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Raven *Corvus corax* ecology in a primeval temperate forest

Ekologia kruka *Corvus corax* w naturalnym lesie nizinnym strefy umiarkowanej

ABSTRACT: Several field studies on common ravens *Corvus corax* were carried out between 1985 and 2004 in Białowieża Primeval Forest (E Poland), one of the best preserved lowland temperate forests in Europe. The surveys focussed on spatial aspects (nest site selection, territory size, territory use), reproduction (breeding success) and foraging patterns (food habits, carrion use). Nests (n = 87) were regularly distributed over the entire forest and located in coniferous forest. More than 90% of the nests were built in pines *Pinus sylvestris*. On average, 61.5% (SD ±15.4) of all breeding pairs were successful, rearing 2.8 (SD ± 0.18) fledglings per year. The occupied raven territories covered 14.1 km^2. Inside the territory boundaries, more than 76% of the exposed baits (n = 57) were used by ravens, even under dense forest canopy. Adult ravens were highly efficient in locating carrion; 79.2% of the exposed baits were detected and used by ravens within the first 24 hours after exposition. Ravens scavenged carcasses (n = 214), mainly of ungulates, intensively during the coldest months, abruptly decreasing the use of carcasses when spring arrived and other food resources became available. Diet analysis showed that carrion and plant material were the dominant food items of ravens in Białowieża Forest. Up to 82% of the analysed pellets con-

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tained items obtained from scavenging. Adult ravens had a more diversified diet than immatures, which consumed more items related to scavenging than to predation. The proportion of squirrels in the diet of adult ravens was remarkably high. Ravens in Białowieża Forest showed efficient strategies to exploit the resources available in the highly productive temperate forests, where they did not depend on artificial food subsidies.

KEY WORDS: *Corvus corax*, Białowieża Forest, habitat requirements, nest site selection, breeding success, diet, territory size, scavengers, temperate forests

STRESZCZENIE: Badania nad krukiem *Corvus corax* prowadzono w latach 1985–2004 na terenie Puszczy Białowieskiej, w jednym z najlepiej zachowanych kompleksów leśnych strefy umiarkowanej w Europie. Badania koncentrowały się na poznaniu aspektów ekologii przestrzennej (wybiórczość miejsc lęgowych, wielkość terytoriów, wykorzystania terytoriów), reprodukcji (sukces lęgowy) oraz odżywiania (miejsca żerowania, korzystanie z padliny). Gniazda (N=87) były równomiernie rozmieszczone w całej puszczy i zlokalizowane w lesie iglastym. Ponad 90% gniazd było umieszczonych na sosnach *Pinus sylvestris*. Średnio 61,5% (SD+15,4) lęgów kończyło się sukcesem i wyprowadzeniem średnio 2,8 (SD ± 0,18) młodych w ciągu roku. Terytoria zajmowane przez kruki miały powierzchnię ok. 14,1 km^2. Wewnątrz swego terytorium kruki wykorzystywały ponad 76% wykładanej przynęty (n=57), nawet na obszarach z gęstym pokryciem koronami drzew. Dorosłe kruki są bardzo wydajne w wyszukiwaniu padliny: 79,2% wykładanej przynęty było wykrywanych i wykorzystywanych przez kruki w ciągu 24 godzin od momentu wyłożenia. Kruki żerowały na tuszach zwierząt (n=214), głównie kopytnych, najintensywniej w zimne miesiące, z nagłym spadkiem zainteresowania padliną wraz z nadejściem wiosny, gdy inne źródła pokarmu stają się dostępne. Analiza pokarmu ukazała, że padlina i materiał roślinny były dominującym składnikiem u kruków z Puszczy Białowieskiej. 82% analizowanych wypluwek zawierało materiał pochodzący z padliny. Dorosłe kruki miały bardziej zróżnicowany pokarm niż ptaki młode), które bardziej koncentrowały się na padlinie niż na polowaniach. Odsetek wiewiórek w składzie pokarmu dorosłych kruków był wyskoki. Kruki z terenu Puszczy Białowieskiej wykazywały wydajną strategię wykorzystania dostępnych zasobów pokarmu w wysoce produktywnej puszczy, gdzie nie są zależne od pokarmu pochodzenia antropogenicznego.

SŁOWA KLUCZOWE: *Corvus corax*, Puszcza Białowieska, wymagania siedliskowe, wybiórczość miejsc lęgowych, sukces lęgowy, pokarm, wielkość terytorium, żerowanie na śmieciach, naturalny las nizinny strefy umiarkowanej

Introduction

The current knowledge on common ravens *Corvus corax* is mainly based upon studies from agricultural, afforested or human-augmented environments (Linz et al. 1992, Ratcliffe 1997, Webb et al. 2004). In heavily transformed ecosystems, opportunistic ravens have adapted well to exploit artificial resources, which partially resulted in extremely high population densities and breeding success. In the deserts of California, raven densities rose by 1,000% due to artificially increased food and water resources (Boarman et al. 1995). Ravens even developed completely new habits and switched from their natural breeding sites in trees to building nests in human-made structures (e.g. houses, car wrecks) (Boarman et al. 1995, Boarman & Heinrich 1999). In Idaho and Oregon ravens actually colonised new areas by using recently constructed electric pylons as nesting substrate (Steenhof et al. 1993).

In contrast to ravens living in natural ecosystems, ravens inhabiting human-shaped habitats may have lost many of their ancestral habits. However, only few studies have been conducted under natural conditions (Skarphèdinsson et al. 1990, Andrén 1992, Stahler et al. 2002). In natural ecosystems, especially at high latitudes, like North American Forests or the Canadian Arctic ravens preferentially associate with large predators in order to feed on their kills (e.g. wolves *Canis lupus*, Gilchrist & Robertson 2000, Stahler et al. 2002). Ravens in boreal areas have been reported to be forest specialists, being present exclusively in forested areas and well adapted to exploit forest food resources (e.g. predation on forest bird nests, Andrén 1992).

In Europe almost all ecosystems have been transformed by men. Thus, human affected landscapes are most abundant and only few natural habitats persisted. Especially natural woodlands have suffered strongly from heavy exploitation. This partly explains the lack of studies in natural forests of Europe. The Białowieża Primeval Forest (E Poland) is regarded as the best preserved woodland of its size in lowland temperate Europe (Okarma et al. 1997, Jędrzejewska & Jędrzejewski 1998). Here, several studies dealing with different aspects of raven ecology have been conducted (Pugacewicz 1997, Müller 2001, Rösner 2002, Selva 2004, Rösner & Selva 2005). In this paper we attempt to summarize the existing data, both published and unpublished, on raven ecology in Białowieża Forest, and to provide a general picture of raven ecology in a primeval temperate forest.

