DANISH REVIEW OF GAME BIOLOGY Vol. 13 No. 2

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by
JOHNNY LUND JEPPESEN

Med et dansk resumé:
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Abstract

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During 1980-84 home range, movements and activity of red deer *(Cervus elaphus)* were recorded in Oksbøl State Forest District in West Jutland, in relation to human disturbances, including hunting, orienteering, military practise, and tourism. The research is mainly based on location of radio-marked deer. Size of annual or seasonal category 1 home ranges (hinds with stable patterns of movements) was 257 ± 28 ha, whereas for hinds with category 2 ranges (those hinds affected by human disturbance) the size was up to 3-4 thousand ha. Some hinds had a single annual home range, others had separate summer and winter ranges; one hind migrated 25 km north in April and returned in September. Some of the radio-marked hinds moved during the rut to rutting grounds outside their home ranges. Mean of daily ranges was 44.5 ± 10.2 ha. Red deer in Oksbøl are mainly nocturnal. Hinds feed in the open at night and stay in cover within the forest during the day. Movements of stags were different from those of hinds, the stags mostly moving in a zigzag pattern within the forests. Various patterns of reaction to disturbance are described: seeking cover, instant flight, and 'delayed flight'. Mean length of flight routes was 3,569 ± 396 m. Flight routes outside home range nearly always ended in a refuge-area specific to the individual hind. Length of stay in refuge-areas was from half a day to more than a week (most often 1-4 days). Another reaction pattern was increased movements, and in periods with repeated disturbances (hunting season, presence of tourists) the result was increased movements in enlarged home ranges. Hunting pressure increased sharply during the period of study. As the deer are not able to distinguish hunters from other humans, this resulted in tourists expelling the deer from near-shore plantations in Easter 1983. This did not happen in Easter 1980, when the hunting pressure was not so great.

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Contents

Introduction

Few studies have assessed the impact of human disturbance on patterns of movements and activity in wild cervids. In Sweden the impact of large orienteering events on moose *(Alces alces)* and roe deer *(Capreolus capreolus)* has been investigated (SENNSTAM 1974, SENNSTAM & STÅLFELT 1976, CEDERLUND et al. 1981), and ALMQVIST & SANDBERG (1979) have recorded the reactions of moose to drive hunts. In the Bavarian Alps GEORGII (1980c) conducted disturbance-trials with red deer *(Cervus elaphus),* and JEPPESEN (1984) gave a few examples of the reactions of red deer and roe deer to hunting and orienteering in Denmark.

NEIL et al. (1975) and BOYLE & SAMSON (1983) have prepared annotated bibliographies of mainly North American works on human-wildlife interactions. These include many different human activities, such as camping, picnicking, trail-walking, horse-riding, boating, cross-country skiing, snowmobile traffic, road- and flight traffic, plus free-roaming dogs. Only a few concern reactions of cervids to human activities.

GEIST (1971a, 1971b, 1978) has pointed out the impact of disturbance on the behaviour of ungulates and the consequences for their energy budget of flight and excitement. Radio telemetry has recently been used taking physiological measurements during disturbances of ungulates. Heart-rate, for example, is a good indication of the first alarm-reaction to disturbing stimuli (MACARTHUR et al. 1979, 1982, MOEN et al. 1982). Heart-rate, and thus metabolism, increased in adult bighorn sheep *(Ovis canadensis canadensis)* and white-tailed deer *(Odocoileus virginianus)* that were subjected to various disturbances (op.cit.). The heart-rate decreased in newborn red deer calves (ESPMARK & LANGVATN 1979, 1985) and white-tailed deer calves (MOEN et al. 1978, JACOBSEN 1979), that reacted to alarm-stimuli by 'freezing' or 'lying prone' (LENT 1974).

This paper presents home range, patterns of movements and activity of radio-marked specimens (mainly hinds) in a Danish population of free-ranging red deer. The population lives in the Oksbøl area in Southwest-Jutland. In order to obtain a good estimate of home range and movements in the area it is necessary to regard the influence of human presence. The movements of red deer are influenced by a variety of human disturbances, and therefore recordings were made of the reactions of red deer (short- and longterm) to hunting, orienteering and tourism.

The few home range studies that have been performed on the European red deer, were made in Scotland (STAINES 1970, 1974, CLUTTON-BROCK et al. 1982) and in the Bavarian Alps (GEORGII 1980a, GEORGII & SCHRÖDER 1983). Further, ANGIBAULT et al. (1985) have reported home range size of one stag in France. These studies have revealed a very large variation in home range size of the species, from 25-50 ha (winter range) on Rhum (CLUTTON-BROCK et al. 1982) up to more than 6,000 ha (annual range) in the Scottish highlands (STAINES 1970).

In addition to radio-telemetry studies of home range, movements and activity-patterns of red deer in the Oksbøl area, regular observations and counts of red deer were carried out in the area. During the first half of the 1980's the hunting pressure increased drastically, and the seasonal variation in group size, and sex and age composition in relation to this, is described in JEPPESEN (1987a). The immediate reactions of red deer to orienteering and hunting assessed from observations and counts, are described in JEPPESEN (1987b).

Acknowledgements

Oksbøl State Forest District provided unrestricted access to carry on research throughout the district. Headquarters of the Oksbøl Military Camp granted permission to use the military areas, and provided lodgings while the research was carried out. Foresters from the district, plus hunters and orienteerers are acknowledged for their collaboration during research involving human disturbances of red deer. Special thanks are directed to radio technician Bo Gaardmand who, together with the author, carried out the time consuming bearings of radio-marked red deer. Catching of red deer for radio collar marking was carried out by gamekeeper Jørgen Andersen. Tommy Asferg, Anders Feilberg, Helmuth Strandgaard, and David R. Klein are thanked for their useful comments on earlier drafts of this paper. Furthermore David R. Klein improved the English. Else-Marie Nielsen is thanked for word processing and proofreading of the manuscript and Poul Hartmann for drawing figures.

The study was financed by the EEC (Contract nos.: ENV - 365 - DK(G) and ENV - 788 - DK(A.D.)), and by the following Danish institutions: The Danish Forest Service, The 'National Agency for the Protection of Nature, Monuments and Sites', The Ministry of Cultural Affairs, the 'Council supporting and encouraging outdoor life, paying the widest possible regard to the Danish Nature', and the Game Biology Station.

Study area

Denmark's largest population of free-ranging red deer lives in the Oksbøl State Forest district in Southwest-Jutland (JEPPESEN 1987a). The area covers 175 km^2 out of which 65 km^2 are dune plantations and 110 km^2 open land (Fig. 1). The plantations consist mainly of conifers, predominantly mountain pine *(Pinus mugo),* but also sitka spruce *(Picea sitchensis)* and other conifers, plus some uncultivated areas (STRANDGAARD 1967). Many sections are covered with dense forests and serve, therefore, as excellent cover for the population of red deer. The open areas consist of 70 km^2 of moorland and grass plains, that are utilized as a military field practise area, while the rest is privately-owned farmland, with the dyked-in Filsø to the north and humid meadows to the east close to Ho bay. The ground is level between 0 and 20 m above sea level. In some of the plantations inland sand dunes may reach 35 m above sea level. The sandy soil is poor, except for the fertilized farmland.

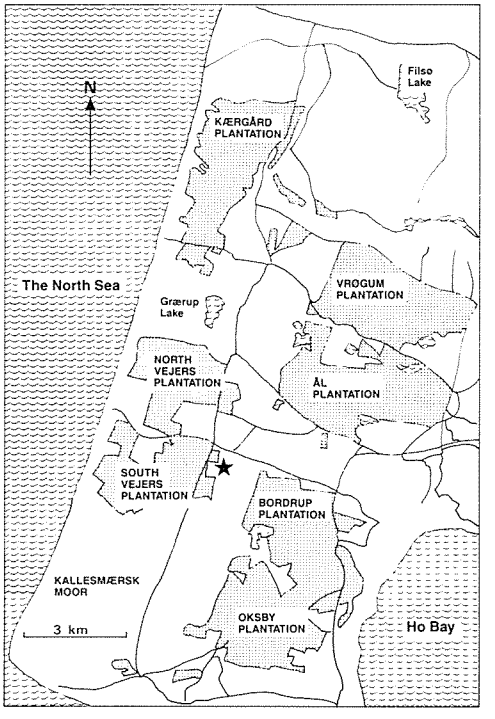


Fig.1. Map of the Oksbøl study area. Asterisk indicates areas named 'Skolestykket' and 'Kirkebjerge'.

Human activities

Hunting

The Danish hunting season for red deer is September-January (stags and calves) and October-January (hinds). Before 1983, February was also included in the hunting season. In the Oksbøl area only stalking of stags is permitted in September and most of October, while drive hunts (and stalking) are common after October 20th, when the rut is over for most of the deer. During the first half of the 1980's the hunting pressure and the number of killed red deer increased sharply for various reasons. From an estimated level of 25% of the population in the 1981/82 season it increased to 60% of the population in 1984/85 (see JEPPESEN 1987a). This was the result of hunters substantially increasing their activities throughout the hunting season in the area (drive hunts and stalking were carried out every second weekend in some plantations, and in others stalking occurred each day for fortnight-periods). Thus, the red deer were subjected to a constant hunting pressure in the whole area and hunting became the most powerful human disturbance for about half the year.

Orienteering

Larger orienteering events, with the number of runners varying from 2-300 up to more than 2,000, take place once or twice each year in the plantations in the Oksbøl area. By means of a map and a compass the runners, in the quickest possible manner, attempt to find their way 'through unknown terrain', from post to post, until they, following different routes reach the goal. In the largest events there are more than 20 'courses', and usually most of the area in a plantation is used in these events. The performance of a large orienteering event constitutes the most intense human disturbance that the red deer are exposed to (JEPPESEN 1987b).

Tourism

In the Oksbøl area, lying close to the North Sea, there are many tourists, especially during Christmas, Easter and Whitsun, in summer and in the 'mushroom season'. In sunshine and warm weather most of these people are concentrated along the shore, close to the summer house areas (see Fig. 1). But in cold and grey weather many people hike throughout the near-shore plantations. Each year there is a massive tourist invasion for a fortnight period in Easter (March-April). The reactions of red deer to these tourists in the forests have been recorded in 1982 (KNUDSEN 1983) and in 1983. The movements of red deer in summer are also under the influence of tourists.

Military activities

A large part of the open area that is used for military practise is former agricultural land. The fact that these areas are administered by the Ministry of Defence means that during the main part of the year the red deer are free to feed peacefully. Several deer stay both day and night on the large moors in the southern part of the study area. On other open areas within the study area the deer only feed at night. Normally only a smaller part of the terrain is used as a military shooting area, thus the military impact on movements of red deer is small. But during large military field practises, especially when large numbers of infantry are involved, most of the red deer are forced to remain in the forests during both day and night.

Civil traffic on the military areas largely takes place in cars on the public roads that cut through the areas, while only pedestrians are allowed in the plantations.

Table 1. Some individual data of 18 radio-marked red deer.

Red deer: no.	sex	Date of marking	Observation period	Number of radio locations: 'Ordinary' recordings	+ 24-hour recordings	= Total
110 B	♀	23.03.82	1982-83	122	57	179
201 B	♀	20.02.81	1981-83(84)	229	300	529
202 B	♀	18.12.80	1981-83(84)	168	20	188
203 B	♀	16.01.81	1981-83(84)	214	36	250
209 B	♀	22.02.81	1981	17		17
210 B	♀	17.03.81	1981-83	133	101	234
211 B	♀	17.03.81	1981-83	186	149	335
212 B	♀	13.03.81	(1981-83)	28		28
302 B	♀	29.03.81	1981-83	110		110
304 B	♀	30.12.81	1982	32		32
305 B	♀	19.01.82	1982-83	175	119	294
308 B	♀	13.03.82	1982-83(84)	169	161	330
403 B	♀	17.03.81	1981-83	125		125
404 B	♀	05.03.83	1983(84)	26		26
406 B	♀	24.03.83	1983	61	40	101
307 B	♂	07.03.83	1983	52		52
310 B	♂	10.02.82	1982	24		24
409 B	♂	26.02.83	1983	42	18	60
				1,913	1,001	2,914

Material and methods

For this study 18 adult red deer (15 hinds and 3 stags) were radio-marked. They were trapped during winter in small enclosures in the plantations. The deer were immobilized within the enclosures and a radio-collar was applied. Table 1 presents information about sex, date of marking, observation period and number of radio locations per deer.

