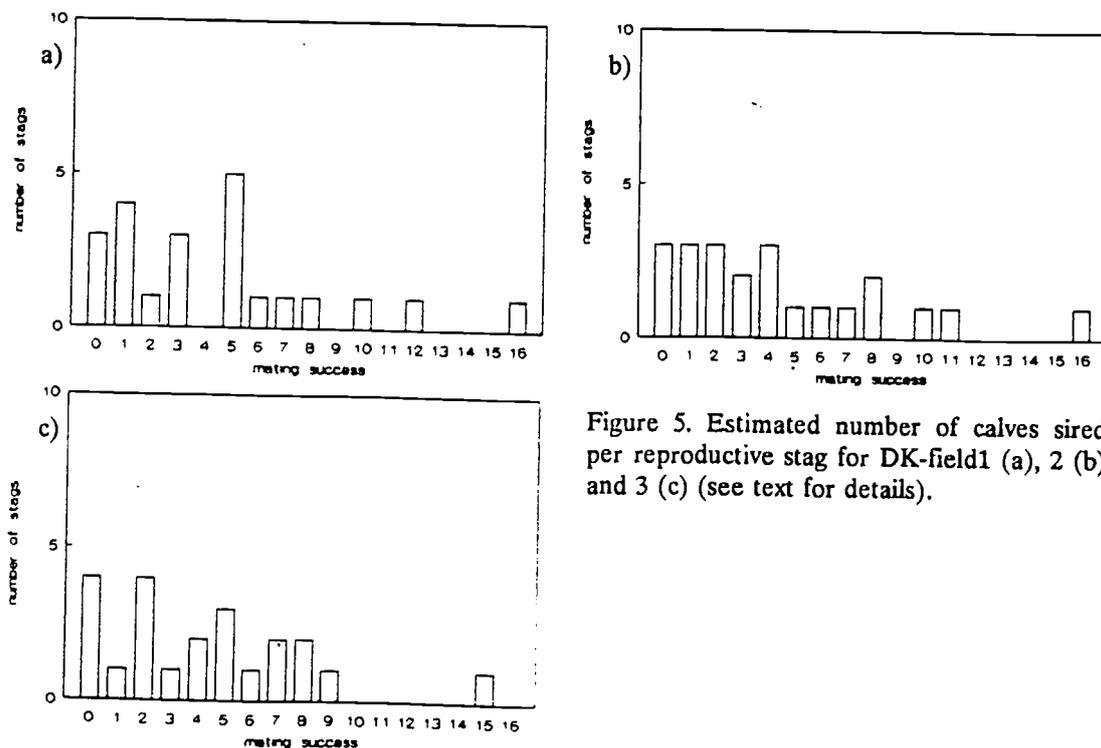


Figure 5. Estimated number of calves sired per reproductive stag for DK-field1 (a), 2 (b) and 3 (c) (see text for details).

DK-field3 does not need so many ad hoc assumptions as DK-field1 and 2, because the rut does not have to be divided into several periods. One ad hoc assumption that is still necessary for DK-field3 is the minimum number of observations for a reproductive stag to regard him as a rutting stag. At least 10

observations between 13 September and 5 October are used for this minimum. When a stag is seen less than 10 times, he is regarded as unsuccessful in fertilizing hinds, because it is very likely that an undetected stag does not have a harem.

In this way 22 different reproductive stags sired an estimated total number of 99 (DK-field1, Fig.5a), 98 (DK-field2, Fig.5b) and 95 (DK-field3, Fig.5c) calves. The coefficient of variation for these distributions is respectively 0.92, 0.93 and 0.86.

4 ANTLER WEIGHT

The calf/hind ratio in the autumn is used as a measure for the reproductive performance of a population. On Rhum this ratio was 0.4 on the first of November 1989. In Jægersborg management aims at achieving a ratio of 0.8 on the first of September (Christiansen: pers.comm.). The other measure used for the reproductive performance is mean antler weight, corrected for the age of a stag, calculated with the use of multiple regression. These regression curves are shown in figure 6. These curves should be split up for the different years of which data are available, because the data are not independent: the weight of the antlers of the same stags are used in different years. Because of this figure 6 is only used to show the rough differences between the two populations. The big differences in antler weight are not only caused by differences in body size between the two populations: the ratio of antler weight to body weight is about 1% on Rhum and 4% in Jægersborg.

