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Reproduction and mortality of invasive raccoon dogs (*Nyctereutes procyonoides*) in the Białowieża Primeval Forest (eastern Poland)

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We investigated reproduction and mortality of raccoon dogs (*Nyctereutes procyonoides*) in the Białowieża Primeval Forest (eastern Poland). The species invaded the forest in 1955 and is more common than native species of medium-sized carnivores. The mean litter size of raccoon dogs, based on placental scars and foetuses was 8.4 (SD = 2.0). Mortality of pups was 61% during the first three months following parturition. Of 82 cases of raccoon dog deaths recorded from 1996 to 2006, 55% were caused by natural factors (predation and diseases), 40% were human-related (vehicle collisions, harvest, poaching), and 5% were indeterminable. Rabies was the most important disease. The main predators of raccoon dogs were wolves (*Canis lupus*) and domestic dogs (*Canis familiaris*). Almost all raccoon dogs killed by cars were dispersing juveniles. We did not find differences in causes of mortality between collared and uncollared individuals. The annual survival rate of radio-tracked raccoon dogs (n = 18, 1997–2000) was 0.38 (SD = 0.05), and did not differ between males and females. Survival of raccoon dogs varied seasonally. It was highest in winter (0.82) when raccoon dogs settle in burrows, which may protect them against predation. The life table constructed based on the age at death indicates that mortality was highest in the first year of the raccoon dog life (0.82), and lower in the following years (0.58–0.68). Most raccoon dogs (98%) died during the first three years of their life and the maximum life span was 7 years. Life expectancy at birth was 0.8 years.

Introduction

The raccoon dog *Nyctereutes procyonoides* is a medium-sized carnivore, which originally comes from eastern Asia. After introduction to the European part of the former Soviet Union during the 1920s–1950s (Geptner *et al*. 1967), raccoon dogs spread over eastern, central and northern Europe. From 1935 to 1984, raccoon dogs colonized by natural expansion 1.4 million km^2 of Europe (Nowak & Pielowski 1964, Nowak 1973, Kauhala & Saeki 2004a). In some of the areas invaded by the raccoon dog, they have become the most numerous species among medium-sized and large carnivores (Jędrzejewska & Jędrzejewski 1998, Sidorovich *et al*. 2000). One of the factors which enabled raccoon dogs to expand and inhabit large areas of Europe is high reproductive capacity, much higher than expected for a medium-sized carnivore (Helle & Kauhala 1995). Other factors of successful expansion are probably great plasticity in adaptation to various climatic and environmental conditions, migratory ability, omnivory, and limited control by humans (Kauhala 1996, Jędrzejewska & Jędrzejewski 1998, Kowalczyk 2006).

Fast expansion of raccoon dogs took place in well preserved wooded areas and marshlands of eastern and northern Europe (e.g. Finland, Baltic states, and Poland), that are inhabited by large carnivores, such as the lynx (*Lynx lynx*) and the wolf (*Canis lupus*) (Nowak & Pielowski 1964, Helle & Kauhala 1991). On one hand, raccoon dogs often utilize animal carcasses, including kills by large carnivores, as food resources. On the other hand, their exposure to predation is probably higher than that of other species of smaller carnivores (Sidorovich *et al*. 2000, Selva *et al*. 2005). Also, life habits of raccoon dogs (high population density, monogamy, cohabitation of burrows with other carnivores, use of carrion) make them vulnerable to disease and parasites (Oksanen *et al*. 1998, Oivanen *et al*. 2002, Kauhala *et al*. 2007), such that the raccoon dog is one of the main vectors of rabies in northeastern Europe (Westerling 1991, Holmala & Kauhala 2006).

Despite its more than 50-year presence in Europe, the species has been studied thoroughly only in Finland, where raccoon dogs are intensively hunted (Kauhala & Saeki 2004a). In the Białowieża Primeval Forest (E Poland), raccoon dogs were first recorded in 1955 (Dehnel 1956). They coexist here amongst a rich predator community and are the most numerous of the medium to large-sized carnivores (Jędrzejewska & Jędrzejewski 1998). We collected raccoon dog carcasses during 1996–2006 and radio-tracked 18 individuals from 1997 to 2002 to study reproduction and mortality of the species in a well preserved natural forest inhabited by large predators. Our specific objectives were to: (1) estimate the reproductive rate of raccoon dogs and the survival of pups; (2) determine mortality factors of raccoon dogs; and (3) estimate seasonal and annual survival and cause-specific mortality rates.

