DANISH REVIEW OF GAME BIOLOGY Vol. 13 No. 1

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by
JOHNNY LUND JEPPESEN

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Abstract

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The size of 1,585 groups containing 13,273 red deer *(Cervus elaphus)* was recorded during 1980 to 1985 in weekly counts in the Oksbøl State Forest District in west Jutland. A sharp increase in hunting pressure peaked in 1984/85 when 60% of the population was killed. Large groups were mainly observed in open areas (mean group size: 9.7) and small groups within forests (mean: 3.7). During Feb.-May large groups predominated, especially hinds, yearlings and calves feeding in the open at night; during July-Sept. small groups were more common, reflecting the fact that hinds with new-born calves were remaining within the forests; and during Nov.-Dec. group size was even smaller, because most deer did not leave the cover of the forests during the peak of the hunting season. The shift from small to large groups occurred during Jan.-Feb. in 1981-82 and in May 1985, thus reflecting the increase in hunting pressure that had taken place. Stags comprised 15% of the observed deer, and were estimated to comprise 20-25% of the population. A summer mortality of new-born calves of 21% was calculated from an observed 55 calves per 100 hinds and an expected birthrate of 70 calves per 100 hinds.

Author's address:
Game Biology Station
Kalø
DK-8410 Rønde
Denmark

Contents

Introduction

Denmark's largest population of wild red deer *(Cervus elaphus)* inhabits the Oksbøl State Forest District in southwest Jutland. Estimation of the population size of red deer in a forested area is difficult. In 1977, therefore, the district instituted, in collaboration with the Game Biology Station, a red deer marking and observation programme, as a basis for estimating the population size (Petersen/Lincoln index). Using this method, annual population estimates are made to enable determination of the number to be killed in the hunting season. Knowledge of the extent of emigration of red deer from the area was also desired, as the general impression was that the number of deer was increasing.

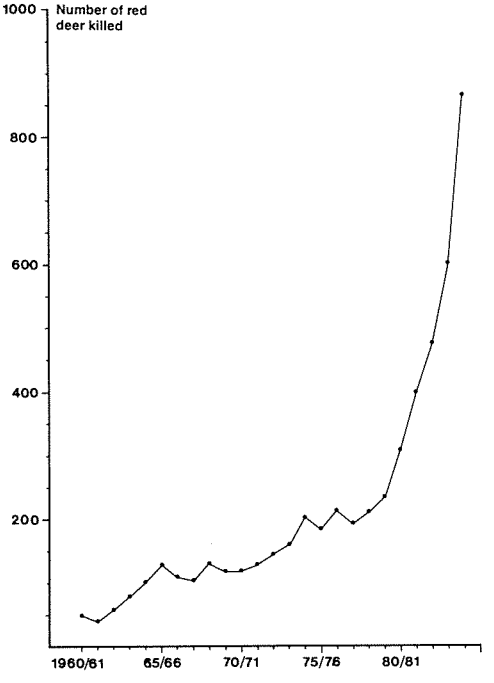

Fig. 1. Number of red deer killed per hunting season in the Oksbøl area during 1960/61 through 1984/85.

From 1981 some of the red deer have been equipped with radio transmitters. They form the basis of research on movements, home range and activity, as well as reactions to human disturbances (see JEPPESEN 1987a,b).

In a population with enough food and cover to fulfil the individual's optimum needs, density is below carrying capacity and birth rate is often high and mortality low (see LACK 1954). Conversely, when the population exceeds the carrying capacity, condition of individual animals becomes poor, birth rate falls and mortality rises.

In areas with high hunting pressure, where the disturbing impact does not displace the surviving deer, compensation for removal of individuals from the population occurs through increased birth rate and lowered mortality. Thus, the rate of increase of the survivors will tend toward the maximum possible, as has been experienced in red deer in New Zealand during control campaigns (BATCHELER 1968).

This paper deals with seasonal variation in group size, and sex and age composition, as revealed from observations of red deer in the Oksbøl area. An assessment is also made of the behavioural adaptations of the deer to compensate for the pronounced increase in hunting pressure during the period of study (Fig. 1, Table 1). Annual estimates of the population size indicate that the hunting cull of red deer in the area rose from about 25% of the population in 1981/82 to 60% in 1984/85. The Danish hunting season for red deer is Sept.-Feb. (stags and calves) and Oct.-Feb. (hinds). Since 1983 no hunting for red deer is permitted in February. In the Oksbøl area only stalking of stags is possible in September and most of October (rutting season), while drive hunts are common after October 20th when the rut is over for most of the deer. In some of the plantations stalking, however, is the predominant way of hunting throughout the season.

Table 1. Estimated population size of red deer in May; expected population size in September, before the hunting season; and the annual cull of red deer during the period of study.

	May[1]	Sept.[2]	Cull[3]	Cull as percentage of Sept.-population	Number of calves/100 hinds in the cull
1981	1,100[4]	1,450	430	29.7	115
1982	1,550	2,100	487	23.2	70
1983	1,350	1,850	620	33.5	88
1984	1,100	1,500	891	59.4	80
1985	800	1,100	(325)	(29.5)	

Notes: 1) Petersen/Lincoln index
2) Summer mortality of new-born calves included
3) Red deer killed in traffic included
4) Population size underestimated

Acknowledgements

For their collaboration Oksbøl State Forest District and the Headquarters of the Oksbøl Military Camp are acknowledged. I am especially appreciative of the help of forester Jørgen Hauskov and gamekeeper Jørgen Andersen. Untiringly and with expertise throughout the years, they systematically made observations and counts of red deer. Also the help from Tommy Asferg, Anders Feilberg, Helmuth Strandgaard, and David R. Klein, who commented critically on the manuscript, is much appreciated. David R. Klein improved the English considerably. Else-Marie Nielsen is thanked for help in word processing and proofreading of the manuscript.