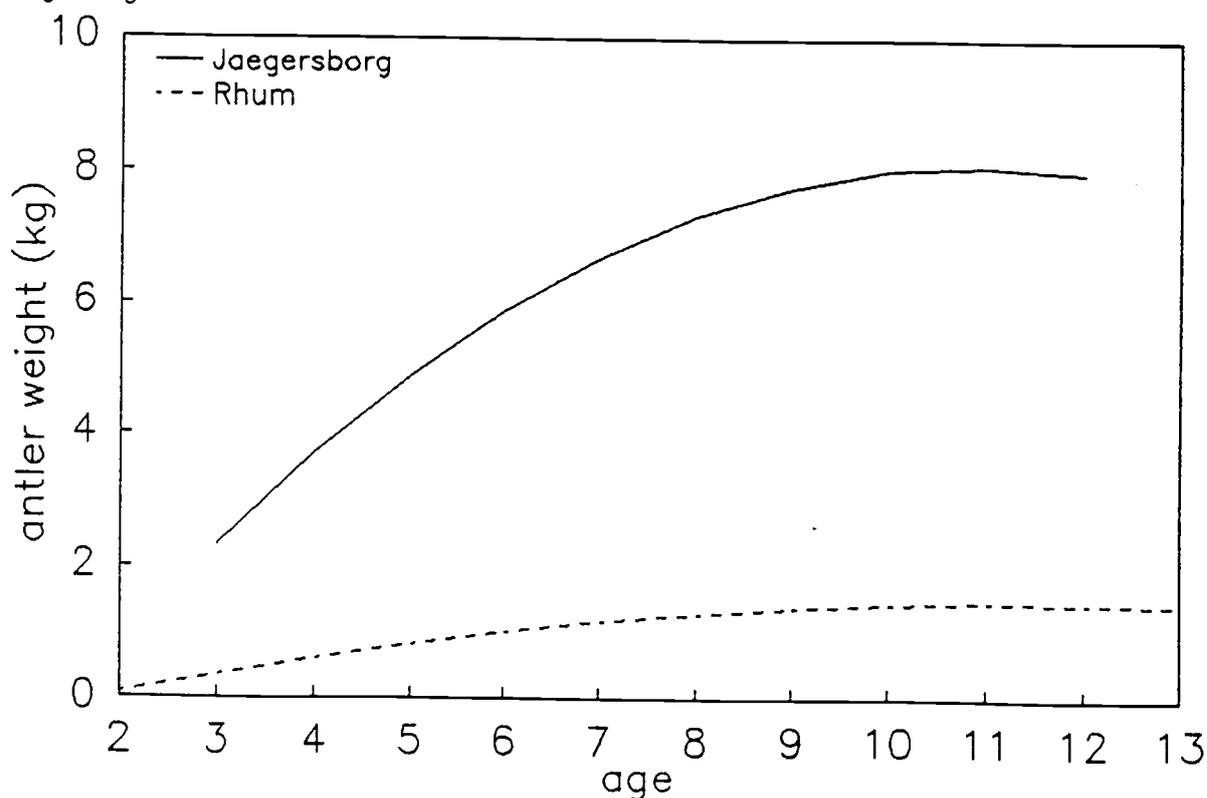


Figure 6. Multiple regression curves for antler weight, plotted against age of the stags, for Jægersborg and Rhum. The curves explain about 65% of the observed variation.

Of 108 stags in Jægersborg (from 1987-1990) and 168 stags on Rhum (from 1985-1989) antlers were weighed. The data of Jægersborg are more complete than those of Rhum. Of the stags in Jægersborg one of the antlers of 6 stags was missing. From the data of Rhum one of the antlers of 101 stags was missing and 11 stags had to be excluded, because both antlers were missing.

Information about the mean antler weight, variance (= opportunity of selection) and coefficient of variation per age class of reproductive stags is given in table 5. Differences between the two populations in mean and variance of the antler weights are significant for all age classes, while differences in coefficient of variation are only significant for stags of six years old.

Table 5. Mean antler weight (\bar{x} in kg), variance (σ^2 in kg²) and coefficient of variation (cv) per age class of reproductive stags on Rhum (UK) and in Jægersborg (DK). The number of stags per age class is also given.

Age	\bar{x} DK	\bar{x} UK	σ^2 DK	σ^2 UK	cv DK	cv UK	n DK	n UK
6	6.0	1.0***	0.8	0.08***	0.15	0.28**	20	27
7	7.2	1.2***	1.2	0.06***	0.15	0.19	16	20
8	7.3	1.4***	1.1	0.06***	0.15	0.18	11	24
9	7.5	1.4***	3.3	0.10***	0.24	0.23	12	17
10	7.3	1.4***	1.4	0.10***	0.16	0.22	7	19
11	8.2	1.4***	5.2	0.07***	0.28	0.18	4	12
12	10.8	1.6***	-	0.04	-	0.13	1	4
13	-	1.4	-	-	-	-	0	1

** = $p < 0.01$, *** = $p < 0.001$ by two-tailed t-test for \bar{x} , two-tailed F-test for σ^2 and two-tailed F-test on the logarithms of the data for cv (Zar 1984)

If differences in phenotypic characters are important for the reproductive success of the stags, it is also important to compare the two populations with all the age classes of six and more together (per rutting season because of independence). The differences in mean, variance and coefficient of variation between the two populations found in this way (Table 6) are of course also dependent on differences in age structure between the populations (Table 7). Table 6 shows the same picture as table 5: big differences between Jægersborg and Rhum in mean and variance of antler weights and no obvious differences between the coefficients of variation. Also for the years of which information about the harem sizes is available (UK89 and DK90), there are no significant differences in the coefficient of variation ($p = 0.86$ by two-tailed F-test on the logarithms of the data).

Table 6. Mean antler weight (\bar{x} in kg), variance (σ^2 in kg²) and coefficient of variation (cv) per rutting season and per population. Only reproductive stags were used (n; see also table 7).