The radio transmitters and collars were a modified Grimsö model (CEDERLUND et al. 1979) and were constructed at the Game Biology Station. The weight of the radio collar was about 350 gram, and the transmitter functioned in the 151 MHz-band. The expected battery-life is 3-10 years. The receiver was an AVM-LA12 type (USA), which in connection with a 6-element yagi antenna was used for radio-location from a mobile unit (a Volkswagen van - Fig. 2). Occasionally a 3-element handheld antenna was used. The antenna and compass in the mobile unit was lifted 6 metres above the ground by means of a pneumatic telescope mast. A repeater-compass could be read in the car.

The location of the deer was determined by triangulation of two to three bearings from the mobile unit, as described by CEDERLUND et al. (1979). The bearings were carried out from 170 fixed stations located throughout the area. A map of the area (1:25,000) with co-ordinates, produced by the Danish Forest Service, was used. Taking bearings were very time-consuming, as two to four red deer were radio-marked in each of the large district plantations. Up to 5 hours could be required to record one location of each of about 10-15 radio-marked deer.

The results in this paper are primarily based on recordings of 13 of the radio-

Fig. 2. Bearings of radio-marked red deer were made from a specially equipped mobile unit, a Volkswagen van. The 6-element Yagi-antenna was lifted 6 m above the ground on a pneumatic telescope mast.

marked hinds. The recordings were made by two persons working in the study area during a total of 225 days, grouped in periods from 2 to 16 days (often one week) during 1980-83, plus a few days in 1984. The recordings were often made in connection with human activities, such as hunting, orienteering, tourism, and military practise. During the intervening periods parallel studies were made of the impact of disturbances on roe deer (JEPPESEN 1987c).

This analysis is based on 2,914 radio location fixes in the study period, of which 1,001 are from 41, 24-hour-recordings on individual deer (daily ranges, Table 1). In the 24-hour-recordings about one location per deer per hour was made. Only 38 daily ranges are included here, as one is concerning a stag (the rest concern hinds), and in two cases a hind was driven away from its home range because of a disturbance (dealt with on page 18). Home range data were analysed, mostly using computer programmes, developed by T. ASFERG (unpubl.). The home range data were, for some deer, divided into a 'summer range' (March-September) and a 'winter range' (September-March). A quadrat-procedure, with a grid size of 200 × 200 m, was used for the description of the home range, while calculations of home range size were made using the minimum area method (MOHR 1947). In 24-hour-recordings of red deer chronologically ordered locations were connected by straight lines, and the distances between fixes were calculated.

Automatic activity recording, as described by CEDERLUND & LEMNELL (1980) for roe deer and mountain hare *(Lepus timidus),* was very difficult to perform on red deer in the Oksbøl area, as many deer moved long distances between day and night habitats. In doing so they moved out of reach of fixed receiving equipment.

Therefore, a mobile trailer was used for the equipment (Fig. 3), a Gould Brush 220 two-channel recorder in combination with two LA12 receivers (see CEDERLUND & LEMNELL 1980). An omnidirectional antenna was placed 8 m above the ground on a telescope mast, and the system received power from a generator. In order to obtain an exact indication of time during activity recording, a time marking device was connected to the recorder (GAARDMAND & JEPPESEN 1984). Thus, some activity patterns of acceptable quality were recorded.

During disturbances like hunting and orienteering events observations were made of the reactions of red deer by foresters, hunters and runners (see JEPPESEN 1987b). In addition, movements and activity patterns, plus flight routes of the radio-marked deer were recorded before, during and after the disturbance. This was primarily during seven larger orienteering events and 12 days of hunting, but also in the hunting season generally and during a tourist invasion.

Results

Home range

Annual and seasonal home range

The use of habitat of red deer in the Oksbøl area is closely connected to human disturbance, such as logging, military practise, hunting, tourism and other recreational use of the area (see also JEPPESEN 1987a). It is, therefore, difficult to distinguish between natural patterns of red deer movements and patterns under the influence of man. The red deer are mainly active at night (see p. 18), which can be seen as an adaptation to human activities.

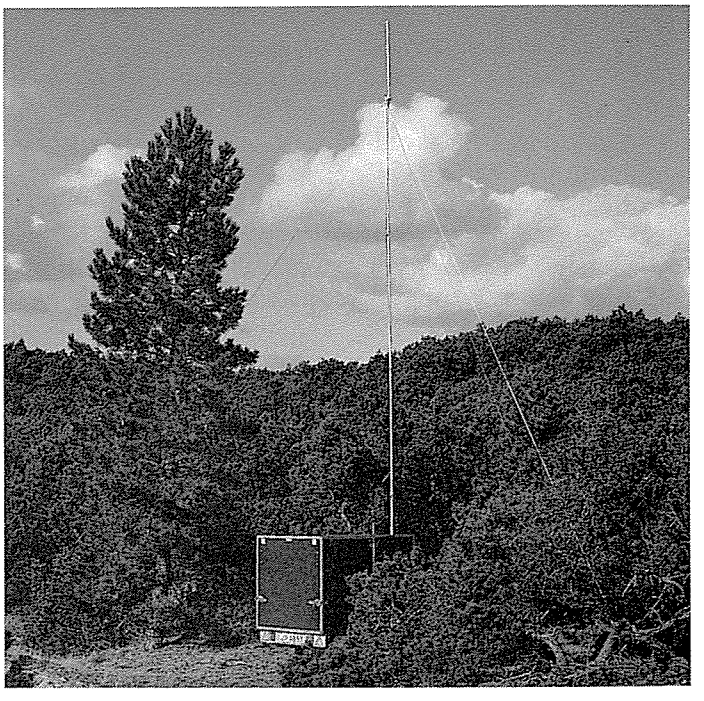


Fig. 3. A mobile trailer containing equipment for automatic activity recording. An omnidirectional antenna placed 8 m above the ground was connected to the activity recorder in the trailer.

Table 2. Home ranges of category 1-hinds (see text).

Hind no.	Type of home range	Home range 1981 ha	1982 ha	1983 ha	Mean of home range ha	Total home range ha	Longest distance within total home range m	Shortest distance within total home range m
210 B	annual range	295	233	228	252	413	2,700	2,200
302 B	annual range		255		255	318	3,100	1,600
406 B	annual range			312	312	312	2,450	2,050
203 B	annual range	327	372	190	296	416	4,000	1,800
305 B	summer range		249	236	243	308	2,900	1,600
305 B	winter range		199		199	269	2,400	1,600
308 B	summer range		205	275	240	392	3,000	1,700
				n:	7	7	7	7
				$\bar{x}$:	257	350	2,936	1,793
				sd:	37	58	539	242
				se:	28	43	399	179

Regarding home ranges and movements of radio-marked red deer hinds in the area it is, however, possible to distinguish between two patterns of movements: 1) Hinds with rather stable movements within small home ranges, and 2) hinds with more varying movements in often very large home ranges (Tables 2 and 3).

Some of the hinds in category 1 were always recorded within the boundaries of only one forest, where they fed in clearings, paddocks and 'game-fields' (Fig. 4(a)). Others fed on open moors, grass plains or farmlands, while they rather constantly utilized a special section of the forest for cover, either the whole year (Fig. 4(b)) or in a summer- or winter period (Fig. 4(c)).

Hinds in category 2 also fed on the open areas, but occasionally they moved around within the areas, remaining in each new place for only a short time, and they also used several different locations for cover. Often they moved between two or more plantations, some for the whole year, others only in winter (Fig. 4(d)). Thus, some hinds were in category 1 in the summer and in category 2 in the winter.

Several hinds had different preferred summer- and winter ranges, which were the same from year to year. The deer fed on grass plains and farmlands from March/April, when the grasses sprout, until September or later, while in winter they mainly fed on heather *(Calluna vulgaris)* in moors and dunes.

Hinds in category 1 had annual or seasonal home ranges of the same size (see Fig. 4(a-c)). When one hind, with a recorded summer range in 1982 of 73 ha, is disregarded, a mean of 257 ha ± 28 s.e. is obtained (Table 2). The overlap of the annual and seasonal home range was not 100%, so the home ranges for the whole period of recordings were larger, with a mean of 350 ha ± 43 s.e.

The shape of these home ranges is rather elongated. Ranges with forest at one end and open land at the other often being tapered. The mean maximum length in category 1 home ranges is 2,936 m ± 399 s.e., while mean maximum width is 1,793 m ± 179 s.e. (Table 2).

Home ranges of hinds in category 2 were generally much larger, with ranges of up to several thousand hectares (Table 3). For some of the hinds this was due to the im-

Table 3. Home ranges of category 2-hinds (see text).

Hind no.	Type of home range	Home range 1981 ha	1982 ha	1983 ha	Mean of home range ha	Total home range ha
211 B	annual range	1,214	1,696	1,426	1,445	2,056
212 B	annual range					855
201 B	annual range	702	3,787	2,893	2,461	4,472
308 B	winter range		2,860		2,860	3,235
403 B	winter range	1,362	887		1,125	1,570
404 B	winter range			897	897	897
202 B	summer range	894	787	208	630	1,731
202 B	winter range	1,354	2,161	1,080	1,534	2,324
202 B	annual range	2,219	2,706	2,072	2,332	3,439

pact of human disturbances (see below), but one hind was, for long periods, a typical open-land deer, and it rarely stayed in the plantations. The mean summer range over 3 years for this hind (Fig. 4(d)) was 630 ha and the winter range was 1,534 ha. In summer she was feeding in the large, uniform farmland of Filsø, and in winter in the open moorlands in the southern part of her range. Her mean annual home range was 2,332 ha, while the total home range over 3 years was 3,439 ha.

One hind made a special case, having a winter range in the Kærgaard-Filsø area of 897 ha, but in the period April-September (in 1983 and 1984) she had migrated to Lønborggård plantation, 25 km north of her winter range.

The annual or seasonal home ranges were in several ways under influence of human activities. Two hinds, whose patterns of movements were regular and stable in their summer ranges (category 1), had substantially larger ranges (category 2) in autumn and winter (the hunting season). For one hind (with a category 1-summer range) it was not possible to acknowledge a 'natural' winter range, as disturbance by human activities (mostly hunting) in the autumn and winter months resulted in her range being considerably enlarged; the total range over 2 years was 5,033 ha. Coincident with the growing hunting pressure from year to year, further two hinds increased their home ranges (both seasonal and annual) over the 3 years of study (for example, summer range of hind no. 201B was in 1981: 267 ha (one plantation); in 1982: 550 ha (three plantations); and in 1983: 1,684 ha (four plantations) (see also Fig. 7). In two winter months (December 1981 - January 1982) the same two hinds remained within areas of 114 ha and 111 ha, respectively; relatively small winter ranges. The winter of 1981/82 was the only one during the study period with a substantial snow-cover. During the same two months the following year their ranges were 943 ha and 597 ha, respectively.

Home range in connection with the rut

In the Oksbøl area roaring of stags during the rut is primarily restricted to the night. Observations made at preferred rutting grounds that are usually in the open, have shown that the stags emerge late in the afternoon from their cover in the forest, and roaring occurs on the rutting ground. The most powerful stag(s) occupies the central part, while younger and less powerful stags stay at the periphery of the rutting ground. The hinds that emerge from cover at night-