Area and Methods

Study area

The study area (Fig. 2) is 175 km² and consists of 65 km² of dune plantations and 110 km² of open land. The open areas include 70 km² of moorland and grass plains that are utilized as a military field practice area, while the rest is private owned farm land, with the diked-in Filsø to the north and humid meadows to the east close to Ho Bay. The area is mostly level and between 0 and 20 m above sea level. Inland sand dunes reach 35 m above sea level. The sandy soils

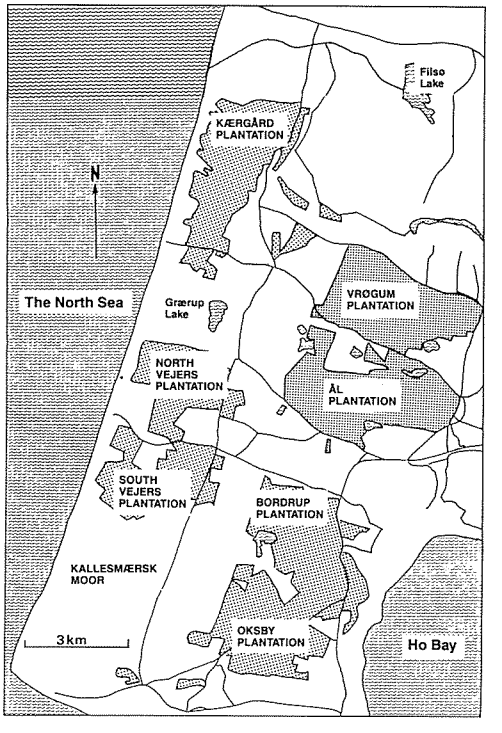

Fig. 2. Map of the Oksbøl study area.

are infertile, except for the fertilized farm lands. The dune plantations consist of conifers, mainly mountain pine *(Pinus mugo),* but also sitka spruce *(Picea sitchensis)* and other conifers, plus some bare areas (see STRANDGAARD 1967).

Traffic by civilians on the military areas occurs largely in automobiles on the public roads that cut through the areas, while traffic on foot (but not in autos) is allowed in the plantations. Near the North Sea lie several summer cottage areas that attract tourists on weekends and during holiday seasons.

Counting procedure

Observations of red deer were made once a week over a period of 41 months (the periods Sept. 1980 - Nov. 1982, Feb.-Aug. 1983, Feb.-May 1984 and Mar.-May 1985) by the same two observers. The observations were made by driving through the area along a specific route, so that no deer were observed more than once per round. The route was not necessarily the same from time to time and traversed both forest and open land. One round could be up to 85 km. During observations of red deer, group size, sex, age (adult/calf), locality, and number of marked deer, were noted. As red deer in the area are mainly active when the sun is close to the horizon and at night (JEPPESEN 1987a), the observations were made in early mornings and late in the evenings when visibility was possible.

In order to record differences in group size in relation to habitat types, the localities where deer were observed, are divided into 1) open land (heather- and grass plains, plus open fields within the forests), and 2) forest.

Treatment of data

The distribution of group sizes is skewed, as many more small groups than large ones were observed. Therefore, the distribution is better characterized by the median than by the mean (CLUTTON-BROCK et al. 1982, WIRTZ & LÖRSCHER 1983). Both are used. As JARMAN (1974) emphasized for antelopes, the numbers of deer observed in each group size better express any preference for certain group sizes than the frequency of these group sizes. The distributions of group sizes in different periods are compared by median tests (5% level of significance, (DOWNIE & HEATH 1970)).

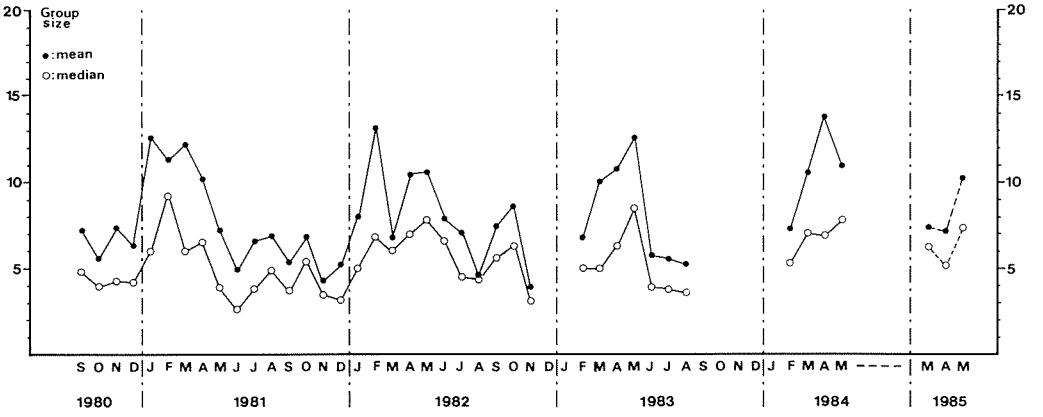

Fig. 3. Monthly mean and median size of red deer groups during the period of study.

A group of red deer enjoying the morning sun before entering the forest.

Results

Group size

During the regular systematic counts, 1,585 groups containing 13,273 red deer were observed. The mean and median of the distributions of group size during each month are shown in Fig. 3.

By testing the frequency of group sizes in each month against other months, and also against the same months in other years (median tests), group size is seen to vary throughout the year. Distinct differences in group sizes can be associated with the three periods: 1) Feb.-May, 2) July-Sept., and 3) Nov.-Dec. (1980-84), as shown in Fig. 4. The period Feb.-May does not include May 1981 which differs significantly from the other monthly values in this period. The group distribution in Feb.-May differs significantly from the distribution in July-Sept. and Nov.-Dec. ($p < 0.001$ in both cases), while the distribution in July-Sept. does not differ significantly from the distribution in Nov.-Dec. ($p < 0.10$). Fig. 4 also shows the number of deer observed in each group size.

The distribution of group sizes in the period Feb.-May is characterized by a majority of large groups (Fig. 4). The largest group observed in these counts contained 95 deer and 50% of the deer observed were seen in groups of 18 or more. Single deer totalled 4.2% of 622 groups, but they only made up 0.4% of all deer observed. In Mar.-May 1985 the mean is 8.4 deer, the median 6.2, and 50% of the deer were observed in groups of 11 or more.

