Re-evaluation of the wolf population management units in central Europe

Authors: Gula, Roman, Bojarska, Katarzyna, Theuerkauf, Jörn, Król, Wiesław, and Okarma, Henryk

Source: Wildlife Biology, 2020(2)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00505

Wildlife Biology 2020: wlb.00505
doi: 10.2981/wlb.00505

Subject Editor: Hans Pederesen. Editor-in-Chief: Ilse Storch. Accepted 13 January 2020

Re-evaluation of the wolf population management units in central Europe

Roman Gula, Katarzyna Bojarska, Jörn Theuerkauf, Wiesław Król and Henryk Okarma

R. Gula (https://orcid.org/000-0002-0619-5123) and J. Theuerkauf (https://orcid.org/0000-0002-7273-3073), Museum and Inst. of Zoology, Polish Academy of Sciences, Warszawa, Poland. – K. Bojarska (https://orcid.org/0000-0001-7141-3118) ✉ (katbojarska@gmail.com), W. Król and H. Okarma, Inst. of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, PL-31-120 Kraków, Poland.

The wolf *Canis lupus* population occupying the lowlands of central Europe is divided into two management units: the Baltic population east of the Vistula river and the Central European population to the west. We re-evaluated arguments for this division in the context of the ongoing wolf recovery and its usefulness for wolf management in Poland. To do so, we 1) compared the recovery stage on each side of the Vistula, 2) investigated the history of wolf occurrence in western Poland after the eradication campaign of 1955–1975, 3) evaluated dispersal corridors, dispersal distances and genetic data for evidence of a possible isolation of the two alleged populations and 4) compared habitat characteristics in Poland on each side of the Vistula.

The total area of forest occupied by wolves was 56 600 km² in 2015 and grew by 5340 km² until June 2017. Wolves in eastern Poland occurred in more areas than predicted by a habitat model, whereas wolves in the west have not yet recolonized all suitable habitats. Wolves have never been extinct west of the Vistula after the eradication campaign, but their recovery started only in the 1980s. Areas currently occupied by wolves on both sides of the Vistula are interconnected by dispersal corridors less than 100 km long, and population genetic studies show that wolves inhabiting the Polish lowlands constitute one genetic cluster. The wolf habitats west of the Vistula have a higher proportion of forests are less fragmented. We conclude that wolves inhabiting the lowlands on both sides of the Vistula river belong to the same population, have similar conservation status, and should be treated as the same management unit.

Keywords: *Canis lupus*, connectivity, habitat suitability, metapopulation, population management units, recolonisation

Wolves *Canis lupus* occur in 28 European countries with an estimated range of ca 800 000 km² (Chapron et al. 2014). Their status is a result of the general recovery of wolves in Europe triggered by the change in policy toward the species. Successful recolonisation was possible due to a high reproductive output in wolves, combined with long-distance (up to 1000 km straight-line distance, on average within 100 km) dispersal by young wolves (Linnell et al. 2005, Kojola et al. 2006, Wabakken et al. 2007). In human-dominated landscapes of Europe, wolves prefer areas with high forest cover, low forest fragmentation and low density of urban areas and roads, where they prey mainly upon wild ungulates (Jędrzejewski et al. 2004, 2008, Karlsson et al. 2007). The distribution and number of wolves in the entire area of Poland have fluctuated during the 20th century, e.g. from 0 to 9.1 individuals/100 km² in the Białowieża Forest at the eastern border of Poland (Jędrzejewska et al. 1996). Persistently persecuted, they recovered during periods of wars (Jędrzejewska et al. 1996). The last Polish eradication campaign lasted from 1955 to 1975 and resulted in the near extinction of wolves (Okarma 1989, 1993, Jędrzejewska et al. 1996). The government ceased persecution and upgraded the wolf status from pest to game species in 1975 (Okarma 1993). At this time, the estimated population of wolves in Poland was <100 individuals, and their range was mainly restricted to north-eastern and south-eastern parts of the country (Okarma 1993). In 1995, wolves became protected in most regions of Poland, and in 1998, the strict protection was extended to the entire country (Gula 2008).

In the European Commission's 'Guidelines for population level management plans for large carnivores' (Linnell et al. 2008), wolves occupying the Polish lowlands were divided into two populations separated by the Vistula river: the Central European and the Baltic population (the latter being part of the north-eastern European population). Wolves in western Poland and Germany were thought to be very low in numbers (less than 50 individuals in 2008), to have a very fragmented distribution, and to be isolated from other areas inhabited by wolves by large distances (several hundred km) (Linnell et al. 2008). Therefore, wolves west of the Vistula river were classified as a separate demographic unit, called the Central European population (Linnell et al. 2008, Kaczensky et al. 2015). It was believed that this population had been extirpated by the eradication programme lasting until the 1970s and that its recovery had only started recently, solely driven by wolves dispersing from eastern Poland, but has then rapidly progressed (Jędrzejewski et al. 2008, Chapron et al. 2014, Nowak and Mysłajek 2016, 2017). Nowak and Mysłajek (2016) estimated that in 2001–2003 only 7–9 wolves lived in western Poland (excluding the Holy Cross region) and that within eight years their numbers grew to 136–142 individuals. In 2018, the IUCN downgraded the Central European population from Critically Endangered to Vulnerable and estimated its numbers to be around 780–1030 individuals (Boitani 2018).