Population and year	n	\bar{x}	σ^2	cv
DK87	14	7.2	1.4	0.17
DK88	17	6.3	2.1	0.23
DK89	18	7.0	1.6	0.18
DK90	22	7.6	2.5	0.21
UK85	24	1.1	0.12	0.31
UK86	18	1.2	0.07	0.21
UK87	34	1.3	0.08	0.21
UK88	19	1.3	0.15	0.29
UK89	29	1.4	0.09	0.21

Table 7. Age structure of reproductive stags on Rhum (UK) and in Jægersborg (DK), based upon the number of weighted antlers

DK: Age	Year				UK: Age	Year				
	87	88	89	90		85	86	87	88	89
6	3	5	6	6	6	9	2	7	3	6
7	4	3	4	5	7	2	5	2	7	4
8	3	3	2	3	8	6	2	7	1	8
9	3	4	3	2	9	2	4	5	4	2
10	1	2	2	2	10	4	2	6	3	4
11	0	0	1	3	11	1	2	5	1	3
12	0	0	0	1	12	0	1	2	0	1
13	0	0	0	0	13	0	0	0	0	1

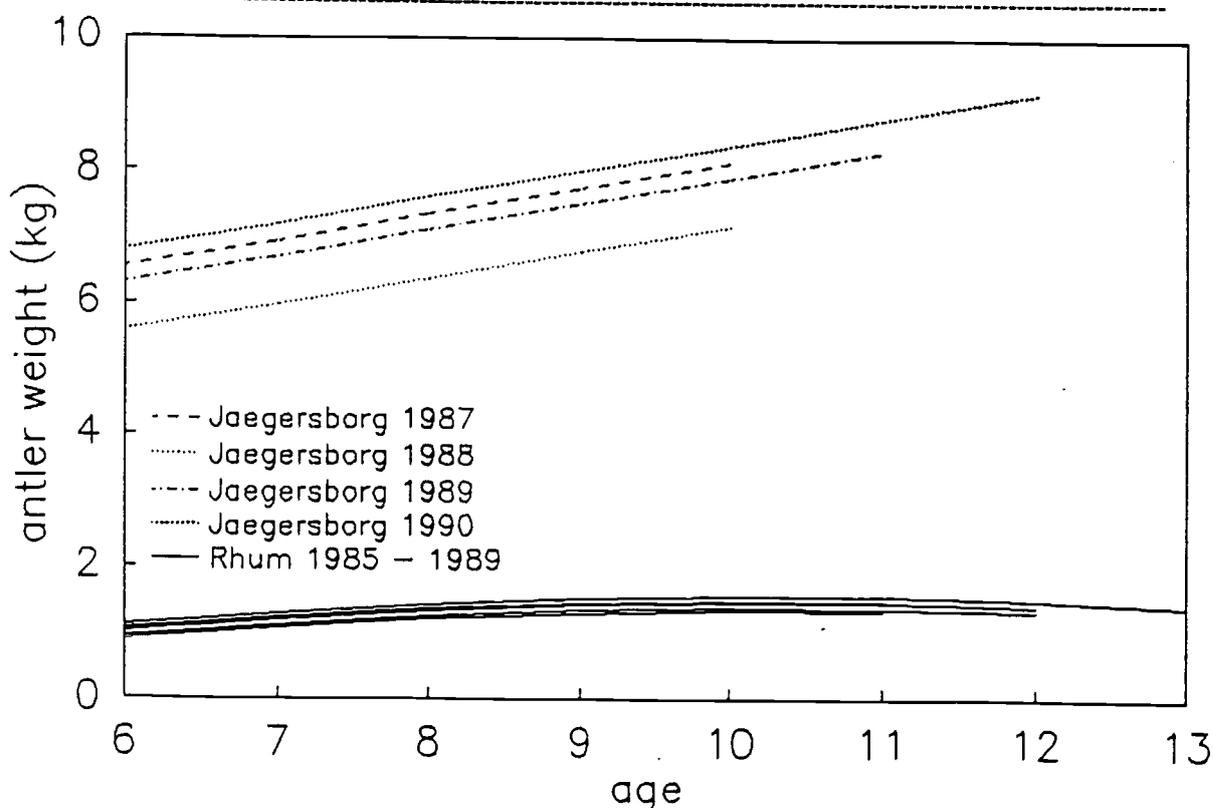


Figure 7. Multiple regression curves for the antler weight of reproductive stags, plotted against their age and split up for the different years, for Jægersborg ($r^2=0.31$) and Rhum ($r^2=0.35$).

To determine if there are differences in importance of the independent variables age, $(age)^2$ and year (= rutting season) in their influence on antler weight between the two populations, these were used in a multiple regression. Year was used as a categorical variable to avoid dependence of the data. The regression was used on age classes six to thirteen. Significance was determined by two-tailed F-test. In Jægersborg age ($p=0.000$) and year ($p=0.04$) were significant, while $(age)^2$ ($p=0.42$) and the interaction between year and age ($p=0.39$) were not significant. On Rhum age ($p=0.001$), $(age)^2$ ($p=0.003$) and year ($p=0.05$) were significant, while the interaction between year and age ($p=0.54$) was not significant. The regression curves are shown in figure 7. In this figure the constant terms (year: 4 levels for Jægersborg and 5 levels for Rhum) and the

significant dependent variables (age for Jægersborg, age and $(age)^2$ for Rhum) were used to draw the curves. All the lines in this figure are parallel, because the interaction between year and age was not significant. Striking is the difference of the significance of $(age)^2$ between Rhum and Jægersborg.

