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Short communication

Wolf denning behaviour in response to external disturbances and implications for pup survival☆

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ABSTRACT

We conducted a 15-year study (1999–2014) of wolf denning behavior in Naliboki Forest, Belarus, to determine the extent to which some external factors (rain, mosquitoes, human disturbances) and litter size are negatively correlated with pup survival until autumn.

For this purpose we entirely documented denning areas of 30 breeding wolf pairs. Initial denning area includes the natal den site and (ii) secondary den sites between which the parent wolves transported sucessively the litter during the rearing season.

The number of den sites per denning area ranged from 1 to 4. The distances in kilometres differed significantly between den sites. The total number of dens (surface dens and burrows) was higher in the natal den site compared with the other den sites. The number of surface dens per den site was higher compared with burrows in den sites 1, 2 and 3 but not den site 4. A total of 168 pups was found over the 15 years. Litter sizes ranged from 1 to 11 (average 5.6 ± 1.9). The rate of pup survival ranged from 0 to 100% and averaged $54.5 \pm 29\%$.

We examined the bivariate association between environmental conditions (mosquitoes, rainfall and human presence) and number of surface dens, total number of burrows and number of den sites. Environmental conditions were assessed from spring to mid-summer. Results show that there was a positive relationship between environmental conditions and number of den sites, and also that more difficult environmental conditions (rainy weather, many mosquitoes) decreased pup survival both in absolute and in relative terms. A cluster analysis showed that pup survival was also influenced by human presence. Wolves probably have a more complicated denning behaviour following stressful event which may lead to less effectiveness for feeding or protecting pups. The number of pups surviving was also found to be lower when there were many (8–10) pups because den shifting is more risky in this case. Burrows improve pup survival. Our results tend to suggest that, in our study area, a high mortality rate of wolf pups could be related to external and internal factors of stress.

The denning area of wolf (*Canis lupus*) is preferentially located at the center of wolf territory to minimize contact with other packs (Ballard and Dau, 1983; Packard, 2003), close to a rich prey supply and water, at least for the natal den site (because lactating females have high hydration needs) and far from other predators territories (Sidorovich and Vorobej, 2013), villages and intensively used roads (Theuerkauf et al., 2003; Trapp et al., 2008; Ahmadi et al., 2013). Usually wolves build many dens close to each other in a given den site, on average within hundred meters radius of the site's centre (unpublished observations). Dens may be dug (i.e. burrows) or simply surface bed. But soil and habitat types also influence the type of den (Ciucci and Mech, 1992; Norris et al., 2002; Kaartinen et al., 2010). For example excavating burrows need soft material (either dug entirely by the wolves or enlarged from the holes of other carnivores), while surface dens need dense vegetation roughly arranged under the roots of fallen trees, in hollow trunks or among bushes or high grasses. Pups are frequently transported from one den to another during the rearing season, in order to improve their safety

☆ Vadim Sidorovich designed the study and carried out almost all the fieldwork needed to build the dataset, test the hypotheses and provide the framework of the manuscript. Annik Schnitzler wrote the manuscript and checked it for consistency and inferences, and took part in the fieldwork in the late stage of the study from 2013 onward. Christophe Schnitzler performed the statistical analysis. Irina Rotenko investigated about 8 cases of wolf denning together with Vadim Sidorovich.

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and comfort, in particular when they are very young. Newborn pups are blind, deaf and unable to move, and it takes them 10–14 days to develop the ability to actively prevent hypothermia (during cold and rainy springs) or hyperthermia (during hot springs), and to cope with unpleasant situations such as an abundance of stinging insects, threat or accumulation of scats. When pups grow older, parents move them in secondary den sites, sometimes at several kilometres within the denning area (Chapman, 1977; Thiel et al., 1998; Theuerkauf et al., 2003; Packard, 2003; Argue et al., 2008). Factors that define the denning behavior of wolves (e.g. the number of dens, the ratio of den types, the displacement distances between the natal den site and secondary den sites) may vary a lot according local environmental situations (e.g. Mech, 1970; Harrington et al., 1983; Fuller et al., 2003; Habib and Kumar, 2007).

The current study focused on investigating the efficiency of wolf denning with regard to pup survival in a protected area of the Naliboki forest, Belarus.

We assessed (1) whether potential threats (i.e. human disturbance) and factors of discomfort (rain, mosquitoes) raised the complexity of denning behaviour (i.e. the number of dens per den site, and the distance between the den sites) and, if so, (2) whether the increasing complexity would lead to lower survival, particularly in cases of many pups. We also tested the efficiency of den type (burrow vs surface den) with regard to pup survival.