Study area

Białowieża Forest is known as the best preserved lowland forest ecosystem in temperate Europe. Once used as strictly protected royal hunting ground, the Białowieża Forest has lost only little of its pristine character. Today, it provides living space for many species that are rare or extinct elsewhere in Europe (Tomiałojć & Wesołowski 2004).

The forest is located on the Polish-Belarusian borderland, covering 1,450 km^2 in total and connected with other large forests in the north (Poland, Lithuania) and east (Belarus). Since 1945, the forest is divided by the Polish–Belarusian border. All studies were conducted in the Polish part (Fig. 1) which encompasses about 600 km^2. It includes a protected area, the Białowieża National Park (100 km^2), and the commercial forest, where timber exploitation and game hunting is practiced. The National Park was established in 1921. In the 1970s it was declared as Man and Biosphere Reserve and World Heritage Site by UNESCO. It protects the most precious part of the forest as a Strict Reserve (47 km^2), with a mean tree age of 130 years (Fig. 1). About one third of the Polish part of the forest is old-growths. The mean tree age in the exploited part of the forest is 72 years (Fig. 1). Numerous forest reserves are spread over the area, covering a manifold of forest types and ages.

Structural characteristics of Białowieża Forest are the multi-storey profiles of most tree stands, including very high trees as well as high portions of woody debris (Tomiałojć & Wesołowski 2004). Many types of forest can be distinguished. The

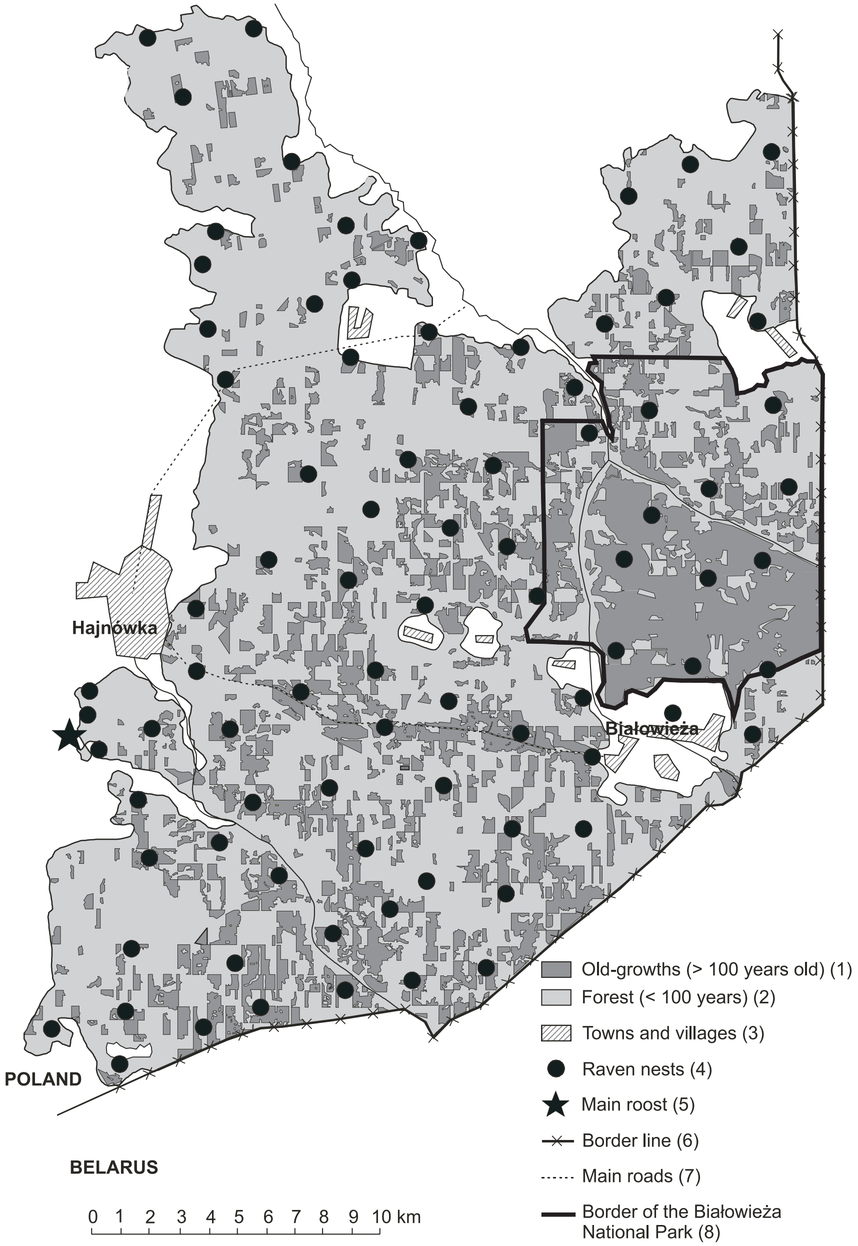

Fig. 1. Map of Białowieża Primeval Forest, Poland. Distribution of raven breeding sites between 1985–87 (after Pugacewicz 1997)

Ryc. 1. Mapa Puszczy Białowieskiej. Rozmieszczenie miejsc lęgowych kruka w latach 1985–1987 (Pugacewicz 1997)
1 – obszary leśne w wieku starszym niż 100 lat, 2 – lasy młodsze niż 100 lat, 3 – miasta i wsie, 4 – gniazda kruka, 5 – główne noclegowisko, 6 – granica państwowa, 7 – główne drogi, 8 – granica Białowieskiego Parku Narodowego

oak-lime-hornbeam (*Quercus robur, Tilia cordata, Carpinus betulus*) forest is the most common association of Białowieża woodland (Jędrzejewska et al. 1994, Jędrzejewska & Jędrzejewski 1998). Coniferous forests, dominated by spruce *Picea abies* and pine *Pinus sylvestris* are also quite common. Wet areas are covered by ash-alder forest (*Fraxinus excelsior, Alnus glutinosa*) and bog alderwoods. Open areas inside the forest, represented by river valleys and glades, cover about four percent of the study area. Only a few small villages are located in glades inside the forest, e.g. Białowieża (13 km^2) or Masiewo (27 km^2) glade. Compared to forests elsewhere in Europe the number of vascular plant species (~1,000), lichens (~300) and mushrooms (~2,500) is extremely high; indicating its primeval character (Faliński 1986, 1994, Wesołowski & Tomiałojć 1995, Tomiałojć 1996). The area is sparsely populated (2–3 people/km^2) and just two public roads are penetrating the forest complex (Jędrzejewska & Jędrzejewski 1998). The forest and its surroundings are characterised by a flat relief (mean height 165 m a.s.l.).

