

## Home Ranges of Red Deer in a European Old-growth Forest

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**ABSTRACT.**—We monitored four male and seven female red deer (*Cervus elaphus*) from Mar. 2001 to Mar. 2003 in Białowieża National Park (BNP), Poland, to determine their home ranges in one of the best preserved old-growth forests in lowland Europe, and with large (>15 kg) carnivores present. Mean home-range size of adult males (36.0 km<sup>2</sup>) was significantly larger than adult females (8.4 km<sup>2</sup>). Seasonal home-range sizes differed significantly among seasons for both males and females, with the largest home ranges being in autumn for males (23.0 km<sup>2</sup>), and winter for females (7.1 km<sup>2</sup>). Inter-sexual differences in home ranges appeared to be influenced by differences in reproductive strategies and physiological needs. Both sexes exhibited strong range fidelity, although home ranges in different years overlapped more for individual males (93–100%) than females (71–90%). Home ranges of red deer in BNP were substantially larger than that reported in previous studies throughout Europe, suggesting that in old-growth forests with large carnivores present (*i.e.*, the historical situation for most of Europe), red deer need large areas to meet their seasonal and annual requirements.

### INTRODUCTION

Red deer (*Cervus elaphus*) are considered big game animals in most areas of Europe, and most populations are heavily hunted (Ueckermann, 1987; Whitehead, 1993). The primary predators of red deer, wolves (*Canis lupus*) and Eurasian lynx (*Lynx lynx*), have been extirpated throughout most of Europe (Nowak, 1999). Additionally, most historic habitats on the continent have been transformed by humans, primarily due to conversion to agriculture and coniferous tree plantations (Ellenberg and Strutt, 1988). For example, temperate Europe historically was dominated by lowland deciduous old-growth forests, although <1% of this habitat remains (Ellenberg and Strutt, 1988). Consequently, most research on red deer has focused on managed populations that are influenced by human hunting, human-altered habitats, and/or lack of large (>15 kg) carnivores. To investigate ecological situations of evolutionary significance, however, research must be conducted in protected communities within natural (*i.e.*, relatively unaltered by human activity) and historical habitat. For example, previous research showed red deer home ranges vary from 1 km<sup>2</sup> in on the Isle of Rhum (Clutton-Brock *et al.*, 1982), to 10 km<sup>2</sup> in coniferous tree plantations in Scotland (Catt and Staines, 1987). In some areas, red deer appear to exhibit strong territoriality (Carranza *et al.*, 1990), whereas in other areas they migrate seasonally over large areas (Szemethy *et al.*, 1998). However, it is unknown which, if any, of these movement patterns are characteristic of red deer under conditions more similar to those in which the species evolved.

Research in North America indicated old-growth forests can provide several advantages to deer species compared to regenerating forests (Schoen *et al.*, 1981; Harestead *et al.*, 1982; Van Horne *et al.*, 1988; Happe, 1990). For example, among North American elk (*Cervus elaphus*), conspecifics to red deer, old-growth forests provided greater benefits in harsh winters, compared to regenerating forests (Jenkins and Starkey, 1993). Previous research in Białowieża Forest showed that red deer densities were highest in the old-growth forest stands

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of BNP, compared to surrounding managed forests dominated by coniferous tree plantations (Jędrzejewska and Jędrzejewski, 1998). Additionally, a review of ungulate densities throughout woodlands in Poland showed that total biomass of deer per unit area was positively correlated with percentage of deciduous forest stand, probably due to higher food availability in this forest type (e.g., browse supply, acorn crop) compared to managed coniferous forests (Jędrzejewska *et al.*, 1994). Thus, deciduous old-growth forests in Europe clearly provide advantages to red deer compared to managed forests, although there is no information regarding red deer movements in this habitat type.

We investigated the seasonal and annual home ranges of red deer in the old-growth forests of Białowieża National Park (BNP), Poland, where large carnivores are present. We also investigated sexual differences in home-range sizes, and range fidelity among red deer. This research provided a unique opportunity to study red deer under relatively natural and historical conditions, and results could be compared to previous studies that occurred in more human-altered environments.

#### METHODS

*Study area.*—The BNP (100 km<sup>2</sup>) is located in northeastern Poland (52°43'N, 23°54'E) and is part of a large (1500 km<sup>2</sup>) primeval forest covering 580 km<sup>2</sup> in Poland and 870 km<sup>2</sup> in Belarus. The BNP is the last remnant of the pristine European lowland forest, and contains three main forest types: oak-lime-hornbeam, mixed coniferous and ash-alderwood. Oak-lime-hornbeam stands cover nearly half of the national park, and are composed of oak (*Quercus robur*), hornbeam (*Carpinus betulus*) and lime (*Tilia cordata*), with scattered spruce (*Picea abies*). Mixed coniferous stands dominant sandy soils, and are composed of spruce and pine (*Pinus sylvestris*). Ash-alderwood stands dominant damp soils, especially near rivers and streams, and are composed of alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) and spruce. Small stands of birch (*Betula verrucosa* and *B. pubescens*) and aspen (*Populus tremulus*) are also scattered throughout the national park.

