Acta Theriologica 52 (2): 113–118, 2007.
PL ISSN 0001–7051

Factors affecting daily ranges of red deer *Cervus elaphus* in Białowieża Primeval Forest, Poland

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Kamler J. F., Jędrzejewska B. and Jędrzejewski W. 2007. Factors affecting daily ranges of red deer *Cervus elaphus* in Białowieża Primeval Forest, Poland. Acta Theriologica 52: 113–118.

Daily ranges of 19 (6 males, 13 females) adult red deer *Cervus elaphus* Linnaeus, 1758 were studied using 24-h tracking sessions in Białowieża Primeval Forest (BPF), Poland, from 2001 to 2004. Overall, size of mean (± SE) daily ranges was larger for males (1.22 ± 0.10 km^2) than females (1.00 ± 0.09 km^2), although the difference was not significant. Similarly, mean daily ranges were 6–46% larger for males than females in each season, although there were no statistical differences in mean daily ranges among seasons for each sex. Abiotic factors, especially temperature, significantly affected daily ranges of females, but not males, suggesting sexual differences in response to weather variables. On a daily basis, males used 3% of their annual home range, whereas females used 12% of their annual home range, indicating females used their annual home ranges more intensely than males. Consecutive daily ranges overlapped little for each sex. Daily ranges of red deer in BPF were considerably larger than previously reported in Europe, suggesting factors unique to BPF also influenced size of daily ranges.

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Key words: *Cervus elaphus*, daily range, Poland, red deer, snow cover, temperature

Introduction

Red deer *Cervus elaphus* Linnaeus, 1758, occurring in most countries in Europe, are sexually dimorphic and gregarious, and adult males and females typically do not associate with each other outside the mating season. Among sexually dimorphic and gregarious ungulates, differences in morphology and/or reproductive strategies result in sexual differences in space and habitat use (Geist and Petocz 1977, Watson and Staines 1978, Clutton-Brock *et al.* 1987, Miquelle *et al.* 1992, Conradt 1998). Consequently, movements of male red deer are influenced by male-male competition and access to females, whereas female movements are influenced by female--female competition, raising young, and distri-

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bution of higher quality food resources (Clutton-Brock *et al.* 1982, Appleby 1983, Carranza *et al.* 1990, Thouless 1990, Albon *et al.* 1992, Post *et al.* 1999).

Although several studies have indicated the above factors result in sexual differences in red deer movement patterns over seasons and years (Clutton-Brock *et al.* 1982, Georgii and Schroder 1983, Catt and Staines 1987, Carranza *et al.* 1991, Koubek and Hrabe 1996), whether they also contribute to differences in specific daily movements are not clear. For example, male and female red deer moved similar distances during a 24-h period in Scotland (Clutton-Brock *et al.* 1982) and Germany (Georgii 1980, Georgii and Schroder 1983), but not in Spain (Carranza *et al.* 1991). Also, seasonal differences in daily movements of red deer occurred in some areas (Clutton-Brock *et al.* 1982, Georgii 1980, Georgii and Schroder 1983), but not others (Jeppesen 1987, Carranza *et al.* 1991). Reasons for these differences among study sites are not clear, but could be related to differences in habitat or deer densities. Daily movements of red deer in the above studies tended to show a high degree of variability, yet no studies looked at the effects of daily fluctuations in abiotic factors on deer movements. This information would help explain if daily movements are more affected by broad differences in reproductive strategies, or by changes in energy requirements due to daily variation in abiotic conditions.

In Białowieża Primeval Forest (BPF), Poland, annual and seasonal home ranges of male red deer were larger than those of females, and seasonal differences in home range size appeared to be influenced by the different reproductive strategies of each sex (J. Kamler, W. Jędrzejewski and B. Jędrzejewska, unpubl.), similar to that reported in previous studies. To determine if daily ranges were also influenced by these same factors, we analyzed continuous 24-h tracking data on 19 adult red deer (6 males, 13 females) monitored from 2001 to 2004. Our hypotheses were that daily ranges of red deer would be larger for males than females, and that daily movements for each sex would respond differently to the seasons. Additionally, we determined if abiotic factors (temperature, rainfall, and snowfall) had different effects on daily ranges of males and females. Finally, we tracked some individuals for several days to determine if sexes differed in overlap of consecutive daily ranges.