As pointed out by Linnell et al. (2008), changes in species range and conservation status may necessitate revision of proposed management units. The recent rapid wolf population growth in Europe (Chapron et al. 2014) suggests the need for such a re-evaluation. To ensure that proper conservation and management measures are taken, there is an urgent need to provide accurate and up-to-date information on the species population structure, range, habitat use, demographic history and recolonisation process.

In this paper, we aim at answering four main questions regarding the current status of wolves in the Polish lowlands: 1) which is the stage of recovery of wolves in western and in eastern Poland? 2) Is the Central European population isolated from the Baltic population? 3) Are there considerable differences in habitat quality on each side of the Vistula? 4) Is it pragmatic to divide wolves inhabiting the Central European lowlands along the Vistula river into two management units?

To address the first question, we assessed the current species range in Poland on each side of the Vistula river. To assess and compare the recovery stage of both alleged populations, we compared the current wolf range with the predictions of the habitat model proposed by Jędrzejewski et al. (2008). We assumed that during recovery, wolves would first colonise suitable habitat patches and later other, less-suitable areas. We also analysed published and unpublished data on wolf occurrence in western Poland to verify whether the Central European wolf population has a different demographic history than the Polish part of the Baltic population. We examined the second question by analysing wolf range, dispersal corridors and genetic structure in the context of potential isolation of the Central European population. To address the third question, we assessed six wolf habitat parameters on each side of the Vistula river. Finally, to address the fourth question, we discussed the current validity of delimiting the central European wolf population along the Vistula river, as well as the implications of this division for planning wolf conservation and management.

We hypothesised that as a result of wolf recovery both east and west of the Vistula river, the Central European population is no longer isolated from the Baltic population, and that the two alleged populations currently represent a continuum, which should be treated as the same demographic unit.

Material and methods

Current wolf status and recovery stage on each side of the Vistula river

We assessed the current wolf distribution in Poland primarily based on data collected during the national wolf monitoring conducted by the Chief Inspectorate for Environmental Protection in 2014 (<http://siedliska.gios.gov.pl/pdf/siedliska/2013-2014/wyniki_monitoringu_zwierzat_1352.pdf>). This information was gathered all over Poland. Data consisted of records of wolf presence (tracks, scats, kills, visual observations) from two main sources: 1) each State Forest District (178 km^2 of forest on average) collected by forestry personnel and 2) each Polish Hunting Association hunting ground (average area of 60 km^2) collected by hunters in 2012 and 2013. These two sources overlapped spatially across most of Poland, except for private forests (ca 17% of forested area) and hunting grounds managed by the State Forestry, for which only one group provided data. Additionally, we included data on wolf range (confirmed records of the species) for the period from 2011 to 2017 collected by the State Forestry, hunters, researchers and workers of the National Parks for the Atlas of Polish Mammals (in squares of 10×10 km, <www.iop.krakow.pl/ssaki/Gatunek.aspx?spID=101>), as well as data on wolf presence from inventories of NATURA 2000 sites, conducted in 2014–2015 and published in Standard Data Forms (<http://natura2000.gdos.gov.pl/datafiles>). We calculated the size of the area occupied by wolves based on the presence data obtained from all sources for the period until 2015, and new areas of wolf occurrence based on the data collected from January 2016 to June 2017 for the Atlas of Polish Mammals. We considered areas occupied by wolves as all the forest (codes 311, 312, 313 and 324 from CORINE Land Cover 2006 digital maps) surface within a unit in which wolf presence was reported by any of the above-mentioned data sources. We compared the area of wolf occurrence in 2015 and in 2017 to the locations of suitable habitat patches as defined by Jędrzejewski et al. (2008) to see if there were differences in model fit on each side of the Vistula. We calculated the proportion of suitable habitat area already occupied by wolves, and the area in which wolves occupied 'non-suitable' patches, as defined by Jędrzejewski et al. (2008).

Chronology of wolf occurrence west of the Vistula river in 1971–2010.

We reviewed all available publications concerning records of wolf occurrence in Poland west of the Vistula river from 1971 to 2010. For further analyses, we only used 14 publications (listed in Supplementary material Appendix 1) that allowed us to assign data on historical wolf presence to one of the 19 large forest patches (varying from 240 to 3100 km^2) west of the Vistula river. We also collected data on wolves observed or shot before the ban on hunting (1995) from the Chief Offices of the State Forestry Districts, which allowed us to obtain additional information from five forest complexes. We grouped all data into five-year intervals. To assess whether recorded wolves might be breeding (territorial) individuals, we divided the data into two categories: 1) general information on wolf presence or absence, observations of wolves or their traces, dead individuals (264 records), and 2) data indicating reproduction, including observations of pups and wolf packs larger than two individuals (46 records).

Connectivity between the central European and Baltic population

We identified forested areas with wolf presence on each side of the Vistula river within 100 km from each other, and then checked if they were connected across the river by least-cost paths, as delineated for wolves in Poland by Huck et al. (2011). We calculated the shortest distance between the wolf-occupied forest patches on either side of the Vistula along these least-cost paths. We examined all publications providing molecular genetic data of wolves sampled in Poland and neighbouring countries in search of evidence for differences in genetic population structure between the Central European and Baltic wolf populations.