The distribution of group sizes in July-Sept. is characterized by many small groups. The largest group contained 37 deer, and 50% of the deer were observed in groups of 10 or more. Single deer totalled

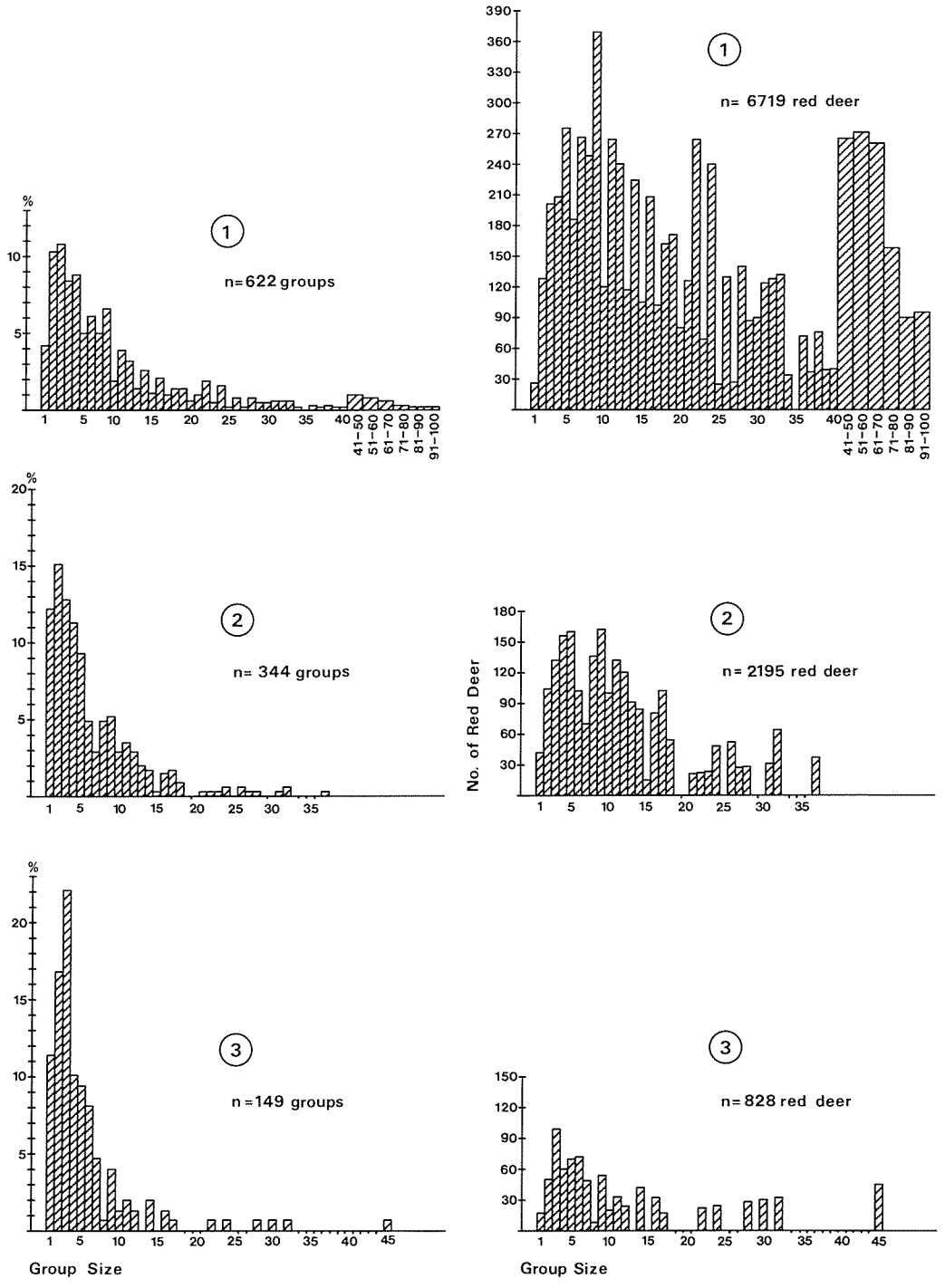

Fig. 4. Group size frequency (left) and number of red deer encountered in different group sizes (right) for the periods: (1) February-May, (2) July-September, and (3) November-December (1980-84).

12.2% of 344 groups, and 1.9% of all deer observed.

In the group distribution for the period Nov.-Dec. the share of small groups is even larger than in the July-Sept. period (see also Table 2). The largest group contained 45 deer, and 50% of the deer were observed in groups of 7 or more. Single deer totalled 11.4% of 149 groups, and 2.1% of all deer observed.

The difference in group size distributions between the three periods also appears clearly in Table 2, which shows the percentage of groups of 1-3 deer. The hinds' core-units consist of 1-3 deer: mother-yearling-calf.

The months of January, June and October constitute intermediate stages between the three main periods. The median for the group size frequency in June 1981 is 2.6; in June 1982: 6.6, and in June 1983: 3.9. The three distributions differ significantly. During the rutting season in October the groups are on the average a bit larger than during the preceding and succeeding periods, the median being 5.2 and the mean 6.8. The difference is significant between October and Nov.-Dec. ($p < 0.02$), but not significant between October and July-Sep. ($p < 0.30$). The median for January is 5.3 and the mean 9.9. Fig. 5 shows this seasonal variation in the median and mean of group size distribution calculated for the years 1980-84. It is, however, over-simplified to regard only January as an intermediate month between the periods of small groups (Nov.-Dec.) and large groups (Feb.-May).

Table 2. Variation throughout the year in percentage of observed red deer in groups containing 1-3 deer during the period of study.

	Feb.-May	Jul.-Sept.	Nov.-Dec.
% of groups	23.6	40.1	50.3
% of deer	5.3	12.7	20.0

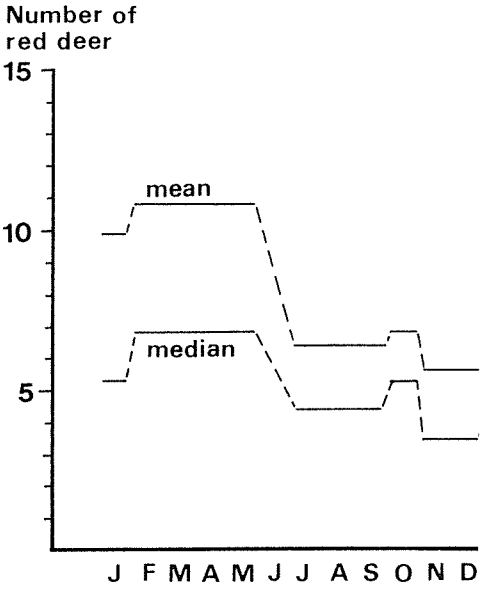

Fig. 5. Seasonal variation in mean and median size of red deer groups, calculated for the years 1980-84 (see text).

As is seen in Fig. 3, the change between the two periods shifted from Dec.-Jan. in 1980-81, to Jan.-Feb. in 1982, and Feb.-Apr. in 1983 and 1984. In 1985, large groups were not seen until May, and they were not as large as in previous years (the same applies to 1986).

