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Wolf recovery and population dynamics in Western Poland, 2001–2012

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Abstract Since the mid-twentieth century, under different management regimes (over 20 years of a wolf control program followed by 20 years of trophy hunting), wolves were absent or rare in Western Poland (hereinafter WPL). They became strictly protected in the whole country in 1998 and started to re-settle the vast forests of WPL, far (376 ± 106.5 km) from the source population in eastern Poland. In 2002–2012, the population increased from several to approximately 140 wolves living in 30 family groups, with an annual rate of increase of 38 % ($\lambda = 1.38$, SE = 0.10). The area of permanent occurrence increased from 600 to 10,900 km^2, with an average density of 1.3 wolves/100 km^2. The nearest neighbour distance between wolf territories decreased from 260 to 25 km. In 2001–2005, half of the settlement efforts by wolves failed after 1–2 years whereas in 2006–2009 only one fifth of newly settled wolves failed to persist >2 years. The number of wolves in groups varied from 2 to 9, and the mean group size increased from 1.8 in 2001 to 4.8 in 2012. The survival of pups from May to the end of November was 50 % (the mean number of pups per litter was 5.1 and 2.5, respectively). Of 28 wolves found dead, 65 % were killed by vehicles, 25 % were poached, and 7 % died because of diseases and natural factors. All road casualties were young wolves, most of them male (67 %), hit on roads on average 11.6 km from the centre of the nearest pack. The re-colonisation of WPL started from jump dispersal, which allowed wolves to establish packs in distant locations. As the recovery proceeded, the dispersal pattern shifted to being stratified, a mixture of diffusion and jump dispersal that resulted in the creation of packs in close vicinity to existing groups. After 12 years of re-colonisation, wolves in Western Poland occupied about 30 % of potential suitable habitats.

Keywords *Canis lupus* · Population growth · Species range · Pack persistence · Group size · Reproduction · Pup survival · Mortality · Dispersal pattern

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Introduction

During the last centuries, dramatic changes have been observed in wolf abundance across Europe (Boitani 2003). Reduced human exploitation during wars or periods of political unrest allowed for rapid increases in the range and number of wolves, which in turn evoked fear and hostility in local societies and resulted in efforts to eradicate the unwanted competitor to game animals and killer of livestock (Jędrzejewska et al. 1996). In modern times, the attitude towards wolves has changed, and such a radical response to wolf population growth is less acceptable, although it still sometimes occurs (Ozoliņš et al. 2001).

Recovery of wolves in different regions provides an excellent opportunity to study the dispersal patterns and dynamics of new populations, but also the obstacles for re-colonisation. Earlier studies in North America showed that wolf population dynamics are mainly shaped by the availability of prey (Keith 1983; Fuller 1989; Mech et al. 1998) and the distance to a source population (Wydeven et al. 1995; Hayes and Harestad 2000). However, in the modern world, other direct and indirect impacts of humans significantly influence

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distribution, number and social structure of wolf populations (Larivière et al. 2000; Murray et al. 2010). Conservation and management strategies seem to be crucial, as protected populations which re-colonised regions of the USA and Canada, where they had previously been extirpated, showed relatively high rates of increase (Fritts and Mech 1981; Peterson et al. 1984; Wydeven et al. 1995; Mitchell et al. 2008).

Wolves, which are legally protected in most western European countries, have recently been returning to central and western Europe to forests that are heavily altered by humans (Miller et al. 2001; Valière et al. 2003; Ansorge et al. 2006; Blanco and Cortéz 2007; Fabbri et al. 2007; Chapron et. al. 2014). Nevertheless, the published data on the dynamics and demography of these recovering populations are scarce (Wabakken et al. 2001, Nowak et al. 2008). Wolves re-populating Europe face not only a risk of illegal killing (Liberg et al. 2011) but also a high risk of mortality on roads and railways, habitat deterioration and lack of connectivity due to human-made constructions, as well as disturbance by people in refuges (Theuerkauf et al. 2003a, 2003b; Jędrzejewski et al. 2004; Huck et al. 2010; Colino-Rabanal et al. 2011). Spontaneous re-colonisation of distant habitats by wolves is possible due to their ability to disperse across long distances. Although most dispersers settle up to 100 km from natal territories (Fritts 1983; Gese and Mech 1991; Kojola et al. 2006, 2009), suggesting a diffuse pattern of dispersal, jump-dispersal events of over 300 km also occur (Linnell et al. 2005; Wabakken et al. 2007; Ciucci et al. 2009). Thus, a mixed, stratified pattern of dispersal is also probable in this species.

In Poland, unlike in many countries in western Europe, wolves were never totally extirpated in the twentieth century. After the Second World War, the range of the wolf population expanded in eastern Poland, numbering—according to hunting estimates—up to 820 individuals in 1951 (Kowalski 1953). This increase prompted the Polish government to introduce a nation-wide wolf control program in the mid-1950s, resulting in deliberate persecution (*ca*. 3300 wolves were killed during 18 years), which caused a significant population decline to about 60 wolves in 1972 (Sumiński 1975). In 1975, the wolf was re-included in the list of game species and a 4-month closed season was introduced across the country in 1981. During the next 23 years, *ca*. 2200 animals were shot during trophy hunts (compiled data of the Polish Central Statistical Office and the Research Station of the Polish Hunting Association). Even though the population range increased in eastern and south-eastern Poland, the population first grew up to 960 animals in the mid-1980s and then declined in the early 1990s because of intensive exploitation (Okarma 1993; Pielowski et al. 1993). Most of the time, however, wolves were very rare in or absent from large woodlands west of the Vistula River (Sumiński 1973; Wolsan et al. 1992; Okarma 1993).

In 1995, wolves became strictly protected in parts of the country (including western Poland) and finally they obtained full protection throughout Poland in 1998 (Mysłajek and Nowak 2015). For the first time in modern history, the species was allowed a reprieve from human control and an opportunity to recover in forests throughout the country. As was suggested by the habitat suitability model for Polish wolves (Jędrzejewski et al. 2008), 63 % of the suitable habitats (about 39,000 km^2) are located in Western Poland (=WPL) together with the Sudetes Mts., while in the lowlands of the eastern part of the country and in the Carpathian Mts., only 37 % (22,600 km^2) are available. Thus, it was expected that wolves would re-establish a viable population in WPL soon after protection was enforced.

In 1998–1999, data about wolves in Poland were scarce: no institution was obliged to survey and report their number and distribution. In 2000–2001, information about wolf occurrence and population size was collected for the first National Wolf and Lynx Census (Jędrzejewski et al. 2002a). While in eastern and south-eastern Poland, the population number reached approximately 500 wolves, in WPL altogether 15–17 wolves, solitary or living in pairs or small packs, were reported by foresters in winter 2000/2001, and no single reproduction was confirmed there at that time (Jędrzejewski et al. 2002a).

At the same time, in 2000, the first reproducing wolf pack was reported in Saxony, Germany, the area adjacent to south-western Poland (Ansorge and Schellenberg 2007). Since 2005, along with the appearance of a second breeding group, the number of wolf groups in Germany increased to 25 in winter 2013/2014 (Reinhardt et al. 2015). As was revealed by genetic analysis, both segments (Polish and German) of this Central European wolf population (Reinhard et al. 2013) were founded by wolves coming from NE Poland (Czarnomska et al. 2013).

