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Litter size, sex ratio, and age structure of gray wolves, *Canis lupus*, in relation to population fluctuations in northern Belarus

V.E. Sidorovich, V.P. Stolyarov, N.N. Vorobei, N.V. Ivanova, and B. Jędrzejewska

Abstract: Gray wolf (*Canis lupus* L., 1758) population fluctuations in northern Belarus (Vitebsk region) between 1990 and 2003 were significantly affected by hunting pressure by humans. Mean litter size was inversely density dependent and varied from 4.8 to 7.7 pups (range 2–10). The increase in litter size with declining density of wolf population concerned only female pups, whereas the number of male pups in a litter was not related to population density. The sex ratio of pups varied significantly: the proportion of females reached 70% in a low-density wolf population and declined to 40%–50% in a high-density population. The age structure also varied. In years following heavy hunting pressure, 55% of individuals shot were juveniles <1 year old (with a strong predominance of females that constituted 69% of juveniles shot), and only 11% of wolves were older than 4 years. The mean age of all wolves shot was 1.5 years. In years following low hunting pressure, 34% of animals shot were juveniles and 20% exceeded 4 years. The mean age was 2.8 years. A female-biased sex ratio of wolf pups conforms to Hiraiwa-Hasegawa's hypothesis of the advantaged daughter, proposed for species in which mothers are able to influence the reproductive success of their daughters through transmission of rank.

Résumé : Les fluctuations de populations de loups communs (*Canis lupus* L., 1758) du nord de la Biélorussie (région de Vitebsk) entre 1990 et 2003 ont été affectées de façon importante par la pression de chasse par les humains. La taille moyenne des portées varie de 4,8 à 7,7 petits (étendue 2–10) et est inversement dépendante de la densité. L'augmentation de la taille des portées en fonction inverse de la densité de populations de loups ne s'applique qu'aux louveteaux femelles, puisque que le nombre de louveteaux mâles n'est pas en relation avec la densité de la population. Le rapport mâles à femelles varie considérablement : la proportion de femelles atteint 70 % lors des faibles densités de populations de loups et diminue à 40 % – 50 % aux fortes densités de population. La structure en âge est aussi variable. Dans les années qui suivent une forte pression de chasse, 55 % des individus abattus sont des jeunes de <1 an (avec une nette prédominance de femelles qui représentent 69 % des jeunes abattus) et seulement 11 % des loups tués ont plus de 4 ans. L'âge moyen des loups abattus est de 1,5 années. Dans les années qui suivent une pression de chasse réduite, 34 % des animaux abattus sont des jeunes et 20 % sont âgés de plus de 4 ans. L'âge moyen est de 2,8 années. Un rapport des sexes avec prédominance de femelles chez les louveteaux est conforme à l'hypothèse d'Hiraiwa-Hasegawa de la fille favorisée qui a été proposée chez les espèces chez lesquelles les mères peuvent influencer le succès reproductif de leurs filles en leur transmettant leur rang.

[Traduit par la Rédaction]

Introduction

The negative effect of population density on reproduction rates in mammals is well documented and has been interpreted as evidence for increasing competition for food with diminishing amount of resources per capita when population numbers grow (e.g., Messier 1991). In gray wolves (*Canis*

lupus L., 1758), a direct relationship between prey (ungulate) biomass available per wolf and litter size was shown in Alaska during large, rapid declines in ungulate populations (Boertje and Stephenson 1992). Density-dependent changes in litter size may also be triggered by human exploitation of wolf populations. Pimlott et al. (1969) reported small litters (mean 4.9 pups) in an unexploited population in

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Table 1. Indices of gray wolf (*Canis lupus*) abundance (number of tracks/km of transect per 2 d and number of wolves/100 km² based on game wardens' assessment of the number of wolves in winter), number of wolves killed, litter size, and percentage of females in all litters found in the Poozere Forest (Vitebsk region, northern Belarus).