Study area

Our study occurred in Białowieża National Park (BNP; 100 km^2) and adjacent managed forests, all of which are part of Białowieża Primeval Forest (BPF) in northeastern Poland (52°43'N, 24°E). The BPF is a large (1500 km^2) mixed-deciduous forest covering 580 km^2 in Poland and 870 km^2 in Belarus. The BPF contains old growth forest stands and is the best preserved woodland of its kind in temperate Europe. Tree stands consist of oak *Quercus robur*, spruce *Picea abies*, pine *Pinus sylvestris*, hornbeam *Carpinus betulus*, black alder *Alnus glutinosa*, ash *Fraxinus excelsior*, birches (*Betula verrucosa* and *B. pubescens*) and mixtures of several other species. The terrain is flat and elevation is 134–185 m a.s.l. Open areas within BPF consist of marshes of sedge *Carex* spp. and reed *Phragmites* spp. in river valleys (< 1 km wide) and several glades next to small villages.

The climate is transitional between continental and Atlantic types, although the continental type prevails (Jędrzejewska and Jędrzejewski 1998). During the study, mean temperature of January ranged from –1.4 to –6.1°C, whereas that of July from 20.9 to 21.9°C. Mean annual precipitation was 534 mm (range: 500–603), and annual mean number of days with snow cover was 77 (range: 66–98). Daylight hours range from 7 h 42 min in winter to 16 h 45 min in summer.

The BPF has one of the most diverse communities of native predator-prey species in Europe. In addition to red deer, other native ungulates are European bison *Bison bonasus*, moose *Alces alces*, roe deer *Capreolus capreolus*, and wild boar *Sus scrofa*. The main predators of red deer in BPF, wolves *Canis lupus* and lynx *Lynx lynx*, occur in stable populations (Jędrzejewska and Jędrzejewski 1998). All hunting by humans is prohibited in BNP, but in surrounding managed forests it is allowed for red deer, roe deer, and wild boar.

Material and methods

We captured red deer in drop-net traps (Jędrzejewski and Kamler 2004) placed in openings and glades at the forest edge in BNP and its buffer zone. Trapping occurred in March and December 2001, January and December 2002, and February 2003. We immobilised captured deer with an intramuscular injection of ketamine hydrochloride and xylazine (2.5:1.5 ratio), and removed them from the nets. We then placed radio-transmitter collars (Margus, Poland), most equipped with activity sensors, on study animals to monitor their movements. Deer were classified as adult (>2 yr) or young (< 2 yr) based on body size, reproductive condition, and for males, antler size.

We recorded telemetry locations of each study animal 1–3 times per week throughout the study. Additionally, 24-h tracking sessions (locations every 30 minutes) were conducted on individuals at least once per season. Seasons were defined as winter (December–March), summer (April––July) and autumn (August–November) to parallel major changes in climate, corresponding changes in vegetation, and main biological periods for red deer (rutting, birthing, etc.). Radio-collared red deer were located and/or followed using a network of paths and roads that dissected the forest into 250-m compartments, which were clearly marked with numbered stones. To estimate deer locations, observers took ≥ 2 bearings (< 10 min apart) from different stone markers, after encircling and approaching within 500–1000 m from the deer. Point estimates (eg, x, y coordinates) were calculated by drawing bearings on 1:25 000 map of the study area, and then entered into a computer database. Mean (± SD) error for reference collars placed in known locations (n = 54) was 90.5 ± 59.0 m.

Based on data from 24-h tracking sessions, we calculated daily home ranges for deer using the minimum convex polygon method (MCP; Mohr 1947) in ArcView (version 3.2, Environmental Systems Research Institute, Inc., Redlands, California, USA) with the Animal Movement extension (Hooge and Eichenlaub 1997). The MCP was the most appropriate method for calculating daily ranges because we collected continuous (ie, not independent) point locations, and assumed all locations reflected the actual area used within a 24-h period. Number of locations per daily home range was relatively constant at 42–48 locations. Mean daily home ranges were compared between sexes and among seasons using a t-test and one-way ANOVA, respectively. For these tests, we assumed all daily ranges were independent, because individual deer were tracked only once per season. Statistical Power (power = $1 - \beta$, where beta is the probability of committing a type II error) was assessed with GPOWER (Faul and Erdfelder 1992).

To determine patterns of home range use, some deer were monitored continuously for 2–4 days. Percent overlap of daily ranges was calculated based on percentage of daily range area overlapping that of the next day. Mean percent overlap was compared between sexes using a t-test.

Meteorological data were provided by the Białowieża Meteorological Station (in central part of BPF), and included mean daily temperatures (°C), daily amount of rainfall (mm), and mean daily snow depth (mm). Multiple regression analyses were used to determine if these abiotic factors influenced daily range size for each sex.