The wolf recovery in WPL offered an excellent opportunity to study the mechanisms of successful growth of populations which settle in human-dominated landscapes far from the source population. The goal of our study was to describe the rate of re-colonisation, the change in number, size and distribution of wolf packs resettling Western Poland, as well as wolf dispersal patterns during their recovery in 2001–2012. Considering the high availability of suitable habitats (Jędrzejewski et al. 2008), high densities of ungulates (Borowik et al. 2013) and the distance to the source population in eastern Poland (Jędrzejewski et al. 2004, 2005), we hypothesised that the rate of increase of the wolf population recolonising WPL was high, with a stratified, rather than diffuse, pattern of dispersal (Cox and Moore 2010).

Methods

Study area

Wolf data were collected in a lowland part of WPL, from 18°48′ E in the east to the Polish-German border in the west

(14°07′) and from 50°00′ N in the south to 54°17′ N in the north (Fig. 1). The total study area covered 136,000 km^2. The region is located in the zone of temperate climate, but with oceanic character, where the mean annual temperature is 7.9–9.3 °C (−1.1 to 0.6 °C in January, 18.1 to 19.5 °C in July). The mean precipitation ranges from 504 to 766 mm (Statistical Yearbook of the Regions-Poland 2012). The length of the vegetation season is 220–240 days, while the snow cover persists from 40 to 60 days.

The landscape of WPL has been shaped by glaciation in the mid and late Pleistocene; thus, the terrain is mostly flat (from 0 to 200 m a.s.l.) with several ranges of frontal and moraine hills. The mean human population density (108 inhabitants/km^2) is lower than for the entirety of Poland (123 inhabitants/km^2) (Statistical Yearbook of the Regions-Poland 2012). About 57 % of the area is farmlands with predominance of arable land. The density of public roads (81 km/100 km^2) is lower than for the whole of Poland (92 km/100 km^2). Between 2000 and 2010, the traffic on national roads increased by 40 % in WPL and reached 9805 vehicles per day in 2010 (Statistical Yearbook of the Republic of Poland 2014; Opoczyński 2001, 2010). There is also an expanding network of motorways and express roads, fenced on each side and creating barriers for animal movements; however, dozens of large fauna passes have been constructed to mitigate this negative impact on habitat connectivity (Nowak and Mysłajek 2010).

The average forest cover of the region is 32 %, slightly higher than the mean for the whole of Poland (29 %). Most forests are coniferous stands (70 % of the total area) dominated by Scots pine (*Pinus sylvestris*, 60 % of the forest area), Norway spruce (*Picea abies*, 6 %) and fir (*Abies alba*, 3 %). Deciduous and mixed forest with oak (*Quercus robur* and *Quercus petraea*), birch (*Betula* sp.), alder (*Alnus glutinosa*), beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*) and poplars (*Populus* sp.) makes up about 30 % of all forests. In WPL, approximately 94 % of forests are public (93 % state owned), while 6 % are private. Most woodlands are commercial stands with only 1.5 % protected as national parks and reserves (Budna and Grzybowska 2012).

State-owned forests in Poland are administered by forest districts (*nadleśnictwo*), with an average area of 175 km^2. A grid of spatial compartments, squares (approx. 500 × 500 m) or rectangles (approx. 300 × 700 m), of 10–35 ha exists in each forest district. Between compartments stretches a regular net of deforested lines (3–10 m wide). The lines are unpaved and serve as logging roads or pathways. All compartments are numbered in the forest and on maps. In every forest, there is also an irregular network of main forest roads, some of which have a hard surface. Although most of these forest roads are closed to public traffic, they can be entered for scientific purposes with permission, issued by the State Forest Service. This spatial division and dense road network make lowland forests accessible by cars and easy to search for tracks and signs of wolves, which leave scent marks in exposed places (Zub et al. 2003).

In forests of WPL, three native species of ungulates: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) are abundant, with densities which are currently the highest in the country (Borowik et al. 2013). Populations of alien species, introduced for recreational hunting, such as fallow deer (*Dama dama*) and mouflon (*Ovis musimon*) are present too, but less numerous. There is an introduced population of native European bison (*Bison bonasus*) (approximately 120 animals) in the north-western part of WPL (Western-Pomeranian Province), and the area is also sporadically visited by moose (*Alces alces*). The only species of large carnivore which has established a substantial population in WPL is the wolf (Nowak et al. 2011), although single observations of Eurasian lynx (*Lynx lynx*) have also been recorded (Niedziałkowska et al. 2006; Nowak et al. 2013).

Data collection and analysis

We collected field data on wolf distribution and numbers in WPL from 2001 to winter 2012/2013. Because we aimed to detect and map wolf groups, and not individuals, in the large study area, we applied similar approaches to other large-scale survey projects, e.g. in Scandinavia, Poland or Spain (Jędrzejewski et al. 2002a; Blanco and Cortéz 2007; Liberg et al. 2012). Our methods were based on territorial marking behaviour of breeding pairs and high detectability of marks (faeces, ground scratching, leg-raised urination) left by reproducing wolf groups in their territories (Wabakken et al. 2001; Zub et al. 2003; Llaneza et al. 2014).

We applied year-round tracking of wolves assuming that good visibility of wolf tracks on snow and numerous sandy forest roads in WPL allow us to follow them and count (Liberg et al. 2012). For surveys, we selected those forests where (1) the presence of wolves was reported by foresters during the National Wolf Census in 2001–2002 (Jędrzejewski et al. 2002a); (2) data about live or killed wolves were reported in the twentieth century; (3) suitable conditions for wolf occurrence were indicated by the habitat suitability model for Polish wolves (Jędrzejewski et al. 2008); and (4) information about the presence of wolves was sent to us by local foresters, hunters and naturalists during the study period. Field works were conducted by authors who have experience in large-scale wolf surveys (Jędrzejewski et al. 2002a, 2008; Nowak et al. 2005, 2008, 2011) and by trained local volunteers. On average, 10 people were involved in data collection each year (Nowak and Mysłajek 2011). We also incorporated recently published data on the number and distribution of wolves in the Bydgoszcz Forest to the analysis (Sewerniak 2010, 2015) and the Cedynia Forest (Żmihorski 2011) (Fig. 1).