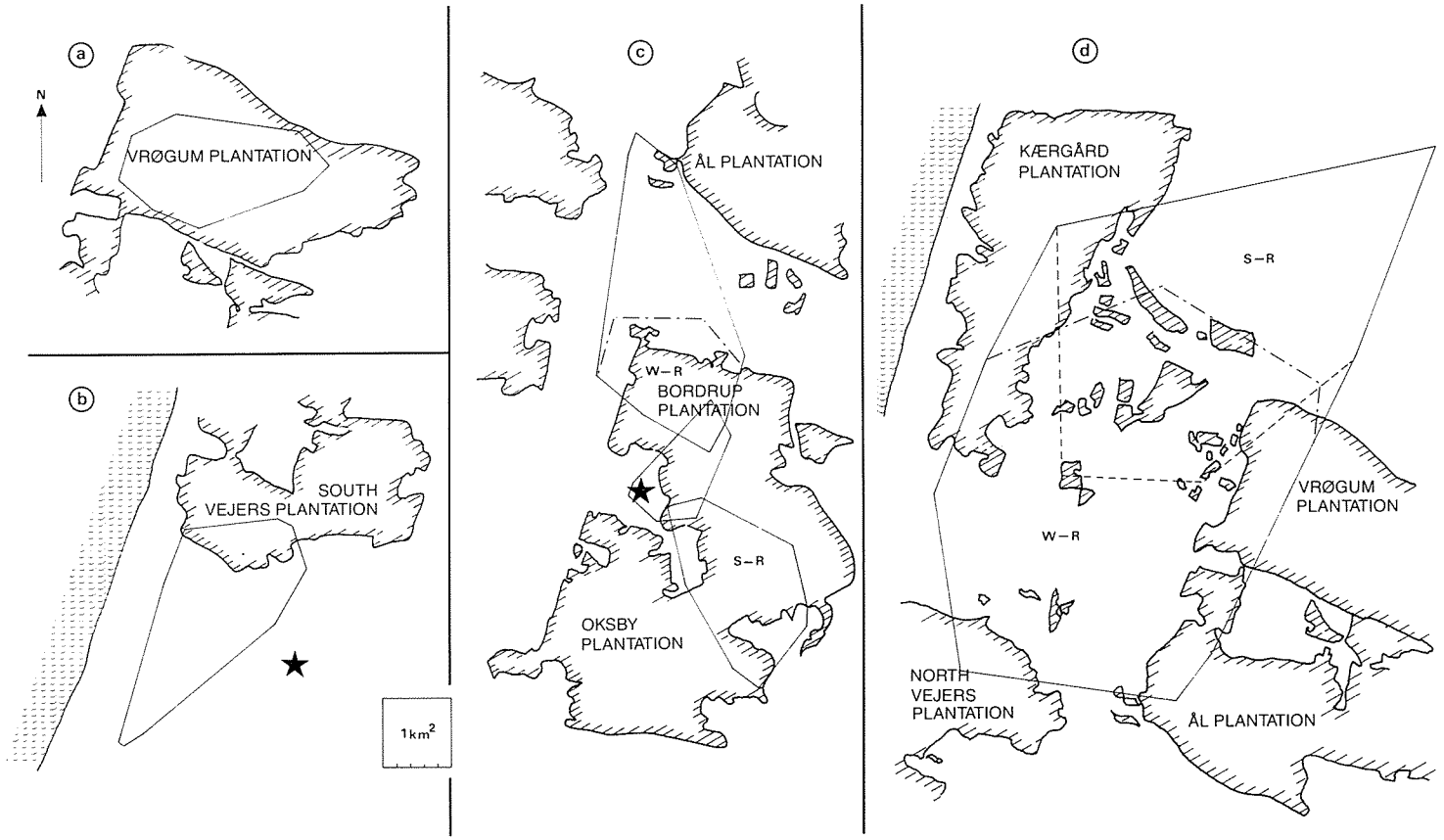


Fig. 4. Home ranges shown by examples of four red deer hinds in the Oksbøl area; – a) Home range of hind no. 302 B for two years in Vrøgum plantation; – b) Home range of hind no. 203 B for three years in South Vejers plantation. The star indicates rutting ground outside home range one year; – c) Summer (S-R) – and winter (W-R) range, plus range during the rut (see text) of hind no. 305 B in Bordrup plantation. The dotted line bounds a winter range without influence from human disturbances (hunting). The star indicates rutting ground each of two years; – d) Summer (S-R) – and winter (W-R) range, plus total home range for three years of hind no. 202 B, which was an open land deer.

fall often have to zigzag past the younger stags that try to cut them off to reach the central part of the rutting grounds. During night and in the morning while the most powerful stag maintains a harem of hinds, the matings take place.

It is only in remote and peaceful sections of the area, and on the large moors of Kallesmærsk, that harems are maintained all 24 hours; on the moors partly without connection with a special rutting ground.

The hinds actively sought out rutting grounds, often located outside the annual or seasonal home ranges (Figs. 4(b-c), and 11). This applies to category 1-hinds, whereas the rutting grounds of category 2-hinds lay within their larger home ranges. Table 4 shows eight instances in which the hinds left their home ranges in favour of a rutting ground that was up to 2,100 m from the nearest home range boundary. This is comparable to the greatest width of these home ranges (see Table 2).

Continuous recordings of hinds during rut showed that their stay in the rutting ground lasted from 24 to 36 hours, after which the hinds returned to their home ranges and resumed their normal patterns of movements. Hinds are in heat for 12-24 hours (CLUTTON-BROCK et al. 1982).

Several hinds have used the same rutting ground during the 2 or 3 years of observations, while other hinds may use different rutting grounds in successive years. One hind whose rutting ground during all 3 years was Bordrup, moved to Bordrup each year for a period of 3-4 weeks during the rutting season, staying in an area of 152 ha (1981) and 227 ha (1982) (the transmitter did not function constantly in the rutting season of 1983).

Size of daily ranges and daily movements

Normally only a small part of the annual or seasonal home range was used within a 24-hour span. In 38 recorded 24-hour periods the mean daily range was 44.5 ha ± 10.2 s.e., within a variation between 5.9 ha and 116.4 ha (Fig. 5). The mean of the largest 'length' in the daily ranges was 1,178 m ± 149 s.e., within a variation between 500 m and 2,550 m. The mean daily distance covered by the deer was 3,953 m ± 513 s.e., with a minimum of 1,419 m and a maximum of 7,590 m.

The mean of daily ranges during the winter months (December-February) was 33.8 ha ± 23.4 s.e. (n=8) while the mean during spring (March-April) was 53.3 ha ±

Table 4. Eight cases where hinds had left their home range in favour of a rutting ground located outside the home range.

Hind no.	Year	Home range ha	Distance from home range m	Date on rutting ground
210 B	1982	233	1,300	13.10.1982
406 B	1983	312	1,600	14.10.1983
203 B	1981	327	700	06.10.1981
305 B	1982	249*	800	12.10.1982
308 B	1982	205*	1,500	14.10.1982
308 B	1983	275*	1,500	11.10.1983
201 B	1981	267*	2,100	06.10.1981
211 B	1981	224*	2,000	?

* Figures indicate summer ranges instead of annual ranges

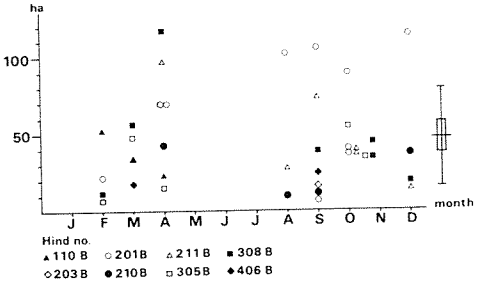


Fig. 5. Size of daily ranges of eight hinds; individual values as well as mean with standard error and standard deviation.

19.2 s.e. (n=11). In August-October the mean daily range was 42.4 ha ± 19.1 s.e. (n=19). The differences are not statistically significant (U-test, $p > 0.05$).

The daily patterns of movements are illustrated for four red deer hinds in Fig. 6. The locations of the hinds during daytime were all within the borders of the forests (open circles), while they moved during the night in the open areas (black circles). Hinds no. 305B and 308B, - and also partly hind no. 406B, returned in the morning into cover at the same locations they had left in the evening. Hind no. 110B moved to a place different from the previous day.

Use of home range

There was a large variation in the way the individual hinds used their habitats. Some were generally attached to one locality, whereas others often moved between various places with cover (also often during the daylight hours). Both categories spent the night in open terrain (paddocks or grass plains), and the daytime in the forest's cover.

As is shown in Fig. 7, some of the areas, especially the more open ones, were used exclusively at night, whereas others (within the forest borders) were used mainly during day. Besides, there were areas (often between the two) that were frequented both during day and night.

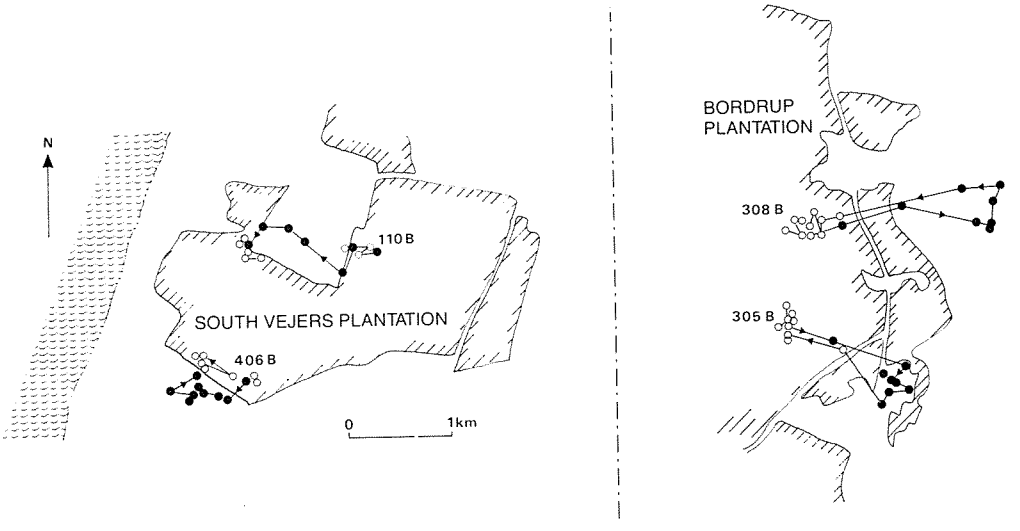


Fig. 6. Patterns of movements during a 24-hour period for four hinds in South Vejers and Bordrup plantations on March 26/27 1983; locations during day (open circles) and during night (black circles).

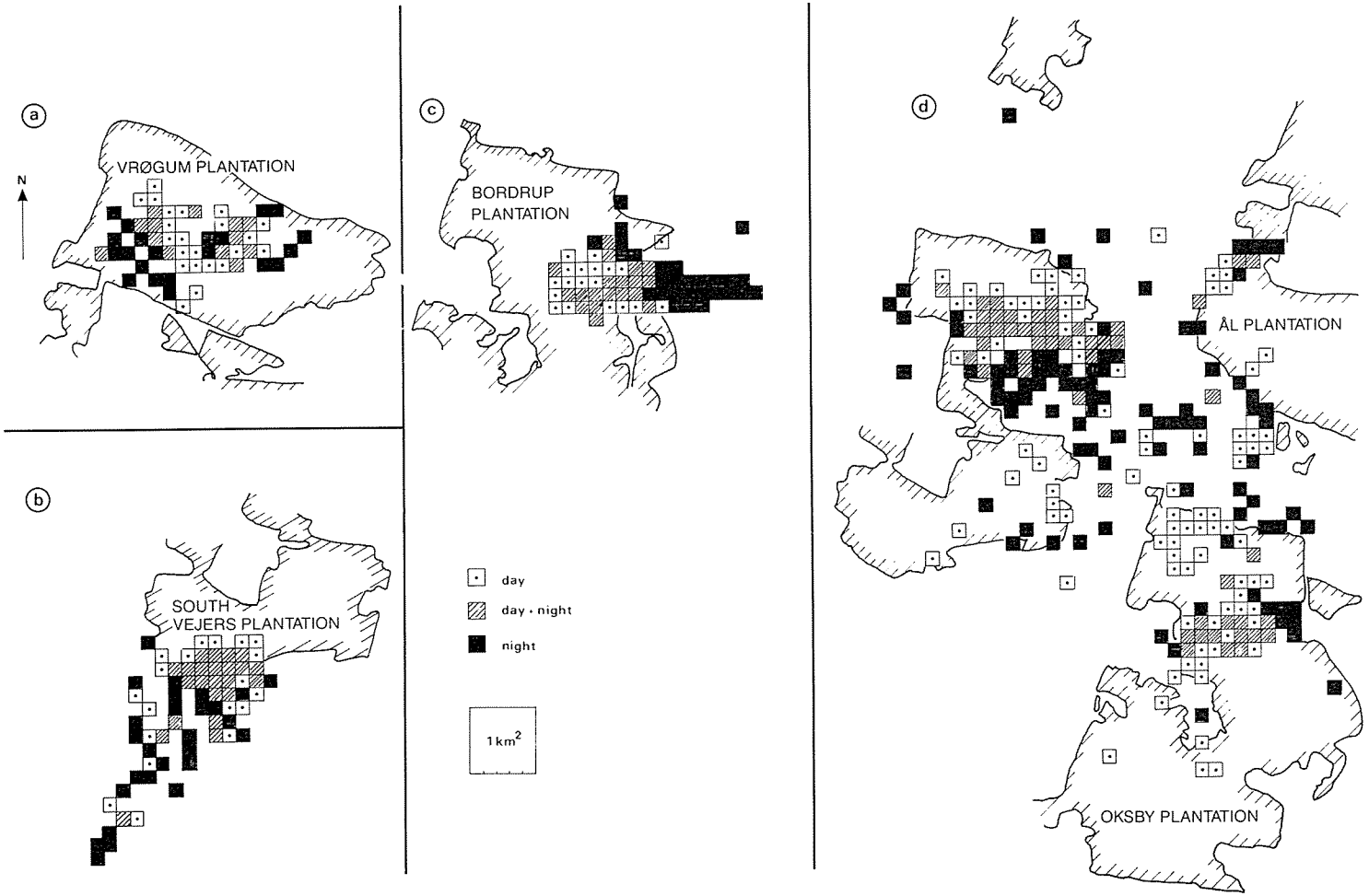


Fig. 7. Use of home ranges shown by examples of four red deer hinds; grid cells indicate areas used only at night (black), and areas used only during the day (white with a dot), plus areas used both during day and night (shaded).
a) Range within Vrøgum plantation of hind no. 302 B.
b) Range in South Vejers of hind no. 203 B.
c) Summer range in Bordrup of hind no. 308 B.
d) Range over four plantations of hind no. 201 B.

