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Survival and cause-specific mortality of red deer *Cervus elaphus* in Białowieża National Park, Poland

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Information is needed from protected populations of game species to help understand natural rates of mortality, and as a means for comparisons with populations hunted by human beings. Additionally, little is known about red deer *Cervus elaphus* survival in historic habitat with large carnivores present. During 2001-2004, we estimated survival and cause-specific mortality of 35 red deer in the Białowieża National Park (BNP), Poland. The BNP contains the last remnant of old-growth lowland forests in Europe, and both predator and prey populations are protected from human exploitation. For all deer, survival did not differ among years or seasons. Annual survival of all deer was 56%, and survival rates were similar for adult males (75%) and females (64%), but was higher for adults (71%) than for young (15%). Predation, primarily caused by wolves *Canis lupus*, was the most common source of mortality (10 of 12 red deer deaths) and contributed most to the differences in survival between adult and young red deer.

Key words: Cervus elaphus, mortality, primeval forest, red deer, survival, wolf predation

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Red deer *Cervus elaphus* are big game animals and, consequently, are heavily hunted throughout Europe (Ueckermann 1987, Whitehead 1993). Thus, human-related mortalities are the major cause of death in most red deer populations (Jeppesen 1987, Mysterud et al. 2000), along with natural causes of death such as starvation (Clutton-Brock & Albon 1982, Clutton-Brock et al. 1985, 1987). To fully understand the effects of anthropogenic factors on ungulate populations, though, information is needed from unexploited populations. Additionally, most previous studies on red deer occurred in human-altered habitats and with large carnivores being absent (Clutton-Brock et al. 1982). To investigate evolutionary significant situations, including predation mortality on ungulates, research must be conducted in protected predator-prey communities.

We investigated the survival and cause-specific mortality of a red deer population in the Białowieża

National Park (BNP), Poland. The BNP contains old-growth deciduous and mixed forest stands, which likely represent the historic habitat of red deer throughout most of Europe. Additionally, wolves *Canis lupus* and lynx *Lynx lynx*, which are the main predators of red deer in European temperate forests, occur in BNP (Jędrzejewska & Jędrzejewski 1998). Furthermore, the red deer population in the BNP is protected from human hunting. Thus, research on red deer survival in the BNP provides a unique opportunity to determine mortality patterns of red deer under historic conditions. The obtained information can be compared to that of other red deer populations that are hunted by humans, thus elucidating the impacts of human management on survival rates in red deer.

Study area

Our study area is situated in the BNP (100 km^2) in northeastern Poland (52° 43'N, 23° 54'E). The BNP is part of the larger Białowieża Primeval Forest (~1,450 km^2) occurring on the Polish-Belarussian border. On the Polish side, the Białowieża Forest (580 km^2) consists of the BNP surrounded by managed forests and small reserves. 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 predominate sandy soils and are composed of spruce and pine *Pinus sylvestris*. Ash-alderwood stands predominate 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. On the Polish side of Białowieża Forest, wolves occur in about three packs with 4-5 members each (2-2.6 wolves/100 km^2), but the BNP usually contains only one pack (Okarma et al. 1998). During the study period, red deer in Białowieża Forest, including the BNP, occurred in densities of 200-350 deer/100 km^2 (Jędrzejewski et al. 2006).

The climate is transitional between continental and Atlantic types, though the continental type prevails (Olszewski 1986). During the years of the study (2001-2004), the mean January daily temperature ranged within -1.4 - -6.1°C, whereas the mean July daily temperature ranged within 20.9 - 21.9°C. Mean annual precipitation was 534 mm (range: 500-603 mm), and the mean number of days with snow cover per winter was 77 (range: 66-98 days). Daylight hours range from 16 hours 45 minutes in summer to 7 hours 42 minutes in winter.

Material and methods

We captured red deer in drop-net traps (Jędrzejewski & Kamler 2004) placed in openings and glades at the forest edge in the BNP and at its buffer zone. Trapping occurred in March and December 2001, January and December 2002, and in February 2003. We immobilised captured deer using 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 of which were equipped with activity sensors, on the study animals to monitor their movements. Deer were classified as adult ($\geq$ 24 months) or young ($<$ 24 months) based on body size, reproductive condition, and for males, antler size. Two female deer were initially classified as young until they became 24 months of age, after which they were subsequently classified as adults.

We recorded telemetry locations for each study animal 1-3 times per week throughout most of the study period. Additionally, 24-hour tracking sessions (with locations every 15 minutes) were conducted on individuals at least once per season. We estimated survival and cause-specific mortality rates using the MicroMort program (Heisey & Fuller 1985). We tested for differences in survival between sexes and among seasons and years. Likelihood ratio tests (G statistic) were used for multiple comparisons (Heisey & Fuller 1985, Zar 1996), and Z-tests were used for 2-way comparisons (Nelson & Mech 1986). Differences were defined significant at $P < 0.05$. 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 major biological periods for red deer (e.g. rutting and birthing). We classified causes of mortality for dead red deer as predation, starvation and human poaching. We identified predators that killed deer by examining features of the carcass (i.e. size and placement of bite marks) and evidence at kill sites (i.e. tracks and scats). Deaths were identified as having been caused by starvation if carcasses showed no signs of trauma and had little body fat.

Results

We collected 7,552 radio-days from 35 red deer (seven adult males, 14 adult females, seven young males and seven young females) monitored from March 2001 to March 2004. During the study, there were 12 confirmed deaths; 10 (83%) caused by predation, one (8%) by a poacher and one (8%) by starvation. Of the 10 predation deaths, nine were caused by wolves, and one by wolves or a lynx (the latter likely killed the deer prior to wolves consuming most of it).