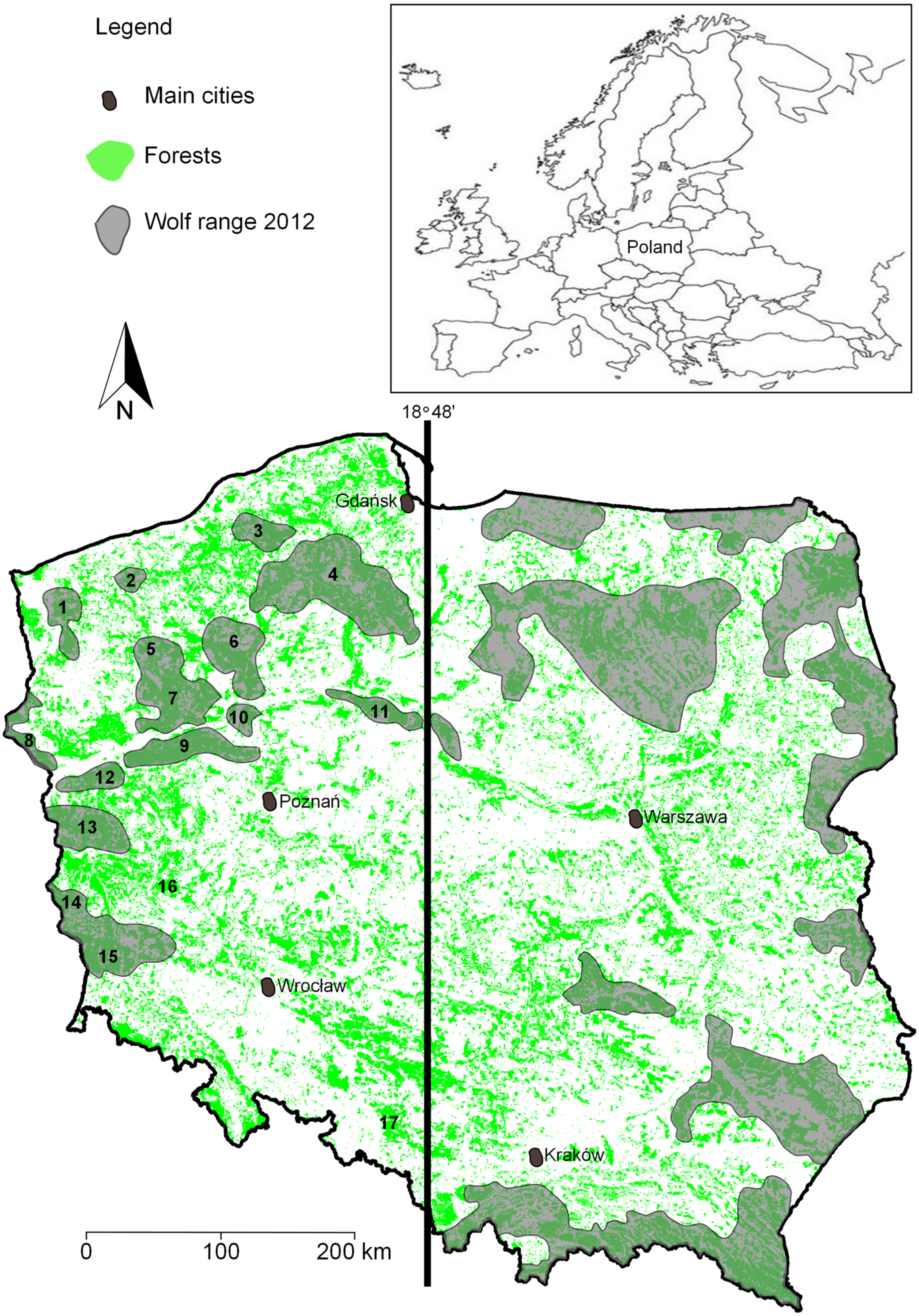

Fig. 1 Study area—Western Poland. Numbers mark the following forests: *1*—Goleniów; *2*—Rymań, *3*—Słupsk, *4*—Tuchola, *5*—Drawsko, *6*—Wałcz, *7*—Drawa, *8*—Cedynia, *9*—Noteć, *10*—Sarbia, *11*—Bydgoszcz, *12*—Lubuskie, *13*—Rzepin, *14*—Lubsko, *15*—Lower Silesian, *16*—Sława, *17*—Rudy

Before we surveyed a forest complex for the first time, we did analyses (with MapInfo Professional software, Pitney Bowes Software Inc., USA) of both topographic and forest maps of the area including the network of forest cells and roads, the tree stand age and composition, to identify regions most preferred by wolves, i.e. those with the highest forest cover, the biggest distance to forest edges, human settlements and main public roads and railways (Jędrzejewski et al. 2004). We then chose forest roads which cross the preliminarily recognised areas. During the field survey, we firstly checked these designated portions of the forest complex. We drove by cars (<10 km h^{-1}) along the main forest roads passing through, with a special focus on distinctive road crossings. We assumed that resident wolves regularly use forest roads to travel through their territories (Musiani et al. 1998; Gurarie et al. 2011) and that the density of faeces and other scent markings are the highest in the core areas of their territories (Zub et al. 2003; Barja et al. 2004, 2005; Llaneza et al. 2014). When faeces, scent markings or tracks were found, we condensed our surveys on adjacent forest compartment lines and cross-roads searching for more signs by foot or by car. After that, we checked the main and secondary roads in other parts of the forest. During later surveys, we checked all the places where wolf signs were found before and then all other probable locations. From early winter, whenever snow cover was present, we searched for wolf tracks on roads and forest compartment lines and followed them by hiking or driving as far as possible. The tracking distances varied from 3 to over 20 km. We repeated such tracking in the same wolf territories at least one or two times per winter season. During the rest of the year, we looked for wolf footprints on unpaved, sandy forest roads, forest compartment lines and pathways. We followed wolf tracks as far as we could recognise them. Whenever it was possible, we estimated the minimum number of individuals in tracked wolf groups (Nowak et al. 2008; Wydeven et al. 2009; Liberg et al. 2012).

Every year during the mating season (February), we searched for ground scratching and joint scent-marking of wolf pairs, as well as evidence of heat in females (oestrus bleeding) and typical mating behaviour (e.g. trampled snow with signs of blood) to confirm attempts of reproduction in the resident group or to discover a new breeding pair. In June-August, we searched for fresh tracks of pups on sandy roads. In selected locations, we conducted direct observations or set up camera traps with a video recording option (Bushnell Trophy Cam and Bushnell Trophy Cam HD, USA) to confirm pup presence and count them. In addition, when in doubt regarding reproduction, we used howling stimulation to detect wolves with pups in different parts of forests (Llaneza et al. 2005; Nowak et al. 2007; Duchamp et al. 2012). After the pup rearing season (from September), we searched for dens in locations where young or their tracks were detected. In autumn and early winter, we measured footprints and pace length in order to distinguish between adults and pups. According to measurements of wolf tracks in WPL, adults were recognised when the length the front paw with claws was >10 cm and the distance between heels of subsequent footprints in the track was >60 cm. The individual was qualified as a pup when these measures were 9–10 and 56–58 cm, respectively, in late autumn/early winter. We also collected all information about recent wolf sightings, remains of kills, wolf howling and tracks, as well as all reported cases of damage to livestock from local foresters, officers of regional directorates for environmental protection, conservationists, tourists, border police, hunters and farmers. Whenever possible, the obtained information was verified by the authors or other experienced persons in the field or on the basis of provided photo documentation.