Białowieża Forest still harbours a great diversity of life; its fauna currently includes 12,000 species (Jaroszewicz 2004). The mammal community is very rich. It comprehends five ungulate species including wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and moose *Alces alces*. Moreover, about 300 free ranging European bison *Bison bonasus* – once extinct in the wild – inhabit the Polish side of Białowieża Forest (Jędrzejewska et al. 1994, Okarma 1995). Large predators are the lynx *Lynx lynx* and wolf *Canis lupus* (Jędrzejewska et al. 1994, Jędrzejewski et al. 2002). Furthermore, Białowieża is also famous for its diverse avifauna, comprising 150 breeding species (Tomiałojć & Wesołowski 2004), including the corvid species nutcracker *Nucifraga caryocatactes*, jay *Garrulus glandarius* and raven (Wesołowski & Tomiałojć 1995). In Białowieża Forest the raven is a common species and – in contrast to elsewhere in central Europe – was never extinct during the last centuries (Bednorz 1991).

The region is influenced by Continental and Atlantic climate types, with clearly marked warm (April–October) and cold (November–March) seasons. The latter is characterised by a mean temperature in January of –5.1°C and a mean snow depth of 10.0 cm (1.0–42.5 cm) (Wesołowski & Tomiałojć 1995, Jędrzejewska & Jędrzejewski 1998). More detailed information on climatic conditions, vertebrate community and vegetation are provided by Faliński (1986), Kwiatkowski (1994) and Jędrzejewska and Jędrzejewski (1998).

Material and methods

The period covered by the different studies summarised in this paper elapses from 1985 to 2004. Intensive field surveys were conducted during this time to estimate raven breeding densities. Additionally, systematic censuses of raven nests were done in plots and transects (see Pugacewicz 1997 for details). The breeding performance was assessed by controlling known raven nests several times during the breeding seasons of 1986, 1987, 2001 and 2004. At the end of the breeding season 2001 a habitat analysis of raven nest sites was conducted. We estimated tree composition at 31 nest sites by registering the tree species in the canopy (>32 cm diameter at breast height DBH) in a 20 m radius around nest sites and the understorey trees (4–10 cm DBH) in a 10 m radius.

To obtain information about carrion use and territory size of breeding ravens, we modified the bait-marking method (for details see Rösner & Selva 2005). In 2001 (January – May) we exposed 57 baits (ungulate intestines and dead chickens) covered with small plastic markers specific for each bait and distinguishable by colour and shape. Following a fixed design, we exposed the baits at different distances and directions from 13 occupied nests. Pellets and droppings containing specific markers were recovered at different raven nests and at the communal roost in systematic visits. This way, we could assess if a bait was used by a certain raven pair or not. Logistic regression analysis were used to calculate the territory size (Rösner & Selva 2005). Forty-eight baits were monitored daily to estimate the time required by ravens to discover the baits.

We collected a total of 570 raven pellets between 1997 and 2000 from different raven nests and from the main roost site close to the garbage dump (Fig. 1). For the diet analysis, we took a random sample of 100 pellets, including 50 pellets from the nests and 50 from the roost. The sample contained equal numbers of pellets from both the cold and warm seasons. The random sample from the nests included pellets from 13 different nests; four of them were located close to villages and/or at the forest edge. All pellets were dried, marked, separated in envelopes and later dissected. The material was analysed under 9–40× magnification and the pellet contents identified with the help of reference material and identification keys (Pucek 1981, Teerink 1991). We used the frequency of occurrence of the food items to investigate differences in the diet between pairs and immature ravens.

From the cold seasons 1997/1998 to 2001/2002 we investigated the use of carcasses by ravens. A total of 214 carcasses, mainly of ungulates, were monitored in systematic inspections (n = 1,784). Ungulate carcasses included all ungulate species, as well as carcasses of different origin: wolf and lynx kills; animals dead from disease, cold or starvation; hunted and later abandoned ungulates; and ungulate entrails discarded by hunters. During each inspection we recorded the presence of ravens at the carcass based on direct observations, tracks in the snow, and other signs (pellets, feathers, droppings and calls). When possible, we assessed the number of scavenging individuals by counting observed birds. To investigate the seasonality of carcass use by ravens, the data from all the carcass inspections (n = 1,784) were pooled in bimonthly periods. The scavenging frequency during each period was presented as the percentage of positive inspections, i.e. the proportion of inspections with ravens recorded from the total number of inspections of carcasses in that bimonthly period. The same procedure was followed to investigate the temporal variation in the mean number of ravens observed at carcasses. The temporal variation in ravens' scavenging frequency throughout the process of carcass exploitation is presented graphically (Fig. 4). The date of animal death or carcass exposition was considered as day "0". Each inspection was assigned to a number of day, according to the number of days elapsed since death/exposition. The data (absence/presence) from inspections belonging to the same number of day were pooled and the scavenging frequency calculated (as the percentage of positive inspections) for each day.

Distribution and numbers

A total of 84–87 raven pairs inhabited the study area in the period 1985–1994. Raven nests were uniformly distributed (Pugacewicz 1997) (Fig. 1). The breeding density for the whole area in this period was 1.4 pairs /10 km^2. However, it was lower in the natural old growths of Białowieża National Park (1.3 pairs/ 10 km^2) than in the commercial forest (1.8 pairs/10 km^2) (Pugacewicz 1997).

The main raven roost was located at a young pine forest in the vicinity of the Hajnówka rubbish dump at the forest edge (Fig. 1). The maximum number of ravens counted roosting together was 74. However, the maximum number of ravens feeding at the dump was around 280 (July). Our observations on raven movements around the dump suggested the presence of other secondary roosts. We also documented temporary roosts in the adjacent trees of large carcasses located deep inside the forest. A maximum of 50 ravens were observed in the vicinity of bison carcasses (Selva et al. 2003). We often noted complete evacuations of the main roost for several days. During one of these incidences we observed more than 70 ravens flying in a long stretched flock to the Belarusian part of the forest.

Territory size and use

The mean size of raven territories during the breeding season 2001 was 13.1 km^2, as estimated by the bait-marking method (Rösner & Selva 2005). Recoveries of specific markers support the idea that raven pairs have a perfect ”knowledge” of their territories. Up to a threshold distance of 2.04 km from their nests, i.e. inside their territories, ravens detected at least 76% of the carrion, independently of the characteristics of the bait exposition sites. Inside their territory, no significant differences in tree density and canopy cover were found between baits used and not used by the raven pair (Mann-Whitney U-test, $n_1 = 17$, $n_2 = 28$, $z = –0.025$, $p = 0.980$ for canopy cover; $z = –0.099$, $p = 0.921$ for tree density) (Fig. 2). Baits exposed outside their territory were more likely to be visited by the corresponding raven pair when they were located at open areas (Mann-Whitney U-test, $n_1 = 105$, $n_2 = 9$, $z = –1.744$, $p = 0.081$ for canopy cover; $z = –1.576$, $p = 0.115$ for tree density). These cases of pairs trespassing territory borders were often related to the presence of flocks of non breeding birds (Rösner & Selva 2005). The snow cover at the bait site also did not affect bait discovering by the raven pair (Mann-Whitney U-test, $n_1 = 12$, $n_2 = 45$, $z = –0.152$, $p = 0.879$).