Habitat quality on each side of the Vistula river

We assessed six main habitat variables in lowlands east and west of the Vistula river to compare habitat quality: forest fragmentation, proportion of forested area (forest cover), proportion of wetlands, proportion of grasslands, proportion of urban area, and density of major roads. To limit the analyses to the Polish lowlands, we excluded the Carpathians and Sudeten Mountains from the analyses. We extracted data on following habitat types from CORINE Land Cover 2006 digital maps (<www.eea.europa.eu/data-and-maps/data/clc-2006-vector-data-version-3>): forest (codes 311, 312, 313 and 324), wetlands (411, 412) and grasslands (231, 321). We used four measures for habitat fragmentation proposed by Jaeger (2000): 1) coherence C (the probability that two animals placed in different areas will find each other), 2) landscape division D (the probability that two randomly chosen places in the landscape are not located in the same undissected area), 3) splitting index S (the number of patches after dividing the total region into parts of equal size in such a way that maintains the same degree of landscape division D) and 4) effective mesh size (the size of the areas if the region is split under the previous conditions). The spatial data on settlements and main roads were obtained from the Chief Centre of Cartographic and Geodesic Documentation (<www.codgik.gov.pl/index.php/zasob/baza-danych-ogolnogeograficznych.html>), updated in 2015. All analyses regarding forest cover and fragmentation, percentage of wetlands and grasslands, dispersal corridors, roads density and urban areas were performed in ArcGIS ver. 10.1 (ESRI 2012) and QGIS ver. 2.8.2 (QGIS Development Team 2016).

Results

Current wolf status and recovery stage on each side of the Vistula river

Most large woodlands in Poland were inhabited by wolves already in 2015 (Fig. 1). Wolf occurrence was reported in 269 (53%) forestry districts and 672 (13%) hunting grounds. Wolf occurrence estimated by these two data sources overlapped spatially; 73% of forestry districts with confirmed wolf presence included hunting grounds with wolves. Accordingly, only 2% of hunting grounds with wolf occurrence were located in forestry districts in which no wolves were recorded. The total area of forest occupied by wolves in 2015 was 56 600 km^2, of which 46% was located in the lowlands west of the Vistula river, and 40% in the lowlands to the east; the remaining area was located in the Carpathians and Sudeten Mountains. The area recolonised by wolves in Poland by 2015 encompassed 126% of the area predicted by Jędrzejewski et al. (2008) as suitable for wolves. Particularly in eastern Poland, wolves did not only settle in all suitable patches defined by Jędrzejewski et al. (2008), but also in many areas outside them (Fig. 1). Thus, the wolf range in the east exceeded the range predicted by the habitat model of Jędrzejewski et al. (2008) by 60%. On the west side of the river, there were still a few patches of suitable wolf habitat in central and northern Poland (Jędrzejewski et al. 2008), which remained unoccupied in 2015 (Fig. 1). However, because wolves occurred in some patches outside the predicted suitable habitats, the size of current wolf range west of Vistula was very similar to the area predicted by Jędrzejewski et al. (2008).

Between 2015 and 2017, wolves recolonised an additional area of 5300 km^2. The majority (77%) of this expansion occurred west of the Vistula river (Fig. 1, Table 1). Fifty-nine percent of the new areas recolonised by wolves were located inside suitable patches predicted by the habitat model of Jędrzejewski et al. (2008), and this proportion was similar on both sides of the Vistula river (Fig. 1, Table 1).

Chronology of wolf occurrence in western Poland

Wolves were continuously present west of the Vistula river throughout the investigated period (1971–2010, Fig. 2, Supplementary material Appendix 2 Table A1). The area of occurrence varied over time, from 10 of the 19 forest complexes (53%) inhabited by wolves in 1976–1980 to 18 (95%) occupied in 1986–1990. Since 1981, wolves have been present in more than 70% of forest patches. Breeding was confirmed in each five-year interval except for 1976–1980. The number of woodlands in which wolves reproduced reached its maximum in 1986–1990, when breeding wolves were recorded in six forest complexes.

In six woodlands (Drawsko, Krajenka, Tuchola, Zielona Gora, Lower Silesia, Holy Cross), the presence of wolves was recorded in each five-year interval (Fig. 2). Two forest complexes (Daleszyce, Goleniow) were occupied for the shortest time (two and three five-year intervals, respectively). Breeding was observed in 10 forest patches (Piaskowa, Drawsko, Krajenka, Bydgoszcz, Notec, Rzepin, Zielona Gora,

