

Home Range and Movements  
of Free-Ranging Roe Deer  
(*Capreolus capreolus*) at Kalø

by  
JOHNNY LUND JEPPESEN

Med et dansk resumé:  
Home range og bevægelser  
hos fritlevende rådyr  
(*Capreolus capreolus*) på Kalø

Резюме на русском языке:  
"Собственные пастбища" и передвижение  
живущих на воле косуль (*Capreolus*  
*capreolus*) на землях имения Калё.

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## Abstract

Jeppesen, J. L., 1990: Home range and movements of free-ranging roe deer (*Capreolus capreolus*) at Kalø. – Dan. Rev. Game Biol. **14** (1).

During 1981-83 positions of 11 radio-marked roe deer (*Capreolus capreolus*) were recorded at Kalø, Denmark. Mean annual range was 42 ha for both sexes. Annual range of deer exclusively inhabiting forest was 29 ha, whereas range of deer occupying both forest and open land was 58 ha; this difference was significant ( $p < 0.001$ ). Mean daily range was 8.5 ha (SE = 1.0). Mean daily range and index of locomotory activity (ILA) were recorded in each of three seasons (summer excluded). Female mean daily range was smallest and ILA lowest during spring, whereas male mean daily range was largest and ILA highest during spring. Seasonal variation in daily range size and ILA was assumed to depend mainly on variations in the relationship between energetic demands of roe deer and production of food plants in the area. An exception to this pattern was the greater movements of males in spring; probably a result of territorial behaviour.

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## Introduction

Resources such as food, shelter and mates are distributed unevenly in time and space. Data on home range, movements and activity patterns of a species provide valuable information on space/time utilisation of these resources. Home range is related to body weight and energy requirements of a species (McNab 1963, Harestad & Bunnell 1979, Mace & Harvey 1983). Size of home range is determined by distribution of food, shelter and foraging patterns (e.g. selective vs. bulk feeders) as well as mating systems, population density, predation and human disturbance (Jewell 1966, Sander-son 1966, Clutton-Brock & Harvey 1978, Jeppesen 1987a). As these parameters vary according to habitat and season of the year, so, usually, does home range size of a species.

This paper describes home range and movements of roe deer (*Capreolus capreolus*) in a habitat of forest and agricultural areas at Kalø, Denmark; activity patterns are treated separately in Jeppesen (1989, and in prep.). Data were gathered from undisturbed deer during a study on effects of human disturbance on roe deer (Jeppesen 1987b) and provide a basis of information in an assessment of the effects of disturbance.

The dissimilar distribution of food and shelter in forest habitats and agricultural areas probably affects movements and home range size of roe deer. In order to test this, home ranges of deer occupying one or both of these habitats were recorded.

Furthermore, availability of utilisable energy from food plants varies according to season (e.g. Drozd 1979), as do the energetic demands of roe deer (Drozd et al. 1975, Weiner 1977, Ellenberg 1978); these parameters probably affect foraging patterns of roe deer. Therefore, daily range and movements were analysed in relation to

season and sex and the relationship between seasonal daily range and index of locomotory activity (ILA) on the one hand and energetic demands and production of food plants in home ranges on the other are discussed.

## Acknowledgments

I am greatly indebted to Dr. R. Terry Bowyer who critically reviewed the manuscript and to Cand. scient. Tommy Asferg who developed computer programmes for the analysis of home range data. Thanks are also due to Radio Technician Bo Gaardmand who participated in locating radio-marked deer, in particular during 24-h recordings, and who kept the receiving system in order.