We documented territory overlap between neighbouring pairs in two occasions. First, a territorial raven trespassed an occupied territory to forage on a cow carcass 5.6 km far from their nest, permanently used by a flock of nonbreeding ravens. Second, we recorded breeding ravens feeding on a fresh wolf kill inside their neighbouring territory together with 20 nonbreeders. The bait-marking method also provided information on movements of immatures. Non-breeding

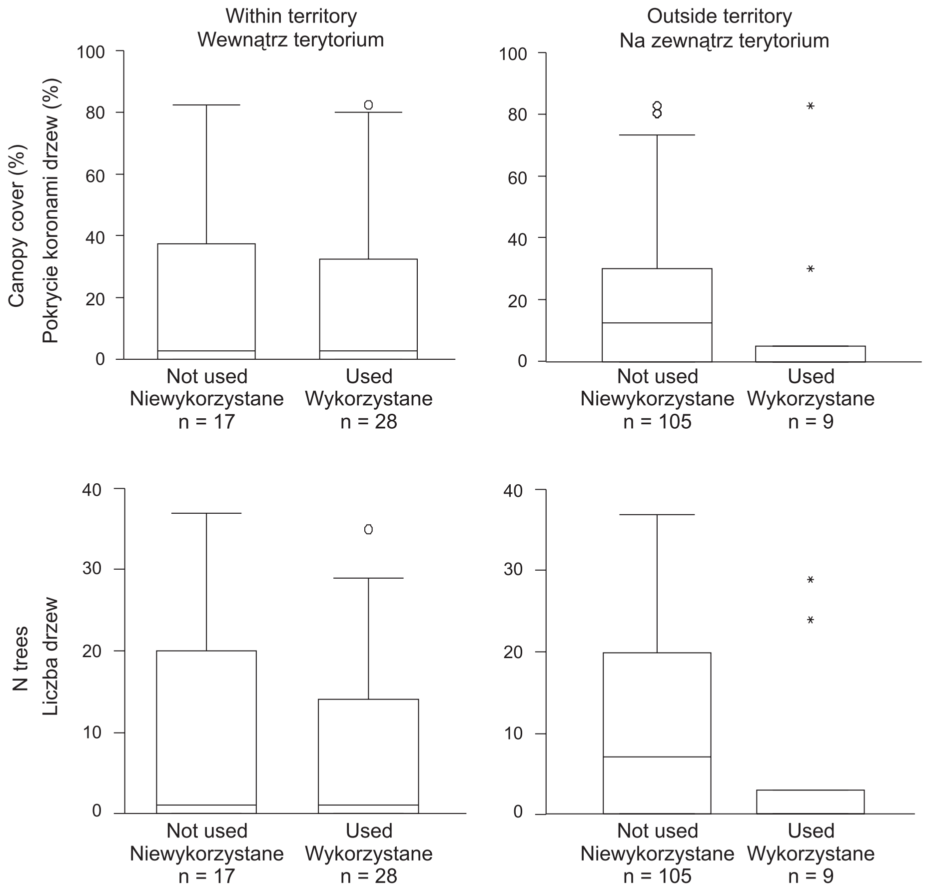

Fig. 2. Influence of habitat characteristics (canopy cover and number of trees) on bait use by adult ravens inside and outside their territory. Mean and standard deviations are shown

Ryc. 2. Wpływ cech siedliska (pokrycie koronami drzew i liczba drzew) na wykrywanie przynęty przez dorosłe kruki wewnątrz i na zewnątrz ich terytoriów. Pokazano średnią i odchylenie standardowe

ravens using the main roost scavenged on carcasses located 14.5 km far inside the forest.

Nest sites

Ravens in Białowieża Forest strongly preferred pines for building their nests. From 98 raven nests found during 1985 and 1994, 91.8% were build on pines, 4.1% on spruce, 2.1% on triangulation towers and 1% on birch *Betula* sp. (Pugacewicz 1997). Nests were usually found in coniferous old growth (mixed coniferous-deciduous, pine-spruce and pure pine forests). The exceptional size of trees in Białowieża Forest resulted in extremely high nest locations. The highest raven nest was found on a pine at a height of 40 m.

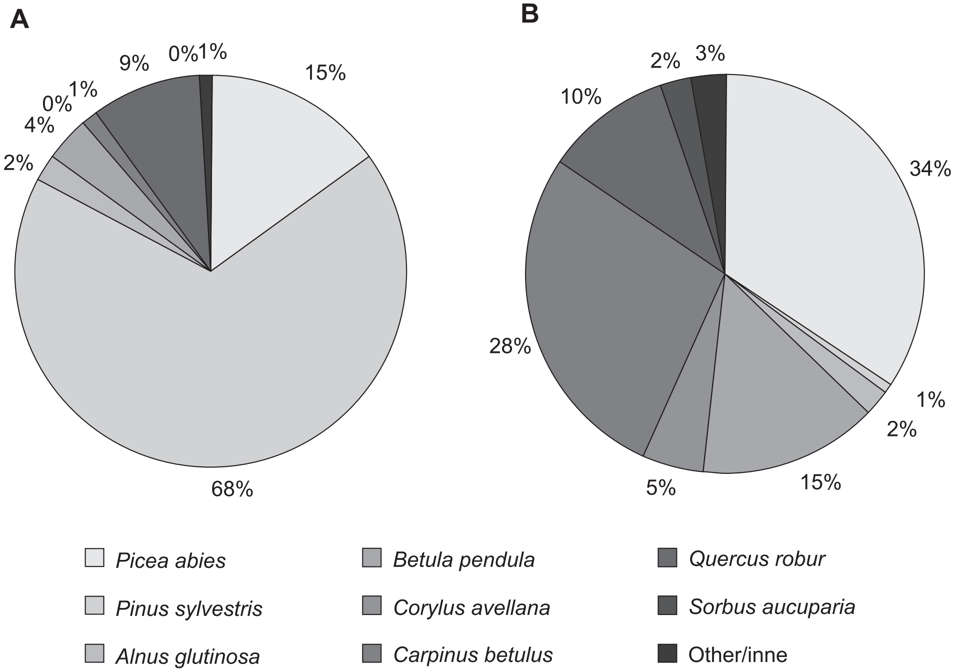

Fig. 3. Comparison of tree composition between canopy and undergrowth at 31 nesting places, Białowieża Forest, Poland

Ryc. 3. Porównanie składu gatunkowego drzew pomiędzy piętrem koron (A) i podszytu (B) dla 31 miejsc gniazdowania w Puszczy Białowieskiej

The composition of canopy trees at nest sites was generally dominated by pines (68%), followed by spruces (15%). The undergrowth was mostly dominated by spruces (34%) and hornbeams (28%), whereas pines barely occurred (<1%). The overall contribution of coniferous trees in the canopy layer was greater (83%) than that of deciduous ones (17%). In contrast, the majority of trees in the undergrowth were deciduous (65%, Fig. 3). Those nest sites located deep inside the forest were typically located in direct neighbourhood to some small opening. Such openings included roads, small clearings, wind-throws and young forest plantations which had not reached the canopy layer yet. Nest site fidelity was generally high and many nests sites found in the 1980s were still present in the 1990s and 2001. However, we do not know whether the same individuals used those nesting sites.