Locations of all findings were recorded with a handheld GPS (Garmin, USA) and entered and analysed in MapInfo Professional software. In total, in 2001–2012, 5057 records of wolf presence were collected, computed and analysed. Based on the concentration of wolf tracks, scent markings, fresh scats, responses to howling stimulation and locations of pup rearing places, we determined core areas of each pack (Zub et al. 2003; Nowak et al. 2007, 2008; Llaneza et al. 2014). Around a central point of each core area, we drew a circle with a radius of 8 km, which is equivalent to an area of about 200 km^2—the average size of wolf territory in Poland (Jędrzejewski et al. 2007, 2008). For each monitoring year, we estimated the average nearest neighbour distance (NND) between wolf territories by measuring distances between the centres of the circular home ranges of the nearest wolf groups.

We considered an area as inhabited by a resident pack (≥3 wolves) or a pair of wolves, when tracks of two or more individuals were observed regularly accompanied by scent-marking or when evidence of pup rearing was recorded. Since 2005, samples from wolf scats were collected for DNA analysis in several larger forests of WPL, allowing results of genetic analysis based on 12 microsatellite DNA markers (S. Nowak, R.W. Mysłajek, unpublished data) as an additional tool to distinguish between packs in these forests. Based on all evidence of wolf presence, we analysed the persistence (in years) of wolf groups (actually wolf territories, because we had no confirmation of persistence of the same individuals in every pack) which were first recorded before 2010, thus confirming that they survived at least 3 years.

To estimate wolf range in WPL, we used a raster map of Poland, with a grid of cells 10 × 10 km (Jędrzejewski et al. 2008). The area occupied by wolves was estimated as a sum of 10 × 10 km cells overlapped by a buffer of 8 km from every wolf sign (when >50 % of a cell was inside of the buffer, the cell was included to the area). We considered a grid cell to be permanently occupied by wolves in a given study season (from April of the first year to the end of March of the following one) if at least two independent hard evidences that unambiguously confirmed the presence of a pair or wolf group (≥2 adult individuals) were collected. Such evidences were tracks, faeces, scent markings, remains of wolf prey, dens, direct observations, genetic proof and photo or video recordings of wolves. If there was only one wolf sign in such a cell in the second year and more evidences in the third year, the cell was also considered as continuously occupied in the second year. Cells were considered as areas with sporadic wolf occurrence if collected evidences confirmed only a short-term (less than few months) presence of lone individuals, or only single observations of loners, groups, roadkill or damage to livestock.

During the study, we distributed a questionnaire survey to forest service and nature conservation agencies in WPL to collect information about wolves hit by vehicles, poached or killed by natural causes in the region. The completed questionnaires were sent back to us together with photo evidence, allowing species identification.

Results

Wolf number, area of occurrence and rates of population increase

In 2001–2003, the number of wolves in WPL was 7–9 individuals. The development of the population slowly began in 2004 with the establishment of two small packs (with confirmed reproduction) and three pairs: a total of 18 wolves. Over the next 8 years, the population increased exponentially to 139 (range 136–142) individuals in at least 30 groups (25–26 packs and 4–5 pairs) (Figs. 2 and 3, Appendix 1). The mean annual rate of population increase, 38 % ($\lambda = 1.38$, SE = 0.10), was estimated for a period from 2002 to 2012 (Appendix 1). Accordingly, the number of wolf groups increased at a mean annual rate of 33 % ($\lambda = 1.33$, SE = 0.07).

The area permanently inhabited by wolves in WPL increased from 600 to 10,900 km^2 (Fig. 3), with the mean rate of increase as high as 34 % per year ($\lambda = 1.34$, SE = 0.09). At the same time, the area of sporadic occurrence rose from 900 to 3600 km^2. Thus, in 2012, wolves occupied in total 14, 500 km^2 of forest in WPL. The average density of wolves in the area of their permanent occurrence was 1.3 wolves/ 100 km^2 (range, 1.0–1.8, SE = 0.06). The nearest neighbour distance (NND) between wolf territories gradually decreased from 163 and 260 km in 2002–2003 to an average of 25 km in 2012 (Appendix 1). The number of forest tracts inhabited by wolves increased from 4 in 2002 to 14 in 2012.

The largest wolf population, which included seven resident groups, occurred in the Lower Silesian Forest (area no. 15 in Fig. 1 and Appendix 2). Other woodlands inhabited by more than one wolf group were as follows: Noteć (area no. 9), Wałcz (6) and Drawa (7) (three wolf groups in each); Bydgoszcz (11), Tuchola (4), Rzepin (13) and Cedynia (8) (two groups in each) (Figs. 1 and 2). The remaining forests were inhabited by single groups. There were also three forests in WPL temporarily occupied by wolves from which wolves retreated (areas nos 10, 16 and 17).

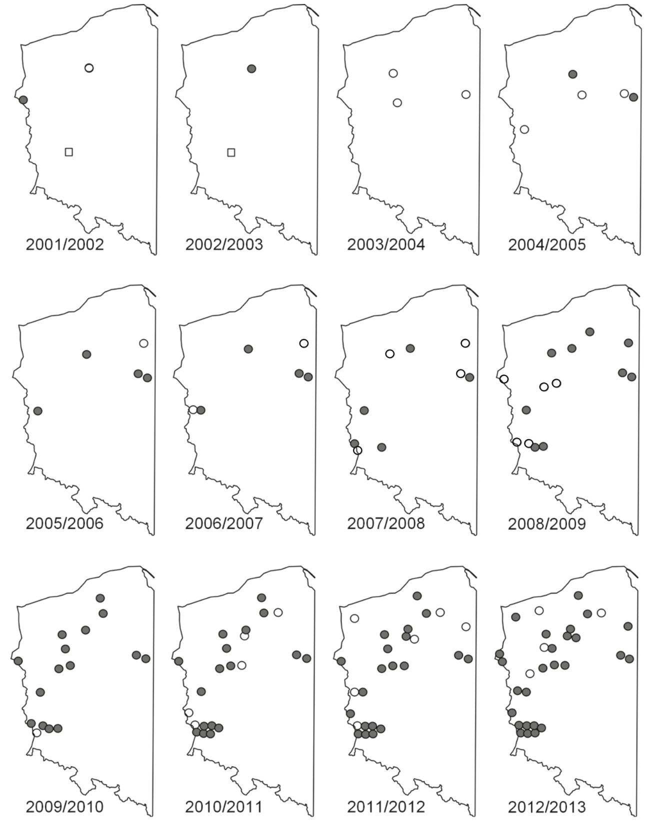

Fig. 2 Distribution of wolf groups in Western Poland in winter seasons 2001/2002–2012/2013. *Filled circles* denote groups with confirmed reproduction, *open circles* groups with no evidence of reproduction, *squares*—group established by wolves that escaped from captivity

The persistence (*N* years of continuous presence of a pack in the same area) was estimated for 27 wolf groups, which first settled in 2001–2009 (Appendix 2). Among them, 9 groups (33 %) lasted only 1 or 2 years, 4 (15 %) were recorded in 4 consecutive years and 14 (52 %) lasted 5–12 years. Ephemeral wolves (those recorded during 1–2 years only) were largely recorded during the first 5 years of population development. Between 2001 and 2005, half of the settlements efforts by wolves (6/12) failed after 1–2 years, whereas in 2006–2009 only one fifth (3/15) of newly settled wolves failed to persist >2 years (Appendix 2).