The results of the estimation of the mating success are shown in figure 2 and 5. These estimates of the number of calves sired were used in Poisson regressions (logarithmic link function) as the dependent variables. The independent variables were antler weight, age and the interaction between antler weight and age. Again the regression was used on age classes six to thirteen and significance was tested by two-tailed F-tests (Table 8). The three different methods used for DK-field give similar results. For the data of Jægersborg the fraction of variance explained is declining with the probability that the used method gives a reliable estimation of the number of hinds served.

Table 8. Poisson regression of mating success of reproductive stags on Rhum (a) and in Jægersborg (b) on antler weight, age and the interaction between weight and age. The r^2 value of the regression, sample size and p-values are given. Only the constant terms and antler weight were used for calculating the regression coefficients.

a)	UK-field		UK-DNA	
	coeff.	p-value	coeff.	p-value
antler weight	1.1	0.12	1.7	0.04
age * antler weight	-	0.55	-	0.46
age	-	0.69	-	0.52
sample size	23		23	
r^2	0.11		0.14	

b)	DK-field1		DK-field2		DK-field3	
	coeff.	p-value	coeff.	p-value	coeff.	p-value
antler weight	0.37		0.0002	0.35		
0.0007	0.32		0.002			
age * antler weight	-	0.63	-	0.38	-	0.73
age	-	0.63	-	0.37	-	0.69
sample size	22		22		22	
r^2	0.52		0.45		0.40	

The slope of the best fitting straight line relating a Lifetime Reproductive Success (LRS) component (mating success) to a character (antler weight), holding other variables constant is usually interpreted as a selection gradient (Grafen 1988). Similarly, the regression coefficient of the Poisson regression may also be considered as a kind of selection gradient. The results show that the influence of age on mating success is only indirect via antler weight and that the selection gradient is stronger on Rhum than in Jægersborg. However, these tables also show that the fraction of variance explained is much lower on Rhum than in Jægersborg.

5 DISCUSSION

5.1 Detecting sexual selection in the field

The evolution of life history traits can be approached in two different ways (Lessells 1991):

- the phenotypic approach, which asks questions about the adaptive value of a trait in terms of the selection pressures acting on it;
- the genetic approach, which also considers the effects of selection but this time the way in which selection will affect gene frequencies.

Only the genetic approach is able to make predictions about the direction and speed of genetic change. It is, however, only applicable if the heritability of the phenotypic characters under study are known. Because there is no information about the heritability of antler weight in red deer, it is not possible to answer questions about genetic change (Clutton-Brock 1988a), so the approach in this study has to be phenotypic.

To determine if a trait, like antler weight, is selected upon, one has to determine the correlation between antler weight and a Lifetime Reproductive Success (LRS) component, like mating success (Grafen 1988). The value of this selection gradient in the analysis of adaptation depends on several factors:

1) Does measured variation in LRS correspond to actual variation?

The data set of individuals is often not complete, because there can be an "invisible fraction" of individuals who do not appear in the regression but should. For example, the penalty for a male red deer "planning" to have a large body size may be that by allocating resources to growth instead of to defense against disease, it is more likely to die as a juvenile. So the "largest" males die young and cannot have their adult size measured (Grafen 1988).

2) Is variation heritable or does it only reflect environmental variation?

Since climatic differences between years often affect birth weight and juvenile growth, a substantial proportion of variation in breeding success may be of environmental origin. One line of evidence supporting this is that in long-lived animals average breeding success calculated across the life span often shows pronounced differences between successive cohorts. Not only can these short-term environmental changes unrelated to phenotype have a major effect on all components of breeding success, also effects of pure chance can influence the estimated force of selection (Clutton-Brock 1988b, Grafen 1988, Newton 1989). Only if differences in reproductive success or survival are caused by genetic variation, is there a possibility for selection.

3) Is the trait studied actually the focus of selection?

If one wants to calculate selection gradients for a character, one needs to measure a whole suite of characters, because selection may actually have acted on correlated characters rather than on the character in focus (Arnold & Wade 1984b, Grafen 1988). The variation in a character that is relevant for the selection gradient is not simply the variance in that character, but only the part of it that cannot be predicted by variation in other characters. If this is small, then it will be difficult to detect an effect that genuinely exists (Grafen 1988).

Genetic correlation between characters means that characters are genetically coupled due to pleiotropy and/or gene linkage (Arnold & Wade 1984a). Because of pleiotropic mutational variance an individual who has a disadvantageous antler weight can have, for example, an advantageous offspring survival and similarly in reverse: Hartl *et al.* (1991) have shown that a certain allele (*Idh-2*¹²⁵) is associated with more antler points in males, while results of Pemberton *et al.* (1988) suggest that natural selection favours heterozygotes of *Idh-2*^{100/125} by a higher viability of heterozygous female calves. According to Wright (1968) the available evidence indicates that pleiotropy is virtually universal.