Forest vs. open land

Of the 1,585 observed red deer groups, 348 were within the forests (22%), while the remaining 1,237 (78%) were out in open areas. Group sizes in the forests were small, the mean being 3.7 and the median 2.8 while mean group size in the open land was 9.7. The proportion of forest-observations during the counts remained rather constant throughout the year, and the variation in group size in the forest was small. The seasonal variation in group size mentioned

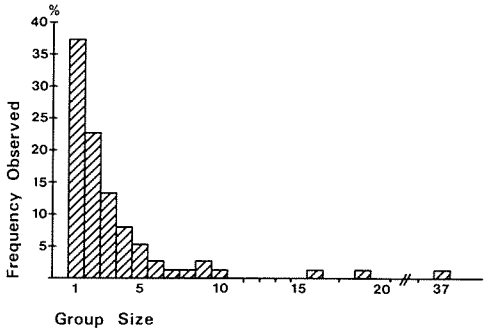

Fig. 6. Group size frequency of red deer stags encountered in pure stag groups during the period of study.

above therefore mainly reflects the variation in red deer groups observed on open land.

Sex and age distribution

Stags represented 15.0% of the red deer counted during 1980-84 (1,357 out of 9,040 sex determined deer). Only 19.4% of the observed stags were in pure stag groups (75 groups or 6.1% of 1,226 groups with known sex and age composition). Most groups thus were of mixed sex and age, mainly containing hinds, yearlings and calves.

The pure stag groups were small compared to mixed groups. A few larger stag groups were, however, observed, the largest included 37 stags and was seen in July (Fig. 6). The mean of pure stag group sizes is 3.5, the median 2.1. Single stags totalled 37.3% of the stag groups observed, and 10.6% of all stags observed.

The percent of stags observed each month was quite variable, from 4.2% to 30.2% of all observed deer (Fig. 7). Each year there was a characteristic decrease in the percent of stags observed in the Jan./Feb. period (>20%) in comparison to the May/June period (<8%). Subsequently there was a sudden rise in June/July to more than 20%, after which stags comprised 15-22% of the red deer observed for the rest of the year.

The ratio of stags to hinds varied in a similar way, with 10% stags/90% hinds in May/June and 20-32% stags at other times of the year (however up to 39.3% stags/60.7% hinds in June 1982 and 35.8%/64.2% in August 1983). This is due to the relatively constant number of calves/100 hinds in the observations (see Table 3).

The size of the antlers was noted (number of points) except for the spring and

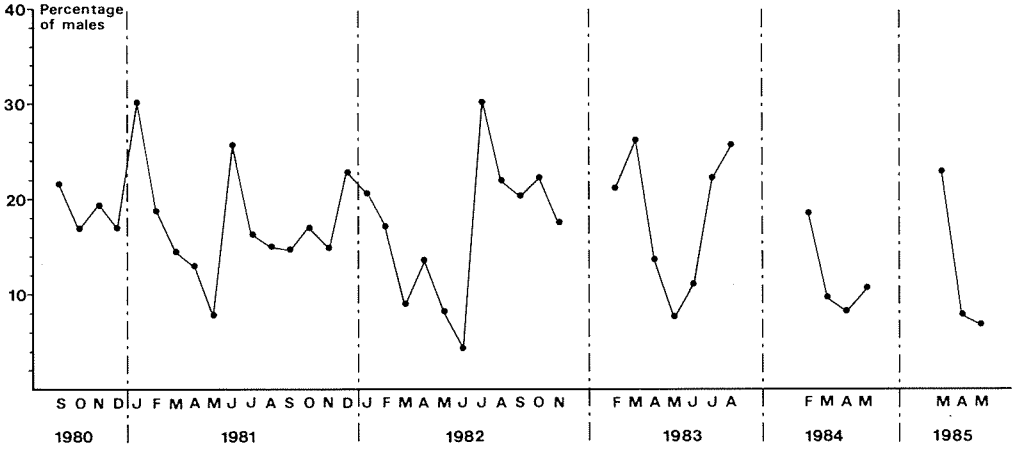

Fig. 7. Monthly percentage of stags in the observations of red deer during the period of study.

Table 3. Monthly number of calves per 100 hinds during the period of study.

	Jan	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1980									46	61	45	58
1981	53	59	59	51	51	3	50	47	55	53	58	54
1982	60						49	56	55	57	58	
1983						10	34	62				

summer months, when the stags' antlers are in velvet. In the months from November until March/April, when the stags in the area cast their antlers, plus August and September, when the new antlers are developed, the percentage of yearling stags (2 points: 1-2 year old stags (JENSEN 1967)) was 52.3, while the rest were older stags with from 6 to 14 points. Yearling stags were almost always observed in mixed groups (hinds, yearlings, calves). Occasionally 6-pointers (2½ - 3½ year old stags (JENSEN 1967)) and rarely an 8-pointer were observed in mixed groups. The pure stag groups mainly consisted of older stags (6-12 points).

During the rutting season which usually peaks in the second week of October, this pattern is broken. Mixed groups observed in October mainly consisted of an older stag (8-12 points) with a harem of hinds, plus calves and occasionally a yearling stag.

The size of the largest harem observed was of 22 hinds. Most harems are reformed each evening, when the deer leave the forest (JEPPESEN 1987a). The percentage of yearling stags among the stags observed in October was only 23.4, the rest were older stags.

Calves per 100 hinds

Calves are easily distinguished from the hinds from the time of birth until the following February, after which their relatively large size makes it more difficult to separate them from adult hinds. Nevertheless, although requiring careful observation, the number of calves/100 hinds was recorded in the period Sept. 1980-Jan. 1982. During the remaining winter and spring observations hinds and calves were noted together, and only during the summer and autumn months in 1982 and 1983 were the number of calves/100 hinds recorded (Table 3).

Except for the period June-August, the proportion of calves in the observations was fairly constant between 50 and 60 calves/100 hinds. In September, in both 1981 and 1982 (the first month of the hunting season) the number of calves was 55/100 hinds, and this level was maintained for the rest of the hunting season.

The relatively large number of calves per 100 hinds in the bag for the 1981/82 hunting season (Table 1) is not reflected in the ratio of calves during the 1981 autumn and winter observations. This is due to the fact, that none of the bagged calves were shot in September, only 25% were shot in October-November and 57% were shot in January-February.

The sex ratio among new-born calves in the study area was found to be equal (P.L. SØRENSEN, pers. comm.). This same sex ratio also occurred among calves in the hunter bag from the area, and therefore an equal sex ratio was assumed for the calves in May. Based on the number of calves per 100 hinds in 1981 and 1982, values of 55 calves/100 hinds for September, and 50 calves/100 hinds for May, just before the

new breeding season, were assumed and used in the folowing calculations which conclude that the summer mortality among new-born calves is 21%. I is assumed that there is no emigration or mortality among hinds in the period May-September.