Results

From June 2001 to March 2004, 102 daily ranges were calculated from 13 adult female and 6 adult male red deer in BPF. Overall, mean (± SE) daily range sizes were 22% larger for adult males (1.22 ± 0.10 km^2, range = 0.19–3.16 km^2, n = 50) than females (1.00 ± 0.09 km^2, range = 0.08–3.24, n = 52), although the difference was not significant (t = 1.604, df = 100, p = 0.353, power = 0.355). In the different seasons, mean daily ranges of males were 6–46% larger than those of females, but none of those differences were statistically significant (summer: t = 1.618, df = 27, p = 0.117, power = 0.314; autumn: t = 1.169, df = 21, p = 0.256, power = 0.199; winter: t = 0.260, df = 48, p = 0.796, power = 0.057; Table 1). Mean daily ranges did not differ among seasons for males (ANOVA: $F_{2,47}$ = 0.463, p = 0.632, power = 0.121) or females (ANOVA: $F_{2,49}$ = 0.436, p = 0.649, power = 0.117; Table 1).

During 24-h tracking sessions, mean daily temperature ranged from –7.1 to 22.4°C, daily rainfall ranged from 0 to 21 mm, and daily snowfall ranged from 0 to 27 mm. Among adult males, multiple regression analysis showed that daily ranges (in hectares, log-transformed) were not affected by ambient temperature, snow cover, or rainfall (R^2 = 0.05, n = 50, p = 0.470). Among adult females, the same set of weather variables explained 20.6% of variation in daily range size (R^2 = 0.21, n = 52, p = 0.010). Of the three independent variables included in the regression

Table 1. Mean (± SE) daily range sizes (in km^2) of adult red deer *Cervus elaphus* during different seasons in Białowieża Primeval Forest, Poland (2001–2004). Summer – April–July, Autumn – August–November, Winter – December–March, n – number of daily ranges analyzed.

Season	Adult males			Adult females		
	n	Mean ± SE	Min–max	n	Mean ± SE	Min–max
Summer	18	1.23 ± 0.15	0.23–2.13	11	0.84 ±0.19	0.08–2.30
Autumn	12	1.36 ± 0.22	0.25–2.67	11	0.97 ± 0.25	0.22–2.44
Winter	20	1.12 ± 0.17	0.19–3.16	30	1.06 ± 0.12	0.39–3.24
Whole year	50	1.22 ± 0.10	0.19–3.16	52	1.00 ± 0.09	0.08–3.24

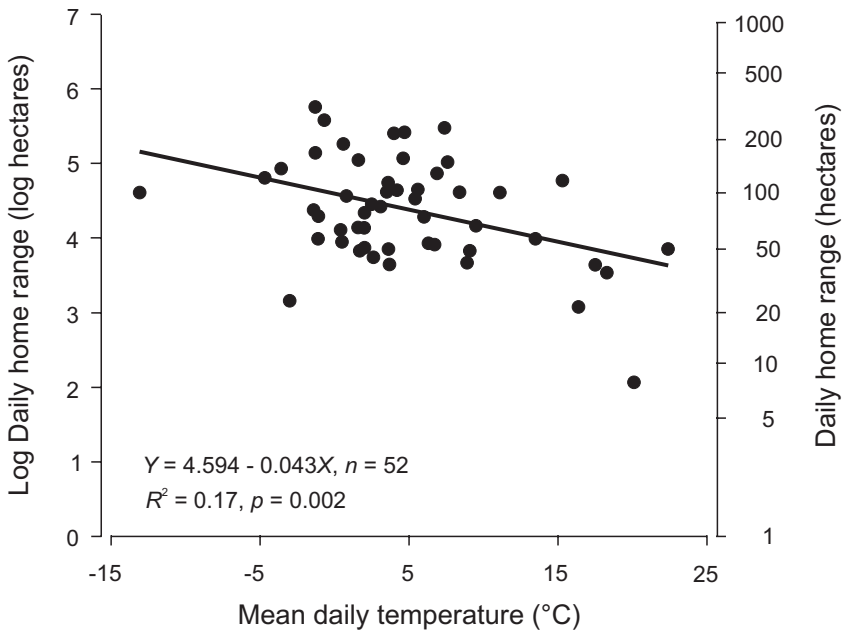

Fig. 1. Daily range sizes (in hectares, log-transformed) of adult female red deer in relation to mean daily temperature in BPF (n – number of daily ranges).

model, only temperature was significant (p = 0.002), as female daily ranges decreased with increasing temperatures (Fig. 1).

In BPF, mean (± SE) annual home ranges of red deer were 36.0 ± 4.7 km^2 for males, and 8.4 ± 0.5 km^2 for females (J. Kamler, W. Jędrzejewski and B. Jędrzejewska, unpubl.). Thus on a daily basis, adult males used 3% of their annual home range, whereas females used 12% of their annual home range. In April and May 2003, 7 red deer (3 males, 4 females) were followed continuously for 2–4 days to collect data on patterns of home range use. Mean (± SE) percent overlap of consecutive daily ranges was similar (t = –0.319, df = 14, p = 0.754) between males (26.3 ± 7.1%, n = 8) and females (23.4 ± 5.9%, n = 8).