Correlations between characters also occur by the "silver spoon" effect (Grafen 1988): a common environmental cause that influences many characters. It can be defined as positive correlations between characters in the adult that are positively associated with fitness, brought about by the common underlying cause of favourable or unfavourable environmental events during development. The syndrome of characters called "quality" may often be determined by the silver spoon effect. If this occurs, one will observe a positive correlation between LRS or fitness and a whole host of characters, most of which will be intercorrelated with each other. The components of LRS would also tend to be intercorrelated. To discover the adaptive significance of antler weight, one has to partial out the effects of all the correlated characters. Because of this it is possible that there are negative genetic correlations but positive phenotypic correlations between characters positively associated with fitness (Lande 1982).

5.2 Comparability of populations living in different habitats

5.2.1 Sampling problems

The intention of the calculation of two methods for the estimation of the mating success of stags on Rhum was to use UK-field for the translation to the situation in Jægersborg (DK-field) and to use UK-DNA as the best possible estimation of the mating success. So in the ideal situation there should be no difference between the estimates of UK-field and UK-DNA. However, several sampling problems, including differences in habitat and management, complicate the comparability of the two populations.

Differences in habitat between Rhum and Jægersborg causes sampling errors in counting the harem sizes, due to difference in visibility of the deer. On Rhum the mean proportion of censuses in which an average hind was seen was 84%, while for stags the same figure was 67%, though some animals were seen in nearly all censuses. Some of the animals not recorded must have been overlooked and a proportion probably was temporarily outside the study area (Clutton-Brock *et al.* 1982). The differences in the number of reproductive stags and hinds between UK-field (39 stags) and UK-DNA (33 stags) is probably also due to the possibility for the animals to leave the study area. In Jægersborg the animals cannot leave the study area, but the chance of overlooking hinds (and stags) is greater than on Rhum because of the presence of cover to hide in. On the other hand, however, the chance of overlooking deer is not particularly great in Jægersborg, because of the dense network of paths.

Differences in habitat quality are also reflected in the quality of food. This probably influences the specific gravity of the antlers (Van Gagern 1953). Since the visual role of antlers in signalling dominance has been demonstrated in several studies (Lincoln 1972), big antlers may be more important than heavy

antlers. If there is a difference in specific gravity of the antlers between Jægersborg and Rhum, antler length is probably a more appropriate measure for mating success than antler weight.

Estimating mating success of stags on Rhum with the use of UK-field gives an underestimation of the variance in mating success. Obviously successful males keep hinds in their harems at exactly the right time of the eleven day period, as opposed to unsuccessful ones ("sneakers"). A hind does not accept a mating before she is in full oestrus, which seldom lasts for more than 24 hours. Estimating mating success with the use of UK-DNA gives no reason to expect any complications in predicting paternity due to sperm competition or precedence, because, in general, females mate only once (Pemberton *et al.* 1992). On Rhum 31 dates of first oestrus from 12 hinds over three years were recorded. A close synchronisation between years and between hinds was found, with the first oestrus falling in the second week of October each year. Although most hinds were successfully fertilized at their first oestrus, some cycled a second and even a third time. The mean cycle time in a sample of hinds kept in an enclosure on Rhum was approximately 18 days (Guinness *et al.* 1971).

Differences in synchronisation of oestrus between habitats are probably caused by differences in habitat quality. The ultimate objective of synchronisation of oestrus is probably to ensure that all calves are born at such a time that the heavy nutritional load of lactation falls on the hind at the time of maximum food availability. Simultaneously the calf can make maximum growth in optimum climatic and grazing conditions before the onset of winter (Fletcher 1974). Because of this it is expected that synchronisation is better in a poor habitat. The more synchronised birth dates in Jægersborg found in this study, suggests that hinds on Rhum are more frequently not served during their first oestrus. This probably explains the more extended rutting season on Rhum, as concluded from the birth dates of the calves (see chapter 3.1.1).

Another complication caused by differences in habitat is its influence on the heritability of a character: the more variable the habitat, the lower the heritability. This causes a smaller effect of selection in Jægersborg than on Rhum (Falconer 1981).

Differences in management between Rhum and Jægersborg causes differences in mean and variance of the antler weights. In Jægersborg the size of the antlers is improved by culling the stags with the smaller antlers (Waage Sørensen: pers.comm.), so the mean antler weight is higher and the variance is lower than it would have been under natural circumstances. This selective hunting also influences the age structure of the population. On Rhum the circumstances are much more natural, because the culling has been completely suspended in connection with the research (Clutton-Brock *et al.* 1982).

5.2.2 Genetic differences or phenotypic plasticity?

The most obvious difference between the two populations is the big difference in antler weight: the antlers in Jægersborg are about five times as heavy as those on Rhum (Figure 5). This can be a consequence of genetic differences between the two populations or of the high degree of phenotypic plasticity in red deer.