Year	Wolf abundance index (<i>N</i> tracks/km per 2 d)	Estimated density (<i>N</i> wolves/100 km ²)	Number of killed wolves	Litter size			Percentage of females in all litters
				<i>N</i>	Mean ± SE	Min.–max.	
1985	?	?	?	5	6.0±1.0	3–9	53.3
1986	?	?	?	4	6.3±1.0	4–8	52.0
1987	?	?	?	4	5.3±0.9	3–7	52.4
1988	?	?	50	4	5.3±0.6	4–7	42.9
1989	?	?	50	5	4.8±0.7	3–7	54.2
1990	1.2	2.2	64	5	5.6±0.7	4–8	47.8
1991	1.0	1.3	66	4	5.8±1.3	3–9	47.8
1992	1.1	1.5	80	4	5.0±1.2	2–7	53.9
1993	0.5	0.9	42	6	7.5±0.6	5–9	60.5
1994	0.6	1.6	34	7	7.1±0.7	4–9	61.1
1995	1.8	3.6	38	9	4.8±0.6	3–8	48.7
1996	3.2	2.1	74	8	5.1±0.7	3–8	39.0
1997	2.4	3.0	62	5	5.6±0.8	3–8	53.6
1998	0.7	0.5	64	5	7.4±0.5	6–9	67.6
1999	0.4	0.8	61	6	7.7±1.0	3–10	69.6
2000	0.3	1.7	54	6	7.0±0.7	5–9	69.0
2001	0.7	0.5	35	4	6.0±0.4	5–7	54.2
2002	0.8	0.7	40	5	7.6±0.4	7–9	57.9
2003	0.9	1.9	36	5	5.8±0.7	5–8	51.7
All years	—	—	850	101	6.1±0.2	2–10	55.5

Note: ?, no data available.

Ontario, Canada, whereas Rausch (1967) documented larger litters (mean 6.5) in the exploited populations in Alaska.

Data on pup sex ratio variation in wolf populations are anecdotal. Mech (1975) reported strongly male-biased sex ratio in a saturated, high-density areas and 1:1 or female-biased ratios in low-density areas in Minnesota. However, as such studies are rather rare, Kreeger (2003) suggested that, based on available empirical evidence, there would be no reason to suspect a skewed sex ratio of wolf pups at birth.

It has been documented that the age structure of a wolf population is affected by hunting: heavy hunting pressure causes a higher proportion of young per adult, shorter mean and maximal ages, and an earlier age of first breeding in females (Smirnov and Korytin 1985; Jędrzejewska et al. 1996; Jędrzejewski et al. 2005).

In this paper, we report on the litter size, the sex ratio of pups, juveniles, and adults, and the age structure of individuals killed in a controlled population of wolves in northern Belarus, eastern Europe. Based on long-term data (1985–2003 for litter size and 1990–2003 for abundance index of wolves), we investigated the effect of varying levels of hunting pressure on (i) the litter size and sex ratio of pups and (ii) the age structure and sex ratio of individuals killed.

Material and methods

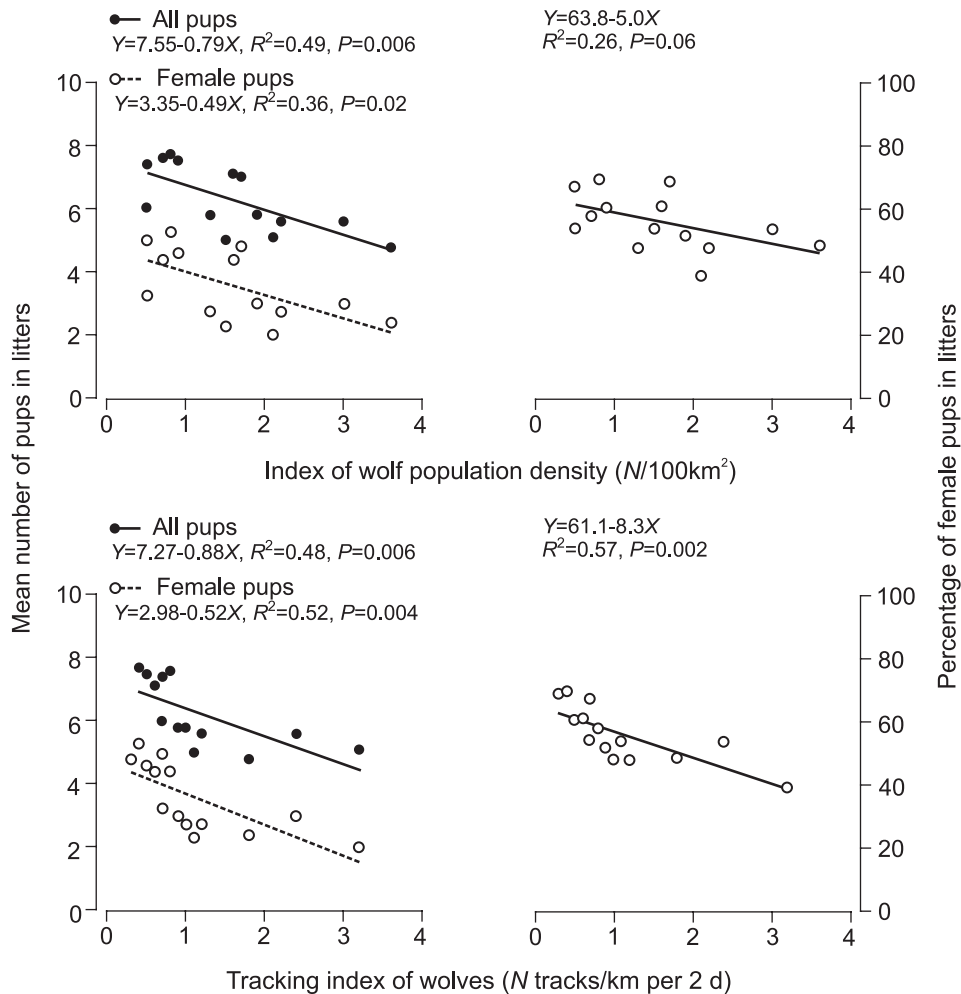
The material was collected in the Poozere Forest in northern Belarus (28°–31°E, 55°–56°N), mainly in the Gorodok, Rossony, and Shumilino districts of the Vitebsk region. The area is part of the transitional region of temperate and boreal forests. The terrain is flat or hilly with numerous lakes. Nor-

way spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) are dominant tree species. Deciduous trees include European black alder (*Alnus glutinosa* (L.) Gaertn.), gray alder (*Alnus incana* (L.) Moench.), European white birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.), and European aspen (*Populus tremula* L.). The mean temperature in January is –6 °C and that in July is 18 °C. Snow cover usually persists for 3–4 months with a maximal depth of 30–90 cm.

The guild of large carnivores consists of three species: the gray wolf, the Eurasian lynx (*Lynx lynx* L., 1758), and the brown bear (*Ursus arctos* L., 1758). The community of wild ungulates includes moose (*Alces alces* (L., 1758)), western roe deer (*Capreolus capreolus* (L., 1758)), and wild boar (*Sus scrofa* L., 1758). In several locations, red deer (*Cervus elaphus* L., 1758) occur in low numbers.

The wolf has a status of game species and is subject to control by two methods: year-round (but mainly winter) hunts with guns and spring (May) searches for den sites with pups usually <1 month old. In both cases, bounties are paid for the wolves killed. Data on 101 litters (4–9 litters per year) found by experienced hunters between 1985 and 2003 yielded information on litter size and sex ratio of pups. Information on annual hunting harvest in 1988–2003 was received from Belarussian hunting organizations (Gorodok and Rossony Raisovet BOOR). Of all wolves killed, 329 specimens (39%) were examined by the authors to identify their age and sex and used in this study. Age was determined based on tooth (mainly canine) cementum banding according to the method of Klevezal (1996). Tooth wear was used as additional information about age (Gibson et al. 2000). As the methods of hunting wolves (mainly hunts with

Fig. 1. Mean number of pups in litters (all pups and female pups) and the percentage of female pups in litters in relation to two indices of gray wolf (*Canis lupus*) abundance in the Poozere Forest, northern Belarus, between 1999 and 2003. Each point is a mean value for 1 year.



“fladry”, i.e., ropes with red flags used to surround wolves in their resting site (see Okarma and Jędrzejewski 1997) but also shooting from helicopters) are little or not selective towards any sex or age class of wolves (e.g., Jędrzejewska et al. 1996), the age structure and sex ratio of killed wolves are believed to reflect those of the whole population.

Data on wolf abundance in the study area are available for 1990–2003. Each year in late winter (January–March), a transect (36 km in the Gorodok district and 44 km in the Rossony district) was walked, and the number of wolf trails crossing the transect were counted, with an attempt to enumerate the wolves traveling together. The transect crossed various forest types, river valleys, lake shores, open marshes, and rural areas to represent the landscape structure and composition of the whole study area. An index of wolf abundance was calculated as the number of tracks divided by the number of kilometres walked and the number of days passed since the last snowfall and multiplied by 2 (N tracks/km per 2 d). As an additional source of data, estimates of wolf numbers from the local departments of the Belarussian hunting organization (Gorodok Raisovet BOOR) were also used for analysis. The estimates covered part of the study area (728 km² in the Gorodok region) and came from game wardens and forest guards, who inspected

their districts many times during each winter and recorded tracks, visual observations, and other signs of wolf presence. Based on all records of wolves, they attempted to count the number of packs living in the area and the size of each pack. The number of wolves obtained from the hunters’ organization was recalculated per 100 km². This estimate was treated as an index of abundance and not the actual density. The two indices of wolf abundance were significantly correlated ($r = 0.642$, $P = 0.013$, $N = 14$ years), so we believe that they reflected trends in the wolf population.