Reproduction and mortality

On average, 61.5% of the raven breeding pairs were successful, rearing 2.8 fledglings per year (Table 1). The mean breeding performance was 1.8 fledged chicks per breeding pair. During the breeding seasons of 1986 and 1987, more than 70% of the raven pairs raised at least one young. In 2001 we observed only 61% of the pairs rearing fledglings successfully. However, this proportion was markedly lower in 2004, when

Table 1. Breeding performance of ravens in 1986, 1987, 2001 and 2004, Białowieża Forest, Poland

Tabela 1. Sukces lęgowy kruków w Puszczy Białowieskiej w latach 1986, 1987, 2001 i 2004

Year Rok	N breeding pairs (nests found) Liczba par lęgowych (znalezione gniazda)	Percentage of successful pairs Odestek par z lęgami zakończonymi sukcesem	Mean number young fledged per successful pair Średnia liczba młodych na parę z sukcesem	Mean number young fledged per breeding pair Średnia liczba młodych na parę przystępującą do lęgu
1986	31	74.2	2.6	2.0
1987	24	70.8	3.0	2.1
2001	31	61.0	2.9	1.8
2004	10	40.0	2.7	1.1
Mean/średnia (± SD)	24 (± 9.9)	61.5 (± 15.4)	2.8 (± 0.18)	1.8 (± 0.45)

only 40% of the pairs bred successfully. Consequently, the mean number of young fledged per breeding pair decreased by two-fold, from a mean of 2.0 fledglings per pair between 1986 and 2001 to 1.1 fledglings in 2004. However, the mean production of young per successful pair did not vary much among years (Table 1).

In the course of all the investigations, 17 complete or partial losses of broods were recorded. Complete losses were caused by extremely low temperatures (n=3), egg predation (probably by conspecifics) (n=1) and strong winds (n=4). In one occasion, strong winds caused felling down of the nesting tree (spruce), perishing the female and the three chicks. Among the losses of single chickens, four were presumably attributed to pine martens; two were confirmed to be due to goshawk *Accipiter gentilis* predation and one to predation by an unknown raptor. Two cases of death could not be determined. Apart from the previously mentioned dead female, three other adult ravens where found dead. One was found under a nest, another inside the forest. The body of a third bird was found about 50 m far from a nest at the beginning of the breeding season. Four weeks later we observed two adults feeding fledglings in the respective nest.

The majority of fledglings in Białowieża Forest left nests in late May. After young ravens left the nests, raptor species used raven nests to breed. We documented four raven nests being subsequently occupied by hobbies *Falco subbuteo* and two nests by long-eared owls *Asio otus*.

Food habits

Carrion from large mammals and plant material were the dominant items in the diet of ravens in Białowieża Forest (Table 2). The main constituents of the diet of immature ravens were livestock carcasses (mainly of pig) and domestic chickens, both discarded by farms in the vicinity of the roost. More than 75% of the pellets from immatures contained carrion from large mammals. When chickens were also

Table 2. Composition of the raven pellets from roost (n = 50) and nests (n = 50), indicating the percentage of pellets containing each type of item, Białowieża Forest, Poland

Tabela 2. Skład wypluwek kruczych zebranych w Puszczy Białowieskiej na noclegowisku (n=50) i z gniazd (n=50); wykazano odsetek wypluwek zawierających każdy ze składników

Item/Składnik	Roost/Noclegowisko	Nest/Gniazdo
Shrews *Soricidae*/ryjówkowate	8	6
Mole *Talpa europaea*/kret	2	2
Insectivores total/owadożerne razem	10	6
Lagomorphs total/zajęczaki razem	2	–
Voles *Microtidae*/nornikowate	10	12
Mice *Muridae*/myszowate	2	12
Squirrels *Sciuridae*/wiewiórkowate	–	12
Undetermined rodent/nieoznaczone gryzonie	2	16
Rodents total/gryzonie razem	12	46
Cervids *Cervidae*/jeleniowate	–	4
Wild boar *Sus scrofa*/dzik	14	12
Livestock/zwierzęta domowe	60	30
Carnivore/drapieżne	2	2
Undetermined large mammal/nieoznaczone duże ssaki	8	6
Large mammals total/duże ssaki razem	76	46
Undetermined mammal/nieoznaczone ssaki	6	4
Eggshells from wild birds/skorupki jaj dzikich ptaków	–	12
Eggshells from chicken/skorupki jaj kury	58	26
Small bird/małe ptaki	–	4
Domestic chicken/kurczaki	28	2
Undetermined bird/nieoznaczone ptaki	2	16
Birds total/ptaki razem	64	48
Anura/płazy bezogonowe	–	2
Fish/ryby	4	10
Beetle/chrząszcze	6	26
Other invertebrates/inne bezkręgowce	2	6
Invertebrates total/bezkręgowce razem	8	30
Cereal/zboże	44	66
Fruits and seeds/owoce i nasiona	6	26
Other vegetal matter/inny materiał roślinny	56	84
Plant material total/materiał roślinny razem	76	92
Refuse (plastic, paper, aluminium foil)/ śmieci (plastik, papier, folia aluminiowa)	74	18

considered as carrion, then at least 82% and 46% of the pellets of immatures and adults contained scavenged material. Probably the remains of lagomorphs and fish found in pellets came also from scavenging. The occurrence of chicken eggshells in pellets from the roost was, at least in part, the result of scavenging at the dump. Cereals were an important component of the diet of both adult and non-adult ravens. Adults consumed more fruits and seeds than immatures (Table 2).

The frequency of occurrence of rodent and invertebrate remains was quite different between the sample from the nests and the roost (Table 2). Raven pairs consumed more rodents and invertebrates. Voles (bank vole *Clethrionomys glareolus*, common vole *Microtus arvalis* and root vole *Microtus oeconomus*) and shrews (*Sorex araneus* and *S. minutus*) had a similar contribution to the diet of adult and immature ravens. However, pairs consumed more mice and squirrels *Sciurus vulgaris*. Rats *Rattus norvegicus* and squirrels were exclusively consumed by raven pairs; squirrels constituted the most frequent rodent species in the pellets of adults (Table 2). Beetles, anuran and fish were more common in samples from nests. Refuse was frequently recorded in pellets from the roost (74% of the pellets), but rarely among those from nests (18%). The presence of other vegetal matter could be partly due to incidental ingestion (together with the animal or other remains, or from the nest) or have a secondary origin (from the guts of dead animals). In general, the diet of adult ravens was more diversified (Table 2).