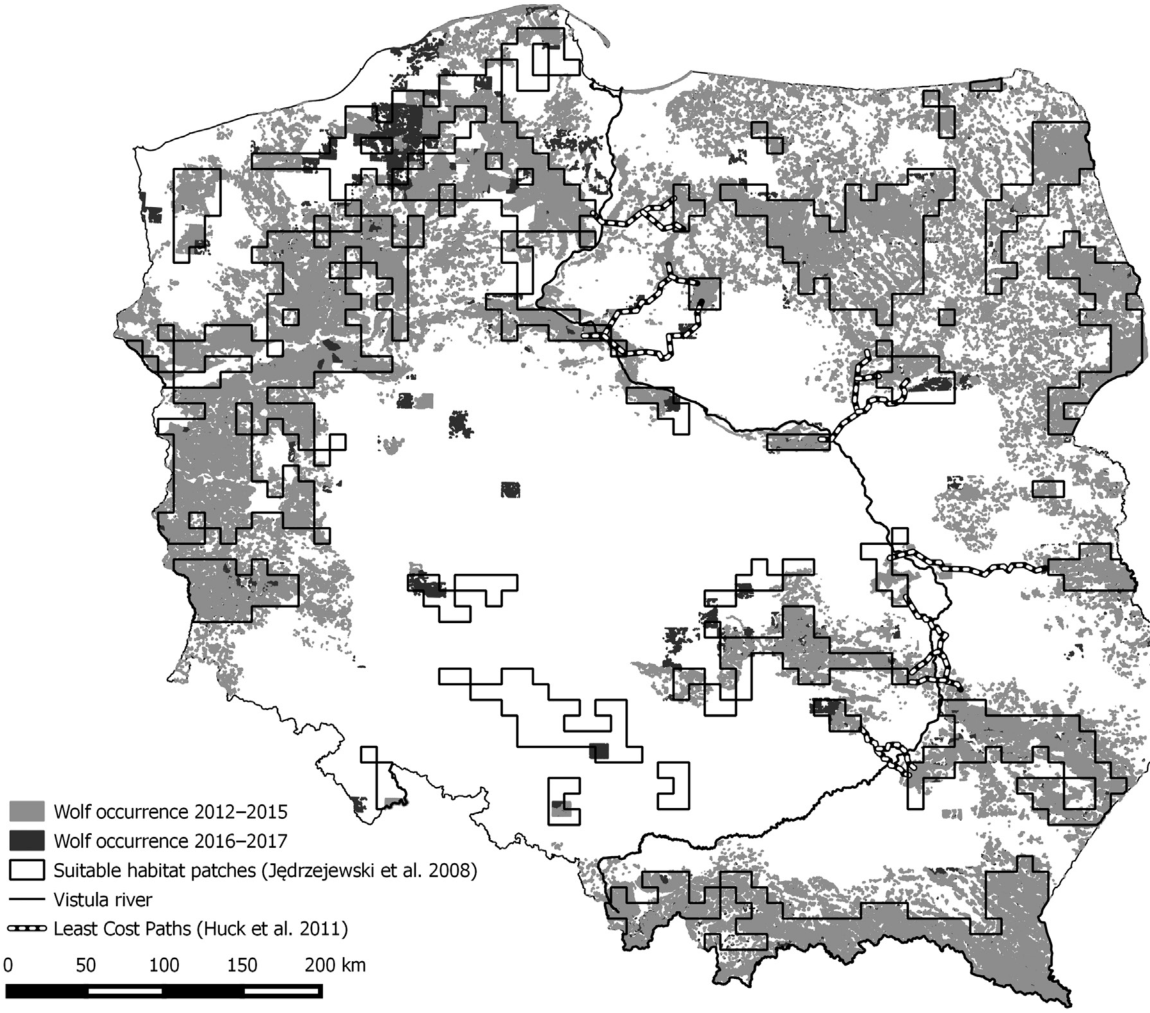

Figure 1. Forests occupied by wolves in Poland in 2015 and new areas of wolf occurrence until 2017, habitat patches classified as suitable for wolves by Jędrzejewski et al. (2008) and least-cost paths (Huck et al. 2011) connecting large woodlands inhabited by wolves on both sides of the Vistula river.

Lower Silesia, Holy Cross, Daleszyce). Wolf breeding was recorded the most frequently in Piaskowa, Notec and Lower Silesia forests (five of eight five-year intervals).

Seventy-four wolves were legally shot or found dead west of the Vistula river in 1971–2010. Dead wolves were recorded in each five-year interval and in every forest complex, except Gorzow and Krajenka forests (Supplementary material Appendix 2 Table A2). Most dead wolves were recorded in the 1980s when wolves were still a game. The highest number of dead wolves was recorded in Notec Forest.

Connectivity between the Central European and Baltic population

Distance and dispersal corridors

There were 11 large woodlands occupied by wolves close to the Vistula river, which are connected across the river by

Table 1. Area of forest (km^2) of wolf occurrence in 2015 and new areas colonised by wolves until 2017 inside and outside of suitable habitat patches (SHP) predicted by Jędrzejewski et al. (2008) in Poland, in lowlands and mountains east and west of the Vistula river.

Area of forest	Whole Poland		Lowlands west of Vistula		Lowlands east of Vistula		Sudeten Mountains		Carpathian Mountains	
	Range in 2015	New areas in 2017	Range in 2015	New areas in 2017	Range in 2015	New areas in 2017	Range in 2015	New areas in 2017	Range in 2015	New areas in 2017
Area of occurrence – total	56 600	5340	26 180	4040	22 540	1010	460	50	7420	250
Area of occurrence – inside SHP	34 640	3140	17 290	2390	11 410	540	190	20	5740	180
Area of occurrence – outside SHP	21 960	2210	8890	1650	11 130	470	270	30	1670	60
SHP uninhabited by wolves	10 410		8800		1110		270		230	