Material and methods

Study area

The Białowieża Primeval Forest (BPF) is one of the best preserved temperate lowland forests in Europe. It covers 1500 km^2 of continuous woodland located on the Polish–Belarussian border (52°30´–53°N, 23°30´–24°15´E). In the Polish part of the BPF (595 km^2), coniferous and mixed forests, dominated by pine *Pinus silvestris* and spruce *Picea abies*, cover 48% of the area, wet forests with alder *Alnus glutinosa* and ash *Fraxinus excelsior* cover 19%, rich deciduous stands dominated by oak *Quercus robur*, hornbeam *Carpinus betulus*, lime *Tilia cordata*, and maple *Acer platanoides* 15%, and aspen *Populus tremula* and birch *Betula* sp. stands 12% of the area (Jędrzejewska & Jędrzejewski 1998, Sokołowski 2006). Open habitats (glades with meadows, riverside open sedge and reed marshes) cover 6% of the area. The Polish part of the BPF consists of the protected area — Białowieża National Park (100 km^2) — and exploited forests (495 km^2). The area is generally flat (134–186 m a.s.l.), with gentle hills and shallow depressions. The density of forest roads suitable for 2-wheel drive cars is about 1.2 km km^{-2}, but only about 50 km of paved roads are used by the public (Theuerkauf *et al*. 2003).

The climate of the BPF is transitional between continental and Atlantic types with clearly marked cold and warm seasons. Mean temperatures during the study period (1996–2006) were –3.6 °C in January and 19.9 °C in July. Recorded temperatures varied from –33.5 to +33.4 °C (min and max, respetively). Snow cover persisted for an average of 85 days per year (range = 60–137 days) with an average maximum recorded depth of 34 cm (range: 13–63 cm). Mean annual precipitation during the study period was 574 mm (range = 490–681 mm).

The BPF is inhabited by 12 species of carnivorans, including two large predators: wolf and lynx. Raccoon dogs reached densities of 0.7 ind. km^{-2}, higher than those of the native species of medium-sized carnivores: red fox *Vulpes vulpes* (0.2–0.5 ind. km^{-2}) and badger *Meles meles* (0.2 ind. km^{-2}) (Jędrzejewska & Jędrzejewski 1998, Kowalczyk *et al*. 2003). Hunting in the BPF is limited to the commercial forest only and focuses on ungulate species (mainly wild boar and red deer). Raccoon dogs are shot occasionally, often when visiting wild boar baiting sites. The hunting season for raccoon dogs extends from 1 August to 31 March.

Data collection and analyses

Raccoon dogs were captured in the central part of the BPF (including both managed forest and national park). Trapping was carried out from September to March (1997–2001). We used box and foot-snare traps set near wintering dens (identified by snow-tracking) and fitted with alarm systems. Additionally net and hand trapping was used. The last two methods were used during snow-tracking or when capturing the second individual of a pair. During snow-tracking, raccoon dogs were captured when found resting on the ground or in hollow trees. They rarely escaped when approached for the first time, so were easily covered with a net or taken by hand from a hollow. If the radio-collared individual had a mate, we tried to capture it by localizing the individual already wearing the collar and capturing the second individual with a net. In total, we captured 19 individuals (including 5 pairs), 11 by hand or net trapping, 6 in box traps, and 2 using foot-snare traps (Appendix). The captured animals were immobilized by an intramuscular injection of a xylazine-ketamine mixture (Kreeger 1997) and fitted with radio-transmitters (Advanced Telemetry System, USA, weight = 125 g). The sex of the raccoon dogs was determined, and age (yearling or adult) was estimated on the basis of body mass and tooth wear. Exact age of radio-collared raccoon dogs was estimated after their death, except for three individuals that were lost. One raccoon dog was excluded from the analyses, because we lost contact with it after three days.

The range of the signal from radio-transmitters was maximally 800–1500 m. Radio-collared raccoon dogs were located from the ground, 3–6 times per week. The average time of active collar wearing per raccoon dog was 313 days (range: 13–901 days). Radio-tracking was used for mortality rate estimation, searching for natal nests to count litter size, and in finding radio-collared individuals to count number of pups accompanying them.