Pack size, litter size and pups survival

From 2001 to 2012, the number of wolves in groups ranged from 2 to 9, and the mean group size was 3.6 (SE = 0.31). The yearly mean group size increased from 1.8 (SE = 0.37) in 2001 to 4.8 (SE = 0.35) in 2012. During the first stage of

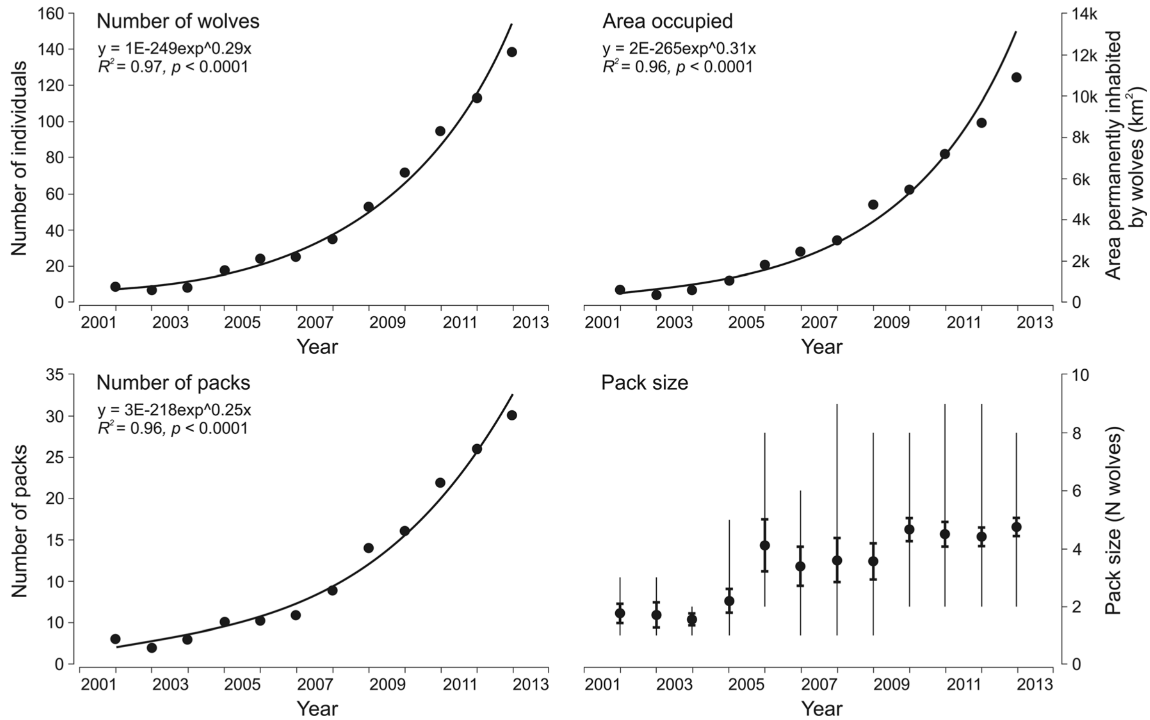

Fig. 3 Changes in number of wolves, area of permanent occurrence of wolves, number of wolf groups, and mean (*dot*), SE (*thick line*) and range (*thin line*) of number of wolves in group in Western Poland, 2001/2002–2012/2013

re-colonisation, the mean group size remained low, and it started to grow from 2005 (Appendix 1). Most of packs with known persistence (15/27) started as a pair of wolves, some of them as groups of three individuals (5/27) or as lone wolves which settled in the territory (4/27). In one case, four wolves appeared together in an area (Appendix 2). The size of groups grew along with years of pack persistence (Fig. 4). During the first winter, the new settlers included mostly two wolves (a parental pair). Those which survived until the second winter consisted of thee to four wolves (a pair with one or two young of the year). In the third winter, packs increased to four or five individuals. Such growth ensured the status of the resident pack. In subsequent years, the size of the resident wolf groups rose and fluctuated between four and nine members, with a mean of 6.8 (SE±0.46) individuals (Fig. 4).

During snow tracking, we observed evidence of oestrus in females from 22 January until 1 March. However, the most intensive urine marking with oestrus discharges and signs of copulation occurred from 14 February to 1 March. In total, we recorded 96 cases of reproduction in WPL (Appendix 1). Most of the places where pups were born or stayed temporarily (57/58) were excavated dens, only one place was a pile of wood debris. Based on direct observations of several-day-old pups and the dates of recorded copulations, we estimated that pups were born from the end of April to the beginning of May. For further analyses, we assumed that 1 May was the first day of the pups' life.

Between 9 May and 30 November, we collected 37 observations of litters. We plotted litter size against consecutive day (9–213) of pups' life (Fig. 5). Survival of pups was estimated separately for days 9–116 (May–August), when pups stayed in dens or were otherwise under the care of older pack members, and days 116–213 (September–November), when pups

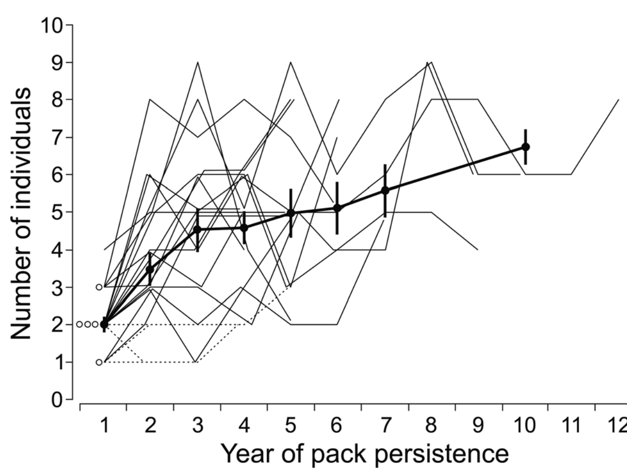

Fig. 4 Changes in wolf group size in consecutive years since their first appearance in Western Poland, 2001/2002–2012/2013. *Thin lines*—all packs, packs and lone wolves recorded (see Appendix 2). *Broken lines*—ephemeral wolves. *Thick line*—mean (±SE) pack size in consecutive years of their persistence (ephemeral wolves not included). Data for years 8–12 combined

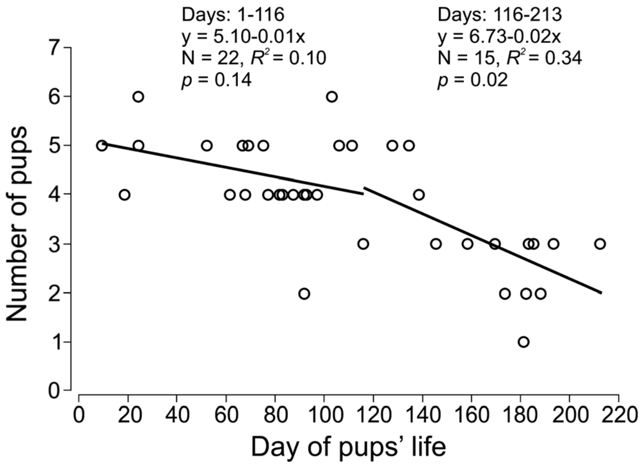

Fig. 5 Number of wolf pups in observed litters in relation to consecutive days of pups' life in Western Poland, 2001–2012

became stronger and were able to join the pack in daily movements in the territory. The mean litter size at birth, estimated from the regression equation, was 5.1 and declined to 4 pups by the end of August (mortality 7 % per month). In the second period, mortality of pups increased to 14 % per month. By the end of November, mean litter size was 2.5 wolves (Fig. 5). Thus, about 50 % of pups survived from birth till the age of 7 months (Fig. 5).