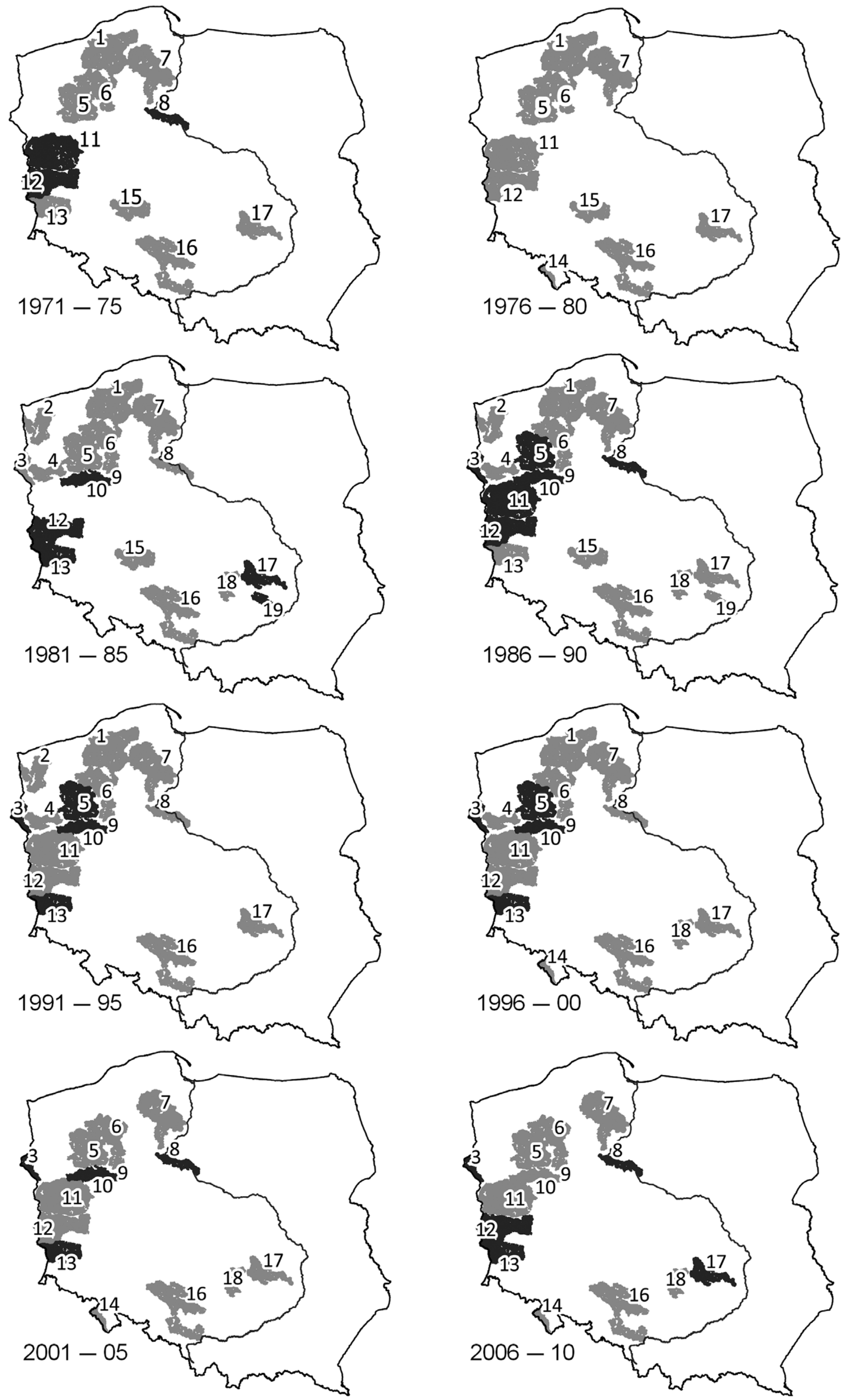

Figure 2. Published records of wolf presence and breeding in 19 large forest complexes in Poland west of the Vistula river (black line) in 1971–2010. Light grey: wolves present, dark grey: wolf breeding. Forest patches: (1) Slupsk, (2) Goleniow, (3) Piaskowa, (4) Gorzow, (5) Drawsko, (6) Krajenka, (7) Tuchola, (8) Bydgoszcz, (9) Sarbia, (10) Notec, (11) Zielona Gora, (12) Rzepin, (13) Lower Silesia, (14) Sudeten Mountains, (15) Milicz, (16) Silesia, (17) Holy Cross, (18) Przedborz, (19) Daleszyce.

nine wolf dispersal corridors (least-cost paths) (Huck et al. 2010, 2011, Fig. 1). The shortest distances between wolf-occupied, large forest patches on either side of the Vistula, calculated along dispersal corridors, ranges from 2 to 83 km (n = 9, average 47 km).

Molecular genetic data on wolf population structure

In a Europe-wide study, Pilot et al. (2010) detected 27 wolf haplotypes (mtDNA 230 bp fragment HV1 region). The two haplotypes found west of the Vistula river occurred also in northern and eastern Europe. In a study of Polish wolves that analysed the mtDNA HV region (333 samples, 33 west of the Vistula river), there was no clustering into eastern and western Poland (Pilot et al. 2010). The results of analyses of 11 wolf microsatellite loci by Czarnomska et al. (2013) also showed no genetic differentiation within wolves inhabiting the Polish lowlands. Likewise, the analyses of 67 K single nucleotide polymorphism (SNP) markers indicated that wolves occupying the Polish lowlands, including areas west of the Vistula river, belonged to the same cluster as wolves in north-eastern Europe including Finland (Stronen et al. 2013). Therefore, neither mtDNA nor nuclear marker-based analyses indicated a genetic division between wolves occupying the lowlands of eastern and western Poland.