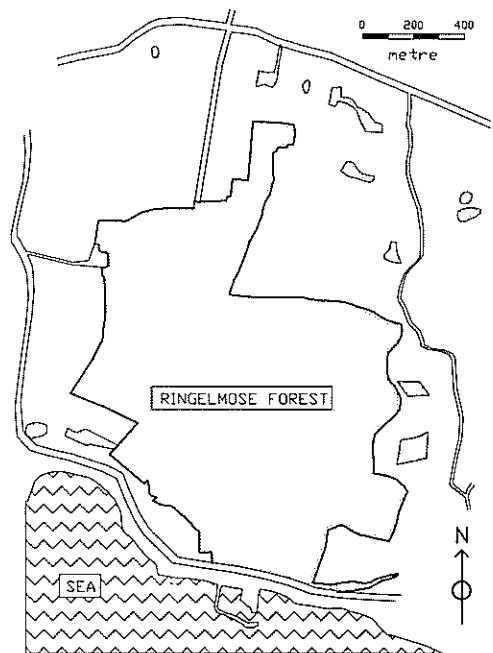


Fig. 1. Map of the Kalø study area.

## Materials and methods

The study area (Fig. 1) and its roe deer population have been thoroughly described by Jeppesen (1989). Additionally it should be mentioned that adult males weigh 21-23 kg and adult females about 1 kg less (Andersen 1953, Strandgaard 1975).

During 1980-84, 35 roe deer were radio-marked for tracking purposes and for automatic activity recordings. They were trapped during winter in small enclosures, following procedure described by Strandgaard (1972), and fitted with radio-collars of different colours. Both transmitters and collars (modified Grimsø design (Cederlund et al. 1979)) were produced at Kalø. Weight of radio-collars was 200-250 g and transmitters functioned in the 151 MHz range. Expected battery life (lithium cells) was 2-3 years.

An AVM-LA12 (USA) receiver was connected to a 6-element yagi antenna. Radio-tracking was performed from a vehicle from which both antenna and compass were raised 6 m above ground by means of a pneumatic, telescopic mast. A repeater compass could be read in the van.

The location of deer was determined by triangulation of two to three bearings, a method described in detail by Cederlund et al. (1979). Accuracy of bearings was  $\pm 2^\circ$  and distance from transmitter-animal to receiver rarely exceeded 1 km. Bearings were obtained from fixed stations located throughout the area, employing a map of the area (1:10,000) with grid squares. The analysis is based on 3,675 radio location fixes on 11 adult deer (8 ♀, 3 ♂) during 1981-83. Positions of deer during and after flights from human disturbance (see Jeppesen 1987b) were not included.

Annual ranges were estimated from data comprising 50-320 fixes per animal per year. For each individual, sample size was tested against home range size; 50 fixes

resulted in home range estimates that averaged 84% of the sizes estimated from samples larger than 50. Therefore, 50 fixes were considered an adequate number to describe the home range of each individual. Seasonal ranges were not estimated because the number of fixes per season (e.g. 50-100 distributed over four seasons), with the exception of a few individuals, was small. A total of 2,248 fixes stem from 108 24-h recordings, each comprising 18-22 locations per deer; 24-h recordings were conducted twice a month during October 1982-May 1983. Technical problems prevented 24-h recordings during summer 1983.

Home range data were analysed using computer programmes, developed by Asferg (unpubl.) at the Game Biology Station. Size of annual and daily ranges was estimated by combining the outermost positions to form a convex polygon (Mohr 1947). As ranges were based on non-statistical estimates, it was not important whether a lack of independence (auto-correlation) existed between successive points with short time-intervals (Swihart & Slade 1985).

Following Bideau et al. (1983) and Vincent et al. (1983), seasonal indices of locomotory activity (ILA, m/h) were calculated, employing 24-h recordings: 1) for each 24-h period, distances between chronologically ordered fixes were calculated, added, and the sum divided by 24. Due to the inherent uncertainty of fixes, only distances  $\geq 100$  m were included 2) each distance ( $\geq 100$  m) between chronologically ordered fixes was corrected to distance per hour and an index per hour for all 24-h obtained.

For comparison of samples of home ranges and samples of ILA's student-t tests (Downie & Heath 1970) were performed.