Discussion

Mean sizes of daily ranges of male red deer tended to be larger than females throughout the year, although differences were not significant, most likely due to the low power of our analyses. Regardless, these results were consistent with other research that showed annual and seasonal home ranges of red deer were always larger for males than for females in BPF (J. Kamler, W. Jędrzejewski and B. Jędrzejewska, unpubl.). Adult male red deer can be more than twice as large as adult females, therefore they should require more foraging to meet their greater energetic requirements (McNab 1963, Clutton-Brock *et al.* 1987). Additionally, red deer exhibit sexual differences in foraging strategies (Staines and Crisp 1978, Clutton-Brock *et al.* 1982, 1987, Staines *et al.* 1982, Conradt 1998) and group sizes and social affiliations (Clutton-Brock *et al.* 1982, Appleby 1983, Jędrzejewski *et al.* 2006). Thus, larger daily ranges for males should be expected in BPF. There were, however, no clear patterns or significant differences in daily range sizes among seasons for each sex, although power of analyses were low, making interpretations of these results difficult.

We found sexual differences of daily range sizes in responses to abiotic factors. Female daily ranges were most influenced by ambient temperature, whereas male daily ranges were not related to any abiotic factors. The results

suggested that as temperatures decreased, especially in winter, daily movements of females increased to meet their energetic requirements. Because male red deer tend to have poorer diets and are more than twice as large as females, their daily movements are probably less affected by abiotic factors than females. Females also used their annual home ranges (12% used on daily basis) more intensely than males (3%). These differences likely reflected their sexual differences in reproductive strategies and diets. Because female movements are more influenced by food quality and rearing young, the utilization of their annual home ranges is more intense and concentrated. In contrast, the broader movements (related to access to multiple females) and poorer diets of males throughout the year result in their annual home ranges being used with relatively low intensity. Both sexes, though, had little overlap in consecutive daily ranges, indicating foraging was not concentrated in the same area on consecutive days, at least during summer. Overall, our data tended to support the hypothesis that daily ranges of red deer were influenced by sexual differences in reproductive strategies.

Finally, daily range sizes of red deer in BPF were up to 10 times larger than those reported in managed boreal forests in Germany (females: 0.14–0.29 km^2, Georgii 1980; males: 0.12–0.25 km^2, Georgii and Schroder 1983) and Denmark (female mean: 0.45 km^2, Jeppesen 1987). Reasons for such large daily ranges in BPF were not clear, but could have been related to several factors such as food resources or even presence of large carnivores. Interestingly, previous research showed deciduous woodlands provided more food to red deer than coniferous forest stands (Jędrzejewska *et al.* 1994), suggesting daily ranges of red deer should be smaller in BPF compared to boreal forests, if food resources were the primary factor determining daily range size. A more important factor might have been presence of large carnivores, especially because recent research in North America showed that wolves had a significant impact on the behavior and movements of elk, which are conspecifics to red deer. For example, the presence of wolves strongly affected vigilance, foraging patterns, movement patterns, and habitat selection of elk (Laundre *et al.* 2001, Ripple *et al.* 2001, Childress and Lung 2003, Fortin *et al.* 2005, Hebblewhite *et al.* 2005, Mao *et al.* 2005). In BPF, predation by wolves and lynx is the largest natural cause of mortality among red deer (Jędrzejewska and Jędrzejewski 1998), and predation was a limiting factor in the red deer population (Jędrzejewski *et al.* 2002) suggesting large carnivores are an important factor affecting the red deer population. Thus, the relatively large daily ranges of red deer in BPF might have been influenced most by the presence of large carnivores, as excessive predation could occur if deer moved within smaller areas as shown in studies from North America. However, more studies in Europe are needed on this subject, because the impacts of large carnivores on their prey under relatively natural conditions are still poorly understood.

Acknowledgements: This project was funded by the Polish State Committee for Scientific Research (grant KBN 5P06H03418) and the Polish Academy of Sciences, Mammal Research Institute, Białowieża. Financial support for J. F. Kamler was provided by the Institute of International Education, U. S. Student Fulbright Program, New York, and the Polish-U. S. Fulbright Commission, Warsaw. Permission to trap deer was granted by the director of Białowieża National Park, Białowieża. Our research and handling protocol was approved by the Local Ethical Commission for Research on Animals, Białystok. We thank R. Kozak and the many students, volunteers and scientists for help with field research and data organization.

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Received 10 August 2006, accepted 23 February 2007.

Associate editor was Andrzej Zalewski.