Habitat quality on each side of the Vistula river

The Polish lowlands west and east of the Vistula river are covered by 54 700 km^2 and 31 000 km^2 of forest, respectively. The western lowlands have a greater proportion of urbanized area and a higher density of major roads than the east (Table 2). All four measures of habitat fragmentation (coherence, landscape division, splitting index and effective mesh size), however, indicated that forests are less fragmented west of the Vistula (Table 2). Compared to the east, in lowlands west of the Vistula, forests are divided into fewer, but larger patches.

Table 2. Comparison of wolf habitat parameters in western and eastern Polish lowlands.

Habitat parameter	West of the Vistula river	East of the Vistula river
Total area (km^2)	171 725	114 251
Forest area (%)	31.9	27.1
Wetland area (%)	0.7	2.2
Grassland area (%)	7.8	10.9
Major road density (km km^{-2})	0.17	0.14
Urbanised area (%)	7.4	5.9
Forest fragmentation:		
Coherence	0.0054	0.0007
Landscape division	0.995	0.999
Splitting index	183.64	1431.25
Effective mesh size (km^2)	935	80

Discussion

Current wolf status and recovery stage on each side of the Vistula river

Today, wolves occupy most forested areas of the Polish lowlands both west and east of the Vistula, and their total range is expanding. The lowland wolf range was already in 2015 26% larger than the area predicted as suitable for wolves (Jędrzejewski et al. 2008). The area of wolf occurrence and the degree of habitat fragmentation are similar on each side of the river. However, the wolf range compared to suitable habitat patches defined by Jędrzejewski et al. (2008) confirms that wolves are at different stages in the recovery process on each side of the Vistula river. In eastern Poland, wolves occupy large areas of less suitable habitat and their range expanded over the last two years four times less than in the west. This demonstrates that the wolf recolonisation of eastern Poland is more advanced than that of western Poland. The advanced stage of wolf recovery in eastern Poland is probably a result of the shorter distance from the large source population in eastern Europe, where wolves have always persisted despite eradication campaigns (Stronen et al. 2013). Moreover, some forest complexes in western Poland remain unoccupied, most likely due to their isolation from other suitable habitat patches already recolonized by wolves, as demonstrated by the lack of least-cost paths (Huck et al. 2011). Thus, while the habitat model seems to well predict earlier stages of recolonisation in western Poland, it is less accurate in predicting the later stages of wolf recovery. A similar pattern was observed in Wisconsin, where the prediction by a habitat suitability model of Mladenoff et al. (1995, 1999) and Mladenoff and Sickley (1998) developed during an early phase of wolf recolonisation, did not match a later stage of recolonisation (Mech 2006). Eradication campaigns usually restrict wolf occurrence to wilderness areas, because these are the only places where wolves can avoid persecution (Mech 2006). During the early stage of recovery after eradication campaigns, wolves tend to spread from these core areas into similar areas of semi-wilderness (Kojola et al. 2006). Therefore, models of wolf habitat suitability may fail to predict later phases of recovery in a non-persecuted population (Mech 2006, 2017). Moreover, the selection of input data and modelling techniques can have an important influence on the outcome of habitat suitability models, especially in the case of habitat generalists like wolves (Fechter and Storch 2014).

In this study, data on wolf presence originated from several sources, which overlapped spatially and were collected within units that were of similar size or smaller than wolf home ranges (Okarma et al. 1998). This increased the chance of detection and minimised the influence of false absence data. However, wolves recolonising areas after longer periods of absence often remain undetected because local foresters and hunters are not familiar with signs of their presence or do not pay attention to them (Okarma et al. 2011). In addition, some of the wolves may be loners dispersing over long distances, which makes them even more difficult to detect, e.g. due to their secretive behaviour and higher travel speed (Gula et al. 2009).

Chronology of wolf occurrence in western Poland

Despite the last state eradication campaign, wolves were never fully exterminated from western Poland after WWII. Signs of wolf presence, dead individuals and evidence of wolf breeding were recorded throughout the 1970s and 1980s. This demonstrates that wolves survived but remained undetected in many areas of the western lowlands because of their low density and the lack of trained observers searching for signs of wolf presence and breeding. This is especially likely in some of the large forested areas in western Poland (e.g. Drawsko Forest, Fig. 2), which were used after WWII by the military as training zones, and where little was known about the status of wildlife. The wolf occurrence in Germany during this period appears to confirm this observation; 20 dead wolves were recorded between 1948 and 1990 in north-eastern Germany (Reinhardt and Kluth 2007), and at least some of them were likely dispersers from western Poland, because median straight-line distances of dispersal are 99 km (Kojola et al. 2006).

The data that we assembled showed that wolf recovery in western Poland began in the early 1980s, and not in 1998, as suggested by Nowak and Mysłajek (2016, 2017). However, wolf recovery in western Poland progressed more slowly than in eastern Poland, due to larger distances from the source population and due to lower initial numbers. This pattern of slower recovery is characteristic of peripheral subpopulations (Reinhardt and Kluth 2007). Additionally, wolf hunting and other human-caused mortality probably further slowed down the expansion of wolves during the first 20 years of recovery (Supplementary material Appendix 3). The fact that wolves were never extinct in western Poland sheds new light not only on the chronology of the species recovery, but also on its potential mechanisms. Our results suggest that long-distance dispersal from eastern Poland was not the only driver of wolf recovery west of the Vistula, as proposed by Nowak and Mysłajek (2016). Instead, a diffuse pattern of dispersal, supplemented by long-distance dispersers, is the most probable scenario for wolf recovery in western Poland, similar to that of other areas recolonised by wolves (Fritts 1983, Gese and Mech 1991, Kojola et al. 2006, 2009).