## Results

### Annual ranges

The size of annual home range varied from 16 to 81 ha, with a mean of 42 ha for both males and females (Table 1). The mean annual range of deer exclusively occupying forest habitat was half the size of that occupied by deer inhabiting both forest and agricultural areas (Table 1); this difference was significant ( $t=5.64$ ;  $df=22$ ;  $p<0.001$ ). Sample size of ranges within each of the habitat types 'forest' and 'forest and open land' was too small to allow comparisons between the sexes.

Home ranges were not uniformly used (Fig. 2); instead, roe deer were frequently located in the parts of their range that provided shelter and/or food. For deer inhabiting both forest and open areas, coverts and hedgerows influenced shape and use of home range (Fig. 2). Agricultural areas were used more often at certain periods of the year according to availability of crops. Thus, during spring roe deer were especially attracted to winter crops and during autumn to fields of sugar beets. During summer, most fields provided shelter for roe deer.

### Daily ranges

Roe deer used only a part of their range during a 24-h period. Size of daily ranges during October-May varied from 1 to 27 ha, with a mean of 8.5 ha. Means for males

and females (Table 2) did not differ significantly ( $t=1.34$ ;  $df=105$ ;  $p>0.10$ ).

For the three seasons tested, mean daily range for females was smallest during spring (Fig. 3a); the difference was significant compared to winter ranges ( $t=2.33$ ;  $df=34$ ;  $p<0.05$ ) but not when compared to autumn ranges ( $t=1.09$ ;  $df=22$ ;  $p>0.10$ ). For males, mean daily range was significantly larger during both winter and spring compared to autumn (Fig. 3b) (autumn:winter,  $t=2.15$ ;  $df=22$ ;  $p<0.05$ ; autumn:spring,  $t=2.67$ ;  $df=14$ ;  $p<0.05$ ). During spring, mean daily range was significantly larger for males than for females ( $t=3.19$ ;  $df=18$ ;  $p<0.01$ ) whereas differences between sexes during autumn and winter were not significant ( $t=0.94$ ;  $df=18$ ;  $p>0.10$  and  $t=1.37$ ;  $df=38$ ;  $p>0.10$ ).

### Locomotory activity

As with daily range, the seasonal ILA (Fig. 3a) for females was significantly lower during spring than during winter ( $t=2.11$ ;  $df=34$ ;  $p<0.05$ ). For males, ILA was highest during spring and significantly higher than during autumn ( $t=2.20$ ;  $df=14$ ;  $p<0.05$ ) (Fig. 3b). Furthermore, male ILA during spring was significantly higher than the value for females ( $t=3.79$ ;  $df=18$ ;  $p<0.01$ ).

ILA for females during the 24-h period

Table 1. Mean & SE of annual ranges (ha) for roe deer at Kalo during 1981-83.