Litter size was estimated in two ways: (1) counts of placental scars (Lindström 1981) and foetuses; and (2) counts of pups in or around the natal nest (before nest abandonment) or accompanying the breeding pairs (after nest abandonment). In total, we investigated 20 females for placental scars and one female for foetuses (14 from the Polish and seven from the Belarussian part of the Białowieża Forest). There are no studies comparing litter size of raccoon dogs based on placental scars and pups born. Studies on other canids showed that the placental scar count is a reliable method of birth litter size estimation (Helle & Kauhala 1995, Strand *et al*. 1995, Elmeros *et al*. 2003, but *see* Green *et al*. 2002). To count pups accompanying their parents, we carefully approached the collared individuals and counted their pups or we observed the natal nests for 1–3 hours. Additionally, all observations of non-collared raccoon dogs with young where recorded. In total, we made 18 observations of 14 litters.

Mortality rates were calculated based on the radio-tracking data using the method described by Trent and Rongstad (1974) and Heisey and Fuller (1985), with the MicroMort programme.

Raccoon dog carcasses were collected during 1996–2006. From carcasses we collected heads for skull preparation, teeth for age determination, uteri from females for reproduction investigation. Body measurements and genetic samples for other studies were also taken as well as rabies examinations were carried out. To increase the sample size for some analyses (age structure, life tables) we used 27 specimens collected from the Białowieża Primeval Forest during 1980–1990, kept at the Mammal Collection of the MRI PAS.

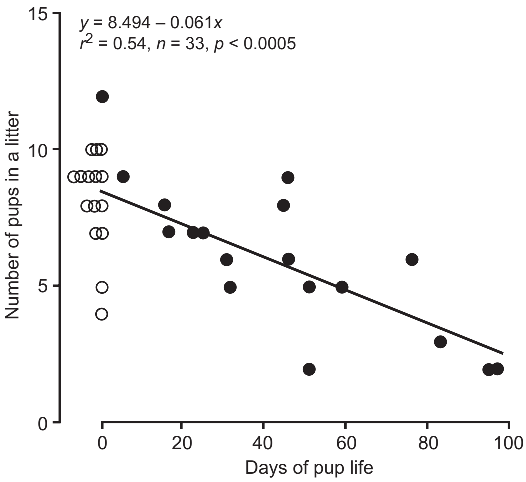

Fig. 1. Litter size of raccoon dogs *Nyctereutes procyonoides* in the Białowieża Primeval Forest in relation to the consecutive days of a pups' life. Empty circles = litter size based on placental scars; filled circles = litter size based on foetus count or observation of pups.

We determined the cause of mortality for each dead individual found (both collared and uncollared raccoon dogs) based on necropsy results (in numerous cases from a veterinarian pathologist's examination) and physical evidence at the site — tracks of predators, location of carcass (e.g. caching, placement near dens, wolf-kills, villages). Determination of the mortality factor was not possible in some cases due to carcass decay. Species of predators were identified based on the size of bite marks and from physical evidence at the kill sites. One raccoon dog killed by a car and recognized as rabies-positive was classified as having died due to rabies.

We used two methods for age determination of collected raccoon dogs. To separate young and adult animals, age estimation was based on tooth abrasion, development of the postorbital constriction and the sagittal crest, obliteration of sutures, roughness of the cranium surface and skull development. Adult raccoon dogs were aged by the configuration of incremental cementum lines of the upper canine. Longitudinal sections, by an efficient method of low speed cutting, produced the number of annual lines which were then used to define age in years (Driscoll *et al*. 1985, Kauhala & Helle 1990, Ansorge 1995). Age was assessed in days (average age) or years (age structure, life span) assuming that all raccoon dogs were born on 25 April (the date estimated based on radio-tracking and pup finding).

The raccoon dog life table was calculated based on the ages recorded at death (Krebs 1989). The number of individuals for age class 0 was estimated based on the assumption that 61% of raccoon dogs died during the first three months of life (decrease of the number of pups per litter from 8.4 to 3.3 — *see* Results). Thus, we assumed that a total sample of 98 raccoon dogs with known age, older than three months, constituted 39% of the individuals born, so the potential number of animals at class 0 was calculated as 250 individuals.