Mortality of wolves

From 2005 (when the first dead wolf was recorded in WPL) to April 2013, we collected data on 28 cases of mortality: 24 adult wolves (86 %) and 4 young of the year (14 %) (Appendix 3). Amongst 27 wolves for which we could recognise gender, there were 14 males (52 %) and 13 females (48 %) (Table 1). The most prevalent cause of recorded mortality was collision with vehicles ($n = 18$; 64 %): 17 wolves died on roads and one on a railway. Most of the detected casualties were males ($n = 12$; 67 %) (Table 1). From 2005 to mid-2012, only two females hit by cars were found, but in autumn 2012 and in winter 2012/2013, four more females were discovered on roads. All wolves hit by vehicles were young (6 months–3 years) (Appendix 3). The average distance from reported locations where wolves were hit by vehicles to the centres of the nearest pack territory was 11.6 km (range 0.6–38.6 km). Only two dead wolves were found outside forests which were inhabited by resident packs at that time. Wolves in the Bydgoszcz Forest (are no. 11) were most affected by road mortality, as at least five individuals (two females and three males) died in collisions with vehicles between 2005 and 2012.

Illegal hunting and snaring contributed 25 % to the recorded wolf mortality (Table 1, Appendix 3). Amongst seven detected poached wolves (four females, two males and one of unidentified sex), five were illegally shot by hunters and two killed in snares. Additionally, one male wolf was found alive in snares and released.

Diseases and other natural factors caused 7 % of recorded mortality. One adult female died during an aggressive intraspecific interaction (Appendix 1).

Additionally during snow-tracking, direct observations and in video footage taken by camera traps, we discovered physically disabled wolves ($n = 2$) and wolves with sarcoptic mange ($n = 2$), which may also be causes for natural mortality in WPL.

Table 1 Number of wolves *Canis lupus* found dead in Western Poland, 2001–2012

Cause of death	Males	Females	All	Percent
Road casualty	11	6	17	61
Railroad casualty	1	–	1	3.5
Poaching	2	4	7[a]	25
Intraspecific strife	–	1	1	3.5
Diseases	–	1	1	3.5
Unknown	–	1	1	3.5
Total	14	13	28	100

[a] In one case, sex of a dead wolf remained unknown

Discussion

This paper presents a process of rapid spontaneous recolonisation of Western Poland by wolves. During 12 years, the population increased exponentially from several individuals to 30 resident packs, the area permanently occupied by wolves extended from 600 to 10,900 km^2 and wolves successfully resettled 14 woodlands.

Because our study covered a large area of about 136, 000 km^2 and wolves are elusive animals, travelling long distances and maintaining large territories, we are aware of possible sources of biases which might have influenced the results of our studies. Firstly, we might not have been able to discover all wolf groups in the first year of their presence in WPL, this is particularly true in case of newly established pairs. There is also a probability that only a small portion of loners was detected. This might lead to underestimation of wolf numbers and the annual rates of their increase. In case of wolf groups, it might lead to underestimation of the number of ephemeral groups and the duration of resident packs. Obviously, not all dead wolves, especially those poached and those which died from natural causes, were recorded in WPL. This might cause the underestimation of wolf mortality and cause bias towards traffic accidents as a main cause of wolf death.

Genetic studies of the Polish wolf population revealed that most wolves settled in WPL were immigrants from northeastern Poland, or their descendants (Czarnomska et al. 2013).

The mean straight-line distance from the western-most edges of the continuous wolf range in northeastern Poland to WPL (midpoint between meridian 18°48′ E and the Polish-German border) was 376 ± 106.5 km in the early 2000s and there were still some unoccupied wolf habitats in eastern Poland (Jędrzejewski et al. 2004, 2008). In the early years of re-colonisation (2001–2003), only loners or wolf pairs appeared in WPL. The large NND between wolf territories at that time showed that pack founders settled after long-distance dispersal and far away from each other. Thus in the first stage of re-colonisation of WPL, the jump-dispersal pattern prevailed, like in some other locations of Europe and North America (Wabakken et al. 2001; Valière et al. 2003; Fabbri et al. 2007, 2014; Wydeven et al. 2009; Andersen et al. 2015).

Persistence of these small wolf groups living far from each other was low, and during that time many of them disappeared. By the mid-2000s however, the permanent wolf range in eastern Poland expanded westward, which shortened the distance to suitable habitats in WPL (Chapron et al. 2014). At the same time, the wolf population in Saxony, Germany, grew quickly (Ansorge and Schellenberg 2007; Reinhard et al. 2013) and became a second source of immigrants for WPL as shown by genetic analyses (S. Nowak, R.W. Mysłajek, unpublished data). This allowed for the strengthening of the recovery process.

Wolf numbers in WPL increased not only due to the appearance of new settlers but also due to the growth of newly established packs. Family groups started from parental pairs and one or two pups of the year. Some of these groups remained at this stage for 2–3 years and disappeared, other continued to develop. When pups survived until the next breeding season, the pack size increased to parents, one or two yearlings and several pups of the year, which ensured the status of resident pack. The relatively high survival of pups in November, recorded in WPL, together with high densities of wild ungulate and mild winters ensured that pack growth continued over the next years. The average size of resident packs in WPL (6.8 wolves) was bigger than in eastern Poland and the Carpathians (Śmietana and Wajda 1997; Okarma et al. 1998; Jędrzejewski et al. 2000, 2002a, 2002b; Finďo and Chovancová 2004; Nowak et al. 2008), Scandinavia (Wabakken et al. 2001; Sand et al. 2012) and some locations in North America (Fuller et al. 2003). Large packs became donors of young dispersers—founders of the next wolf groups in WPL.

Over the course of the recovery process, the NND between the territories of packs gradually decreased. More new wolf groups were established in the close vicinity of already existing packs, while relatively fewer groups appeared in more distant areas. Thus in the second phase of the recovery process the dispersal pattern of re-colonisation shifted to being more stratified, being a mixture of diffusion dispersal and long-distance dispersal of individuals. This allowed for better persistence of wolf groups (or pack territories), especially those living in close proximity to each other, because of easier access to potential mates. In WPL, immigration of wolves from northeastern Poland, the increase in pack size and the increase in their number exceeded the mortality of wolves, which caused the population to grow exponentially until end of our study.