Hind no. 302B was located only within one forest's borders (category 1), and stayed during the day in the central part of the forest (Fig. 7a), whereas the hours of dark often were spent in the more peripheral areas of the home range. Hinds no. 203B and 308B (Figs. 7b and c) both shifted between the forest at day and the open areas at night. However, there was a difference. While hind no. 308B was never located during the day in the open farmland (Fig. 7c), hind no. 203B now and then spent several days in the open moorland, - especially during periods of rest in the military activities on the moor. When there vere military activities, hind no. 203B spent both days and nights within the plantation (Fig. 7b). Actually hind no. 203B spent most of her time in the forest. This is seen in Fig. 8 that shows, in which areas she was most frequently located. The pattern of movements of hind no. 201B (Fig. 7d), with shifts between open land and cover, was identical with those of other hinds; often she merely spent the days in scrub in the open moorland between the plantations.

In hinds that were exclusively located within one forest's borders, a large percentage of the grid squares were used both days and nights. This percentage was smaller in hinds with greater distances between day- and night areas of use, or in hinds that often moved around.

Home range of stags

In spite of very few recordings of radio-marked stags, it clearly appears, that stag and hind movements differed very much. While the hinds moved daily between the same feeding- and cover area during undisturbed periods, the stags very rarely returned to the same cover area in the morning, that they had left in the evening. The patterns of movements of stags tended to follow a slow zigzagged route for several days through a larger home range, than was found in category 1-hinds (Fig. 9). Most of

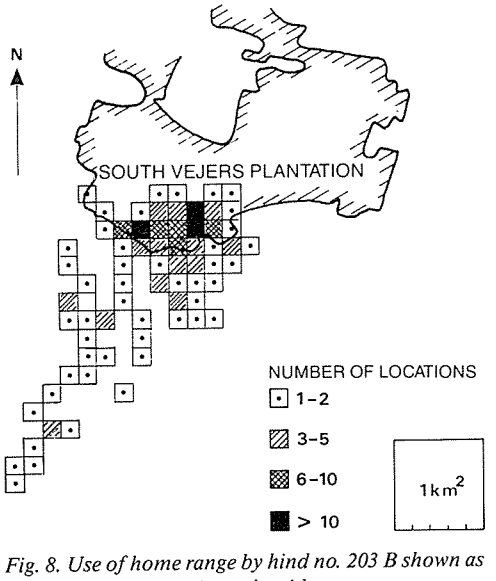


Fig. 8. Use of home range by hind no. 203 B shown as number of locations in each grid square.

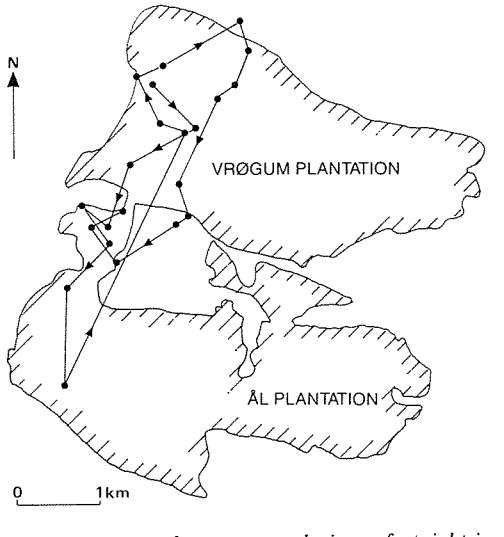


Fig. 9. Pattern of movements during a fortnight in March/April of stag no. 307 A, based on 1-2 locations per day.

Table 5. Size of home range of three stags in the periods they were recorded.

Stag no.	Number of points in antlers	Period of registration	Range ha
310 B	12	16.02. - 26.04.1982	756
307 B	12	25.03. - 17.09.1983	1,408
409 B	8	25.03. - 30.10.1983	2,650

the time the stags stayed within the plantations' borders (see also JEPPESEN 1987a).

The home range sizes of three stags in the period of recordings, are shown in Table 5. The youngest stag (no. 409B) was roaming much more from day to day over large areas, than were the two older stags.

Activity patterns

In spite of many gaps in the recordings we succeeded in obtaining several registrations of activity patterns of acceptable quality, and Fig. 10 shows the daily activity patterns during two selected periods.

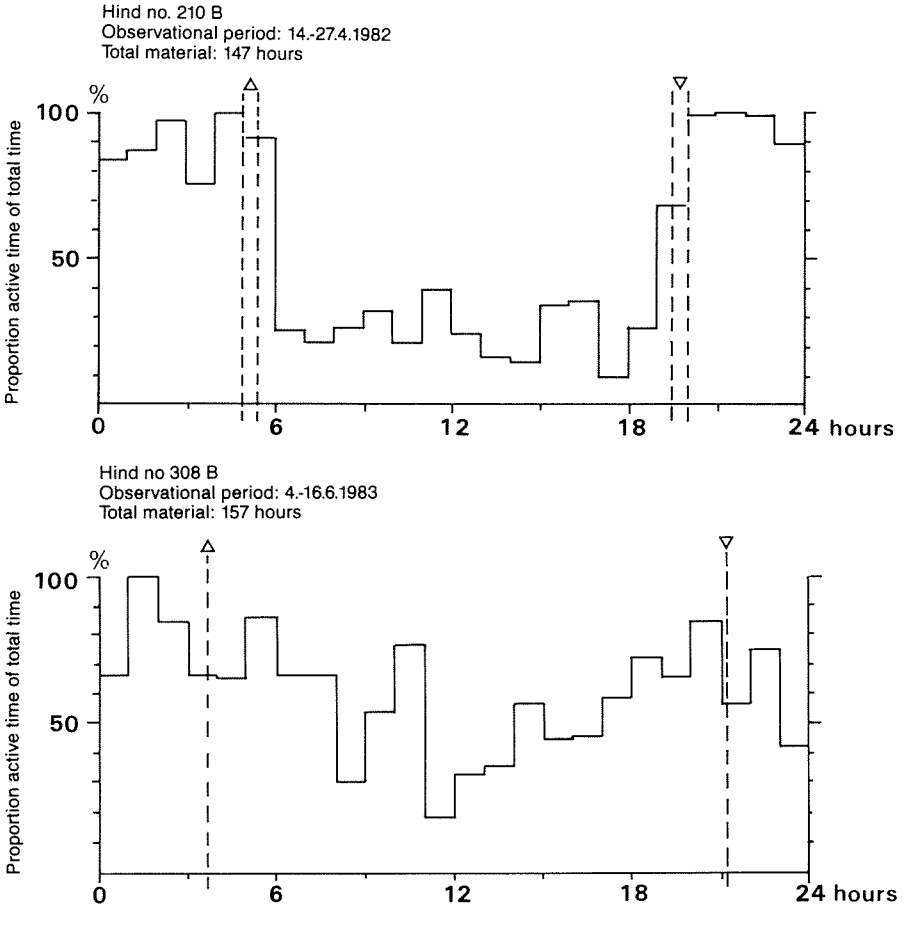


Fig. 10. Daily activity pattern of two female red deer in two selected periods. Arrows indicate sunrise and sunset.

Table 6. Median length of activity and inactivity periods in different seasons of the year. Recordings involved hind nos. 210 B, 211 B, 308 B, and 406 B.

Season	Activity: Median length minutes	n	Inactivity: Median length minutes	n
February - primo April	•50 - 75*	109	•46 - 85*	120
medio April - primo May	•23 - 27*	89	•60 - 65*	105
June	39	74	33	79
September - October	•63 - 135*	29	•85 - 105*	31

Minima (•) and maxima (*) median values for activity and inactivity in the periods of registration

There were typical long activity periods around and after sunset and in the hours towards sunrise. Thus, a bimodal activity distribution was seen, with the two peaks after sunset and around sunrise. During these hours the deer were almost constantly active. At night red deer were active for most of the time (thus blurring the bimodal pattern), the periods of inactivity being relatively short. During day hinds were mainly inactive, with interruptions of relatively short activity bursts.

Activity patterns in the June-observation period (Fig. 10) show a comparatively smaller height of the two peaks, and hinds were generally more active in daylight hours, and less active in the middle of the day.

The length of periods of activity and inactivity varied much. Often the first period of activity from sunset lasted 3-6 hours, but the longest period recorded was 685 minutes (all night!). The longest periods of inactivity were recorded in the afternoon, the longest being 348 minutes.

The variation in period-lengths that was found in the scanty material, shows that the median lengths of activity periods were largest in autumn (September-October) and winter months (February-March) (Table 6). Activity periods were shortest in spring (April) and summer (June). Also, period lengths of inactivity were greatest in autumn and winter, but also in April. In June they were much shorter (Table 6).

The number of activity periods per 24 hours (in 20 fully recorded days and nights) varied seasonally over the two years of observations as follows: February 7; March/April 8; June 12; and September 5.

Thus, it seems that there were shorter activity periods in March/April than in February, but that the length of inactivity periods during these months did not change appreciably. In June there were frequent shifts between active and inactive periods. In September/October both active and inactive periods were longer than in February.

Disturbance

Reaction patterns in red deer

Seeking cover

Red deer in the Oksbøl area reacted to disturbances such as hunting and orienteering in various ways. Often they immediately sought dense cover. Here they stayed for some time, either as long as the disturbing event lasted, - or for shorter periods until their threshold of tolerance towards disturbances was crossed, and they fled, - or for longer periods until peace was restored. As the radio signals revealed, the deer were

almost always 'active', - that is, they followed attentively the noise around them, - while staying in cover. Often, though, without movement or with only slight movement within the cover. An example was presented in JEPPESEN (1984, example 6) of a hind (no. 201B) that stayed in cover during a beat, while the men and dogs passed.

Instant flight

Most red deer in the Oksbøl area reacted to a major disturbance by taking flight at once, either a short flight into cover in the same plantation, or a longer flight to a neighbouring plantation (Fig. 13 and JEPPESEN 1984, example 2), of often more than 5,000 m (Table 7). See also JEPPESEN (1987b).

'Delayed flight'

Fig. 11 deals with the reaction of a hind, that stayed in a beat during a drive hunt in South Vejers plantation. The beat lasted one hour and although the radio signals revealed that she was 'active' throughout this period she remained in cover in the same place. She stayed in the same spot during the next several hours until sunset, after which she left the plantation at a rapid pace (flight). She crossed the moor and ran to Oksby plantation, - a flight-route of 5,900 m, - and stayed there for the rest of the night and the following day. She

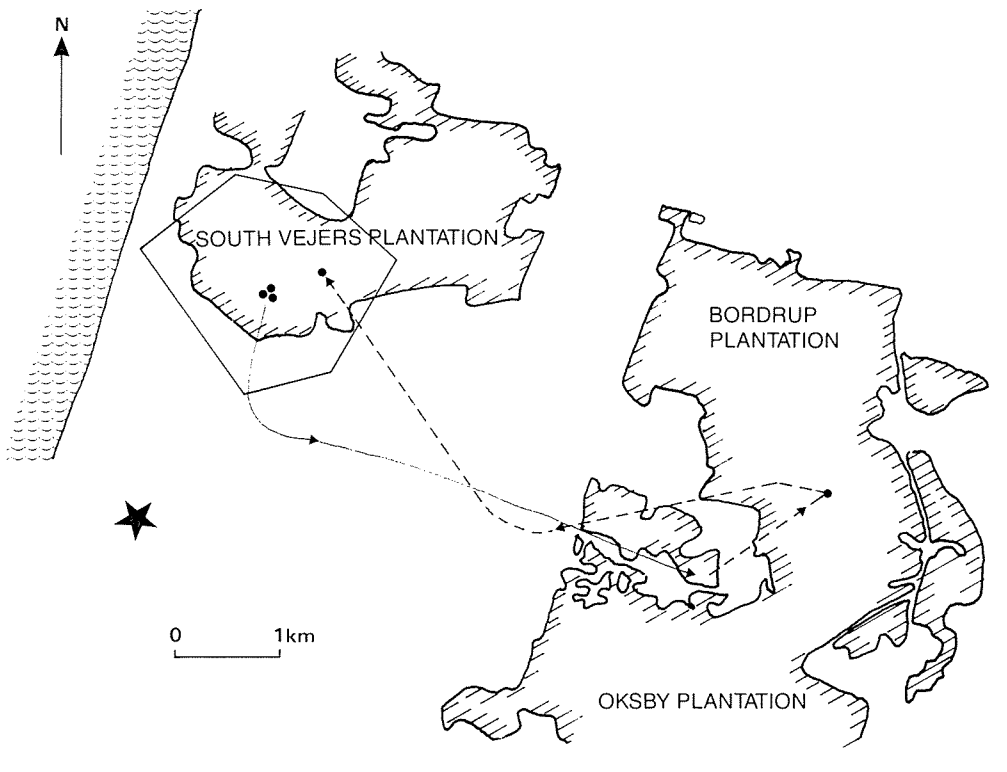


Fig. 11. 'Delayed flight' of hind no. 406 B (see text); the polygon indicates home range, solid line: flight route, dashed line: walk. The star indicates rutting ground outside home range.