Annual survival of all deer was 0.56. As survival did not differ among seasons ($G = 1.51$, $P = 0.471$) or years ($G = 1.89$, $P = 0.388$), seasons and years were pooled to provide more robust annual analyses. Annual survival did not differ ($Z = 0.55$, $P = 0.500$) between adult males (0.75) and adult females (0.64). Sensitivity analyses showed that only if four additional females had died at least six months before the termination of the study, a statistical significance ($P < 0.05$) would have occurred between adult groups. Similarly, annual survival for young did not differ ($Z = 0.96$, $P = 0.2553$) between males (0.20) and females (0.07). Sensitivity analyses showed that only if two additional males had lived, a statistical significance ($P < 0.05$) would have occurred between juvenile groups. Therefore, sexes in each age class were pooled for subsequent analyses. Annual survival was higher ($Z = 3.70$, $P = 0.001$) for adults (0.71) than for young (0.15). Cause-specific mortality from predation was higher ($Z = 2.51$, $P = 0.001$) for young (0.71) than for adults (0.24), indicating that this mortality factor contributed the most to the differences in survival.

Discussion

Predation, primarily by wolves, was the only major cause of mortality among red deer in the BNP during our study. Only one deer was killed by humans during our study period, and this individual was killed in an illegal snare set near the border of the BNP. In contrast, human hunting is a major cause of death in most red deer populations in Europe (Jeppesen 1987, Ueckermann 1987, Mysterud et al. 2000). Even in the forests surrounding the BNP, research during the 1990s showed that human hunting was the largest source of mortality for red deer, being larger than wolf and lynx predation (Okarma et al. 1995, Jędrzejewska & Jędrzejewski 1998). Similarly, only one deer in our study died from starvation (i.e. a < 1-year old female). In contrast, previous studies on the Isle of Rhum, Scotland, showed that starvation during winter was the primary cause of death among young red deer (Clutton-Brock & Albon 1982, Clutton-Brock et al. 1985, Coulson et al. 1997), however deer were culled in this area, large carnivores were absent and habitats differed from those in the BNP.

Predation was the mortality factor that affected survival of red deer in the BNP the most. Previous research on red deer in Europe found that survival was most influenced by other factors including deer density (Clutton-Brock et al. 1985, Clutton-Brock et al. 1987, Coulson et al. 1997), winter temperatures and rainfall (Clutton-Brock & Albon 1982), birth weight (Loison et al. 1999), spring temperatures (Albon et al. 1987) and human hunting (Jeppesen 1987, Mysterud et al. 2000), although wolves were absent in all the above-mentioned studies. Although we did not test for many of the above factors, previous research in Białowieża Forest, Poland, has shown that wolves limit red deer numbers through predation (Jędrzejewski et al. 2002), and thus starvation and other natural death causes are not likely to be as important in the BNP as in the previously mentioned studies. However, wolves are still a poor predictor of red deer numbers in Białowieża Forest, as wolves have alternative prey, and deer suffer from other mortalities such as lynx predation and human hunting outside the BNP (Okarma et al. 1995, Jędrzejewska & Jędrzejewski 1998, Jędrzejewski et al. 2002).

Survival of adult red deer was significantly higher than that of young, and mortality from predation contributed most to this difference. Our results support those obtained in previous research in the Białowieża Forest, Poland, which showed that wolves and lynx preyed selectively on young versus adult red deer, causing greater mortality among young red deer (Jędrzejewski et al. 1993, Okarma et al. 1995, Jędrzejewski et al. 2000). Wolves and lynx probably prey selectively on young deer because they are easier to catch and bring down, and because they are more inexperienced at avoiding predators than are adults. Additionally, young deer have smaller fat reserves and generally are in weaker condition than adults in winter, which makes them more susceptible to predation (Jędrzejewski et al. 2002).

Previous research in the Białowieża Forest, Poland, also showed that wolves preyed more selectively on young deer and adult females than on adult male red deer (Table 1). Furthermore, lynx prey on adult female red deer, but not on adult males (Okarma et al. 1995, Jędrzejewska & Jędrzejewski 1998). As adult male red deer can be twice as large as adult

Table 1. Mean and 95% Confidence Intervals (CI) for annual survival and mortality rates from predation of radio-collared red deer in Białowieża National Park, Poland, during 2001-2004.

Parameter	All deer (N=35) Mean rate (95% CI)	Adult male (N=7) Mean rate (95% CI)	Adult females (N=14)[1] Mean rate (95% CI)	Young (N=14) Mean rate (95% CI)
Annual survival	0.56 (0.40-0.78)	0.75 (0.51-1.00)	0.64 (0.44-0.95)	0.15 (0.03-0.68)
Annual mortality from predation	0.37 (0.19-0.55)	0.25 (0.00-0.54)	0.29 (0.05-0.52)	0.71 (0.39-1.00)

[1] Two females captured as young were also included as adults when they became 24 months of age.

females, they may experience lower mortality from predation simply because they are harder for predators to hunt and bring down than are adult females. Indeed, survival of adult males (0.75) tended to be higher than that of adult females (0.64), although this difference was not statistically significant.

In general, our results supported the previous research in the BNP, which determined red deer mortality factors by examining carcasses found during winter (Jędrzejewski et al. 1992). In that study, predation from wolves or lynx accounted for 94% of red deer deaths, whereas starvation accounted for 6%. Excluding deer poached by humans, our study showed that predation accounted for 91% of red deer deaths, whereas starvation accounted for 9%. Thus, in a protected predator and prey community in historic habitat, predation has the greatest effect on red deer survival and accounts for nearly all red deer deaths. Under these circumstances, deaths due to starvation/malnutrition are minimal and have little effect on red deer survival. This clearly contrasts previous research on red deer from predator-free areas, in which deaths from starvation/malnutrition have the greatest effect on red deer survival and are the largest non-human source of mortality.

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