Results

We did not find a significant difference (Mann-Whitney test: $U = 51.0$, $p = 0.63$) between litter size estimated by placental scar count (mean ± SD = 8.1 ± 1.7, $n = 15$, range = 4–10), and that based on the number of pups found in natal nests during 30 days after parturition (five cases) and foetus count (one case, female two weeks before whelping) (mean ± SD = 8.3 ± 2.0, $n = 6$, range = 7–12) (Fig. 1). The litter size of raccoon dogs at birth based on placental scar and foetus counting ranged from 4 to 12, and averaged 8.4 ± 2.0 (SD). Litter size decreased to 3.3 ± 2.5 (SD) (range = 2–6) in the third month of a pup's life (Fig. 1). During the first 3 months after parturition, mortality of pups was 61%. There was a significant negative relationship between litter size and days of pup life (Fig. 1). Of 21 females of known reproductive status, reproduction was recorded in 64% of 1-year old females ($n = 11$) and 100% in ≥ 2-year-old females ($n = 10$).

Of 82 deaths recorded, 55% were caused by natural factors (27% predation, 27% diseases), 40% were human-related (vehicle collisions, harvest, poaching), and 5% were indeterminable (Table 1). Among diseases, rabies and sarcoptic mange were the most important. Of 22 raccoon dogs killed by predators, 13 were preyed upon by large predators: wolves and dogs *Canis familiaris* (6 and 7 cases, respectively) (Table 1). Three raccoon dogs killed by predators were found in the vicinity of predator kills or dead ungulates. When killed by predators, raccoon dogs were rarely consumed (27%). Vehicle collisions (24% of all cases) were the most important source of human-caused mortality. Of 20 raccoon dogs killed by cars, 18 were juveniles. Hunting and poaching together made up 16% of raccoon dog mortality (Table 1).

To check if estimation of mortality factors based on incidentally located carcasses is a reliable source of data, we compared causes of mortality of radio-collared and uncollared raccoon dogs found during the study. Among uncollared individuals, we selected animals older than 5 months as all radio-collared individuals were fully grown animals. Among uncollared raccoon dogs, the percentage of animals which died due to predation was lower than in the sample of radio-collared individuals, while deaths from disease, vehicle collisions, hunting and poaching occurred more frequently (Table 2). However, the differences were not statistically significant (G-test: $G_3 = 7.740$, $p > 0.05$). There were 49% males and 51% females in the collected sample ($n = 59$ individuals with known sex, dead and captured together). Among dead animals with known age ($n = 98$), 54% were juvenile (≤ 1-year-old), 27% were 1.1–2 years old, 13% were 2.1–3 years old, and 6% were older than three years of age (Fig. 2).

Table 1. Causes of death of dead raccoon dogs found in the Białowieża Primeval Forest during 1996–2006 (n = 82 individuals).

Causes	Percentage of cases
Natural	55
Predation	27
Dog *Canis familiaris*	9
Wolf *Canis lupus*	7
Badger *Meles meles*	2
White-tailed eagle *Haliaeetus albicilla*	1
Unidentified predator	7
Diseases	27
Rabies	15
Sarcoptic mange	6
Other diseases	6
Drowning in a drain	1
Human-related	40
Collisions with vehicles	24
Hunting	12
Poaching	4
Unidentified	5

Annual survival rate of radio-tracked raccoon dogs (older than five months) was 0.38 (SD = 0.05, range = 0.25–0.55) (Table 3), and did not differ between males and females (0.31 and 0.47, respectively) (G-test: $G_1 = 1.83$, $p > 0.05$). Mortality due to predation was higher for males than for females (G-test: $G_1 = 4.45$, $p < 0.05$) (Table 3). Seasonal survival significantly differed between December–March (0.82) and August–November (0.51) (G-test: $G_1 = 7.292$, $p < 0.05$). Predation was an important source of mortality in all seasons, while diseases were important mainly in August–November.

The life table constructed based on age at death (x) indicates that the rate of mortality (q_x) was highest in the first year of raccoon dog life (0.82), and decreased in the following years (0.50–0.68) (Table 4). Most raccoon dogs (98%) died during the first three years of life. Among radio-tracked individuals, 71% died in age < 3 years, but 93% before reaching the age of 3.3 years. Maximal life span of raccoon dogs was 7 years; the oldest raccoon dog found dead during the study was 6.6 years old. Life expectancy at birth was 0.8 years (Table 4).

In seven pairs of raccoon dogs (five radio-tracked and two uncollared), we recorded death of one (two cases) or both individuals of a pair (five cases) (Table 5). We recorded a relatively short time-span between the deaths of both individuals from a pair (0–114 days). In one of two pairs for which we recorded death of one individual only, the surviving individual was observed

Table 2. Comparison of mortality causes of uncollared (n = 46) and radio-collared (n = 15) raccoon dogs found dead in the Białowieża Primeval Forest during 1996–2006.