Table 7. Reactions of red deer to human disturbances; distances that the deer took flight (instant flight and 'delayed flight'), and duration of stay in refuge-areas.

	Instantly seeking cover No. of occasions /no. of events	No. of instant flights		No. of 'delayed flights'		No. of flights within home range	No. of flights outside home range	Stay in refuge area		
		Flight distance		Flight distance						
		<5,000 m	>5,000 m	<5,000 m	>5,000 m			0-1 day	2-4 days	>4 days
Hunting	11/18	7	3	5	3	8	10	1	8	2
Orienteering events	5/11	3	2	4	2	5	6	3	2	2
Other human disturbances	0/3	3					3	2		

Hunting		Orienteering		Total
Instant flight	'Delayed flight'	Instant flight	'Delayed flight'	Flight
n = 10	n = 8	n = 5	n = 6	n = 32
$\bar{x}$ = 3,410 m	$\bar{x}$ = 3,775 m	$\bar{x}$ = 4,020 m	$\bar{x}$ = 3,200 m	$\bar{x}$ = 3,569 m
sd = 2,560	sd = 2,243	sd = 2,860	sd = 2,276	sd = 2,242
se = 1,587	se = 793	se = 1,279	se = 926	se = 396

returned to her home range the following night after having been away for about 36 hours.

This reaction pattern, where the disturbed deer seeks and remains in cover, even when subjected to hard pressure (dogs, men), and after which it takes flight, typically after dark, then staying away for a number of days, has been recorded almost as often as the instant flight (see Table 7). Often, however, the deer did not succeed in avoiding detection by staying in the first cover, but were forced by disturbance to flee to a new cover, or leave the plantation.

Yet another sort of 'delayed flight' has been observed in red deer, that have been exposed to human disturbance in their home range for one or more days. This disturbance was caused by hunters deer stalking, or a drive hunt in another part of the forest. Under cover of darkness the deer left the area and moved to a neighbouring plantation. The same pattern was observed in connection with the presence of tourists in the deers' home range (see p. 25), and also, when small posts were placed throughout a plantation the day before an orienteering event.

The mean distance that deer took flight, whether instant or delayed, was 3,569m ± 396 s.e. (Table 7).

Movements in the period after the disturbance

A deer that had moved into cover during a disturbance was sometimes observed later moving to its usual feeding grounds after dark, - and also returning to its usual cover in the morning. Thus, the only visible reaction was, that the deer stayed in cover all day. This is, of course, not different from its normal patterns of movements, - except for the enhanced level of activity.

Whether the flight was instant or 'delayed', it lasted from half a day to more than a week, before the deer returned to its original location (Table 7). This especially applies to category 1-hinds (with small home ranges, see p. 10), whereas several category 2-hinds (with large home ranges) did not return to the same area for a longer period of time.

For the deer that returned to their home ranges, 1 to 4 days elapsed before they did so (Table 7). During their stay in the refuge area, the patterns of movements were mainly as usual, as they fed in open areas at night, and took cover during the day. The return to their home ranges lasted from a few hours (JEPPESEN 1984, example 2) up to several days or even weeks with stops on the way.

After reacting to disturbances several red deer continued to show increased movements. Instead of the usual movements between the same feeding and cover locations, the deer made zigzag-movements over large areas, often continuing for several days, as examplified in Fig. 12. Thus, during this period, they did not return in the morning to the same location of cover, they had left in the evening. This pattern of movements is more similar to that of stags in the area (see p. 16).

Movements after repeated disturbances

Under repeated disturbances the reaction patterns varied in individual deer, depending on the situation at the moment of disturbance. If the deer sought cover within its home range (category 1-hinds), it did so in a variety of places. Mostly it would be in dense forest. But in flights out of home ranges the goal of the flight was almost always the same for the individual deer, and the actual flight-route was also often the same (Fig. 13). Thus, the individual deer nearly always used the same area for shelter or refuge; an area which after repeated dis-

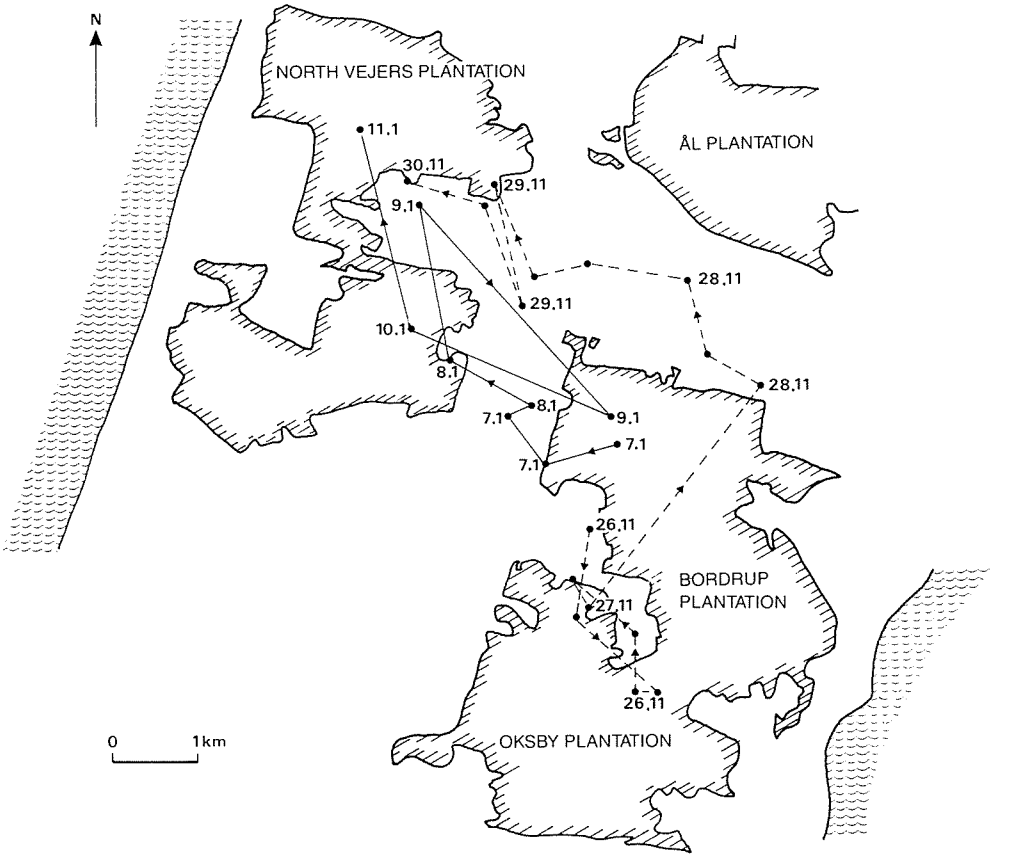


Fig. 12. Increased movements during the days after disturbances (hunting) of hind nos. 201 B (dashed line) and 211 B (solid line); dates are indicated.

turbances the deer learns to know. Distance from home range to refuge-area was for some deer considerably longer than the distance to the nearest plantation.

During the hunting season red deer were frequently disturbed (JEPPESEN 1987 a,b). Hunting also took place in the refuge-areas. Thus, most deer had larger ranges during the hunting season as a consequence of either: 1)instant or 'delayed' flight to the refuge-area, and often also flight back, or flight to another locality; or 2) by reacting for a period after each disturbance with increased movements (Fig. 12), the boundaries of home ranges being crossed several times, so that all the area over which the deer roamed had to be regarded as enlarged home range.

But as is described below, the presence of tourists also gives rise to many disturbances, and thus changed movements and enlarged home ranges of the red deer.

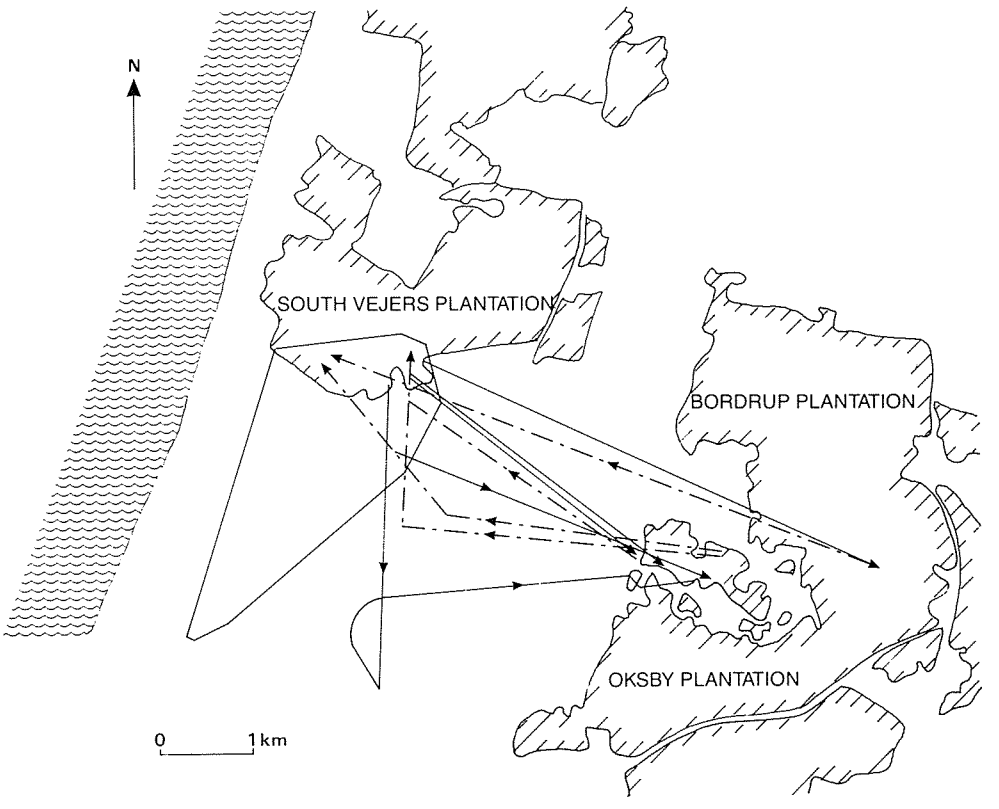


Fig. 13. Flights out of home range (polygon) of hind no. 203 B (from South Vejers) caused by various human disturbances. Both instant flight and 'delayed flight' were recorded. Refuge-area was situated in Oksby plantation.