The use of carcasses by ravens was significantly different among bimonthly periods (G-test for homogeneity of percentages, $G = 62.78$, $p < 0.001$) (Fig. 4). They scavenged intensively during the coldest months, abruptly decreasing the use of carcasses when spring arrived and other food resources became available. Scavenging frequency remained low during summertime and increased rapidly again at the beginning of the cold season. The number of ravens recorded at carcasses followed the same pattern as their scavenging frequency, being also significantly different among periods (one-way ANOVA, $F_{5,\ 535} = 3.82$, $p < 0.005$) (Fig. 4). Carcasses were used mainly by raven pairs during the breeding season, whereas the rest of the year was attended by larger groups. The scavenging frequency of ravens tended to decrease throughout carcass exploitation ($r_s = -0.41$, $p = 0.001$); ravens being less frequent at older carcasses (Fig. 4).

The mean group size of ravens observed at carcasses was 5.7 (SD ± 5.98). In the case of bison carcasses, we observed a manifest difference in group size of ravens scavenging on carcasses exposed in forest and openings (Mann-Whitney U-test, $U = 1{,}105$, $n_1 = 10$, $n_2 = 130$, $p < 0.001$, see Selva et al. 2004 for details). Bison carcasses exposed in clearings (more visible) were mainly consumed by flocks of immatures, while those under the forest canopy were utilised by the territorial pairs of ravens. Mean number of individuals observed at bison carcasses was 1.5 (SE ± 0.17) in forest and 12.8 (SE ± 1.21) in clearings (Fig. 5).

Ravens were highly efficient in discovering carcasses. During the bait-marking experiments, 79.2% of the baits were detected and used by ravens within the first 24 hours after exposition (Fig. 6). By day number four (> 72 h) all baits were already visited by ravens. In two cases, we could record ravens scavenging 30 and 50 minutes just after carrion exposition.

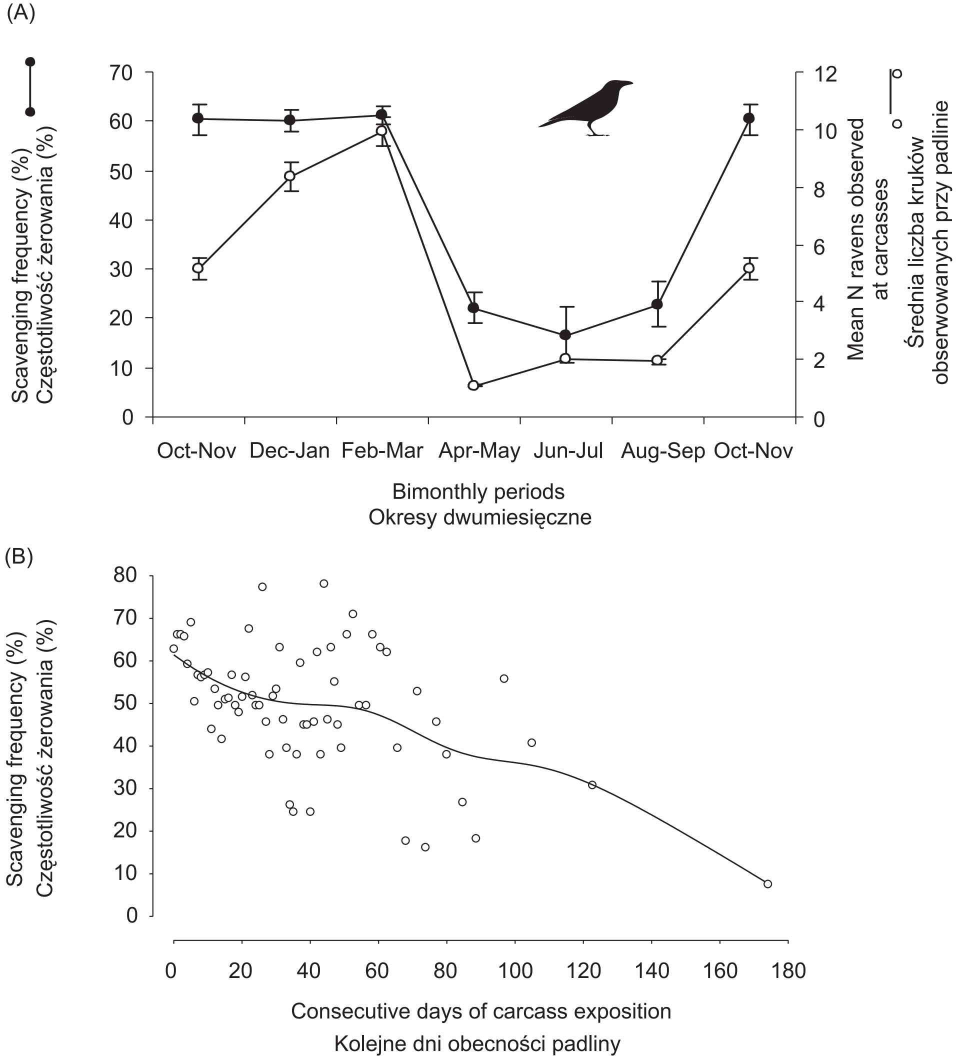

Fig. 4. Raven scavenging frequency throughout both the year and carcass exploitation process. (A) Bimonthly variation in the raven scavenging frequency and mean number (±SE) of ravens observed at carcasses; scavenging frequency expressed as mean percentage of inspection (±SE) with ravens recorded. (B) Variation in the raven scavenging frequency, expressed as percentage of positive inspections in a given day of the carcass exploitation. Scatterplot data smoothed by the Distance Least Square Method

Ryc. 4. Częstotliwość żerowania na padlinie kruka zarówno w ciągu roku jak i sam proces wykorzystywania padliny. (A) Zmienność w cyklu dwumiesięcznym częstotliwości żerowania kruka na padlinie i średnia liczba (±SE) obserwacji kruka na padlinie; częstotliwość żerowania na padlinie wyrażono jako średni odsetek kontroli (±SE) ze stwierdzeniem obecności kruka. (B) Zmienność częstotliwości żerowania kruka na padlinie, wyrażona jako odsetek pozytywnych kontroli w danym dniu korzystania z padliny. Obszar rozrzutu danych wyrównano poprzez użycie metody Distance Least Square Method