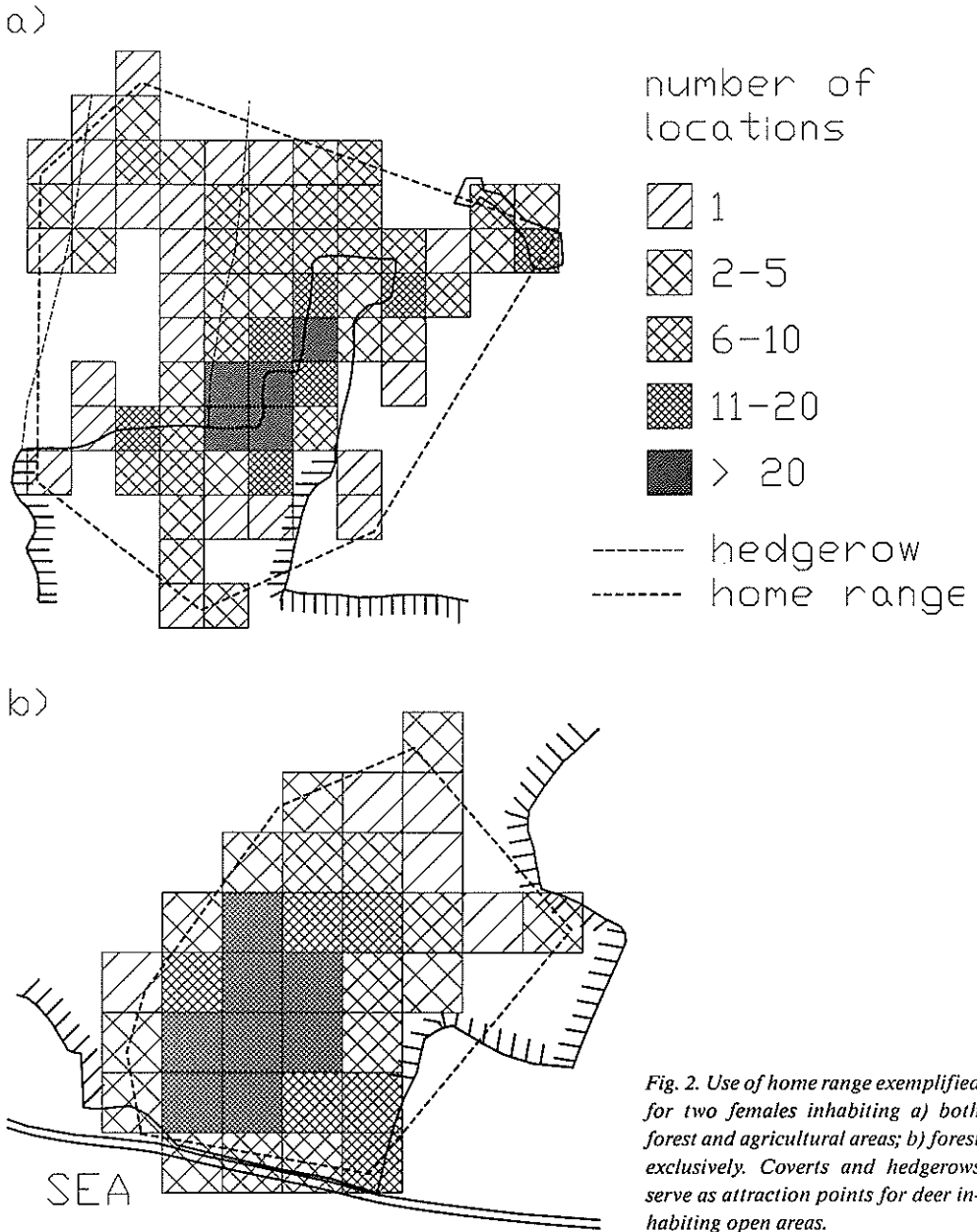
	Roe deer in study area	Females	Males	Deer inhabiting	
				forest + open land	forest only
N	24	16	8	11	13
$\bar{X}\pm SE$	42 $\pm$ 8	42 $\pm$ 11	42 $\pm$ 10	58 $\pm$ 9	29 $\pm$ 5



Home Range and Movements of Free-Ranging Roe Deer

Table 2. Mean & SE of daily ranges (ha) for roe deer at Kalo during October 1982-May 1983.

	Both sexes	Females	Males
N	108	72	36
$\bar{X} \pm SE$	$8.5 \pm 1.0$	$8.1 \pm 1.1$	$9.4 \pm 2.0$