Year 1, May: (X adults + (100-X) yearlings) + (25 ♂ + 25 ♀) calves (1 year old)
Year 2, May: (100 adults + 25 yearlings) + (31.3 ♂ + 31.3 ♀) calves
Year 3, May: (125 adults + 31.3 yearlings) + (39.1 ♂ + 39.1 ♀) calves

As it may be assumed that the birth rate in the area is of the same size as it was in the 1950's, that is 0.9 calves per adult hind (more than 2 years old) and 0.75 calves per yearling hind (JENSEN 1967), we get:

Year 2, June, births:	
from 100 adult hinds:	90.0 calves
from 25 yearling hinds:	18.8 calves
from 125 hinds:	108.8 calves

108.8 calves correspond to 87.0 calves per 100 hinds (adults + yearlings), which corresponds to: 69.6 calves per 100 hinds (one year old and older, including the calves from May) (the yearling hinds make up 20% of the hinds (= 100-X, year 1)).

So, it is to be expected, that 69.6 calves per 100 hinds (adults + yearlings + new yearlings) would appear in the observations in September.
In September, year 2, the observations show 55 calves/100 hinds (one year old and older).

This corresponds with 68.8 calves per 125 hinds (adults + yearlings), and 86.0 calves per (125 + 31.3) hinds (one year old and older).

Thus, 86.0 × 100/108.8 = 79.0% of the new calves survive until the end of September – corresponding to a summer mortality among calves of 21%.

Discussion

In the Oksbøl area, with its large plantations and open areas (Fig. 2), red deer are mainly active at dawn and dusk and at night (JEPPESEN 1987a). A large portion of the deer forage in open areas at night, while spending the daylight hours in cover in the dense coniferous plantations.

In red deer group size is smaller in forest than in open areas (BURCKHARDT 1958, AHLÉN 1965, STAINES 1974, MITCHELL et al. 1977, CLUTTON-BROCK et al. 1982), and the observations in Oksbøl show similar behaviour. Groups observed during evening counts are often heading towards the forest edge. Gradually various small groups join together into a larger group, that moves into the open to forage at night (Fig. 8). Movements of red deer show relatively stable patterns (MITCHELL et al. 1977), and in the Oksbøl area larger groups consistently enter open areas from the same spots at the forest edge each evening. This has also been recorded for radio-marked hinds in the area (JEPPESEN 1987a).

In a population of red deer there are

small units, usually consisting of a hind with its calf and yearling, that remain together, while most larger groups vary in size and composition (BURCKHARDT 1958, AHLÉN 1965, SCHLOETH 1966, CLUTTON-BROCK 1974, STAINES 1974). In an undisturbed population of red deer on the Scottish island Rhum, the hinds live in matriliniar groups that consist of female relatives (CLUTTON-BROCK et al. 1982). This was described earlier by DARLING (1937) in his classic studies of red deer in the Scottish highlands, and seems to be in evidence in Oksbøl as well, as revealed by marked deer. Groups of stags are often more loosely structured (SCHLOETH 1961, DARLING 1937).

Seasonal variation in group size among red deer in Oksbøl (Figs. 3, 4, 5) is in part influenced by hunting. After the rut in October drive hunts are permitted. In Nov.-Dec. the observed groups are small; this is the result of more secretive habits as most of the deer do not leave the forest cover in the hunting season. The number of deer observed at this time per round is the smallest. Groups observed in the open leave the forests in the usual way (as illustrated in Fig. 8), but they are smaller as much fewer deer leave the forests.

This pattern of behaviour corresponds with what BATCHELER (1968) found in New Zealand, when red deer were subjected to an intensive hunting campaign. The deer became more shy and wary, stayed close to cover and fed in the open mainly at night. DOUGLAS (1971) found that red deer recommenced diurnal feeding on open grass land two years after the hunting ceased. At this time the mean group size of hinds was significantly larger than during the hunting campaign (DOUGLAS 1971).

Distribution of group sizes in Feb.-May (Fig. 4) with many large groups is a reflection of large numbers of deer exploiting forage in open areas at this time. The number of deer per observation-round in this period is also larger than in the rest of the year. In 1981 and 1982 when hunting pressure was lighter than in the following years (Table 1), deer had already begun to use the open areas in large numbers before the end of the hunting season. Whereas, with the rise in hunting pressure in the following years, many deer did not start using the open areas until March/April (Fig. 3). After the unusually large bag in 1984/85 (Fig. 1), it was not until May 1985 that large groups could be observed (Fig. 3).

Studies on the quality of food eaten by red deer in winter (STAINES & CRISP 1978, STAINES et al. 1982, CLUTTON-BROCK et al. 1982, OKARMA et al. 1985) show that hinds have a greater demand for high-quality food than stags. Hinds, therefore, often use areas with food of higher quality than is the case in areas where stags feed (BURCKHARDT 1958, AHLÉN 1965, WATSON & STAINES 1978, STAINES et al. 1982, CLUTTON-BROCK et al. 1982). Stags, possibly because of their larger rumen ca-

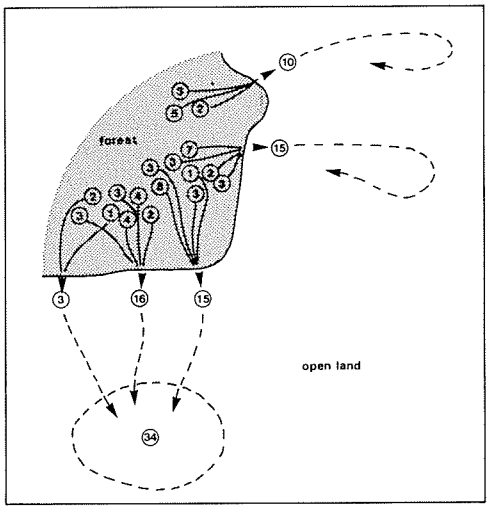

Fig. 8. Model of the movements of red deer in the Oksbøl area throughout a 24-hour period. During the day the deer stay in smaller groups within the forests. During the night they gather in larger groups on their feeding grounds in the open.

pacity, can exist on a diet of poorer food quality (STAINES et al. 1982). In winter and spring hinds need high-quality food, because many are lactating and/or pregnant, and therefore have higher energy and other nutrient demands (WATSON & STAINES 1978). During late pregnancy and in early lactation ARMAN et al. (1974) found that feed intake of hinds rose to 2.5 times maintenance requirements of non-breeding animals. This is reflected in a pronounced increase in activity of hinds at the end of April (GEORGII 1981). Further, assessment of reproductive success of hinds must include consideration of the size and vigor attained by calves during their first year of life (CLUTTON-BROCK et al. 1982).