Such exponential growth cannot continue without limits. How high the wolf population can increase not only depends on access to suitable habitats but also depends on public acceptance, legal status and the mitigation of conflicts (Kaczensky et al. 2013). According to the habitat suitability model for Polish wolves (Jędrzejewski et al. 2008), about 790 ± 60 wolves are able to live in an area of 35,570 km^2 of suitable habitats, west from 18°48′. Thus in winter 2012/2013, the population number reached about 18 % of that estimate, and wolves occupied 30 % of suitable habitats. Therefore, forests in WPL are far from being saturated, and further wolf population development can be expected. However, the growing impact of human activity on wolf habitats, and habitat fragmentation caused by the development of transportation infrastructure, may decrease their suitability for wolves (Jędrzejewski et al. 2005; Huck et al. 2010, 2011). On the other hand, increasing densities of wild ungulates support wolf population growth in WPL (Borowik et al. 2013). In parallel to wolf recovery in WPL, a rapid development of the wolf population was observed in Germany (Reinhardt et al. 2015). There is also evidence of long-distance (800 km) dispersal of wolves from packs living near the German-Polish border to Denmark, which shows that the European Lowlands wolf population expands further to the west of Europe (Andersen et al. 2015).

The increase in wolf range and population size has recently been recorded in the whole of Europe (Chapron et al. 2014). However, the population in WPL (together with its source population in eastern Poland) and Germany is the only lowland wolf population re-establishing in central and western Europe, in areas of high human density. The majority of recent re-colonisations in human-dominated parts of Europe have taken place in uplands (Nowak et al. 2008; Marucco et al. 2009, Kaczensky et al. 2013). In Finland and the Baltic states, where wolves also live on plains, human density is much lower (18–47 inhabitants per km^2, http://ec.europa.eu/eurostat), while in Sweden (24 inhabitants per km^2), most of the current wolf range covers uplands (Wabakken et al. 2001; Liberg et al. 2011).

The dense network of public and forest roads and high human density causes increased human pressure on wildlife (Selva et al. 2011). Therefore, we can expect that the recovery of wolves in lowlands will be slower and limited by human-caused disturbance and mortality. Yet, the mean annual rate of population increase in WPL was higher than the average growth rates in recovering wolf populations studied in the uplands of Europe (Wabakken et al. 2001; Nowak et al. 2008) and most of North America (Wydeven et al. 1995; Pletscher et al. 1997; Hayes and Harestad 2000). This shows that wolves are adapted to human presence in WPL: similarly to other exploited forests, we believe it is a behavioural adaptation of spatio-temporal character (Theuerkauf et al. 2003a, b).

Giving birth to young almost exclusively in excavated dens, raising pups as far as possible from human settlements and public roads, might also help to avoid a high risk of disturbance by people in the managed lowland forests of WPL. The high survival of pups in the first 120 days of their life, when they were still not very mobile and stayed in relatively safe rendezvous sites under the supervision of older pack mates, seems to confirm this assumption. In contrast, in October-November when pups were bigger, more active and had begun to move with the pack to more peripheral parts of their territory (Packard 2003), where the risk of mortality, especially human-caused, is higher, the pups' survival decreased. However, in general, the recorded pups' survival in WPL was higher than in other parts of Poland (Jędrzejewska et al. 1996; Jędrzejewski et al. 2002a; Nowak et al. 2008).

The mortality of wolves in WPL, similarly to other protected populations (Wabakken et al. 2001; Blanco and Cortéz 2007; Smith et al. 2010), was mostly human-caused and was dominated by collisions with vehicles. Although some underestimation of the number of illegal shootings and snarings of wolves is possible, it is also likely that poaching was much lower in WPL than in other regions, e.g. Scandinavia (Liberg et al. 2012). In general, the total human-caused and natural mortality during the recovery period 2001–2012 did not hamper the wolf population increase, contrary to periods of wolf control and exploitation, when wolves were absent from or very rare in western Poland (Sumiński 1973; Okarma 1989; Wolsan et al. 1992).

In conclusion, our study showed that the fast spontaneous recovery of wolves in distant suitable areas is possible due to two patterns of dispersal. At the beginning, the most frequent is jump-dispersal, which allows wolves to settle and form packs in locations very distant from their continuous range. The first settlers face a risk of short persistence of groups. When the number of packs and their size increases, the growing packs become a source of migrants and the dispersal pattern shifts to being more stratified—a mixture of long-distance and diffusion dispersal. This results in the creation of small local populations. After 12 years of successful re-colonisation, wolves in Western Poland still show exponential population increase while occupying an estimated 30 % of potential suitable habitats.

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Appendix 1. Development of the wolf population in Western Poland in 2001–2012

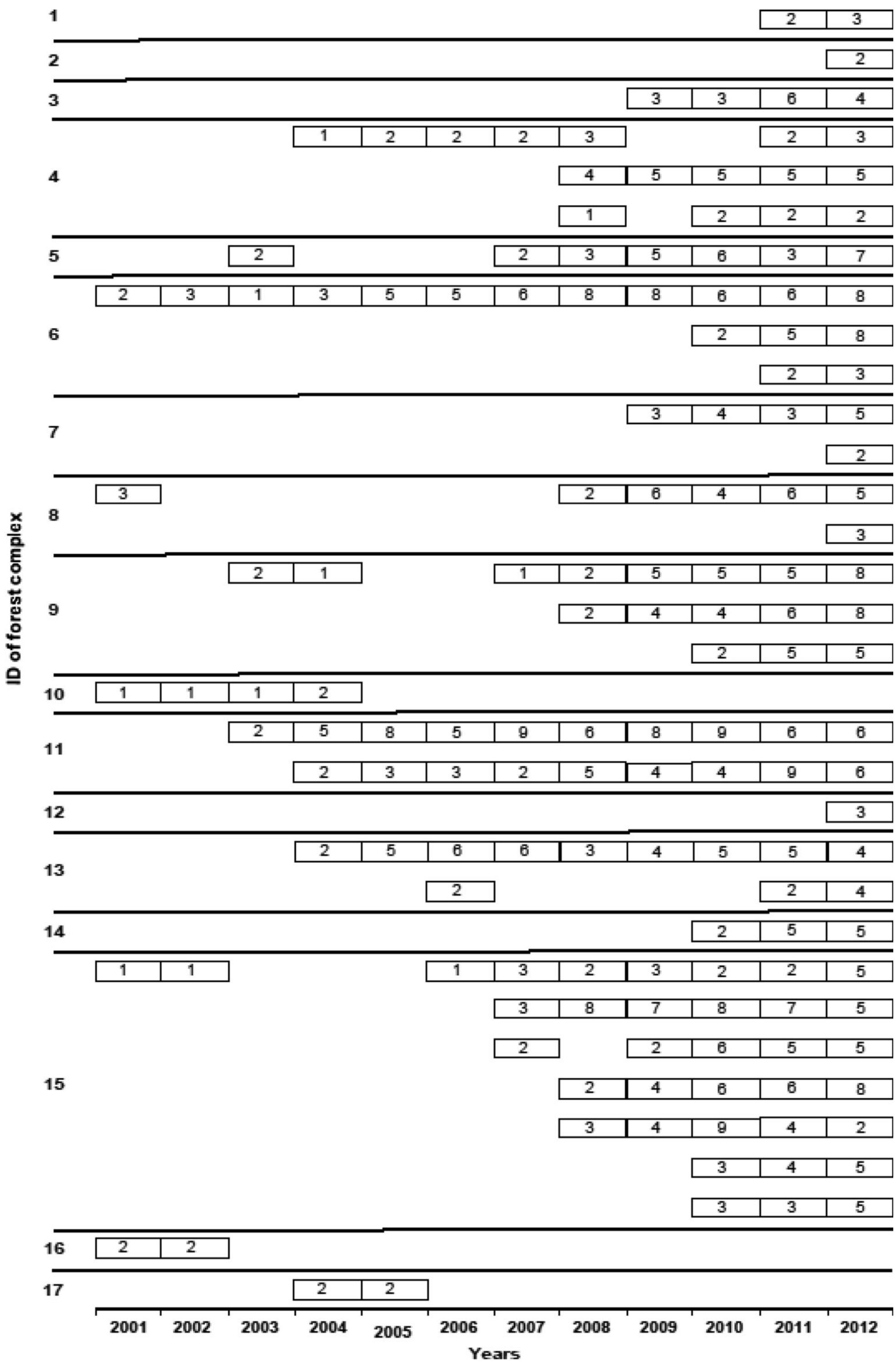
In 2001, WPL was inhabited by a small pack of wolves (with one to two young): one pair and a small group which probably escaped from an illegal enclosure. There was also evidence of at least two loners (see Fig. 2). In 2002, we found signs of one pack, one group of fugitives and no less than two single wolves in the study area. In 2003, wolves disappeared from some forests to appear in other forests, without a single reproduction confirmed. In total, we recorded the presence of *ca.* 8 wolves at that time. In 2004, the development of the population slowly began by the establishment of three pairs and two small packs with confirmed reproduction: a total of 18 wolves. In 2005, altogether four packs and a pair were present in WPL (about 23–25 wolves); all four family groups reared pups. In 2006, the number of groups rose to six (including four packs and two pairs), and in 2007, the population increased to nine groups (five packs and four pairs): altogether 34–36 wolves were confirmed. At this point, wolves occurred in seven forest tracts, and more than one pack was recorded in two big woodlands (see Fig. 2). In 2008, 14 wolf groups (nine packs and five pairs, 49–56 wolves) lived in nine large forests, and at least nine family groups had reproduced. In 2009, altogether 15 resident packs and a pair were found (69–75 wolves). In 2010, at least 22 groups (17 packs and five pairs, 89–100 wolves) were recorded in 12 forests; four forests were inhabited by more than one pack. In 2011, about 26 groups (20 packs and six pairs, 111–116 wolves) were confirmed to be present. At the end of the study period, in the winter of 2012/2013, the wolf population reached at least 30 groups (25–26 packs and 4–5 pairs, 136–142 wolves) (see Fig. 2 and Table 2). We recorded reproduction in at least 25 packs. These groups occurred in the 14 largest woodlands in WPL.