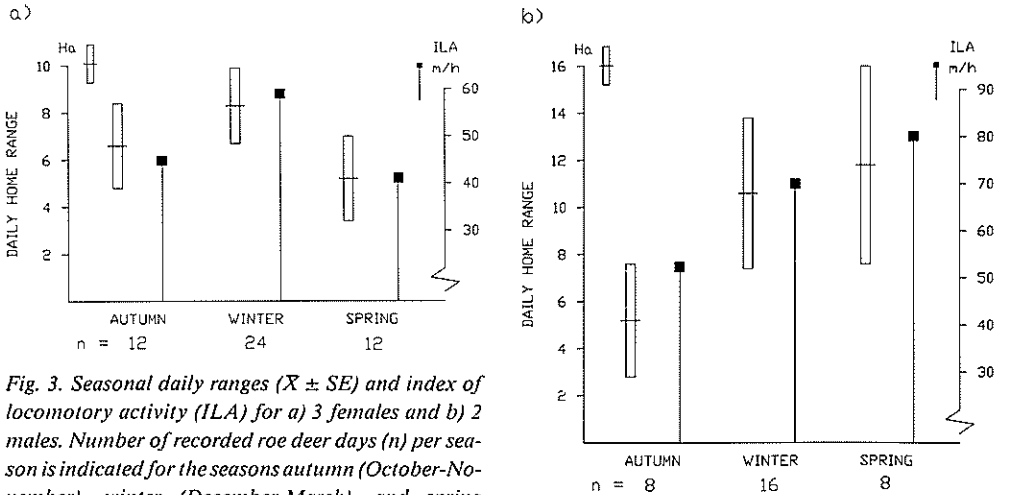
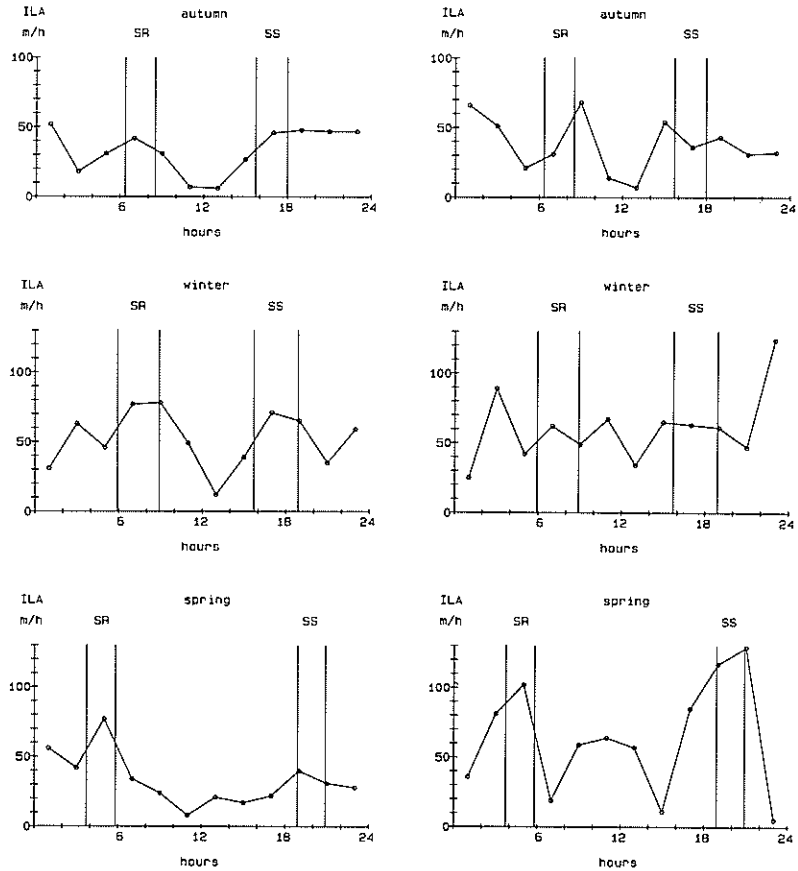


Fig. 3. Seasonal daily ranges ( $\bar{X} \pm SE$ ) and index of locomotory activity (ILA) for a) 3 females and b) 2 males. Number of recorded roe deer days (n) per season is indicated for the seasons autumn (October-November), winter (December-March), and spring (April-May).



showed a mid-day minimum through all seasons with peaks at sunrise and sunset (Fig. 4a). This two-peaked pattern also appeared for males: distinct during spring but not during winter (Fig. 4b).