The food of red deer in the Oksbøl area is dominated by heather *(Calluna vulgaris)* and wavy hair grass *(Deschampsia flexuosa)* (JENSEN 1968). These plants are predominant on open moorland and grass plains, and to a smaller extent in the plantations. It seems as if red deer in autumn and the first part of winter are able to maintain themselves by staying within the forests, and this behaviour results mainly from the impact of the hunting pressure. During the second half of winter it appears necessary for the hinds to feed increasingly in the open areas, because of increasing demands for high-quality food.

During winter and spring the percentage of stags in the observations falls rapidly (Fig. 7), so that by spring it is predominantly only hinds, calves and yearlings that utilize the open areas. Stags, with their lower demands for food-quality, are able to remain more dispersed and more secretive within the forests' borders (see also AHLÉN 1965 and JEPPESEN 1987a). The reduced proportion of stags in the spring observations may also result from the yearling stags leaving their mother during their second year of life.

By the end of May and in June the majority of the calves in the Oksbøl area have been born. Hinds occur separately or together with their calf of the year, while yearlings occur in smaller groups. That group size frequencies in June in three successive years differ significantly, results from June (and partly May, - see May 1981) being a month of change, with many hinds still being pregnant and living in larger groups. Group sizes of red deer in Sweden and Poland are smaller at this time than during the rest of the year (LAVSUND 1976, DZIECIOLOWSKI 1979). The peak of the rut may vary a fortnight from year to year (J. HAUSKOV and J. ANDERSEN, pers. comm.), therefore the date of birth varies in the same manner. From the time of birth hinds become more secretive, so that many do not come out in the open (see also JEPPESEN 1987a). Hinds have high energy demands during lactation (ARMAN et al. 1974), and spend much more time feeding than hinds without calves (CLUTTON-BROCK et al. 1982), but at this time of year there is sufficient food in the forests. That the median of the group size frequency in May 1981 is significantly smaller than in May in the remaining years (Fig. 3) may be due to an earlier breeding season, whereas the relatively high median in June 1982 may be due to a later breeding season.

The abrupt increase in the percentage of stags in observations in June 1981, July 1982 and June/July 1983 (Fig. 7) thus reflects the shift of hinds from an open to a secretive way of life. At the same time more stags with their antlers in velvet begin to appear in open areas outside the forests.

In the period of June until September many hinds in the Oksbøl area maintain their secretive habits and this is reflected in the small group sizes (Figs. 2, 3, 4 and Table 2). Whereas, the percentage of stags in observations in this period is considerably larger than in the spring months (Fig. 7). SCHLOETH (1961) and GOSSOW (1973) mention that group size for stags is largest in summer. In this period, when antlers are in

Red deer groups vary in size and composition, but mother, calf and yearling remain together and form a small, stable unit.

velvet, there is very little aggression among stags (LINCOLN et al. 1970). High foraging efficiency results in accumulation of a thick layer of fat (MITCHELL et al. 1976), in preparation for the rut, during which they spend very little time feeding (CLUTTON-BROCK et al. 1982). In Oksbøl the largest stag-groups are observed in June-August (up to 30 stags have been observed in addition to those seen in the regular counts).

Thus, stags utilize open areas to a larger extent during summer months, when their energy demands are highest, and when six months have elapsed since the last hunting season. In contrast the strategy of hinds at this time of year is to protect the calves by becoming secretive.

Stags older than two years are observable to some extent in Oksbøl only during summer and the rut, therefore it is difficult to estimate the percentage of stags in the population. About half of the stags in the observations were yearlings, consequently the percentage of older stags was only 7-8. This corresponds to AHLÉN's experience in Sweden, where observations showed 9.2% older stags, and not the expected 20% (AHLÉN 1965). The 30% representation of stags in observations of red deer in Oksbøl in June/July is probably too high to be used as a measure of the actual proportion of stags in the population. Considering their secretive habits, the 15% representation of stags for the entire year may give rise to a conservative estimate of 20-25% stags in the population. Also the proportion of yearling stags to older stags (52.3% for the entire year; 23.4% during the rut) confirms this estimate. The percentage of stags in observations during the rut was the same as in all the autumn months. Thus, during the rut older stags are much more visible than in the months preceding and following it (1.5 times the normal share in the observations; (15% stags in observations all year)$\times$1.5 = 22.5% stags in the population). The sex and age distribution in the red deer population in Oksbøl, thus, is esti-

mated to be: 22.5% stags, 50% hinds, and 27.5% calves (on the basis of 55 calves/100 hinds).

Reproduction

JENSEN (1967) reported that among red deer hinds 93% of those older than 2½ years carried a foetus in contrast to 71% of the yearling hinds. This was based on hunter-killed red deer in Jan.-Feb. from different Danish forest districts, 2/3 of which came from the Oksbøl-area. This corresponds to levels of reproduction found in red deer populations in Norway (WEGGE 1975), Sweden (LAVSUND 1976), Holland (CROMBRUGGHE 1964) and Yugoslavia (VALENTINCIC 1960).

With the proportion of yearling hinds in the population being 20%, this corresponds to a birth rate of 70 calves/100 hinds one year old or older. This figure is substantially higher than found in highland red deer in Scotland (MITCHELL et al. 1977, CLUTTON-BROCK et al. 1982), but lies within the limits mentioned by RATCLIFFE (1984) for Scottish forest-living red deer populations, where 30-90% of yearling hinds and 60-100% of older hinds become pregnant each year.

A birth rate of 70 calves/100 hinds is close to the biological maximum for the species (RATCLIFFE 1984), if the possibility of twins is excluded. In Oksbøl in the 1980's, there were two corpora lutea in the ovaries in 40% of the hinds killed by hunters (P.L. SØRENSEN, unpubl.), but not more than one foetus per pregnant hind. There have been few observations in the Oksbøl area of hinds with two calves and adoption cannot be ruled out in these cases. Twinnings are not likely important in the population dynamics of these red deer.