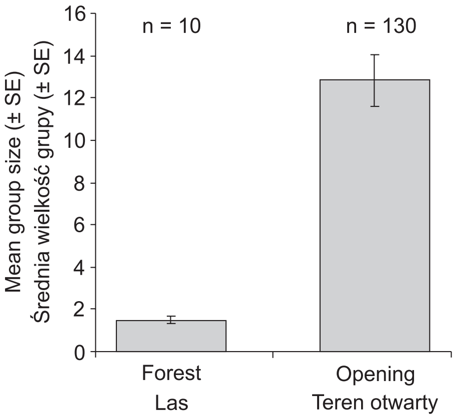

Fig. 5. Mean group size of ravens (±SE) observed at bison carcasses located in forest and open areas in Białowieża Forest

Ryc. 5. Średnia wielkość grup kruków (±SE) obserwowanych na padlinie żubra umieszczonej w lesie oraz na otwartym terenie w Puszczy Białowieskiej

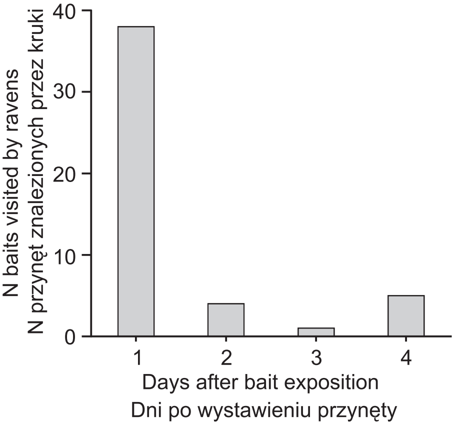

Fig. 6. Time required by ravens for bait discovering, expressed as number of days elapsed since bait exposition. Bars show the number of exposed baits found by ravens in each consecutive day from exposition

Ryc. 6. Czas potrzebny krukom na wykrycie przynęty, wyrażony przez liczbę dni, jakie upłynęły od momentu wyłożenia padliny. Słupki ukazują liczbę znalezionej przez kruki (z całkowitej liczby wyłożonej) przynęty w każdym kolejnym dniu od dnia wyłożenia

Discussion

Raven nests in Białowieża were regularly distributed throughout the forest. This indicates that the whole forest is both, suitable breeding ground and foraging habitat for ravens. In contrast, surveys from other areas in Europe have reported that forest interiors are rather avoided by ravens. In these areas, nests are predominantly located at the forest edge and ravens are likely to forage mainly outside the forest (e.g. in farmlands and open areas) (Dunk et al. 1997, Ratcliffe 1997). Thus, transformed forests might merely provide nest sites rather than foraging habitats. Natural forests, like Białowieża woodland, offer suitable habitats in terms of both enough food supply and nesting sites, as shown for ravens in North America (Boarman & Heinrich 1999). Findings from boreal forests in Sweden have revealed ravens as forest specialists, breeding and foraging inside large natural forests (Andrén 1992). These forests were uniformly occupied by ravens. Opposite, ravens living in more transformed ecosystems (farmlands, urban areas) are more likely to be distributed less regularly and rather clustered at places with abundant supply of artificial food, as dumps and/or nest sites (Boarman et al. 1995, Boarman 2003, Grünkorn 1999).

Nests in Białowieża Forest were predominantly found in old pines and the nest heights were the highest ever documented. This is probably due to the availability of exceptionally high trees in the forest. Several authors have pointed raven preference for high trees (or high cliffs) and widely spaced tree stands (Davis & Davis 1986, Dunk et al. 1997). Optimised breeding conditions, namely easier approach to the nest for the raven itself and higher visibility of potentially approaching predators (aerial or terrestrial) might be explanatory reasons (see Dunk et al. 1997). Additionally, old pine trunks typically lack branches up to the crowns. This reduces the access to nests by terrestrial predators such as the pine marten *Martes martes*. This is partly supported by the study by Davis and Davis (1986), who found a positive correlation between breeding success of ravens and nest height above ground and at least a slight tendency towards higher breeding success of ravens in coniferous trees.

The population density in Białowieża Forest (1.4 breeding pairs per 10 km^2) is intermediate among densities found in other forests. Densities in forested areas ranges from 0.3 pairs per 10km^2 in Virginia (Hooper 1977) or 0.6 pairs per 10km^2 in Britain (Ratcliffe 1962) to the slightly higher value of 1.7 pairs per 10km^2 found in Wigry, also in eastern Poland (Zawadzka 1996). Data from agricultural landscapes with interspersed forest fragments (where ravens mainly forage in open meadows and fields) showed markedly higher densities: 2.0 pairs per 10km^2 (Sellin 1991), 3.0–4.0 pairs per 10km^2 (both in Germany) (Grünkorn 1993) or 3.6 pairs per 10 km^2 in the Canary Islands (Nogales 1994). In more transformed ecosystems (farmlands, afforested areas) ravens frequently gather around rich artificial food resources (e.g. dumps, landfills, livestock), which, in turn, may result in higher abundance of ravens (Grünkorn 1999). Similarly, one of the highest raven densities have been found in the heavily human-transformed landscape of the Mojave Desert in California. There, raven densities have been additionally increased by a) water resources (Boarman et al. 1995, Boarman 2003) and/or b) man-made nest sites (Boarman et al. 1995, Bednorz 2000). Boarman et al. (1995) has suggested the presence of landfills as the main factor responsible for raven population increases to over 1,000%. Food bonanzas may supply ravens with plentiful food, which may result in very high breeding densities, such as 10.0 pairs/10 km^2, at least on a small spatial scale (Grünkorn 1999). Further support has been given to the fact that high food availability goes along with low intraspecific competition (Nogales 1994, Kochert et al. in Nogales 1994). In this sense, Dare (1986) found evidence for a chronological increase of raven densities in Snowdonia caused by a simultaneous increase in sheep stockings, which resulted in turn in a higher carrion availability. In addition, artificial nesting substrates may enhance breeding success and thus promote an increase in raven populations by a) providing more available nest sites and b) decreasing the predation risk at the nests (due to a reduced access to terrestrial predators) (Steenhof et al. 1993). Thus, it seems that highest breeding densities in common ravens might only be supported in strongly humanized landscapes with overabundance of food and nesting substrates.

To our knowledge, the territory size data presented here are the first for natural forest ecosystems in Europe (Rösner & Selva 2005). It is known, that territory sizes and breeding densities are strongly connected with food availability and intraspecific competition. Thus, one can assume that the higher the food supply the smaller the territory size or home range. Already Ratcliffe (1997) mentioned that raven territory sizes vary in close relation to food availability. Thus, raven territory size may vary strongly between habitats (Table 3). The value from Białowieża is the smallest compared to other forests. Forests in Virginia are fragmented by pastures and urban areas (Hooper 1975, 1977); indicating less natural conditions. The upland deer forest in Scotland is even more transformed (or rather afforested) with much larger territories of ravens although carrion is often plentiful. Ratcliffe (1997) explained this due to a strong interspecific competition with golden eagles *Aquila chrysaetos*, which are numerous and also feed on carrion. The values from cliff breeding raven populations in Ireland are comparable to those from forests in Virginia (Table 3). However, the territory sizes in coastal California are extremely small (1.2 km^2). This may be due to the high availability of nest sites (large cliffs) and food resources such as large sea bird colonies (Linz et al. 1992). Published data concerning territory sizes are mainly gathered from agricultural landscapes. In Wales (grass- and moorland, farmland) as well as in northern Germany (farmland), raven populations are strongly supported by additional food supply in form of sheep carcasses (Wales) or dump sites for organic material (Germany). Both may cause high breeding densities which accordingly lead to smaller territories.