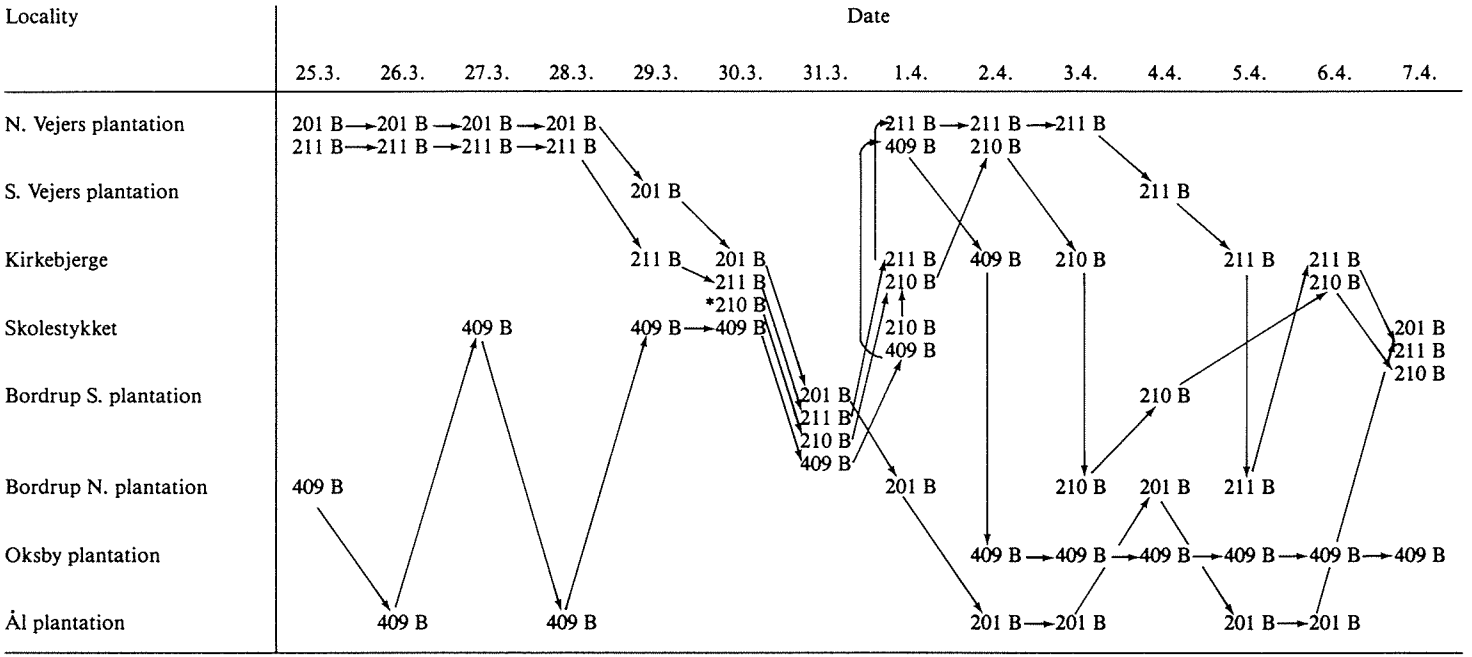
The impact of tourism on the movements of red deer

During the Easter holidays several thousand tourists arrive at their summer cottages along the coast. Judging from the number of caravans, many arrive in the weekend of Palm Sunday and on the Wednesday before Maundy Thursday. Within a few days many people are hiking in the forests, on forest roads and smaller tracks. This especially applies to the plantations along the west coast (Vejers and Kærgaard, see Fig. 1); but also large parts of the other plantations are visited by people during all the Easter holidays.

Normally deer in dense sections of the forests accept people passing by on foot on the forest roads, sometimes only 10-20 m away. The deer also accept logging activities occurring close to their dense cover.

During Easter 1983 the locations of radio-marked red deer were recorded from Friday, March 25th (the weekend up to Palm Sunday) until Thursday, April 7th, when most tourists had left the area. In Table 8 are shown the movements of four red deer.

Table 8. Increased movements of four red deer (1 ♂, 3 ♀), caused by the presence of tourists during a fortnight in Easter 1983 (March 25th – April 7th).



(Hind nos.: 201 B, 210 B, 211 B; Stag no.: 409 B)

* hind no. 210 B, a category 1-hind with home range in North Vejers, was only recorded from March 30th.

Table 9. Ranges of three hinds during three fortnight periods. Due to the presence of tourists, ranges in Easter 1982 were larger than ranges during a comparable period without tourists four weeks earlier. During Easter 1983 ranges had been further enlarged. These data are, however, not directly comparable with 1982-data.

Red deer no.	Range, ha		
	March 8th - 21st 1982*	April 5th - 18th 1982* (Easter)	March 25th - April 7th 1983 (Easter)
210 B	156	220	333
211 B	232	464	808
201 B	384	460	1,280

* 1982 - home range data (grid cell method) from Knudsen (1983)

During the first 3 or 4 days of the fortnight-period nothing unusual was recorded in the movements of the radio-marked deer. But from the 5th and 6th day five out of six radio-marked hinds in the two Vejers plantations moved eastwards, three leaving North Vejers and two remaining in the eastern part of South Vejers. The three hinds from North Vejers and a radio-marked stag from Ål plantation gathered in the open areas between South Vejers and Bordrup plantations, and were together for two days (Table 8). After that they dispersed to different areas, some to North Vejers, and returned later after varying periods of time. During the second week of the fortnight period several deer moved much between different areas. The 6th radio-marked hind in Vejers took flight three times to Oksby plantation (hind no. 203B, see Fig. 13), from where she returned after 1, 1, and 2 days, respectively. Two marked hinds remained within their summer ranges in Bordrup plantation for the entire Easter period. Only one showed reaction to humans and it stayed south of her usual cover in an impassable section of the forest.

For the rest of the radio-marked red deer in the area, especially in the northern part, the pressure from tourists was small. Several deer probably were not aware of the tourists, as the deer stayed on the farmland of Filsø.

As is shown in Table 8 these four deer very rarely stayed in one place more than one day at a time, after they had left North Vejers. This pattern of movements meant that their ranges during this period - and very likely for some time thereafter - were much increased (Table 9). The comparatively small range size of hinds no. 203B and 210B was due to the large distances, they moved away from their home ranges, viz. 4.5 km and 5.5 km, respectively, - thus creating a range of elongated, but very narrow shape.

Observations revealed that many red deer aggregated in the open areas between South Vejers and Bordrup in 'Kirkebjerge' and 'Skolestykket'. The four radio-marked deer also repeatedly returned and stayed in this area, often together. During the actual days of Easter more than 200 red deer were observed in Kallesmærsk moorland, dispersed along a wide front of 2-3 km. Thus many deer left the dune plantations and stayed in the open moors, in areas so far away from public roads that they were difficult to locate.

The patterns of movements during Easter 1983 for the three hinds from North

Vejers, dealt with in Table 8, correspond with the patterns shown during Easter 1982 (KNUDSEN 1983). Also in Easter 1982 all three deer moved eastwards and their ranges were enlarged (see Table 9). Their reactions to the presence of tourists were as described for Easter 1983, just not so pronounced. Observations in North Vejers during Easter 1982 also revealed that the deer were unusually uneasy during the day, as they often passed roads and fire tracks in a rapid pace (KNUDSEN 1983). The human impact on the movements of red deer during the Easter period in 1983 was even further intensified, because of three large orienteering events (with 2,300 participating runners in each race) from Maundy Thursday to Easter eve: March 31st: in Kærgaard South plantation; April 1st: in Bordrup/Oksby; and April 2nd: in Vrøgum plantation (JEPPESEN 1987b). Observations and countings of red deer in these plantations during the orienteering events further elucidate the impact from tourists on the distribution of red deer in the area. In Kærgaard South plantation (a near-shore plantation) there were almost no red deer, as only 13 were reported by posted spotters, and 31 by the runners. On the other hand about 150 red deer were spotted in the open areas near Grærup lake between Kærgaard and North Vejers, and almost 200 red deer in the farmland at Filsø.

Bordrup plantation was crowded with red deer on April 1st; the spotters reporting 139 and the runners 475. Many of the animals were observed more than once but at least 75 red deer took flight away from Bordrup plantation during the event (JEPPESEN 1987b). The large number of red deer in Bordrup at this time resulted from influx of many deer living in Vejers plantation that had been disturbed by the tourists as well as many deer on the open moors between the plantations. The orienteering event in Vrøgum plantation gave 68 observations of red deer by spotters, while the runners saw 193.

Thus, the presence of tourists in the Oksbøl area in Easter 1983 displaced many of the red deer in the plantations near the shore eastwards, either to the neighbouring plantations of Bordrup, Ål, Vrøgum, or to the farmland of Filsø, - or to the intervening open areas. The situation in summer was probably similar, as few deer are seen in the western part of North Vejers at that time. Red deer are also scarce in Kærgaard plantation during summer as most have moved to the farmland of Filsø.

The military does not practise during Easter, because it is not possible to keep the tourists out of the practise area. This is fortuitous as most of the red deer are unable to use the open areas at night during several weeks before and after Easter, because of the military activity (pers. comm. J. HAUSKOV and J. ANDERSEN, plus own observations). Thus, roughly speaking, the red deer have to stay within the forests during several weeks before and after Easter, whereas during Easter they are forced to stay away from the near-shore plantations.

In Easter 1980, there were also a lot of tourists in the Oksbøl area with associated large orienteering events in Kærgaard and North Vejers plantations (JEPPESEN 1987b). At that time many red deer in these plantations were observed leaving during the orienteering events. This means that the red deer had not left these plantations near the shore in advance, due to the presence of tourists. Thus the red deer did not react as drastically to the pressure of tourists in the near-shore plantations in 1980 as in 1983. In 1980 they stayed in these plantations. This must be viewed in connection with a very drastic increase in hunting pressure during the first half of the 1980's, in the number of red deer killed per year in the area, - and in the number of days hunting took place in the area (JEPPESEN 1987a).

Discussion

Home range and movements

All terrestrial mammals spend their lives in a confined area that forms the individual's home range (JEWELL 1966). Fundamentally the home range is an area with a certain productivity that meets the energy requirements of the individual, or group, that occupies it (MCNAB 1963, JEWELL 1966). The individual that lives in a home range benefits by a relatively stable and predictable habitat structure in different seasons (food and cover).

Home range size is determined by the size of the animal and its energy needs (MCNAB 1963, MACE & HARVEY 1983), by the distribution and quality of food, and by the population density (JEWELL 1966, SANDERSON 1966, CLUTTON-BROCK & HARVEY 1978). It is also influenced by the reproductive strategy especially in males (territorial vs. non-territorial species). The degree of persecution and disturbance, and the distribution of cover are further factors, influencing the home range size.

The annual or seasonal category-1 home ranges for hinds in the Oksbøl area (the 'natural' situation, see Table 2) are larger than the home ranges of red deer on the Scottish island of Rhum (CLUTTON-BROCK et al. 1982), and of red deer in the Alps (GEORGII 1980a), but much smaller than the range of red deer in the Scottish highlands (STAINES 1974). These differences in home range size within the same species are usually due to differences in habitat structure with regard to the distribution of preferred food and shelter (STAINES 1974). Category-2 hinds in Oksbøl have large home ranges of the same size as red deer in the Scottish highlands. But except for hind no. 202B (Fig. 4), the large size of home ranges of category-2 hinds is due to the reactions of the deer to human disturbance. The movements of hind no. 202B are likely to be comparable with the movements of Scottish deer, as her preferred habitat was the open grass plains and heather moors, and rarely the large plantations.

There is a large element of tradition in the movements of deer (STAINES 1974, 1977). Individuals use the same seasonal home range in successive years (GEORGII 1980a). As also BLANKENHORN et al. (1978) and GEORGII (1980a) found in red deer in the Alps, some of the hinds in Oksbøl have one annual home range, whereas others shift periodically and traditionally between a summer- and a winter range (either separate or overlapping). A radio-marked (hind no. 404B) from Oksbøl that migrated 25 km between her summer- and winter range, showed the same migration pattern as red deer in Switzerland (BLANKENHORN et al. 1978) and populations of North American elk *(Cervus elaphus canadensis)* (KNIGHT 1970, CRAIGHEAD et al. 1972). Finally, there were also, as described in red deer by BLANKENHORN et al. (1978) and GEORGII & SCHRÖDER (1983), a few marked deer, that emigrated from the Oksbøl area to plantations in the middle of Jutland. These were mainly young stags (2½ - 3½ years old) and were recorded up to 100 km away.

It is well-known that stags often leave their home range, and may wander several km away, and appear in rutting grounds that may be the same from year to year (DARLING 1937, LINCOLN et al. 1970, STAINES 1974, GEORGII & SCHRÖDER 1983). This has also been observed in identifiable stags in the Oksbøl area. On the other hand, the fact that hinds may leave their home range to stay in a rutting ground, as it happens in the Oksbøl area (Table 4, Figs. 4, 11), has not been recorded earlier elsewhere. That they do so, is probably due to the rutting grounds being dispersed in or adjacent to the open land, so that not all hinds have a rutting ground

within their home range. This especially applies to hinds feeding in the privately-owned farmlands. In these areas harems and actual rutting grounds are very rare or absent.

The mean daily range of hinds in the Oksbøl area is larger than that of hinds in the Alps (GEORGII 1980a), and the daily distance that the Oksbøl-hinds move is longer than in red deer on Rhum which during winter move daily 1.8 km and during summer 3.0 km (CLUTTON-BROCK et al. 1982). The daily distance of Oksbøl hinds falls within the daily distance recorded in elk (CRAIGHEAD et al. 1973, LIEB 1981a, BOWYER 1981).