## Discussion

Annual home range size of roe deer at Kalø lies well within the extent of ranges documented for other European populations. Ranges with means below 15 ha are known from English (Bramley 1970, 1977, Loudon 1978) and Polish (Bobek 1977, Fruzinski et al. 1983) populations inhabiting forested areas. Other populations occupy ranges comparable in size to those at Kalø (Bobek 1977, von Berg 1978, Sempéré 1979a, b, Janeau et al. 1981, Cederlund 1983, Vincent et al. 1983, Bideau et al. 1983, 1985, Maublanc et al. 1985, Putman 1988). The largest annual ranges ( $\bar{x}$ =380 ha) were documented for 'field roe deer', living in habitats with large monocultures of agricultural crops in Eastern Europe (Zejda & Bauerova 1985).

In several populations, males occupy larger annual ranges than females (Bobek 1977, Putman 1988). In a population of field roe deer, however, females had larger ranges than males (Zejda & Bauerova 1985). Differences between sexes were not found for roe deer in the present study, but differences in range size between habitat types were obvious. A difference in home range size between sexes would not be predicted from the small difference in mean body weight between sexes at Kalø (cf. p.5).

For deer inhabiting both forest and open land, seasonal changes in distribution of

food plants and cover according to farming practices were probably major factors in determining the large ranges compared to animals occupying forest habitat exclusively. Use of annual home range (Fig. 2) showed that large parts, especially the fields, were not utilised at all; other parts were used intensively for only a portion of the year.

The size of daily ranges found in the present study was about half the size reported for French and Swedish roe deer (Bideau et al. 1983, Vincent et al. 1983, Cederlund 1983). Seasonal variation in daily range and ILA may be related to foraging patterns and to behaviour associated with the reproductive cycle; both differ according to sex. If the hypothesis that an animal utilises the minimum area that can sustain its energetic requirements (Harestad & Bunnell 1979) is correct, size of home range would be determined by the amount of utilisable energy available and the energy requirements of the deer and would vary with season. Geist (1982) suggested that when the amount of utilisable energy increases, movements within the home range should decline. Results from this study support Geist's hypothesis: daily ranges of roe deer at Kalø were small and ILA was low during autumn; a period when fat deposits are built up (Hoffmann 1977) and the amount of utilisable energy is high. Males have abandoned territoriality and small groups of roe deer feed together (cf. Jeppesen 1989). Thus, during autumn social interactions are probably not major factors governing daily range use.

During winter, the energetic requirements of roe deer decline (see Jeppesen 1989), as does production of utilisable

Fig. 4. Index of locomotory activity (ILA) throughout the 24-h period for three seasons (see text to Fig. 3) presented as mean values per 2 hours for a) females, b) males. See Fig. 3 for number of recorded roe deer days per season.

energy from the habitat. In accordance with the previously mentioned hypotheses, a more rapid decline of productivity than of requirements during winter may explain the increase from autumn to winter in both daily home range and movements of both sexes. Snow rarely impedes movements of roe deer at Kalø. Daily home ranges during winter in a French population of roe deer (Bideau et al. 1983, Vincent et al. 1983) did not differ from autumn ones although daily movements of females declined. Daily home ranges of Swedish roe deer declined from autumn to winter (Cederlund 1983) and were strongly affected by deep snow.

Large numbers of new shoots become available during spring and deer feed to a great extent on the herb layer of the forest floor, especially on *Anemone nemorosa* (Strandgaard 1972). Basal metabolism and, consequently, energy requirements, increase during spring in both males and females (Drozdz et al. 1975, Weiner 1977, Ellenberg 1978). However, productivity at Kalø apparently shows an even steeper increase. In spring females exhibit limited movements and smaller daily home ranges compared to winter. This same trend was noted for roe deer females in France (Vincent et al. 1983). In spring, gestating females demonstrate more solitary behaviour prior to parturition (Bubenik 1965, Kurt 1968, own observations). High productivity ensures that they are able to remain within a limited area. In contrast, Swedish females increased their daily range

from winter to spring, probably because of a scattered distribution of early green plants (Cederlund 1983); nevertheless, mean daily range of Swedish males during spring was significantly larger than that of females.