On the basis of 55 calves/100 hinds in the Oksbøl area by the end of September, the estimated calf mortality in summer is 21%. This is close to the 20% CLUTTON-BROCK et al. (1982) found at Rhum. Nearly 80% of the calves that died during their first summer at Rhum, did so within the first week after birth (CLUTTON-BROCK et al. 1982). Winter mortality of calves at Rhum was 11%, but in Oksbøl it may be assumed that calf mortality after the hunting season is small.

Dansk resumé

Sæsonmæssig variation i rudelstørrelse, køns- og alderssammensætning i en dansk krondyrbestand (Cervus elaphus) *under stort jagttryk*

Den store bestand af krondyr i Oksbøl Statsskovdistrikt blev i første halvdel af 1980'erne af forskellige grunde udsat for et stigende jagttryk, som toppede i sæsonen 1984/85, hvor ca. 60% af bestanden blev skudt (Fig. 1, Tabel 1). Under ugentlige observationsrunder i perioder fra september 1980 til maj 1985 blev der talt 1.585 rudler med 13.273 krondyr. Middel- og medianværdi af fordelingen af rudelstørrelser pr. måned ses i Fig. 3, mens fordelingen af rudelstørrelser for perioderne: 1) feb.-maj, 2) juli-sept. og 3) nov.-dec. (1980-84) ses i Fig. 4.

I Fig. 8 er illustreret krondyrenes døgnrytme, idet de opholder sig i småruddler i skovene om dagen (gennemsnitlig 3,7 dyr pr. rudel) og vandrer ud på de åbne arealer i større rudler for at fouragere om natten (gennemsnitlig 9,7 dyr pr. rudel).

Rudelstørrelsesfordelingen i nov.-dec. er karakteriseret ved mange små rudler, og dette skal ses som et resultat af dyrenes mere skjulte levevis, da mange dyr ikke forlader skovens dækning, mens jagtsæsonen er på sit højeste.

Fordelingen af rudler i feb.-maj er karakteri-

seret ved mange store rudler, idet mange dyr udnytter de åbne arealer til fødesøgning. I 1981 og 1982, da jagttrykket var mindre end de følgende år, begyndte dyrene allerede at udnytte de åbne arealer i stort tal før jagtsæsonen sluttede (jan.-feb.), mens mange, med stigningen i jagttrykket de følgende år, ikke begyndte at bruge de åbne arealer før i marts/april. Efter det usædvanligt store jagttryk i 1984/85 sås ikke store rudler på de åbne arealer før i maj (Fig. 3). Det er især hinder med kalve og smaldyr (af begge køn), der om foråret ses på de åbne arealer, mens hjortene holder sig skjult i skovene. Dette skal ses i sammenhæng med hindernes store energikrav om foråret.

Rudelstørrelsesfordelingen i juli-sept. er karakteriseret ved mange små rudler; dog ikke så små som i nov.-dec. Dette afspejler, at når kalvene fødes i juni, skifter hinderne fra en åben til en mere skjult levevis. Derfor ses også en pludselig stigning i procentdelen af hjorte i observationerne i juni/juli (Fig. 7). Hjortene udnytter endvidere i større udstrækning de åbne arealer i sommermånederne, hvor deres energikrav er størst (gevirdannelse, dannelse af fedtlag før brunst).

Ca. halvdelen af de observerede hjorte er spidshjorte (1-2 års dyr), der ses sammen med hinder og kalve i blandede rudler. I oktober (brunsttid) ses 1,5 gange så stor en andel ældre hjorte som sædvanlig. Disse lever ellers skjult i skovene. Hjorte udgør 15% af samtlige observerede dyr, og andelen af hjorte i bestanden vurderes til 20-25%.

Der er observeret 55 kalve pr. 100 hinder (Tabel 3), og med en forventet fødselsrate på 70 kalve pr. 100 hinder, er der udregnet en sommerdødelighed blandt nyfødte kalve på 21%.

Резюме на русском языке:

Сезонные изменения численности стай и состава по полу и возрасту одной датской популяции благородных оленей (Cervus elaphus) при интенсивной охоте на них

Многочисленная популяция благородных оленей в Государственном Лесном Районе Оксбёль в первой половине 1980-ых годов по разным причинам подвергалась интенсивной охоте, достигшей высшей степени в сезоне 1984/1985 г., в котором было убито около 60% этой популяции (Фиг. 1, Табл. 1). При еженедельных наблюдениях в периодах с сентября 1980 г. по май 1985 г. было подсчитано 1.585 стай с 13.273 благородными оленями. Средние и медианные величины распределения численности стай по месяцам указаны в Фиг. 3, а распределения численности стай в периоды: 1) февраль-май, 2) июль-сентябрь и 3) ноябрь-декабрь (1980-1984 г.) указаны в Фиг. 4.

Фиг. 8 иллюстрирует суточный ритм благородных оленей. Днем они небольшими стайками (средним числом по 3,7 особей за стайку) находятся в лесах, а ночью более многочисленными стаями выходят на открытые пространства для фуражирования (средним числом 9,7 особей за стаю).

Распределение численности стай в ноябре-декабре характеризуется тем, что наблюдается много небольших стаек, что следует считать результатом более скрытого образа жизни оленей, так как многие из них в разгар охотничьего сезона не покидают скрывающего их леса.

Распределение по стаям с февраля по май характерно множеством больших стай, так как многие олени используют открытые пространства для розыска пищи. В 1981 и 1982 годах, когда охота велась менее интенсивно, чем в последующие годы, олени большими стаями уже начинали пользоваться открытыми пространствами до окончания сезона охоты (в январе-феврале), а при возрастающей интенсивности охоты в последующие годы многие из них не выходили на открытые пространства до марта-апреля. После необычайно интенсивной охоты в 1984-1985 годах, большие стаи не наблюдались на открытых пространствах до мая (Фиг. 8). Весной на открытых пространствах преимущественно наблюдаются лани с оленятами (обоих полов), между тем как самцы скрываются в лесах. Это следует рассматривать в связи с повышенной весной потребностью ланей в энергии.

Распределение по численности стай с июля по сентябрь характерно большим числом небольших стаек, но не таких малочисленных,

как в ноябре-декабре. В этом отражается то, что лани, когда они в июне родили оленят, переходят с открытого на более скрытый образ жизни. Поэтому также наблюдается внезапное повышение процента наблюдаемых в июне-июле самцов (Фиг. 7). Кроме того, самцы в летние месяцы в более высокой степени используют открытые пространства, так как в это время их потребность в энергии особенно высока (образование рогов, образование слоя жира перед течкой).