The BNP has one of the most diverse communities of native predator-prey species in Europe. In addition to red deer, four other native ungulates occur in BNP, including European bison (*Bison bonasus*), moose (*Alces alces*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Wolves and Eurasian lynx occur in relatively stable populations within BNP (Jędrzejewska and Jędrzejewski, 1998) and human hunting is prohibited.

The climate is transitional between continental and Atlantic types, although the continental type prevails (Jędrzejewska and Jędrzejewski, 1998). During the years of the study (2001–2003), the mean Jan. daily temperature ranged from –1.4 to –6.1 C, whereas the mean Jul. daily temperature ranged from 20.9 to 21.9 C. Mean annual precipitation was 534 mm (range = 500–603 mm) and mean number of days with snow cover per winter was 77 (range = 66–98 d). Daylight hours range from 16 h 45 min in summer, to 7 h 42 min in winter.

*Data collection.*—We captured red deer in drop-nets traps (Jędrzejewski and Kamler, 2004) placed in openings and glades at the forest edge inside BNP, in Mar. and Dec. 2001. Captured deer were immobilized with an intramuscular injection of ketamine hydrochloride and xylazine (2.5:1.5 ratio), removed from the nets, and fitted with radio-transmitter collars (Margus, Białystok, Poland), most equipped with activity sensors. We classified deer as adult ( $\geq 24$  mo) or young ( $< 24$  mo) based on body size, reproductive condition and, for males, antler size. Red deer were captured and radio collared without regard to gender, although the sex ratio of adults captured (1 M:2.3 F) was similar to the sex ratio of adults estimated for the local population (1 M:1.7 F; Jędrzejewska and Jędrzejewski, 1998).

We recorded telemetry locations of for each study animal 1–3 times per week throughout the study period (Mar. 2001 to Nov. 2003), randomly during a 24-h period. Additionally, 24-h tracking sessions (locations every 30 min) were conducted on individuals at least once per season. We defined seasons as winter (Dec.–Mar.), summer (Apr.–Jul.) and autumn (Aug.–Nov.) to parallel major changes in climate, corresponding changes in vegetation and major biological periods for red deer (rutting, birthing, etc.). All radio locations from each relevant period were used in analyses, but individual home ranges were included only if area observation curves (Odum and Kuenzler, 1955) showed an asymptote of home-range size plotted against number of locations.

We located and monitored radio-collared red deer using a network of paths and roads that dissected the forest into 250-m<sup>2</sup> compartments that were clearly marked with numbered stones. To estimate deer locations, observers took  $\geq 2$  bearings ( $< 10$  min apart) from different stone markers, after encircling and approaching within 500–1000 m of the deer. Estimated locations (*e.g.*, *x*, *y* coordinates) were calculated by drawing bearings on 1:25,000 map of the study area, then these coordinates were entered into a computer database. Mean ( $\pm$ SD) error of estimated locations was  $90.5 \pm 59.0$  m when using reference collars ( $n = 54$ ) placed in known locations approximately 1 km away from observers.

Seasonal and annual home-range sizes for deer were calculated from estimated locations using the minimum convex polygon method (Mohr, 1947) in ArcView (version 3.2, Environmental Systems Research Institute, Inc., Redlands, California, U.S.A.) with the Animal Movement extension (Hooge and Eichenlaub, 1997). If individual deer were tracked during the same season in different years (for seasonal home ranges) and multiple years (for annual home ranges), then only the home range calculated during their first season and year, respectively, were used in analyses. We calculated seasonal and annual range fidelity for individual deer by determining percent home-range overlap between the same season (in different years) and between different years, respectively. Mean seasonal home-range sizes were compared among seasons within each sex using a 1-way ANOVA (Zar, 1996) and mean annual home-range sizes were compared between sexes using a *t*-test. Mean home-range overlaps were compared among seasons within each sex using a 1-way ANOVA and annual mean home-range overlap was compared between sexes using a *t*-test.