Causes	Percentage of dead raccoon dogs > 5 months old	
	Uncollared	Radio-collared
Natural	67	67
Predation	30	40
Diseases	37	27
Human-related	28	13
Vehicle collisions	4	–
Hunting and poaching	24	13
Other and unidentified	4	20

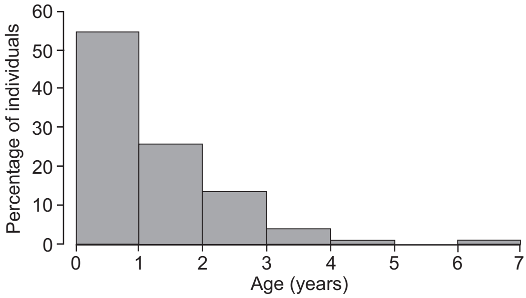

Fig. 2. Age structure of raccoon dogs found dead in the Białowieża Primeval Forest; n = 98 animals.

paired with another individual (probably a new mate). The age difference between individuals in a pair ranged from 0 to 4 years (Table 5).

Discussion

Reproductive rates of raccoon dogs in the Białowieża Primeval Forest were among the highest observed in the species (range = 4.9–10.2, based on placental scars; Geptner *et al*. 1967, Ansorge & Stiebling 2001, Kauhala & Saeki 2004b). Reproductive rates higher than in other canids of corresponding body size (Moehlman 1986) might compensate for high mortality. In raccoon dogs, both males and females take care of pups, which rarely stay alone (Kauhala *et al*. 1998, Drygala *et al*. 2008). However, even with such thorough care, pups suffer very high mortality. As reported by Helle and Kauhala (1993), only 11% of young raccoon dogs survived the first year of their life. Compensatory reproduction is known for some species of canids (e.g. red foxes: Schofield 1958, Cavallini & Santini 1996; coyotes *Canis latrans*: Knowlton 1972; wolves: Sidorovich *et al*. 2007) and this is likely to occur in raccoon dogs as well. The high reproductive potential of raccoon dogs was not only expressed by large litters, but also by a high proportion of breeding females (81%). In Finland, the proportion of reproducing females averaged 78% (Helle & Kauhala 1993).

During our study we found only three dead pups (two killed by badgers and one by sarcoptic mange). Carcasses of pups are probably consumed totally or taken out of natal nests by predators or scavengers, and their remains quickly disappear. Raccoon dog pups may be easily accessible to predators, because the natal lairs are often located in fallen hollow trees or on the ground in dense vegetation (R. Kowalczyk unpubl. data). This might result in high mortality of pups from predation and explain our finding that the percentage of juveniles in the population was lower than in other studies (e.g. 68% in Japan (Obara 1983); 70%–75% in Germany (Ansorge & Stiebling 2001); 74%–87% in Finland (Helle & Kauhala 1993)). In the BPF, raccoon dogs often settled in active badger setts for wintering and — less frequently — for reproduction (Kowalczyk *et al*. 2008). This increased the chance of aggressive interactions, including interspecific killing of pups, as observed in other studies on medium-sized carnivores (review in Palomares & Caro 1999).

Table 3. Mean and 95% confidence intervals (CI) for annual and seasonal survival rates and cause-specific mortality rates of radio-collared raccoon dogs in the Białowieża Primeval Forest (September 1997–August 2000). N = number of individuals radio-tracked by sex group or season.

Group of animals or season	*N*	Survival rate (95% CI)	Cause-specific mortality rates (95% CI)		
			Predation	Disease	Human
Raccoon dogs					
All animals	17	0.38 (0.17–0.89)	0.22 (0.01–0.51)	0.22 (0.01–0.51)	0.07 (0–0.17)
Males	8	0.31 (0.10–0.99)	0.28 (0–0.72)	0.27 (0–0.61)	0.07 (0–0.20)
Females	9	0.47 (0.16–1)	0.15 (0–0.30)	0.15 (0–0.41)	0.08 (0–0.21)
Season					
August–November	14	0.51 (0.20–1)	0.12 (0–0.27)	0.18 (0–0.36)	0.06 (0–0.17)
December–March	13	0.82 (0.65–1)	0.12 (0–0.27)	0	0.06 (0–0.17)
April–July	11	0.72 (0.44–1)	0.12 (0–0.27)	0.06 (0–0.17)	0

Table 4. Life table for the raccoon dog in the Białowieża Primeval Forest constructed on the basis of age at death recorded (1996–2006). x = age at death (years), n_x = number of alive at start of age interval, l_x = proportion surviving at start of age interval, d_x = number of dying within age interval, q_x = rate of mortality, p_x = rate of survival, e_x = life expectancy.