Connectivity between the Central European and Baltic population and habitat quality

Dispersal corridors connect the two alleged populations in several places along the Vistula, which indicates that there are no barriers that could seriously impede dispersal across the river. The Central European wolf population is no longer isolated by distance, because the distances that wolves must travel between occupied areas on both sides of the Vistula are smaller than distances usually covered by dispersing wolves (Kojola et al. 2009). Moreover, the wolf range is continuous on both sides of the Vistula in some regions of northern and central Poland. In the north of Poland, there is even a continuous wolf-occupied habitat from the western to the eastern state border. Dispersing wolves have been shown to use this route even eastwards (Reinhardt and Kluth 2016). These results are supported by molecular studies, which showed no differential genetic structuring across the Polish lowlands (Pilot et al. 2010, Czarnomska et al. 2013, Stronen et al. 2013).

We demonstrated that wolf habitat quality in eastern and western Poland is at least similar regarding forest cover and fragmentation but habitat quality in the west is slightly lower in terms of degree of urbanisation and density of roads. Additionally, habitat patches suitable for wolves in western Poland are larger and support a higher biomass of ungulates (Jędrzejewski et al. 2008). Wolves on both sides of the Vistula river occupy forest patches that are all large enough to support several packs, and these patches are interconnected by dispersal corridors, which provide a bi-directional gene flow, as evidenced by dispersal routes of radio-tracked individuals (Reinhardt and Kluth 2016).

Division between the Central European and Baltic population

The findings that we present in this study indicate that the division of wolf populations along the Vistula river, as proposed by the European Community Guidelines (Linnell et al. 2008) and adopted later by Chapron et al. (2014), Nowak and Mysłajek (2016) and Hindrikson et al. (2017), although appropriate in the early 2000, should now be re-evaluated because of the advanced wolf recovery. Currently, the two alleged populations represent a continuum in terms of range, genetic structure, habitat characteristics and management regimes. They inhabit state forests managed in a similar way and there are no pronounced climatic differences between the two areas (Okarma et al. 2011). They also share a common demographic history, recolonization patterns and conservation status. The only difference between wolves east and west of the Vistula is that western wolves are in an earlier stage of recovery, related to the distance to the source population in eastern Europe. Within the territory of Poland, we do not see the need for three management zones, but only two, the lowlands and the Carpathians, which are distinctive regarding their population genetics, conflict with humans and habitat characteristics (Pilot et al. 2010, Czarnomska et al. 2013, Stronen et al. 2013). Two zones would also be more practical from the perspective of a state level wolf management for planning and reporting to the European Commission. Although western Polish wolves generally seem to be in an earlier recovery stage, there is considerable variation in the status among smaller wolf subpopulations (i.e. wolves occupying different forest patches) on both sides of the Vistula river. Therefore, different management scenarios that were applicable in certain areas of both sides, have been discussed on the national level (Okarma et al. 2011). In our opinion, such a fine-scale zoning adjusted to the status of local subpopulations, habitat structure and level of wolf-human conflict is currently a more appropriate management strategy than the general division along the Vistula river. We are therefore advocating for it on the national level.

On the European level, in our opinion, there is currently no reason for a general division of the wolf population occupying the central European lowlands into two management units. However, present wolf recovery in Germany, Denmark, Belgium and the Netherlands may create the necessity to delimitate new subpopulation management units that unify areas in an early stage of recolonisation, which are more vulnerable to human mortality and disturbance. In this case, the border between the current central European and Baltic management units should be moved west (and maybe renamed Western European wolf management unit), while wolves occupying western Poland and possibly eastern Germany should be incorporated into the Baltic unit. Thus, we propose that the division of the central European–Baltic metapopulation into management units should be re-evaluated by the European Commission based on current population data after consultation with a wide array of national experts.

Acknowledgements – We thank Elizabeth Gosling for revising an earlier version of this manuscript and helpful comments.

Funding – This study was funded by the Polish National Science Centre (grants NCN2011/01/B/NZ8/04233, NCN2012/05/N/NZ8/00860, N N304 170439) and SAVE Wildlife Conservation Fund.

Author contributions – The first and the second author contributed equally to this work.

References

Boitani, L. 2018. *Canis lupus* (errata version published in 2019). – The IUCN Red List of Threatened Species 2018: e.T3746A144226239.

Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. – Science 346: 1517–1519.

Czarnomska, S. et al. 2013. Concordant mitochondrial and microsatellite DNA structuring between Polish lowland and Carpathian Mountain wolves. – Conserv. Genet. 14: 573–588.

ESRI 2012. ArcGIS, Ver. 10.1. – ESRI, Inc., Redlands, California, USA.

Fechter, D. and Storch, I. 2014. How many wolves (*Canis lupus*) fit into Germany? The role of assumptions in predictive rule-based habitat models for habitat generalists. – PLoS One 9: e101798.