Increased movements and enlarged daily ranges of male roe deer during spring, as recorded in the French and Swedish studies (Mauget & Sempéré 1978, Sempéré 1979a, Bideau et al. 1983, Cederlund 1983), are probably not explained by the relationship between requirements and productivity since they should then exhibit a pattern similar to females. Instead, territorial behaviour is probably the dominant factor (see Jeppesen 1989).

Sempéré (1979a) and Bideau et al. (1983) noted a pattern of territorial movements at the periphery of ranges of males during spring. Such peripheral movements were not documented for males at Kalø; rather, fixes indicated a greater use of central areas (Jeppesen, unpubl. data), as also noted for Swedish males (Cederlund 1983).

Peaks in movements (ILA) at dawn and dusk coincided with the two peaks in daily activity noted previously for roe deer at Kalø (Jeppesen 1989). The largest movements were recorded when deer moved to and from feeding areas, in particular from forest cover to open fields and back. 'Travelling activity' in French roe deer also peaked during twilight (Mauget & Sempéré 1978, Bideau et al. 1983, Vincent et al. 1983).

## Dansk resumé

### Home range og bevægelser hos fritlevende rådyr (*Capreolus capreolus*) på Kalø

Elleve radiomærkede rådyr (*Capreolus capreolus*), 8 råer og 3 bukke, blev i perioden 1981-83 fulgt ved hjælp af pejleudstyr i og omkring Ringelmoseskoven på Kalø i Østjylland. Positionsbestemmelser blev foretaget på alle årstider og udgjorde det basismateriale, der gjorde det muligt at vurdere den forstyrrende effekt af menneskelige aktiviteter i skoven (se Jeppesen 1987). Fra oktober 1982 til maj 1983 blev der to gange om måneden udført en 24-timers registrering af rådyr, med 18-22 positioner pr. dyr pr. døgn. På grund af tekniske vanskeligheder blev der ikke udført 24-timers registreringer i sommeren 1983.

Home range for det enkelte dyr blev bestemt ved at forbinde de yderste af de registrerede positioner, så en konveks polygon dannedes. Størrelsen af det årlige home range for rådyr på Kalø varierede fra 16 til 81 ha, med et gennemsnit på 42 ha for begge køn. Rådyr, som udelukkende opholdt sig i skovbiotopen, havde et gennemsnitligt home range på 29 ha, mens det var dobbelt så stort for dyr, der dels opholdt sig i skoven, dels i det åbne land (Tabel 1).

Dyrene blev overvejende registreret, hvor der var føde og/eller dækning, og i det åbne land havde remiser og levende hegn stor indflydelse på formen og brugen af home range (Fig. 2). Markarealer kunne benyttes intenst i en periode, f.eks. om foråret, og ellers ikke resten af året, hvor arealerne, afhængig af afgrøde, kunne være uden værdi mht. føde eller dækning.

Rådyrene udnyttede kun en del af deres home range i det enkelte døgn. Størrelsen af det dagli-

ge home range varierede fra 1 til 27 ha, med et gennemsnit på 8,5 ha.

Hos råerne var både det daglige home range og bevægelses-indekset ILA (index of locomotory activity), der på basis af 24-timers registreringer udtrykker de tilbagelagte meter/time, mindst om foråret (Fig. 3a); bukkene derimod havde det største daglige home range om foråret, og bevægelses-indekset (Fig. 4) toppede omkring solop- og nedgang.

Variationerne i den sæsonmæssige størrelse af dagligt home range og bevægelses-indekset kan for efterårs- og vinterperioderne ses som et samspil mellem svingninger i rådyrenes energikrav og områdets produktion af fødeplanter. Om efteråret behøver dyrene ikke at bevæge sig meget efter den rigelige føde. Om vinteren aftager rådyrs energikrav, men områdets produktivitet falder sandsynligvis endnu mere. Dette kan forklare stigningen fra efterår til vinter i bevægelser (m/time) og dagligt home range. Sne udgør sjældent nogen hindring for rådyrs bevægelser på Kalø.