## RESULTS

We obtained  $> 10,000$  locations from three adult male, one yearling male and seven adult female red deer in BNP. Mean ( $\pm$ SE) annual home-range size of adult males ( $36.0 \pm 4.7$  km<sup>2</sup>) was larger ( $P = 0.027$ ) than for adult females ( $8.4 \pm 0.5$  km<sup>2</sup>). The yearling male had an annual home-range size ( $13.5$  km<sup>2</sup>) intermediate to that of adult males and females. Seasonal home-range sizes differed significantly among seasons for both adult males ( $P = 0.027$ ) and females ( $P = 0.006$ ). Mean ( $\pm$ SE) home ranges of adult males were  $13.6 \pm 1.2$  km<sup>2</sup> in summer,  $23.0 \pm 3.6$  km<sup>2</sup> in autumn and  $11.6 \pm 1.2$  km<sup>2</sup> in winter. Home ranges of females were in  $4.6 \pm 0.2$  km<sup>2</sup> in summer,  $5.5 \pm 0.9$  km<sup>2</sup> in autumn and  $7.1 \pm 0.6$  km<sup>2</sup> in winter.

Both sexes exhibited strong range fidelity, although home ranges in different years and seasons always overlapped more for adult males (93–100%) than females (71–90%). Mean ( $\pm$ SE) annual home-range overlap for adult males ( $96.1 \pm 2.1\%$ ) was marginally greater ( $P = 0.108$ ) than for females ( $82.9 \pm 6.0\%$ ). Seasonal home-range overlap was similar among seasons for adult males ( $P = 0.397$ ) and females ( $P = 0.465$ ). Mean ( $\pm$ SE) home-range overlap for males was  $92.3 \pm 2.1\%$  in summer,  $91.7 \pm 8.4\%$  in autumn and  $76.5 \pm 11.9\%$  in

winter. Mean ( $\pm$ SE) home-range overlap for females was  $83.1 \pm 7.0\%$  in summer,  $72.9 \pm 10.9\%$  in autumn and  $70.9 \pm 4.5\%$  in winter.

#### DISCUSSION

Red deer in BNP were not migratory as seen in other red deer populations (Szemethy *et al.*, 1998). Adult males tended to have stronger range fidelity than females in BNP, and this was likely related to breeding strategies and physiological needs. Previous research showed that males can be strongly territorial, especially during the rut (Carranza *et al.*, 1990), and that males return to the same rutting grounds year after year (Clutton-Brock *et al.*, 1982). The same was likely true in BNP, as adult males showed the strongest range fidelity in summer and autumn, which coincides with the rutting period. Adult females showed the strongest range fidelity in summer, which suggested that females choose the same areas for birthing year after year.

Male home ranges were always larger than females, and this was likely due to several factors, including differences in body size, physiological needs, foraging strategies, group sizes and reproductive behavior. Adult males are more than twice as large as adult females, therefore may need to forage over larger areas to meet their greater energetic demands (McNab, 1963; Clutton-Brock *et al.*, 1987). However, annual home ranges of males were more than four times larger than females, much larger than expected based on differences in energetic requirements (McNab, 1963). Sexual segregation occurs in red deer, and in other ungulates, which results in different foraging strategies and diets (Clutton-Brock *et al.*, 1982; Staines *et al.*, 1982; Clutton-Brock *et al.*, 1987; Main *et al.*, 1996; Conradt, 1998). Also, adult male ungulates tend to be more solitary than adult females, which results in different sized groups and social affiliations (Clutton-Brock *et al.*, 1982; Appleby, 1983; Jędrzejewski *et al.*, 2006). Sexual differences in reproductive strategies also results in different movement patterns, because male reproductive success is related to breeding opportunities, whereas female reproductive success is related to rearing young (Main *et al.*, 1996). Thus, male movements can be influenced by access to breeding females and forage quality (Clutton-Brock *et al.*, 1982; Appleby, 1983; Carranza *et al.*, 1990; Main *et al.*, 1996), whereas female movements are influenced by protective cover for young, forage quality and possibly female competition (Clutton-Brock *et al.*, 1982; Thouless, 1990; Albon *et al.*, 1992; Main *et al.*, 1996). Different reproductive strategies and physiological needs also likely explain why male home ranges were largest in autumn (*i.e.*, the rut), whereas female home ranges were largest in winter when food is most limiting.

Annual and seasonal home ranges of red deer in BNP were the largest reported from non-migratory red deer populations in Europe (Table 1). Reasons for such large home ranges in BNP compared to other European populations are not clear, but could be related to differences in deer density, food resources, lack of human hunting or presence of large carnivores. Density of ungulates is often related to food resources (Jędrzejewska *et al.*, 1994), both of which could influence home-range size. For example, home-range size in mammals is often negatively related to density (Sanderson, 1966) and a review of previous studies showed that the highest density of red deer exhibited the smallest home ranges (Table 1). However, several studies had similar or lower densities of red deer than in Białowieża Forest, yet home ranges of red deer in BNP were still considerably larger (Table 1), suggesting density alone was not influencing home range sizes. The effects of food resources on home-range size are less clear. Previous research showed that deciduous woodlands in Poland provided more food to deer than boreal forest stands (Jędrzejewska *et al.*, 1994), suggesting home ranges should be relatively small in the former. However, this