Results

The indices of wolf abundance in year n are significantly, negatively correlated with the summed harvest in the two preceding years, which suggests that fluctuations in wolf numbers between 1990 and 2003 were significantly affected by hunting pressure by humans ($R^2 = 0.36$, $P = 0.025$ for wolf tracks and $R^2 = 0.30$, $P = 0.04$ for index of wolf density, $N = 14$ years; data in Table 1).

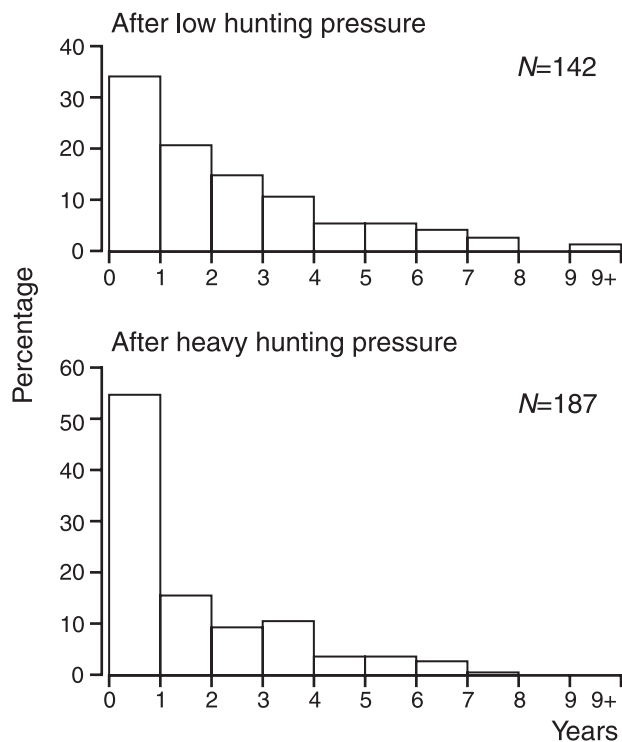
The litter size of wolves varied from 2 to 10 pups, averaging 6.1 (Table 1). There was a marked between-year variation in the mean litter size, from 4.8 to 7.7 pups, which was significantly, negatively related to the indices of wolf

Table 2. Sex ratio of wolves in various age classes based on analysis of tooth cementum banding ($N = 329$ wolves) in two periods differing in hunting pressure in the Poozere Forest.

Age class	Percentage of females after low hunting pressure	Percentage of females after heavy hunting pressure	P for G test
Juveniles (0.5–1 year)	45.8	68.6	<0.05
Yearlings (1–2 years)	43.3	58.6	ns
Adults (>2 years)	53.1	57.1	ns

Note: See explanation to Fig. 2 for samples of years with low and heavy hunting pressure. ns, not significant.

Fig. 2. Age structure (determined by tooth cementum banding) of gray wolves shot in two periods of differing levels of hunting pressure. The first age class includes juveniles 0.5–1 year old (does not include dependent pups). Low hunting pressure occurred between 1993 and 1995 (see Table 1), and the sample of wolves shot in the years following low hunting pressure comes from 1995 to 1997. Heavy hunting pressure occurred between 1996 and 2000, and the sample of wolves shot in the years after heavy hunting pressure comes from 1998 to 2003.



population numbers (Fig. 1). However, the inversely density-dependent increase in litter size concerned only female pups. The average number of females in a litter varied from about 1.6 pups at the highest population density to 3 pups at the lowest density (Fig. 1). The number of male pups in a litter was not related to wolf density ($P = 0.96$ for density index and $P = 0.09$ for the tracking index) and averaged 2.8 pups ($SE = 0.15$) for all litters between 1990 and 2003. Overall, the sex ratio of pups did not differ significantly from 1:1; 55.5% were females and 44.5% were males (G test for homogeneity of percentages, $G = 1.212$, $df = 1$, $P > 0.1$). However, the sex ratio significantly changed between years: the proportion of females reached 70% in a low-density wolf population and declined to 40%–50% in a high-density population (Fig. 1).