The sparce information about home range and movements of stags in Oksbøl is in accordance with information given by GEORGII & SCHRÖDER (1983) on movements of stags in the Bavarian Alps (the day-to-day movements of which are rather unpredictable. There the home range of stags is also larger than of hinds (GEORGII 1980a, GEORGII & SCHRÖDER 1983). The home range size of stags in the Oksbøl area is, however, much larger than of stags in the Alps, and is more in agreement with the size of 3,850 ha, over 8 months, that ANGIBAULT et al. (1985) found for one stag in France. DARLING (1937) found that the Scottish highland stags were more wide ranging than hinds. AHLÉN (1965) also mentioned that stags covered much larger areas than the hind-groups, and that the hinds occupied the optimum areas. This corresponds with stags in Oksbøl remaining mainly within the forests both day and night (JEPPESEN 1987a). On Rhum the home range of hinds is larger than of stags (CLUTTON-BROCK et al. 1982).

Together with habitat use, home range, and movements, activity patterns provide a good insight into the overall ecology of a species. The relatively few activity studies existing on cervids all give evidence of a bimodal pattern with two peaks of activity at dusk and dawn, respectively (for references, see GEORGII (1981) and CEDERLUND (1981)). Red deer hinds in Oksbøl do not constitute an exception in this respect. The daily cycle of light and darkness acts as a so-called 'Zeitgeber' that synchronizes the animals' activity patterns to the rhythm of the day.

Red deer in the Oksbøl area are mainly active at night, and this is closely related to their need for shelter during the day, as shown by their use of habitat. It is the food (and shelter) that determines daily and seasonal red deer distribution (STAINES 1974). Activity patterns and movements of red deer hinds in Oksbøl reflect the separation of areas of food and shelter. Freedom from disturbance that is provided by forest cover is one of the most important factors determining movements and location of red deer during day time (STAINES 1974). Thus, red deer hinds in the Alps are normally active at night whereas they are inactive and stay in cover during the day; apparently an adaptation to human disturbance and hunting. Only in summer when the deer stay in the alpine highland, with food and shelter evenly distributed does the activity pattern diverge from this, with activity periods evenly distributed during day and night (GEORGII & SCHRÖDER 1978, GEORGII 1980a, b, c, 1981). In the undisturbed population of red deer on Rhum movements of deer in the area are largest during the daylight hours (CLUTTON-BROCK et al. 1982), and the same has been registered in elk (CRAIGHEAD et al. 1973, LIEB 1981a).

The recordings of activity of red deer hinds in Oksbøl are too sporadic to show seasonal variation in daily activity. The length of activity periods in different seasons shows, however, the same tendency as in red deer on Rhum (CLUTTON-BROCK et al. 1982), with long activity periods during winter, and short during summer. This is contrary to what GEORGII (1981) found in

red deer hinds in the Alps, but the pattern there is probably atypical, because of their attachment to winter feeding stations.

Among cervids in the northern hemisphere metabolic rate and food intake decline during winter which is associated with weight loss (for references, see CLUTTON-BROCK et al. 1982). Deer conserve energy during winter by reducing activity and movements within a restricted home range (CRAIGHEAD et al. 1973, MOEN 1976, GEORGII 1980a, GEORGII & SCHRÖDER 1983, CEDERLUND 1981, LIEB 1981a,b, CLUTTON-BROCK et al. 1982). The presence of snow especially reduces activity and home range (RONGSTAD & TESTER 1969, DROLET 1976, GEORGII 1980a, GEORGII & SCHRÖDER 1983, CEDERLUND 1982, BÜTTNER 1983). This explains the small range that hinds no. 201B and 211B had in the winter 1981/82 (see p. 11), as this was the only winter during the study period with a considerable amount of snow. GATES & HUDSON (1979) have shown that a 'thermoregulatory penalty' increased with increased activity in elk exposed to cold, the converse is that an energetic advantage can be obtained by reducing activity as much as possible in winter.

This is contrary to the recordings of home range size of red deer hinds in Oksbøl where winter ranges in most cases were much larger than summer ranges. These large winter ranges must be seen in connection with the reactions of deer to human disturbances.

Human disturbances

When red deer in open habitat in the Oksbøl area are alerted by an approaching car or person they react by crowding together while focusing their senses on the source of disturbance. After a short time, that is from a few seconds to several minutes, the leading hind initiates flight from the area. The rest of the deer then follow her immediately. Red deer alerted within the forest take cover instantly.

The flight distance for a species ('the distance to which a person can approach a wild animal without causing it to flee' (ALTMANN 1958)) varies with a seasonally changing threshold of sensitivity due to reproductive and nutritional status. It varies also due to type of habitat, and to the specific experience of the individual or the group (ALTMANN 1956, 1958). For example, the flight distance is longer in blesbok females *(Damaliscus dorcas phillipsi)* during the first 2 to 4 weeks post partum (ROWE-ROWE 1974). Alarm and flight distances in June were longer in groups of chamois *(Rupicapra rupicapra)* with many kids (and thus a higher number of mothers on the alert), in comparison with groups with a small number of kids (CEDERNA & LOVARY 1985). Moose cows with calves that are old enough to follow their mother, also have longer flight distances, whereas the flight distance is short when the moose cow hesitates to leave her concealed newborn calf (ALTMANN 1958).

Sensitivity also may vary between the sexes. In red deer hinds are generally more wary than stags (MITCHELL et al. 1977). This also applies to a Danish population of roe deer (ANDERSEN 1953) where the percentage of females became still larger, when the population was heavily persecuted, because the males were less wary than the females, and thus were killed first. Reactions to dogs and ranching operations showed that white-tailed deer reacted differently, dependent on sex; the males usually reacted with a long, straight flight out of home range whereas the females usually followed a circuitous escape route that began and ended within their home range (SWEENEY et al. 1971, HOOD & INGLIS 1974).

Humans usually can approach closer in a car than on foot, before flight is released in white-tailed deer (KUCERA 1976), elk

(SCHULTZ & BAILEY 1978) and roe deer (STRANDGAARD 1972). Also flight distance and escape routes in roe deer (NÄSLUND 1979) and white-tailed deer (ECKSTEIN et al. 1979) are shorter when disturbed by snow mobiles than by skiers. Flight distance is shorter during the night than during the day (STRANDGAARD 1972, SCHULTZ & BAILEY 1978, ECKSTEIN et al. 1979). There is also individual variation within a population in their reaction to disturbance (STRANDGAARD 1972 for roe deer).

Cervids appear to have a strong attachment to their home range. STAINES (1977) found that when red deer were disturbed at the edge of their home range they always ran back towards the centre of the range. Red deer in the Oksbøl area often took evasive actions during drive hunts in order to stay within their home range (took cover, or moved in the opposite direction of the beat) (see JEPPESEN 1987b)). GEORGII (1980c) found that when red deer were deliberately startled they did not leave their home range. White-tailed deer that were exposed to heavy hunting pressure, stayed within their home ranges (MARSHALL & WHITTINGTON 1968), and DASMANN & TABER (1956) could not drive black-tailed deer out of their home ranges by means of dogs. In Sweden moose were not driven out of their home ranges during drive hunts (ALMQVIST & SANDBERG 1979).

In some situations dogs have been able to chase white-tailed deer several kilometres from their home ranges (MARCHINTON et al. 1970, CORBETT et al. 1971, SWEENEY et al. 1971, GIPSON & SEALANDER 1977), and the same applies to roe deer (NÄSLUND 1979). In the vast majority of cases the deer returned to their home ranges within 24 hours after the disturbance; although a few deer have remained away for up to 7 days (CORBETT et al. 1971). Radio-marked roe deer in Denmark that left their home ranges when exposed to battues and orienteering events, always returned within 7 hours (JEPPESEN 1987c). Red deer in the Oksbøl area showed analogous reaction patterns following an instant flight out of home range and in far the most cases the deer returned within 4 days (Table 7). The same was seen in red deer that reacted with a 'delayed flight' (see p. 19). 'Delayed flight' seems, however, not to have been described earlier in cervids.

In Oksbøl flight out of home range, almost always ends in a 'refuge-area'. It seems advantageous that red deer are able to flee to specific refuge-areas where they can stay for some days free from repeated disturbances. Presumably refuge areas are learned by the calf when it accompanies its mother in flight from the home range.

Increased movements in an enlarged home range as a reaction to disturbance seem to be a general behavioural adaptation in cervids. It has been recorded in red deer in the Oksbøl area as a reaction to human activities such as hunting, orienteering and tourism. It has also been recorded in male white-tailed deer as a reaction to ranching operations (HOOD & INGLIS 1974), and as a reaction of white-tailed deer to snowmobile traffic (DORRANCE et al. 1975). White-tailed deer also increased their movements when exposed to intensive hunting pressure (MARSHALL & WHITTINGTON 1968). Elk also increased their movements as a reaction to seismic activities (KNIGHT 1981), and elk calves moved over larger areas as a reaction to surface-mining activities and direct human disturbances (KUCH et al. 1985).

Increased movements in an enlarged home range may be advantageous in that the deer learns to know a larger area, and therefore rarely is forced to move into totally unknown terrain. When it is moving much, it is also difficult to track. But often the deer have to leave preferred areas, and the negative effect of increased energy expenditures as a result of the increased

stress-level, and the increased movements and flight may be considerable. As stress factors are cumulative (BAILEY 1984), the effect presumably could be fatal in periods that for other reasons are critical (for example severe winter, breeding season, - see also GEIST (1975)).

Wild ungulates are able to learn and respond, on the basis of their past experience (GEIST 1971a). They generalize from one stimulus to classes of similar stimuli (GEIST 1971a), - for example, they easily become accustomed to predictable events that are at first alarming, but are not followed by painful events, such as highway traffic (GEIST 1971b). The behaviour of ungulates toward human beings is largely a consequence of our behaviour towards them; they are as 'wild' as we teach them to be (GEIST 1971a).

Most species become tolerant to humans if their activity is regular and not in direct conflict with them (STAINES 1974). Elk, that experienced little or no hunting, were very visible and accepted most human activities, such as road traffic and tourists (SCHULTZ & BAILEY 1978). BEHREND & LUBECK (1968) and GRAU & GRAU (1980) showed that white-tailed deer on unhunted areas allowed humans to approach closer than did deer on areas where hunting was permitted.

During hunting seasons the flight distance in cervids is longer than in the rest of the year, the deer become more attentive and wary, and stay in cover in dense forest, or leave preferred areas. This has been recorded in red deer (BATCHELER 1968, DOUGLAS 1971, STAINES 1977), elk (MCCULLOUGH 1969, IRWIN & PEEK 1980, MORGANTINI & HUDSON 1980, LIEB 1981a), white-tailed deer (BEHREND & LUBECK 1968, SPARROWE & SPRINGER 1970, ROSEBERRY & KLIMSTRA 1974, GRAU & GRAU 1980), black-tailed deer *(Odocoileus hemionus)* (DASMANN & TABER 1956), moose (ALTMANN 1958), and roe deer (ANDERSEN 1953, BÜTTNER 1983). It is also the case in red deer in the Oksbøl area, where fewer deer feed in open areas during the hunting season (JEPPESEN 1987a).

As mentioned earlier red deer become nocturnal when exposed to heavy hunting pressure (BATCHELER 1968, DOUGLAS 1971, GEORGII 1980a). This is a general feature in the behaviour of many species when heavily hunted (CLOUDSLEY-THOMPSON 1960). This may be a short-term adaptation (=reversible), as was seen in chamois and red deer (DOUGLAS 1971), which, two years after intensive hunting ceased, returned to their preferred habitats and recommenced diurnal feeding on open grassland.

In the Oksbøl area the hunting season lasts from September to January; a lot of tourists are present in Easter, Whitsun, and during summer (June-August); occasionally a large orienteering event takes place; and the military practises in part of the open areas. Thus, the red deer have to respond to a variety of human activities throughout the year. It is the accumulated effect of all human activities that determines the behaviour of deer in an area. But when hunting becomes intense, as it did in Oksbøl at the end of the study period, the deer become very wary. They are not able to distinguish hunters from other humans, and therefore they react strongly to humans in their area. This is illustrated in the different reactions of red deer in Oksbøl to tourists in Easter 1980 and in 1983, viewed in relation to the large difference in hunting pressure, which was 'normal' in the season 1979/80 and heavy in 1982/83. In Easter 1980 the deer did not leave the near-shore plantations while the tourists were present. But in Easter 1983 the deer were more disturbed by the tourists and left the near-shore plantations. As is described by JEPPESEN (1987b) large orienteering events are the most violent disturbance that the deer are exposed to, and thus this adds to the wariness of deer caused by hunting.