TABLE 1.—Summary of seasonal and annual home-range sizes of non-migratory red deer (*Cervus elaphus*) in Europe

Country (region)	Habitat	Deer density (n/km <sup>2</sup> )	Home range size (km <sup>2</sup> )	Sex/age class	Comments	Hunted/ culled	Large carnivores
Austria (Austrian Alps) <sup>1</sup>	Mainly spruce forests with some meadows	Not given	1.2–5.9	Mixed herds	Winter range	Yes	No
Czech Rep. (Jeseníky Mts) <sup>2</sup>	Mainly spruce forests	Very high (>6?)	0.8–4.4	Males	Monthly ranges	Yes	No
Denmark (SW Jutland) <sup>3</sup>	Pine-spruce plantation	6–9	0.4–1.7	Females	Monthly ranges	Yes	No
Germany (Bavarian Alps) <sup>4</sup>	Mainly coniferous trees	3–4	2.6	Females	Annual mean	Yes	No
Hungary (near Godollo) <sup>5</sup>	Forested coniferous hills	Low	1.1–3.9	Adult males	Seasonal ranges	Yes	No
Poland (Białowieża) <sup>6</sup>	Temperate-mixed forest	5–7	0.7–1.7	Females	Seasonal ranges	Yes	No
			6.7	Females	Annual mean	Yes	No
			36.0 (27–41)	Adult males	Annual mean	No	Yes
			8.4 (7–10)	Adult females	Annual mean (range)		
Scotland (South Argyll) <sup>7</sup>	Sitka-spruce plantation	Not given	10.6–11.8	Young males	Annual range	Yes	No
			4.1–10.1	Females	Annual range		
Scotland (Isle of Rhum) <sup>8</sup>	Heath, bog, and grassland	14	1.1	Males	Annual mean	Yes	No
			1.8	Females	Annual mean		
Spain (Monfrague Nat. Park) <sup>9</sup>	Mediterranean shrub	Not given	6.6	Adult male	Annual	Yes	No
			2.6	Adult females	Annual mean		

Sources: 1 = Schmidt, 1993; 2 = Koubek and Hrabec, 1996; 3 = Jeppesen, 1987; 4 = Georgii, 1980; Georgii and Schroder, 1983; 5 = Szemethy *et al.*, 1994; 6 = This study; Jedrzejewska and Jedrzejewski, 1998; 7 = Catt and Staines, 1987; 8 = Clutton-Brock *et al.*, 1982; 9 = Carranza *et al.*, 1991

was not supported by our results (Table 1). In North America, elk in old-growth forests had home ranges considerably larger than in managed coniferous forests (Jenkins and Starkey, 1982). Although old-growth forests contained more food resources than managed forests, they were more widely and unevenly dispersed in the former, causing elk to move over larger areas in old-growth forests (Jenkins and Starkey, 1982). This suggests the distribution of food resources in BNP could have contributed to the relatively large home ranges of red deer.

Human hunting was shown to increase movements of elk in North America (Ruth *et al.*, 2003; Vieira *et al.*, 2003), and increase home-range sizes of red deer in Denmark (Jeppesen, 1987). With the exception of our study, all previous studies of red deer occurred in hunted or culled populations (Table 1), suggesting that reasons other than lack of human hunting were responsible for the large home ranges of red deer in BNP.

Another possibility is that the presence of large carnivores affected home ranges of red deer, because all previous studies occurred in areas without large carnivores (Table 1). Although no previous research investigated the effect of wolves on ungulate home ranges, recent research in western North America showed that wolves can have a significant impact on elk behavior. The presence of wolves appeared to affect movement patterns, habitat use and vigilance of elk (Ripple *et al.*, 2001; Laundre *et al.*, 2001; Childress and Lung, 2003), resulting in a trophic cascade that continues to affect vegetative growth patterns (Ripple *et al.*, 2001; Fortin *et al.*, 2005; Hebblewhite *et al.*, 2005; Mao *et al.*, 2005). In BNP, red deer are the main prey of wolves (83% of wolf diet) and lynx (52% of lynx diet; Jędrzejewska and Jędrzejewski, 1998), which together account for 94% of red deer deaths (Jędrzejewski *et al.*, 1992). Wolves in BNP are active day and night (Theuerkauf *et al.*, 2003), and move throughout their territories in a rotational way, hunting in a particular area once about every 6 d (range = 2–8 d; Jędrzejewski *et al.*, 2001). Thus, red deer in BNP are constantly hunted by packs of wolves, which could result in red deer increasing their overall movements to avoid excessive predation. However, more research is needed on this subject, because only studies comparing predator-free and high-predator areas could show impacts of large carnivores on home-range sizes of red deer. Nevertheless, our results indicate that in deciduous old-growth forests with large carnivores present (the historical situation for temperate Europe), red deer need relatively large areas to meet their seasonal and annual requirements.

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