According to Bützler (1986) the red deer in Denmark belong to the subspecies *elaphus*, while the red deer in Scotland belong to the subspecies *scoticus*, but it is not known how much genetic differences there are between those subspecies. There are no records of whether red deer occurred naturally on Rhum or

whether they were originally introduced by man (Clutton-Brock *et al.* 1982). The main strain of red deer in Jægersborg is of original Danish breed, but the population has several times been improved through blood renewal. For example, at the end of the seventeenth century a large number of deer was transferred from the island Bornholm. In 1737 twelve white deer were imported from Germany. In this century in 1910, 1912, 1913 and 1939 one stag was imported and in 1934 two hinds were imported into the park. Since 1939 no red deer have been admitted to the park (Waage Sørensen: pers.comm.).

Not only the origin of the populations is important for the genetic differences between the two populations, but also the occurrence of bottlenecks in population size and the resulting degree of inbreeding. According to Fiedler *et al.* (1991) the degree of inbreeding in Žehušice park in Czechoslovakia, where numbers of the stags in the main pen was between approximately five and eighteen (Bartoš: pers.comm.), may at present attain 50-83% in the white variant of the red deer population. A high degree of inbreeding gives harmful recessive genes more chance to become expressed. If this happens, purifying selection will be the result (Uyenoyama & Waller 1991). In Žehušice park the high degree of inbreeding is a possible explanation of the long-term low natality of the population, which does not even attain 50% (Fiedler *et al.* 1991). According to Uyenoyama & Waller (1991) the influence of inbreeding on fertility is still under discussion. Other explanations for the low natality of the white deer population are also given by Fiedler *et al.* (1991), for example the possibility that a certain combination of genes connected with the white colouring may have lethal effects on the developing embryo.

The degree of inbreeding, which reduces the genetic variation, is expected to be low in Jægersborg and on Rhum, although it is not known how many deer were reintroduced in 1845 on Rhum (Clutton-Brock *et al.* 1982). In Jægersborg the population started with at least several tens of red deer, because the original population of deer in the forest and surroundings was gathered before the fence of the park was closed in 1669 (Waage Sørensen: pers.comm.). The degree of inbreeding is expected to be lower in a rich habitat than in a poor one if equal numbers of deer are present in both habitats, because the distribution of the mating success of the stags is more skewed in the poor habitat (see chapter 3 and 5.3.3).

Although not much can be said about genetic differences between the two populations, the degree of phenotypic plasticity in red deer appears to be high. According to Clutton-Brock *et al.* (1982) the differences in body size and relative antler size between Scottish deer and Eastern European forms appears to be a result of phenotypic plasticity rather than of genetic changes: not only were the recent ancestors of Scottish red deer similar in size to contemporary Eastern European forms, but Scottish red deer imported in New-Zealand attain weights and antler sizes comparable to those of Eastern European deer.

5.3 Differences between the populations on Rhum and in Jægersborg

5.3.1 Reproductive performance and antler weight

The big difference in autumn in calf/hind ratio between Rhum and Jægersborg is a consequence of the fact that hinds on Rhum usually conceive for the first time in their third year and a substantial proportion fail to breed following the years when they have reared a calf successfully (Mitchell 1973), while hinds in Jægersborg usually conceive each year and for the first time in their second year of life (Christiansen:

pers.comm.). The difference in calf/hind ratio is not likely to be caused by difference in resorption or fetal loss, because both appear to be uncommon in red deer (Clutton-Brock *et al.* 1982). The long recovery of mature Scottish hinds from producing and rearing a calf (often a full year) suggests strongly that nutrition is the main proximal factor limiting the performance of red deer in the Scottish hill-environment. Under better food conditions, like in Warnham Park, West Sussex, at least 90% of hinds are known to become sexually mature as yearlings. Here only about 17% of the hinds fail to breed each year (Mitchell 1973).

Not only the calf/hind ratio, but also the body and antler weight are probably limited by nutrition. There are many records of red deer of Scottish origin showing a much higher rate of growth in different environments, including parks, so they are not genetically incapable of a higher growth rate (Mitchell 1973). This probably explains the big difference in mean and variance in antler weight between Rhum and Jægersborg (Table 5). The coefficient of variation seems to be a bit greater on Rhum, but this is, just like the variance, in Jægersborg smaller than it would have been under natural circumstances, because of selective hunting (see chapter 5.2.1).

In both populations there is a positive correlation between antler weight and age, although the fraction of variance explained is low (Figure 7). On Rhum the antler weight declines with age after about ten years of age, because $(age)^2$ is significant on Rhum and not in Jægersborg. According to Geist (1971) growth should be completed at a younger age in a rich habitat. Perhaps this difference arises from the fact that there are more stags over ten years old on Rhum: at this age the mean antler weight seems to be decreasing, so $(age)^2$ will more easily be significant.

5.3.2 Female choice and sexual competition between males

The fundamental difference between males and females is the size of the gametes. Large ova bias organisms toward female nurture wherever fertilization takes place inside the female's body. Since females are the chief providers of resources for the zygote in red deer, they might be expected to choose their mates carefully in order to get something in return, while males of polygynous species invest in quantity of offspring instead of quality (Daly & Wilson 1983, Krebs & Davies 1987). According to Bartoš (1982) it is likely that in red deer the female determines the choice of the sexual partner. Observations in Jægersborg suggest that hinds can have an obvious preference for a particular stag (Christiansen: pers.comm.). However, there is little firm evidence that females choose among adult males either in red deer or in other ungulate species (Gibson & Guinness 1980). Mating preferences are usually difficult to demonstrate, particularly where inter-male competition is also involved (Clutton-Brock 1983).