Age (years)	n_x	l_x	d_x	q_x	p_x	e_x
0	250*	1.000	205	0.820	0.180	0.796
1	45	0.180	26	0.578	0.422	1.144
2	19	0.076	13	0.684	0.316	1.026
3	6	0.024	4	0.667	0.333	1.167
4	2	0.008	1	0.500	0.500	1.500
5	1	0.004	0	0	1.000	1.500
6	1	0.004	1	1.000	0	0.500
7	0	0	–	–	–	–

* Zero frequency calculated from fecundity rates — *see* Material and methods.

Intra-guild predation is often recorded among canid species (Palomares & Caro 1999). On one hand, large predators might be a limiting factor for smaller carnivores (Lindström *et al.* 1995, Ralls & White 1995, Helldin *et al.* 2006). On the other hand, large carnivores may ensure scavengers, such as raccoon dogs, access to food resources (carcasses), thereby securing them survival in severe winters (Viro & Mikkola 1981, Sidorovich *et al.* 2000, Selva *et al.* 2005). Raccoon dogs are very efficient scavengers (Sidorovich *et al.* 2000, Selva *et al.* 2005) and, in some areas, carrion or kill remnants left by larger predators are a very important component of their diet (Jędrzejewska & Jędrzejewski 1998, Sidorovich *et al.* 2000, 2008). In the BPF, 47% of ungulate carcasses were scavenged by raccoon dogs (Selva *et al.* 2005). However, use of carcasses by raccoon dogs is risky because they may become prey themselves when carrion remnants are revisited by wolves or lynx or utilized by larger birds of prey (e.g. white-tailed eagles *Haliaeetus albicilla*). We recorded three such cases during our study (one raccoon dog killed by an eagle and two killed by wolves).

One of the factors which make raccoon dogs especially susceptible to predation is their behaviour. When approached, they usually remain still without escaping. As described earlier, we were able to cover raccoon dogs with a net or hand-trap them. In Finland, domestic dogs were used to capture raccoon dogs for radio-collaring (Kauhala & Helle 1994). In late autumn, their mobility is additionally limited by excessive fat reserves. Their body mass then is 50%–70% higher than in the spring (Kauhala 1993, R. Kowalczyk unpubl. data). In winter, when raccoon dogs settle in burrows (mainly badger setts; Kowalczyk *et al.* 2000, 2008) and stay inactive for longer periods (Kauhala *et al.* 2007, Kowalczyk *et al.* 2008), they become unavailable for large predators. It results in a higher survival of raccoon dogs in winter than in summer.

The raccoon dog is one of the main vectors of rabies in northeastern Europe (Westerling 1991, Holmala & Kauhala 2006). In the 1990s, from 7% to 50% of all rabies cases in Poland, Lithuania, Latvia and Estonia were found in raccoon dogs (Mól 2005, Kowalczyk 2006). In the late 1980s, during a rabies epizootic in

Table 5. Mortality of pairs of raccoon dogs in the Białowieża Primeval Forest.

Pair of raccoon dogs	Age (Female/Male) (years)	Days between deaths of individuals from a pair	Sex of individual dying first	Cause of mortality (Female/Male)
F1–M2	1/5	114	Male	Predation/predation
F4–M5	1/2	42	Male	Predation/unknown
F5–M4	?/3	> 60*	Male	Survived*/predation
F10–M11	2/1	8	Female	Disease/predation
F14–M13	?/2	> 174*	Male	Survived*/disease
Uncollared pair	1/1	0	Together	Predation/predation
Uncollared pair	?/?	0	Together	Shot/shot

* We were not able to estimate the exact date and source of mortality of the second individual due to collar loss or failure.

Finland, 77% of the cases identified were in raccoon dogs (Westerling 1991). Oral vaccination campaigns against rabies conducted recently in Poland and other European countries may diminish the role of rabies in raccoon dog mortality, as it has already been reported for the red fox (Goszczyński *et al*. 2008).