Около половины наблюдаемых оленей-самцов составляется из молодых особей I-2 летнего возраста. Они наблюдаются в смешанных стаях, вместе с ланями и оленятами. В октябре (во время течки) наблюдается в полтора раза больше самцов старшего возраста, чем обычно. В другие времена года они живут скрыто, в лесах. Самцы составляют около I5% всех наблюдаемых оленей, и доля самцов в популяции по оценке составляет 20-25%.

Наблюдалось 55 оленят за I00 ланей (Табл. 3), и предполагая, что родятся 70 оленят за I00 ланей, вычислена летняя смертность в 2I% новорожденных оленят.

References

AHLÉN, I. 1965. Studies on the red deer, *Cervus elaphus* L., in Scandinavia. III. Ecological Investigations. Viltrevy 3:177-376.

ARMAN, P., R.N.B. KAY, E.D. GOODALL & G.A.M. SHARMAN. 1974. The composition and yield of milk from captive red deer (*Cervus elaphus* L.). J. Reprod. Fert. 37:67-84.

BATCHELER, C.L. 1968. Compensatory response of artificially controlled mammal populations. Proceedings of the New Zealand Ecological Society, 15:25-30.

BURCKHARDT, D. 1958. Observations sur la vie sociale du cerf *(Cervus elaphus)* au Park National Suisse. Mammalia 22:226-244.

CLUTTON-BROCK, T. 1974. Why do animals live in groups? New Scientist 63(905):72-74.

CLUTTON-BROCK, T.H., F.E. GUINNESS, S.D. ALBON 1982. Red deer: Behavior and Ecology of Two Sexes. University of Chicago Press, Chicago.

CROMBRUGGHE, S.A.DE. 1964. Untersuchungen über die Reproduktion des Rotwildes in den Niederlanden. Z. Jagdwiss. 10:91-101.

DARLING, F.F. 1937. A herd of red deer. Oxford University Press, London.

DOUGLAS, M.J.W. 1971. Behaviour responses of red deer and chamois to cessation of hunting. New Zealand Journal of Science 14:507-518.

DOWNIE, N.M. & R.W. HEATH. 1970. Basic statistical methods. - New York.

DZIECIOLOWSKI, R. 1979. Structure and Spatial Organization of Deer Populations. Acta Theriologica 24(1):3-21.

GEORGII, B. 1981. Activity patterns of female red deer *(Cervus elaphus* L.*)* in the Alps. Oecologia (Berlin) 49:127-136.

GOSSOW, H. 1973. On some environmental effects on sociology and behaviour in alpine red deer. Trans. XI Int. Congr. Game Biol. Stockholm:99-101.

JARMAN, J.P. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:215-267.

JENSEN, B. 1967. Køns- og aldersfordeling, vækstforhold og bestandsomsætning hos dansk kronvildt belyst ved jagtudbyttet. Danske Vildtundersøgelser, 13:77-106.

JENSEN, P.V. 1968. Food selection of the Danish red deer *(Cervus elaphus* L.*)* as determined by examination of the rumen content. Dan. Rev. Game Biol. *5* (3):1-44.

JEPPESEN, J.L. 1987a. Impact of human disturbance on home range, movements and activity of red deer *(Cervus elaphus)* in a Danish environment. Dan. Rev. Game Biol. *13* (2). In press.

JEPPESEN, J.L. 1987b. 'Immediate reactions of red deer *(Cervus elaphus)* to orienteering and hunting in a Danish environment' (in Danish with an English summary). Danske Vildtundersøgelser, 43: in press.

LACK, D.L. 1954. The natural regulation of animal numbers. Oxford University Press.

LAVSUND, S. 1976. 'The ecology of red deer, *Cervus elaphus* L., in areas in southern Sweden with recently established populations' (in Swedish, with an English summary). In-

stitutionen för Skogszoologi. Rapporter och Uppsatser, Nr. 25:80 pp + app.

LINCOLN, G.A., R.W. YOUNGSON & R.V. SHORT. 1970. The sexual behaviour of the red deer stag. J. Reprod. Fert., Suppl. 11:71-103.

MITCHELL, B., D. MCCOWAN & I.A. NICHOLSON. 1976. Annual cycles of body weight and condition in Scottish red deer. J. Zool., Lond. 80:107-127.

MITCHELL, B., B.W. STAINES & D. WELCH. 1977. Ecology of red deer. Institute of Terrestrial Ecology, Cambridge:74 pp.

OKARMA, H., J. ZIELINSKI & T. NOWAKOWSKA. 1985. Food of red deer *(Cervus elaphus* L.*)* in montane forest of southeastern Poland. Trans. XVII Int. Congr. Game Biol. Brussels: 457-463.

RATCLIFFE, P.R. 1984. Population dynamics of red deer (*Cervus elaphus* L.) in Scottish commercial forests. Proceedings of the Royal Society of Edinburgh. 82B:291-302.

SCHLOETH, R. 1961. Einige Verhaltensweisen im Hirschrudel. Rev. Suisse Zool. 68:241-247.

SCHLOETH, R. 1966. Verwandtschaftliche Beziehungen und Rudelbildung beim Rothirsch *(Cervus elaphus* L.). Rev. Suisse Zool. 73:434-440

STAINES, B.W. 1974. A review of factors affecting deer dispersion and their relevance to management. Mammal Review, 4:79-91.

STAINES, B.W. & J.M. CRISP. 1978. Observations on food quality in Scottish red deer *(Cervus elaphus)* as determined by chemical analysis of the rumen contents. J. Zool., Lond. 185: 253-259.

STAINES, B.W., J.M. CRISP & T. PARISH. 1982. Differences in the quality of food eaten by red deer *(Cervus elaphus)* stags and hinds in winter. J. Appl. Ecol. 19:65-77.

STRANDGAARD, H. 1967. En undersøgelse over kronvildtets tilpasning til det danske kulturlandskab. Danske Vildtundersøgelser, 13:9-75.

VALENTINCIC, S.I. 1960. Komparative Studie einiger Reproduktions-erscheinungen beim Rotwild des Alpen und Au-Gebietes. Trans. Congr. Int. Union Game Biol. 4:188-197.

WATSON, A. & B.W. STAINES. 1978. Differences in the quality of wintering areas used by male and female red deer *(Cervus elaphus)* in Aberdeenshire. J. Zool., Lond. 186:544-550.

WEGGE, P. 1975. Reproduction and early calf mortality in Norwegian red deer. J. Wild. Mgmt. 39(1):92-100.

WIRTZ, P. & J. LÖRSCHER. 1983. Group sizes of antelopes in an East African National Park. Behaviour 84:135-156.

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