The disturbance that the individual red deer in the Oksbøl area is exposed to varies. It depends on the location of their home ranges in relation to human activities and the response of the individual deer varies due to its past experience and its temperament.

In the plantations in the Oksbøl area bark-stripping by red deer occurs. This is accepted by the forest management, as most of the plantations serve to stabilize the sandy soils and protect them from wind erosion. They are not of commercial importance for wood production. Recordings by VAN DE VEEN (1979) and PRIOR (1984) have shown that red deer when forced by disturbance to stay in dense forest cause damage by bark-stripping. Frightened animals stop ruminating and consequently rumen pH will drop (acidosis), which may cause the rumen epithelium to become damaged (ruminitis) (CHURCH & HINES 1978, VAN DE VEEN 1979). Consumption of bark appears to cure acidosis (VAN DE VEEN 1979).

In the Danish cultivated landscape there is a need for control of the number of red deer, because of the damage they can cause in the forests and in the farmland. The most considerate way of hunting red deer would be to aim at an annual shooting cull that keeps the population at a stable level. Thus, periods of exceptionally heavy hunting pressure causing the stress-effect as experienced in the survey area in 1982/83 could be avoided (see p. 6).

Dansk resumé

Indvirkning af menneskeskabte forstyrrelser på home range, bevægelses- og aktivitetsmønster hos krondyr *(Cervus elaphus)* i Oksbøl området

Danmarks største bestand af fritlevende krondyr *(Cervus elaphus)* lever i klitplantagerne og de omgivende militære hedearealer ved Oksbøl i Vestjylland. I perioden 1980-84 er der i området (175 km²) foretaget undersøgelser over krondyrenes home range, bevægelses- og aktivitetsmønstre, set i forhold til forskellige menneskelige friluftsaktiviteter. Undersøgelserne er især baseret på 2.914 positionsbestemmelser af 18 radiomærkede krondyr (15 hinder, 3 hjorte, se Tabel 1), og der er tillige benyttet automatisk aktivitetsregistrering (Fig. 10).

I løbet af undersøgelsesperioden steg jagttrykket i området drastisk fra et »normalt« jagtudbytte af bestanden på 25% i 1981/82 til 60% i 1984/85 (se JEPPESEN 1987a). Som en tilpasning til jagten er krondyrene i Oksbøl området hovedsagelig nataktive, mens de om dagen opholder sig i dækning i tykninger i skoven.

Hos hinderne er der foretaget en inddeling i: 1)ret stabile bevægelsesmønstre indenfor relativt små home ranges (Tabel 2), og 2)hinder med mere varierende bevægelsesmønstre i ofte meget store home ranges (Tabel 3). Årligt home range i kategori 1 var gennemsnitligt på 257 ± 28 ha, mens det drejede sig om op til 3-4 tusinde hektar i kategori 2. Her skyldtes de store home ranges dog, for langt de fleste hinder, indvirkningen af menneskelige forstyrrelser.

Nogle hinder havde ét årligt home range, mens andre blev registreret i et sommer-range (hvor de søgte føde på græsarealer) og et vinter-range (lyng-arealer). En enkelt radiomærket hind vandrede i april (i de to år hun blev registreret) 25 km nordpå, og vendte tilbage i september. Nogle få radiomærkede hjorte udvandrede. - En del hinder søgte i oktober til brunstpladser udenfor deres home range (Tabel 4, Fig. 4, 11).

Kun en mindre del af de årlige eller sæsonmæssige home ranges blev benyttet indenfor ét døgn. Dagligt home range var i 38 tilfælde 44,5 ± 10,2 ha (Fig. 5).

Hjortenes bevægelsesmønster er meget forskelligt fra hindernes. Hjortene opholdt sig ho-

vedsagelig indenfor skovenes grænser og bevægede sig nærmest siksakkende gennem større arealer end hinderne (Fig. 9).

Der er beskrevet følgende reaktionsmønstre hos krondyrene overfor forstyrrelser foranlediget af jagt, orienteringsløb og turisme: søge dækning; øjeblikkelig flugt; og »forsinket flugt«, hvor dyret bliver i dækning til mørkets frembrud, hvorefter det i ly af mørket i hastigt tempo flygter til en naboplantage. Den gennemsnitlige flugtdistance var på 3.569 ± 396 m (Tabel 7), den længste på 8.000 m.

For kategori 1 hinderne, med små home ranges, varede det fra ½ dag til over en uge, inden de vendte tilbage til det sted, hvorfra de var jaget væk (hyppigst 1-4 dage, Tabel 7). Kategori 2 hinderne, med de store home ranges, vendte ofte først tilbage længe efter (over en uge senere).

Ved gentagne forstyrrelser flygtede kategori 1 hinder næsten hver gang til et for det enkelte dyr ganske bestemt tilflugtsområde (Fig. 13). Flere af hinderne (især i kategori 2) reagerede på forstyrrelser med et stærkt udvidet bevægelsesmønster (Fig. 12), og i perioder med gentagne forstyrrelser, som i jagtsæsonen, strejfede disse dyr over store arealer. Deres home range blev, som følge af det forøgede jagttryk, forstørret betydeligt.

Hvert år i påsken er der en massiv turistinvasion i Oksbøl området. I 1983 bevirkede denne, at flere af de radiomærkede dyr bevægede sig over et større areal med forøget intensitet (Tabel 8). Deres stress-niveau var hævet som i jagtsæsonen. På grund af turisternes tilstedeværelse flyttede en stor del af krondyr-bestanden i de kystnære plantager (Kærgaard, Vejers) østpå til naboplantagerne eller til de åbne arealer imellem. Der var derudover tre store orienteringsløb (med 2.300 deltagere hver gang) i påsken 1983, hvilket forårsagede voldsomme forstyrrelser af krondyrene (se JEPPESEN 1987b). Tre år før, i påsken 1980, var dyrene ikke så skræmte af turisternes tilstedeværelse, og de forlod ikke de kystnære plantager.

Konklusionen er, at dyrene i 1983, på grund af det store jagttryk i sæsonen før påsken 1983 (i forhold til før påsken 1980), var mere skræmte af mennesker generelt. Dyrene kan ikke skelne jægere fra andre mennesker og reagerer derfor stærkere overfor alle mennesker i deres område. Omvendt lærer dyrene i områder uden jagt (og store orienteringsløb), at mennesker er ufarlige. I det danske kulturlandskab er det nødvendigt at holde antallet af krondyr i de forskellige bestande på et stabilt niveau for at begrænse skader på markafgrøder og i skovene. Den mest hensynsfulde måde at drive jagten på vil være at tilstræbe en jævn årlig beskydning af bestanden. Herved undgås unormalt høje jagttryk i perioder, og man undgår den stressende effekt, som sås ved den forøgede jagtintensitet i 1982/83 i forsøgsområdet.

Резюме на русском языке:

Самая многочисленная датская популяция живущих на воле благородных оленей (Cervus elaphus) обитает на засаженных лесом дюнах и окружающих их военных полигонах на пустоши у г. Оксбёль в Западной Ютландии. В периоде с 1980 по 1984 г. в этом районе (175 км^2) проводились исследования "собственных пастбищ", режима передвижения и активности оленей, с точки зрения их зависимости от разных видов человеческой деятельности на открытом воздухе. Исследования в особенности основаны на 2.914 определениях местонахождения 18 оленей, помеченных радиопередатчиками (15 ланей, трех самцов, см. Табл. 1), а кроме того применялась автоматическая регистрация активности (Фиг. 10).

В течение периода исследования в районе резко повысилась интенсивность охоты, с "нормальной" охотничьей добычи, соответствующей 25% популяции в сезоне 1981/82 г. до 60% в сезоне 1984/85 (см. ИЕППЕСЕН 1987 а). Приспособляясь к охоте, олени в районе Оксбёль главным образом активны ночью, а днем скрываются в лесной чаще.

У ланей проведено подразделение на 1) довольно постоянные режимы передвижения в пределах сравнительно небольших "собственных пастбищ" (Табл. 2), и 2) лани с более разнообразными режимами передвижения по часто очень обширным "собственным пастбищам" (Табл. 3). Площадь годового "собственного пастбища" ланей категории 1 в среднем составляла 257 + 25 га, между тем

как у категории 2 она составляла до 3 - 4 тысяч гектаров. Однако, эти обширные площади "собственных пастбищ" у подавляющего большинства ланей объяснялись воздействием вызванных человеком нарушений покоя.

У некоторых ланей было годовое "собственное пастбище", а другие были зарегистрированы на одном летнем пастбище (где они паслись на травянистых пространствах), и на другом зимнем (заросшим вереском). Одна помеченная радиопередатчиком лань в апреле (в двух годах, в которых она была зарегистрирована) ушла на 25 км на север, и возвратилась в сентябре. Немногие из помеченных радиопередатчиком оленей-самцов ушли из района. Многие лани в октябре переходили на места течки вне их "собственных пастбищ" (Табл. 4, Фиг. 4, II).

В течение суток использовалась только небольшая часть годовых или сезонных "собственных пастбищ". Площадь "собственного пастбища" за день в 38 случаях составляла 44,5 + I0,2 га (Фиг. 5).

Режим передвижения оленей-самцов сильно отличается от режима ланей. Самцы главным образом держались в пределах лесов, и передвигались как-то зигзагообразно по более обширным пространствам, чем лани (Фиг. 9).

Описываются следующие неодинаковые реакции оленей на нарушения их покоя, вызванные охотой, состязаниями в беге по лесу и туристами: уходят в укрытие; немедленно убегают; "убегают с запозданием", т. е. животное остается в укрытии до наступления темноты и затем, скрытое темнотой, быстро убегает в соседний лес. Среднее расстояние бегства составляло 3.569 + 396 м (Табл. 7), а самое далекое = 8.000 м.

У ланей категории I, с небольшими "собственными пастбищами", проходило от I/2 дня до целой недели до их возвращения на место, с которого их угнали (чаще всего от I до 4 дней, Табл. 7). Лани категории 2, с обширными "собственными пастбищами", часто возвращались только по истечении долгого времени (дольше недели).

При неоднократных нарушениях покоя, лани категории I почти каждый раз убегали в один и тот-же определенный участок, служивший убежищем каждой отдельной особи (Фиг. I3). Некоторые лани (особенно категории 2) реагировали на нарушения покоя сильно расширенным режимом передвижения (Фиг. I2), и в периодах с неоднократными нарушениями покоя, напр. в сезоне охоты, эти животные скитались по обширным пространствам. Вследствие повышенной интенсивности охоты их "собственное пастбище" значительно расширялось.

Каждый год на пасхе в районе Оксбёль происходит массовое вторжение туристов. В I983 г. это привело к тому, что некоторые из помеченных радиопередатчиками животных более интенсивно передвигались по более обширному пространству (Табл. 8). Уровень их раздраженности был таким-же повышенным, как в сезоне охоты. Вследствие присутствия туристов большая часть популяции благородных оленей из ближайших к морскому берегу лесов (Кэргорд, Вейерс) перешла в соседние леса восточнее их, или на открытые пространства между лесами. Кроме того, на пасхе I983 г. состоялись три больших состязания в беге по лесу (каждое с 2.300 участниками), вызвавшие страшные нарушения покоя оленей (см. ИЕППЕСЕН I987 б). Три года перед этим, на пасхе I980 г., животные были не так сильно испуганы присутствием туристов, и не оставляли ближайших к морю лесов.

Из этого следует, что животные в I983 г. вследствие интенсивной охоты в сезоне перед пасхой этого года (по сравнению с сезоном перед пасхой I980 г.) в общем сильнее боялись людей. Животные не могут различать охотников от других людей, и поэтому сильнее реагируют на любых людей в их районе. И наоборот: животные в районах без охоты (и без больших состязаний в беге по лесу) сообразили, что люди не опасны. В датской культурной среде, численности разных популяций оленей необходимо поддерживать на постоянном уровне, чтобы ограничить вред, причиняемый ими злаковым культурам и лесам. Самым внимательным к оленям порядком ведения охоты было-бы стремление к получению постоянного ежегодного количества убитых животных. Этим было-бы возможно избегать периодических ненормальных повышений интенсивности охоты и того повышенного раздражающего эффекта, который наблюдался в исследованном районе при повышенной интенсивности охоты в I982/83 г.

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Continued cover page 4

Vol. 13

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Part 2. Johnny Lund Jeppesen: Impact of Human Disturbance on Home Range, Movements and Activity of Red Deer *(Cervus elaphus)* in a Danish Environment. pp. 1-38.