The bait-marking data indicate that adult ravens in the Forest of Białowieża have very good knowledge of their territories and are well adapted to find carrion even under dense forest conditions. Already Heinrich (1990), Promberger (1992)

Table 3. Raven territory sizes in different ecosystems in Europe and North America
Tabela 3. Wielkość terytoriów kruka w różnych ekosystemach Europy i Ameryki Północnej. A – las, B – wybrzeże, C – krajobraz rolniczy

Ecosystem type Typ ekosystemu		Territory size (km^2) Wielkość terytorium	Location Lokalizacja	Source Źródło
Forest (A)	upland deer forest/wyżynny las chroniony dla zwierzyny płowej (trees/drzewa)	61.9–87.3	Scotland/ Szkocja, UK	Ratcliffe (1997)
	forest/las (trees/drzewa)	30.6	Virginia, USA	Hooper et. al (1975) in Hooper (1977)
	lowland forest/ las nizinny (trees/drzewa)	13.1	Białowieża, PL	Rösner & Selva (2005)
Coast (B)	coast/wybrzeże (cliffs/klify)	35.7	Ireland/ Irlandia	Noonan in Ratcliffe (1997)
	coast/wybrzeże (cliffs/klify)	1.2	California/ Kalifornia, USA	Linz et al. (1992)
Farmland (C)	gras/łąki, pastwiska moorland/wrzosowiska	23.9	Wales/ Walia, UK	Dare (1986)
	farmland/ krajobraz rolniczy	9.5	Wales/ Walia, UK	Dare (1986)
	agricultural country/ użytki rolnicze	>5.0	Germany/ Niemcy	Sellin (1991)

and Stahler et al. (2002) characterised ravens to be generally efficient in discovering carcasses and new food resources. This is an important attribute, especially in natural ecosystems where food is distributed randomly. Nevertheless, this attribute enable ravens to explore new and locally clustered food bonanzas also in heavily transformed landscapes.

The breeding performance documented for Białowieża (percentage of reproductive pairs and fledged chickens) is comparable to values from other forest ecosystems in Wyoming and Virginia (see Dunk et al. 1997, Hooper 1977). Markedly lower breeding success (0.2–0.5 fledglings/pair) has been found in agricultural landscapes where raven nests were built in small insular woods (Lo & Müller 2000, Grünkorn 1999). The low breeding success has been discussed as a result of increased intraspecific predation under conditions of high breeding densities (Glandt 2003, Grünkorn 1999). However, in strongly transformed ecosystems where ravens switch from natural to (or even rely on) artificial nesting substrates like electric towers, breeding success might be artificially increased. The steely and high constructions provide secure nest places: reduced predation by terrestrial predators, protection against fire and anchoring against strong winds (Boarman & Heinrich 1999). Anyhow, breeding performance may fluctuate strongly among years. For example, Dunk et al. (1997) reported fluctuations of 238% in three years. Extreme weather conditions, shortage of food – especially at the beginning of breeding season – and nest predation are well known reasons for breeding failure (Ratcliffe 1997). Observations of rapid rematings during breeding season, when “stepmothers or stepfathers” are recruited and look after the chicks have been also recoded by other authors (Stiehl 1985, Ratcliffe 1997).

In Białowieża Forest, the predominant items in raven diet were carrion and cereal, as reported in other studies (Newton et al. 1982, Engel & Young 1989, Zawadzka 1996). Ravens in temperate forests may depend heavily on carrion, mainly of ungulates, especially during winter, when carrion is more abundant but other food resources are unavailable or depleted. The availability of wild ungulate carrion during winter may play a key role in the fitness of raven pairs for the breeding season. In Wales, raven breeding performance clearly depended on sheep carrion supplies (Newton et al. 1982). Recent studies have shown (Kristan et al. 2004) that rubbish dumps may supply ravens constantly with carrion and may be important in maintaining large numbers of ravens, especially non-breeders.

We found clear differences between the food habits of territorial pairs and non-breeders, as also found by Newton et al. (1982). Immature ravens roosting close to the city dump depended on collecting and scavenging on discarded food and remains from domestic animals, which has been shown by the high frequency of refuse, livestock and chicken remains in their pellets. However, ravens pairs kept more ancestral food habits, even though many of them nested close to village glades or openings whenever possible. For these pairs nesting at the forest edge, cereal constituted an important food item. The distance from the nests to points of food subsidies (e.g. dumps, agricultural fields) seems to strongly influence diet composition (Kristan et al. 2004). Adults seemed to be more efficient in taking alive prey or were forced to hunt more often inside the forest. This is supported by the frequent occurrence of squirrels in the pellets of adult ravens, never reported in previous studies on diet. The diet of raven pairs also included more items related to predation in a Mediterranean island, whereas raven flocks showed a pronounced scavenging strategy and fed mainly on the dump (Sarà & Busalacchi 2003). In agreement with our findings, Newton et al. (1982) found that adult ravens consumed more sheep carrion, voles and invertebrates, but much less refuse. With increasing forest cover, the amount of small mammals consumed also increased.

These differences between the food habits of immature and territorial ravens may be a consequence, not only of different foraging abilities, but also of using different foraging habitats. Even raven pairs have been shown to have different diets in different habitat types within the same area (Stiehl & Trautwein 1991, Zawadzka 1996, Kristan et al. 2004). Immature ravens may be relegated to less productive or low-quality areas. This hypothesis is supported also by raven flocks scavenging only on bison carcasses placed in open areas – more visible – whereas those bison carcasses located inside the forest were exclusively used by territorial pairs (Selva et al. 2003). Similar habitat segregation has been described for other avian scavengers foraging in groups (Kirk & Houston 1995, Donázar et al. 1998).

To sum up, the whole Białowieża Forest represents a suitable habitat for ravens, which are perfectly adapted to pristine forest conditions. Ravens selected the best breeding sites (secure old pine stands) and showed efficient strategies to exploit forest food resources such as association with large predators, hunting of forest rodents or fast location of ungulate carcasses. In this respect, their ecological requirements differed much from those of raven populations in highly transformed ecosystems of Europe and North America. Raven populations in these landscapes, facing the appearance of new conditions, have easily adapted to the exploitation of human-provided resources, and thus loosing most of their ancestral habits.

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