If females do actually choose males with regard to *absolute* differences in phenotypic characters, it is expected that the skewness of the distribution of mating success among males is more extreme in Jægersborg than on Rhum, because the variance in antler weight is much higher in Jægersborg (Table 6). However, the skewness of this distribution is more extreme on Rhum ($cv=1.18$ and 1.72) than in Jægersborg ($cv=0.9$) (see chapter 3), so it is more likely that females choose with regard to relative differences in phenotypic characters. There are no *relative* differences in antler weight between Rhum and Jægersborg, regarding the differences in coefficient of variation in table 5 and 6, but this is probably partly caused by the

selective culling in Jægersborg (see chapter 5.2.1). The relation between variation in antler weight and female choice is further complicated by a negative feedback mechanism: if females choose males with certain phenotypic characters, then phenotypic variation will facilitate the choice of females, causing selection to be more intense. This more intense selection decreases the genetic variation, which in turn decreases the phenotypic variation.

In red deer, where females are responsible for all parental care, the potential reproductive rate of males exceeds that of females. As a result the operational sex ratio (the ratio of sexually receptive females to males) is biased towards males, generating more intense competition between males for mates (Clutton-Brock & Vincent 1991). If equal numbers of the two sexes come into breeding condition at the same time, the degree of (sexual) selection is reduced, because there is less chance for a few males to control access to a very large number of females. In contrast, when females come into breeding condition asynchronously, there is a chance for a small number of males to control many females one after the other. With such high potential pay-offs, sexual competition can be very intense (Krebs & Davies 1987). Because it is likely that the hinds are more synchronously served in Jægersborg than on Rhum (see chapter 3.2), it is expected that competition among males is more intense on Rhum. Also the operational sex ratio suggests a more intense competition on Rhum ($\text{♀}/\text{♂} = 74/39 = 1.9$ for UK-field and $\text{♀}/\text{♂} = 64/33 = 1.9$ for UK-DNA) than in Jægersborg (DK-field: $\text{♀}/\text{♂} = 102/22 = 4.6$). This difference in operational sex ratio is partly due to the fact that the hinds on Rhum fail to breed each year (see chapter 5.3.1). The less intense competition between males in Jægersborg is probably the reason for the relatively few fights observed (Table 4).

However, when oestrus is strongly synchronised, it is also possible that "sneakers" have a lower chance to steal copulations compared to a situation with a badly synchronised oestrus, because the dominant males have the chance to fertilize all hinds in a very short period. In addition, the condition of harem holders would not be affected so much if oestrus is strongly synchronised, because a situation with a badly synchronised oestrus forces harem holders to spend a much longer time guarding hinds. This reduces the possibility to eat for a much longer time. So it is necessary to know more about the speed with which the condition and the alertness of the males is declining during the rut to predict the chance of "sneakers" to fertilize hinds. Perhaps "sneakers" have the best chance to have some successful copulations when oestrus of the hinds is very strongly or very badly synchronised.

It is possible that antler weight is more important on Rhum than in Jægersborg for the mating success of the stags: the stronger selection gradient on Rhum in comparison with Jægersborg (Table 8) could be caused by the more intense competition on Rhum. However, the low fraction of variance explained on Rhum makes firm conclusions about the strength of selection impossible.

5.3.3 Consequences for Lifetime Reproductive Success

Differences in mating success among stags do not have to result in differences in LRS. Cross-sectional data, like in this study, can lead to overestimations of the force of selection (because seasonal differences between individuals cancel out over the entire lifetime) or underestimations (because size-related differences in fitness are exaggerated over lifetimes) (Arnold & Wade 1984b). Also the antler weights on Rhum and in

Jægersborg both show significant differences between years from which data are available (see chapter 4). Clutton-Brock *et al.* (1988) estimated LRS by the product of mating success and offspring survival per stag for each rutting season, summed over the entire reproductive lifespan of the stags. Variance in LRS of stags was split up in the components mating success, reproductive life span and offspring survival. Mating success and the interaction between mating success and reproductive life span explained together 58% of the variance in LRS (Clutton-Brock *et al.* 1988). Because differences in reproductive life span and offspring survival between successful and unsuccessful stags are not pronounced (Gibson & Guinness 1980), it is likely that differences in mating success is the most important component of LRS for stags. Pemberton *et al.* (1992) found that variance in mating success among stags was much greater than predicted by Clutton-Brock *et al.* (1988) (see chapter 3.1.2). The LRS of the most successful stag was estimated at 32 by Clutton-Brock *et al.* (1988), which was corrected to 86 by Pemberton *et al.* (1992). It was one of the conclusions of Clutton-Brock *et al.* (1988) that variance in lifetime breeding success was greater among males than among females, but that the data showed that the difference was not as large as was often supposed and was exaggerated by calculations within breeding seasons. However, Pemberton *et al.* (1992) concluded that the distribution of mating success among males was extremely skewed: 84-88% of all calves were fathered by one of the two top-ranked males. The LRS of males is estimated to vary between 0 and 86 (Pemberton *et al.* 1992) while that of females is estimated to vary between 0 and 13 (Clutton-Brock *et al.* 1988).