The Naliboki forest and surroundings (2750 km^2) is part of the East European plain in central-western Belarus (53°55′N; 26°20′E, elevation 100–200 m asl). The climate is moderately continental with a mean winter temperature (December) ranging from −6 °C to −8 °C (all surface water is ice-bound). The mean temperature in June ranges from 17°C to 19°C. Annual rainfall ranges from 580 to 690 mm, with frequent summer droughts. The area is characterized by flat boggy zones gently undulating between sandy dunes, moraine zones, and crossed by two large meandering rivers. The landscape is forested at 84% with forest habitat-types of spruce (*Picea abies*), oak (*Quercus robur*), pine (*Pinus sylvestris*), spruce-birch (*Betula alba, B. pubescens*), dry pine and black alder (*Alnus glutinosa*) swamps, and bogs with suppressed pines. There are also some agrarian land and sparse small human settlements. We estimated a yearly density of 0.9-2.5 wolves per 100 km^2, for a mean of 1.8 individuals per 100 km^2. The local population size of wolves ranged from 27 to 70 individuals. This predator coexists here with the lynx (*Lynx lynx*), and the brown bear (*Ursus arctos*). Prey availability is diverse and flourishing over the rearing period, with five species of large herbivorous mammals: elk (*Alces alces*), bison (*Bison bonasus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*).

A natural reserve of about 0.9 km^2 was found in the core area of the forest, where there is no human persecution of wolves. Outside the reserve, they are theoretically subjected to year-round control but this in fact occurs only in winter (December–February), outside the breeding season.

In the study area, wolves select den sites in clearcuts with early reforestation, swpruce tree falls, abandoned peatory and meadows, all characterized by good cover for hiding. Small openings at the border with boggy habitats rich in fallen trees (mostly spruce) or in grassy small areas are also selected (Sidorovich 2011, 2016). They are also generally built in places where ungulates are not too active, because they can trample and kill pups (unpublished observations). Water is abundant in the forest and is thus not a limiting factor.

Each year in January-February we first evaluated the structure of packs and their spatial distribution in the forest, before searching den sites. The den sites (natal den site and secondary den sites) were progressively found by carefully searching the area several times from mid-April to mid-June (for a complete description of the method, see Sidorovich and Vorobej, 2013). Den sites differ from kill sites because they consist in a cluster of dens within several hundred meters.

We documented in detail 30 denning areas over 15 years. The number of den sites ranged from 1 to 4 den sites (mean 2.9, SD: 1.1), with 70% of the denning areas having at least 3 den sites. Some den sites have many dens (a range from 5 to fifty, to 79 in one of them !). Displacement distances were calculated between the center of the natal den site to the center of secondary den sites as the straight line distance between them, and were measured using a GPS. The spatial distribution of den sites was analysed after checking normality of distribution (Kolmogorov-Smirnov test) and homogeneity of variance (Bartlett's test). A two-ways ANOVA for repeated measures (fixed factor: distance between den sites in kilometres; repeated factor: den site number) was performed. Tukey's post hoc test was applied to specify the existence of differences between the distances of the den sites within each denning area. The ANOVA showed that distance in kilometres differed between den sites. Tukey post-hoc test showed that the distance between den site 1 and 2 was significantly greater than the distance between den 3 and 4 (3.3 ± 1.4 vs 1.7 ± 2.4 km, $P < 0.05$). These distances were relatively short in the forest compared with findings from other studies. Chapman (1977) recorded more variable distances for shifting from natal dens to secondary dens in Alaska, with average distances of 3 km and a range from 0.3 to 11.2 km. In Canada, Argue et al. (2008) reported that packs tended to move pups farther and farther away from the denning area as the pups grew older. We have no explanation for these differences in behaviour, perhaps based on available preferred denning habitat differences.

We also examined whether the number of burrows differed from the number of surface dens between the den sites. The Mann-Whitney test showed that the median number of surface dens per den site was higher compared with burrows in den sites 1 (25 surface dens vs 4.1 burrows, $P < 0.05$), 2 (16.4 surface dens vs 1.8 burrows, $P < 0.05$) and 3 (9.3 surface dens vs 0.6 burrows), but not den site 4 (median = 0 for both surface dens and burrows).

168 pups were found during the study period. Litter sizes range from 1 to 11 (average 5.6 ± 1.9); They were handled and counted. There occurred no bias (such as relocation after the counting) because the method was the same for all packs during the whole period of the study. The night after we discovered the pups in a den, the parents relocated them to another den site. Finally we did not include earlier findings (end of April–May) because parents were still not fully exposed to factors of rain, mosquitoes or human disturbance long enough.

In autumn, we assessed the number of surviving pups in a given litter by howling at night to locate them within the pack home range (usually they answer easily). After that, we inspected the discovered area of pups stay, which scared the parents. They usually relocated the pups, travelling on or crossing one of the numerous sand roads in the Naliboki Forest. On such a road we could count pups.

All these data helped to determine the litter size in early autumn. Later in November, we could count the number of surviving pups because of their smaller footprints in the first snow.

Pup survival assessment corresponds to the percentage of surviving pups in autumn in a given litter compared to the initial total number of pups in the litter. The rate of survival ranged from 0 to 100% and averaged $54.5 \pm 29\%$. We also estimate pup survival by considering only the number of pups in autumn. The number of surviving pups ranged from 0 to 6 and average 2.9.

Environmental conditions were assessed from spring to mid-summer using a Likert-type scale with a few categories (1–4 or 5) (Likert, 1932). Insect abundance was evaluated from our own assessments (no insects; low, medium, high and very high abundance) several times during spring and mid summer; rainfall from our own assessments and some registrations from