Om foråret skifter drægtige råer fra at leve i flokke til at leve enligt. En meget stor produktion af nyspirede planter gør det muligt for råerne at ernære sig inden for et begrænset areal, og så selvom råernes energikrav i perioden op til fødslen stiger kraftigt.

Bukkens store bevægelses-indeks og daglige home range om foråret kan ikke forklares af forholdet mellem dyrenes energikrav og områdets produktivitet; det må sandsynligvis tilskrives deres territoriale adfærd.

Резюме на русском языке:

"Собственные пастбища" и передвижение живущих на воле косуль (*Capreolus capreolus*) на землях имения Калё.

При помощи радиолокаторов в периоде с 1981 по 1983 г. проводились наблюдения за одиннадцатью помеченными радиоаппаратами косулями (*Capreolus capreolus*), 8 самками и 3 самцами, в лесу Рингельмозе и его окрестностях на имении Калё в Восточной Ютландии. Местоположения определялись во все времена года, и служили основным материалом, позволявшим оценку воздействий нарушений покоя, вызванных человеческой активностью в лесу (см. Йеппесен 1987).

С октября 1982 г. по май 1983 г. два раза в месяц производились круглосуточные регистрации косуль, с 18–22 местоположениями за косулю за сутки. Вследствие технических затруднений, летом 1983 г. круглосуточных регистраций не производилось.

"Собственные пастбища" отдельных косуль определялись соединением между собой крайних местоположений, так что образовался выпуклый многоугольник. Величина годового "собственного пастбища" косуль на Калё колебалась от 16 до 81 га., со средней величиной в 42 га. у особей обоих полов. Косули, исключительно проживавшие в лесном биотопе, средним числом имели "собственное пастбище" в 29 га., а у косуль, проживавших отчасти в лесу, а отчасти в открытой местности, оно было вдвое обширнее (Табл. I).

Косули главным образом регистрировались, где были пища и/или прикрытие, и в открытой местности убежища для дичи и живые изгороди оказывали значительное влияние на форму и использование "собственного пастбища" (Фиг. 2). Кивами животные иногда интенсивно пользовались в течение определенного периода, например весной, но не в остальные времена года, когда эти пространства, зависимо от вида злаков, не были пригодны для пищи или прикрытия.

В отдельные сутки косули использовали

только часть своего "собственного пастбища". Величина ежедневного "собственного пастбища" колебалась от одного до 27 га., и средним числом составляла 8,5 га.

У самок как ежедневное "собственное пастбище", так и показатель передвижения ЦА, на основании круглосуточных регистраций указывающий пройденное число метров/час, были наименьше весной (Фиг. 3а); у самцов же наибольшее "собственное пастбище" было весной, а максимум показателя передвижения (Фиг. 4) наступал около восхода и захода солнца.

Сезонные изменения величины ежедневного "собственного пастбища" и показателя передвижения в осенние и зимние периоды могут объясняться как результаты взаимодействия колебаний потребности энергии косуль и продукции пищевых растений на данном участке. Осенью животным не нужно много передвигаться для обильного питания. Зимой потребность энергии у косуль понижается, но продуктивность местности вероятно понижается еще сильнее. Этим можно объяснить повышение передвижения (м/ч) и увеличение ежедневного "собственного пастбища" с осени до зимы. Снег передвижению косуль на Калё мешает только редко.

Весной стельные самки переходят от образа жизни табунками на жизнь поодиночке. Очень значительная продукция молодых растений предоставляет косулям-самкам возможность питаться на ограниченном пространстве, невзирая на то, что их потребность энергии в периоде до родов сильно повышается.

Более высокий показатель передвижения и более обширные "собственные пастбища" самцов весной не могут объясняться соотношением между требуемой ими энергии и продуктивностью местности; они вероятно объясняются их территориальным поведением.

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