The age structure of the wolf population in two contrast-

ing periods, heavy hunting pressure and relatively low hunting pressure, differed markedly ($G = 9.85$, $df = 4$, $P < 0.05$) (Fig. 2). During and after heavy hunting pressure, 55% of individuals killed were <1 year old and only 11% of wolves were older than 4 years; the mean age of killed wolves was 1.5 years. After low hunting pressure, 34% of individuals killed were juveniles and 20% were older than 4 years. The mean age of wolves was 2.8 years. In the sample of wolves collected after heavy hunting pressure, females were more numerous than males among juveniles, yearlings, and adults. However, when compared with the sample obtained after low hunting pressure, a significant difference was only found for juveniles (Table 2).

Discussion

Under conditions of heavy hunting pressure, the proportion of young (0.5–1 year old) in the studied wolf populations markedly increased. For the former Soviet Union, Smirnov and Korytin (1985) reported that in decades of most intense wolf control (1950s–1970s), the percentage of juveniles among wolves killed was 49%, whereas in a decade of moderate or weak control (1940s), it was 32%. In the 1980s and 1990s, wolves were moderately harvested in the Belarussian part of the Białowieża Forest, and the percentage of juveniles among wolves killed reached 35% (Jędrzejewska et al. 1996). These data correspond well to our findings on age structure of the wolf population in northern Belarus during differing levels of hunting pressure.

In terms of litter size, our studied population of wolves from northern Belarus falls within the observed variation recorded in the Holarctic zone. In 16 Eurasian populations of gray wolves, mean litter sizes varied from 4.4 to 7.7 pups, averaging 5.9 (reviews in Danilov et al. 1985; Jędrzejewska et al. 1996). In North America, the mean litter size of gray wolves in 17 local populations ranged from 4.2 to 6.9 pups, averaging 5.4 (review in Fuller et al. 2003). The studies in Eurasia and North America reported markedly smaller litters in the least productive ecosystems (e.g., in the High Arctic of North America and deserts of Central Asia) than those in the productive ones (Vyrypaev and Vorobev 1983; Danilov et al. 1985; Mech 1995).

In line with the theory of intrinsic population limitation, the elevated productivity of heavily exploited wolf populations has been interpreted as a population-level response to territory vacancies and reduced social limitations (Vyrypaev and Vorobev 1983; Danilov et al. 1985). Additionally, Danilov et al. (1985) proposed that heavy control of wolves would result in more female pups born to better compensate for the losses. Recent studies suggest that while social factors might play a role, it was the available food per wolf

that shaped the productivity of wolf populations (review in Fuller et al. 2003). In our study area, data on ungulate abundance (available for the Gorodok district, 1990–2000; see Sidorovich et al. 2003) suggest that, with the declining abundance of wolves, the ratio of ungulate biomass per wolf increased. Thus, also in northern Belarus, the observed inversely density-dependent growth in litter size can be explained by the growing food supply per wolf.

Yet the question remains as to why with an increase in litter size the number of female pups increases but the number of males does not. The very early age of pups reported in our study (<1 month) suggests that sex-biased maternal investment takes place at the stage of conception, mortality in utero, and (or) during the first few weeks following birth. Sex-biased maternal investment has not been studied so far in canids, although it was investigated in ungulates (review in Hewison and Gaillard 1999), primates (e.g., Brown 2001; Ostner et al. 2005), and rodents (e.g., Koskela et al. 2004). Researchers frequently addressed the model of Trivers and Willard (1973), developed for caribou (*Rangifer tarandus* (L., 1758)) as an exemplary species. The model predicts that, in a highly dimorphic, polygynous species in which the variance in male reproductive success exceeds that of females, mothers with extra resources should bias investment towards sons. The life history of the gray wolf is rather different. This species is characterized by monogamous pairs with long-term bonds and biparental care of young, so the reproductive success of females and males is most likely similar. Therefore, although not explicitly stated by Trivers and Willard (1973), it can be expected from their model that in conditions of extra resources, maternal investment in wolves will *not* be male-biased. Rather, it should be female-biased, as predicted by the advantaged daughter hypothesis (Hiraiwa-Hasegawa 1993). According to that hypothesis, a female-biased sex ratio of young is expected in species in which mothers are able to influence the reproductive success of their daughters through transmission of rank or some other quality. Population genetic studies conducted in the Białowieża Primeval Forest, eastern Poland, and western Belarus documented that, when the breeding females were killed or otherwise lost their position, their daughters became successors. The successors of breeding males were less predictable: they could be either their sons or alien males (Jędrzejewski et al. 2005). Thus, in a heavily exploited population of wolves, producing more daughters may be an adaptive strategy.

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