Fritts, S. H. 1983. Record dispersal by a wolf from Minnesota. – J. Mammal. 64: 166–167.

Gese, E. M. and Mech, L. D. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. – Can. J. Zool. 69: 1946–1955.

Gula, R. 2008. Legal protection of wolves in Poland: implications for the status of the wolf population. – Eur. J. Wildl. Res. 54: 163–170.

Gula, R. et al. 2009. Evidence of wolf dispersal in anthropogenic habitats of the Polish Carpathian Mountains. – Biodivers. Conserv. 18: 2173–2184.

Hindrikson, M. et al. 2017. Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management. – Biol. Rev. 92: 1601–1629.

Huck, M. et al. 2010. Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. – Acta Theriol. 55: 177–192.

Huck, M. et al. 2011. Analyses of least cost paths for determining effects of habitat types on landscape permeability: wolves in Poland. – Acta Theriol. 56: 91–101.

Jaeger, J. A. 2000. Landscape division, splitting index and effective mesh size: new measures of landscape fragmentation. – Landscape Ecol. 15: 115–130.

Jędrzejewska, B. et al. 1996. Population dynamics of wolves *Canis lupus* in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. – Mamm. Rev. 26: 103–126.

Jędrzejewski, W. et al. 2004. Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. – Divers. Distrib. 10: 225–233.

Jędrzejewski, W. et al. 2008. Habitat suitability model for Polish wolves based on long-term national census. – Anim. Conserv. 11: 377–390.

Kaczensky, P. et al. 2015. Status, management and distribution of large carnivores – bear, lynx, wolf and wolverine – in Europe. – Prepared for the European Commission. IUCN/SSC Large Carnivore Initiative for Europe.

Karlsson, J. et al. 2007. Predicting occurrence of wolf territories in Scandinavia. – J. Zool. 272: 276–283.

Kojola, I. et al. 2006. Dispersal in an expanding wolf population in Finland. – J. Mammal. 87: 281–286.

Kojola, I. et al. 2009. Dispersal behaviour and the connectivity between wolf populations in northern Europe. – J. Wildl. Manage. 73: 309–313.

Linnell, J. D. et al. 2005. The origins of the southern Scandinavian wolf *Canis lupus* population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice. – Wildl. Biol. 11: 383–391.

Linnell, J. D. et al. 2008. Guidelines for population level management plans for large carnivores in Europe. A large carnivore initiative for Europe report prepared for the European Commission (contract 070501/2005/424162/MAR/B2) 83. <https://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/guidelines_for_population_level_management.pdf>..

Mech, L. D. 2006. Prediction failure of a wolf landscape model. – Wildl. Soc. Bull. 34: 874–877.

Mech, L. D. 2017. Where can wolves live and how can we live with them? – Biol. Conserv. 210: 310–317.

Mladenoff, D. J. and Sickley, T. A. 1998. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. – J. Wildl. Manage. 62: 1–10.

Mladenoff, D. J. et al. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. – Conserv. Biol. 9: 279–294.

Mladenoff, D. J. et al. 1999. Predicting gray wolf landscape recolonization: logistic regression models vs new field data. – Ecol. Appl. 9: 37–44.

Nowak, S. and Mysłajek, R. W. 2016. Wolf recovery and population dynamics in western Poland, 2001–2012. – Mamm. Res. 61: 83–98.

Nowak, S. and Mysłajek, R. 2017. Response of the wolf (*Canis lupus* Linnaeus, 1758) population to various management regimes at the edge of its distribution range in western Poland. – Appl. Ecol. Environ. Res. 15: 187–203.

Okarma, H. 1989. Distribution and number of wolves in Poland. – Acta Theriol. 34: 497–503.

Okarma, H. 1993. Status and management of the wolf in Poland. – Biol. Conserv. 66: 153–158.

Okarma, H. et al. 1998. Home ranges of wolves in Białowieża Primeval Forest, Poland, compared with other Eurasian populations. – J. Mammal. 79: 842–852.

Okarma, H. et al. 2011. Krajowa strategia ochrony wilka *Canis lupus* warunkująca trwałość populacji gatunku w Polsce. – Warsaw Univ. of Life Sciences, Warszawa, Poland.

Pilot, M. et al. 2010. Phylogeographic history of grey wolves in Europe. – BMC Evol. Biol. 104: 1–11.

QGIS Development Team 2016. QGIS Geographic Information System. – Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>.

Reinhardt, I. and Kluth, G. 2007. Leben mit Wölfen. Leitfaden für den Umgang mit einer konfliktträchtigen Tierart. BfN-Skripten Band 201. – Bundesamt für Naturschutz, Bonn., Germany.

Reinhardt, I., Kluth, G. 2016. Abwanderung und Raumnutzungsverhalten von Wölfen (*Canis lupus*) in Deutschland. Ergebnisse einer ersten Telemetriestudie. – Natur and Landschaft 91: 6.

Stronen, A. V. et al. 2013. North-south differentiation and a region of high diversity in European wolves (*Canis lupus*). – PLoS One 8: e76454.

Wabakken, P. et al. 2007. Multistage, long-range natal dispersal by a global positioning system-collared Scandinavian wolf. – J. Wildl. Manage. 71: 1631–1634.

Supplementary material (available online as Appendix wlb-00505 at <www.wildlifebiology.org/appendix/wlb-00505>). Appendix 1–2, File 3.