Table 2 Characteristics of the wolf population during winter seasons in WPL, 2001/2002–2012/2013

Winter	Estimated number of wolves	Annual rate of population increase	*N* packs (≥3 wolves)	*N* pairs	*N* loners	Mean group size ± SE	Largest group	Annual rate of pack number increase	Area occupied (km^2)	Annual rate of increase of occupied area	Nearest neighbour distance between wolf groups (km) ± SE	*N* litters	*N* dead wolves
2001/2002	9	–	1	2	1	1.8±0.37	3	–	600	–	163	1	0
2002/2003	7	0.78	1	1	2	1.8±0.48	3	0.67	400	0.67	260	1	0
2003/2004	8	1.14	0	3	2	1.6±0.25	2	1.50	600	1.50	97 ± 4.9	0	0
2004/2005	18	2.25	2	3	4	2.3±0.45	5	1.67	1100	1.83	59 ± 6.8	2	0
2005/2006	23–25	1.33	4	1	0	4.2±0.95	8	1.00	1800	1.64	81 ± 7.1	4	2
2006/2007	25	1.04	4	2	1	3.4±0.72	6	1.20	2500	1.39	44 ± 6.8	3	2
2007/2008	34–36	1.40	5	4	1	3.6±0.81	9	1.50	3000	1.20	41 ± 3.6	5	0
2008/2009	49–56	1.51	9	5	1	3.6±0.57	8	1.56	4700	1.57	39 ± 3.7	9	1
2009/2010	69–75	1.36	15	1	0	4.7±0.45	8	1.14	5400	1.15	33 ± 3.5	11	2
2010/2011	89–100	1.32	17	5	1	4.5±0.47	9	1.38	7200	1.33	27 ± 3.2	15	4
2011/2012	111–116	1.20	20	6	0	4.5±0.37	9	1.18	8700	1.21	28 ± 3.4	20	5
2012/2013	136–142	1.22	25–26	4–5	1	4.8±0.35	8	1.15	10,900	1.25	25 ± 2.7	25	12

Appendix 2

Chronology of wolf appearance and persistence of wolf groups in forests of Western Poland, 2001–2012. ID of forest complex refers to number of forest in Fig. 1. *Numbers in blocks* are numbers of wolves in groups



Appendix 3

Mortality of wolves in Western Poland from 2001 to the end of April 2013

No.	Season	Forest	Age, sex of wolf	Cause of death
1	2005, November 17	Bydgoszcz	2 years, male	Road casualty
2	2006, February 02	Bydgoszcz	1 year, female	Road casualty
3	2006, April 08	Wałcz	3 years, male	Poached/snared
4	2007, January 16	Rzepin	3 years, male	Road casualty
5	2008, October 30	Rzepin	Ad, unknown	Illegally shot
6	2009, May 14	Bydgoszcz	1 year, male	Road casualty
7	2009, November 30	Notecka	3 years, male	Road casualty
8	2010, October 29	Wałcz	2 years, female	Road casualty
9	2010, December 15	Słupsk	2 years, female	Illegal shooting
10	2011, January 11	Rzepin	2 years, male	Road casualty
11	2011, March 21	Drawa	2 years, male	Road casualty
12	2011, May 30	Bydgoszcz	3 years, male	Road casualty
13	2011, August 04	Lower Silesian	2 years, male	Road casualty
14	2011, November 15	Rzepin	Juv, male	Railway casualty
15	2011, December 10	Drawa	2 years, female	Illegally shot
16	2011, December 10	Drawa	2 years, male	Illegally shot
17	2012, April 12	Drawa	2 years, female	Intraspecific strife
18	2012, August 07	Goleniów	2 years, male	Road casualty
19	2012, summer	Lower Silesian	2 years, female	Unknown cause
20	2012, September 14	Noteć	Juv, female	Disease
21	2012, September 29	Noteć	2 years, male	Road casualty
22	2012, October 08	Wałcz	Juv, female	Road casualty
23	2012, October 19	Bydgoszcz	2 years, female	Road casualty
24	2012, December 18	Goleniów	Juv, female	Road casualty
25	2013, January 10	Lower Silesian	2 years, female	Road casualty
26	2013, February 08	Bydgoszcz	9 years, female alpha	Illegally shot
27	2013, March 13	Cedynia	2 years, male	Road casualty
28	2013, late April	Cedynia	2 years, female	Poached/snared
Death not confirmed				
29	2009, January 26	Wałcz	Ad, male	Snared, but released

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