The results of this study suggest that there is a difference in the distribution of mating success among males between a population in a rich versus a poor habitat. The coefficient of variation is used to represent the degree to which reproductive success varies among breeders (Grant 1990). Although there is a difference in the coefficient of variation of UK-field and UK-DNA (1.18 resp. 1.72), these are both higher than in Jægersborg (0.9): on Rhum there are more stags excluded from reproduction.

It is not very surprising that the skewness of the distribution of the mating success among stags is more extreme on Rhum than in Jægersborg since there are almost five females per male available in Jægersborg but only two females per male on Rhum: the "bad" males in Jægersborg have a much better chance to father some calves than the "bad" males on Rhum. The greater skewness of this distribution on Rhum could also be a consequence of differences in food distribution: it is likely that food is more patchily distributed over the study area on Rhum than in Jægersborg, probably causing a more patchy distribution of the hinds. If this is true, hinds will be more easily monopolisable on Rhum and the "sneaky strategy" will be more successful in Jægersborg. Also the presence of a lot of cover in Jægersborg makes the formation of a harem more difficult than on Rhum and gives "sneakers" more chance of "stealing" copulations. It is also possible that hinds in a poor habitat are switching between harems more often to avoid competition with other hinds, so the quality of the habitat may have consequences for the stability of the harems.

6 CONCLUSIONS

The results of this pilot study suggest that the distribution of the mating success among stags is more skewed in a poor habitat when compared to a rich one (Figure 2 and 5). This suggests that the extremely skewed distribution of mating success among stags on Rhum described in Pemberton *et al.* (1992), is likely to be valid for a poor habitat, but not for a rich one. If this is true, genetic variation of a population will tend to decrease faster in a poor habitat than in a rich one. However, there are several problems to be solved before firm conclusions can be formulated:

- The comparison in this pilot study is based on only two populations. The study of more populations of different performance are needed to confirm the conclusions described here. One of the problems that has to be solved is whether the more skewed distribution in a poor habitat is a consequence of the quality of the food and/or the distribution of the food.
- The quality of the habitat can have an influence on the type of characters which are important for the mating success of the stags. For example, it is possible that females in habitats of different quality use other criteria to choose a sexual partner. Another example is the possible difference in specific gravity of antlers in habitats of different quality (Van Gagern 1953).
- One of the problems of this pilot study is that it is not known how far these conclusions are determined by genetic differences between the two populations. A possible solution to solve this problem is to compare the relation between antler weight and mating success of the stags within one population by using good years versus bad years. However, within one population the phenotypic variance between years rarely exceeds 10% (Langbein 1990). Because of this it can be difficult to get significant differences in phenotypic characters between years within a population.
- The method used to determine the distribution of the number of hinds served during the rut and the median date of conception in Jægersborg has to be improved by trying to get more data about harem sizes, roaring frequencies, number of chivies, fights and copulations and their relation with the number of hinds served. It is much easier to use populations where the dates of birth are known, but this may be difficult for rich habitats, because those are often covered with woods and bushes where the hinds can hide their calves.
- It is useful to combine studies of selection and inheritance to make predictions about the rate of changes in gene frequencies (Arnold & Wade 1984b). Studies about the heritability of antler weight and other characters are complicated by the fact that the heritability is dependent on the environmental variance and the gene frequencies of the character under study (Falconer 1981).
- It is also useful to know more about genetic correlations between antler weight and other characters, so these correlated characters can be scored. This makes it possible to partial out the effects of correlated characters when calculating the selection gradient (see chapter 5.1).
- Additional progress could be made by measuring Lifetime Reproductive Success, as well as its components, but this requires many years of long-term study in each population.

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SUMMARY

The influence of the quality of the habitat on sexual selection in red deer was investigated by comparing the relationship between antler weight and estimated mating success of stags on Rhum, a poor habitat, and in Jægersborg, a rich habitat. Two methods were used for the estimation of mating success of the stags on Rhum, both based on the frequency distribution of the estimated date of conception, calculated by backdating the gestation length from the birth date of the calves. In one method (UK-field) the estimated date of conception was determined over a period of 20 years and used as an estimation for the distribution of the number of hinds served during the rutting season. This gave an estimation of the mating success of the stags when multiplied with their harem sizes. In the other method (UK-DNA) the estimated date of conception was used to determine the chance with which stags, in whose harem that particular hind was seen about his estimated date, served the mothers of the calves born in the spring of 1990. This method was corrected for the results which were found with DNA fingerprinting analysis. Because for Jægersborg the birth dates of the calves were unknown, UK-field was used for the translation to the situation in Jægersborg (DK-field), while UK-DNA was used as the best possible estimation for the distribution of the mating success among stags on Rhum. The results of this pilot study suggest that the distribution of mating success among stags is more skewed in a poor habitat when compared to a rich one. This suggests that the extremely skewed distribution of the mating success among stags on Rhum found in other studies, is likely to be valid for a poor habitat, but not for a rich one.