Another important factor of raccoon dog mortality was vehicle accidents. Traffic mortality affected mostly dispersing young, who were more susceptible to accidents than adults (*see* Takeuchi & Koganezawa 1994, Saeki & Macdonald 2004). Also in Japan, the mortality of raccoon dogs on roads increased during dispersal in the autumn (Saeki & Macdonald 2004).

As argued by Ciucci *et al*. (2007), mortality analyses based on incidentally found dead animals (opportunistic sampling) are inadequate, because different causes of death may not have the same probability of detection. This was shown for Florida panthers *Puma concolor coryi* (Taylor *et al*. 2002), where 88% of uncollared individuals died due to vehicular trauma and illegal killing, while those factors were responsible for deaths of only 19% of collared animals. In our comparison, we did not find significant differences in mortality causes between collared and uncollared raccoon dogs, but we excluded all juveniles < 5 months old from the analyses, as all the collared individuals were fully grown animals of age > 5 months. Most of the uncollared juveniles (18 of 21) were killed by cars. Comparable shares of natural and human-related causes of mortality among collared and uncollared raccoon dogs most likely resulted from the character of the study area: the Białowieża Primeval Forest is a large woodland with a very low density of human settlements and paved roads (Theuerkauf *et al*. 2003).

Mortality rates, life expectancy and longevity of raccoon dogs in the BPF were similar to those observed in Finland (Helle & Kauhala 1993). In the BPF, natural factors of mortality such as predation and diseases might have a similar effect on population dynamics as heavy hunting pressure in Finland (Helle & Kauhala 1993), where 75 000–130 000 individuals are shot annually (Kauhala & Saeki 2004a). In Poland, annual hunting bag is only 6000–10 000 individuals (data from the Research Station of the Polish Hunting Society in Czempiń, Poland). It is worth mentioning that the population density of raccoon dogs in Poland and Finland are comparable (Jędrzejewska & Jędrzejewski 1998, Goszczyński 1999, Kauhala *et al*. 2006).

The relatively short period between deaths of individuals in a pair might result from their social behaviour. Because individuals of a pair most often rest, move and forage together (R. Kowalczyk unpubl. data), there is also a high probability of being simultaneously killed by predators or hunters, as well as of disease transmission.

Despite a high mortality rate, the life strategy of raccoon dogs make them ideally suited to invading new areas. Western Europe seems to be especially suitable due to a lack of large predators and the elimination of rabies (oral vaccination programs). This poses a special conservation concern, as the raccoon dog is listed as an invasive species, which have proved to be a threat to biological diversity (*see* e.g. Kauhala & Auniola 2001) and should be eradicated (Kowalczyk 2006).

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Appendix. Raccoon dogs *Nyctereutes procyonoides* radio-tracked in the Białowieża Primeval Forest during 1997–2002. F1–F16: females, M1–M15: males.

No.	Raccoon dog	Age (year of life)	Radio-tracking period	Cause of mortality
1	F1	1	25 Sep. 1997–14 Mar. 2000	Predator
2	F3	2	10 Feb.–6 May 1998	Unknown
3	F4	1	16 Feb.–1 Dec. 1999	Predator
4	F5	> 1*	11 May–13 Aug. 1998	Faith unknown (collar lost)
5	F6	1	25 Sep.–23 Oct. 1998	Sarcoptic mange
6	F7	1	26 Sep.–29 Oct. 1998	Poached
7	F8	1	28 Sep.–23 Dec. 1998	Unknown
8	F10	2	15 Dec. 1998–28 Aug. 2000	Disease
9	F14	> 1*	14 Jan. 1999–4 Jane 2001	Faith unknown (collar failure)
10	F16	1	7 Nov. 2001–10 June 2002	Unknown
11	M1	3	14 Sep.–23 Oct. 1997	Infection
12	M2	5	21 Sep. 1997–20 Nov. 1999	Predator
13	M4	3	28 Mar.–15 June 1998	Predator
14	M5	2	16 Feb.–21 Oct. 1999	Unknown
15	M9	1	2 Oct. 1998–13 Apr. 1999	Predator
16	M11	1	15 Dec. 1998–5 Sep. 2000	Predator
17	M13	2	14 Jan. 1999–15 July 2000	Disease
18	M15	> 1*	16–28 Jan. 1999	Shot

* The exact age was not estimated.