

Genetic support for the current discrete conservation unit of the Central European wolf population

Authors: Szewczyk, Maciej, Nowak, Carsten, Hulva, Pavel, Mergeay, Joachim, Stronen, Astrid V., et al.

Source: Wildlife Biology, 2021(2)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00809>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



Genetic support for the current discrete conservation unit of the Central European wolf population

Maciej Szewczyk, Carsten Nowak, Pavel Hulva, Joachim Mergeay, Astrid V. Stronen, Barbora Černá Bolfíková, Sylwia D. Czarnomska, Tom A. Diserens, Viktor Fenchuk, Michał Figura, Arjen de Groot, Andželika Haidt, Michael M. Hansen, Hugh Jansman, Gesa Kluth, Iga Kwiatkowska, Karolina Lubińska, Johan R. Michaux, Natalia Niedźwiecka, Sabina Nowak, Kent Olsen, Ilka Reinhardt, Maciej Romański, Laurent Schley, Steve Smith, Renata Špinkytė-Bačkaitienė, Przemysław Stachyra, Kinga M. Stępnia, Peter Sunde, Philip F. Thomsen, Tomasz Zwijacz-Kozica and Robert W. Mysłajek

M. Szewczyk (<https://orcid.org/0000-0001-7424-1120>) ✉ (maciej.szewczyk@ug.edu.pl), Dept of Vertebrate Ecology and Zoology, Faculty of Biology, Univ. of Gdańsk, Gdańsk, Poland. – C. Nowak (<https://orcid.org/0000-0002-3139-1951>), Senckenberg Research Inst. and Natural History Museum Frankfurt, Gelnhausen, Germany. – P. Hulva (<https://orcid.org/0000-0002-4968-4859>), Faculty of Science, Charles Univ. in Prague, Prague, Czech Republic, and: Faculty of Science, Univ. of Ostrava, Ostrava, Czech Republic. – J. Mergeay (<https://orcid.org/0000-0002-6504-0551>), Research Inst. for Nature and Forest (INBO), Geraardsbergen, Belgium, and: Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Leuven, Belgium. – A. V. Stronen (<https://orcid.org/0000-0002-5169-6736>), Dept of Biology, Biotechnical Faculty, Univ. of Ljubljana, Ljubljana, Slovenia. – B. Černá Bolfíková (<https://orcid.org/0000-0001-8059-4889>), Dept of Animal Science and Food Processing, Faculty of Tropical AgriSciences, Czech Univ. of Life Sciences Prague, Prague 6, Czech Republic. – S. D. Czarnomska (<https://orcid.org/0000-0002-8081-0956>), Museum and Inst. of Zoology, Polish Academy of Sciences, Gdańsk, Poland. – T. A. Diserens (<https://orcid.org/0000-0002-0693-4168>), Mammal Research Inst., Polish Academy of Sciences, Białowieża, Poland, and: Faculty of Biology, Univ. of Warsaw, Warsaw, Poland. – V. Fenchuk, APB-BirdLife Belarus, Minsk, Belarus. – M. Figura (<https://orcid.org/0000-0001-8367-5828>), N. Niedźwiecka (<https://orcid.org/0000-0002-9352-8546>) and S. Nowak (<https://orcid.org/0000-0002-7771-8032>), Association for Nature 'Wolf', Twardorzeczka, Lipowa, Poland. – A. de Groot (<https://orcid.org/0000-0001-7308-9200>) and H. Jansman, Wageningen Environmental Research, Wageningen Univ. and Research, Wageningen, Netherlands. – A. Haidt (<https://orcid.org/0000-0002-3570-8899>), Dept of Forest Ecology, Forest Research Inst., Sekocin Stary, Raszyn, Poland. – M. M. Hansen (<https://orcid.org/0000-0001-5372-4828>) and P. F. Thomsen (<https://orcid.org/0000-0002-9867-4366>), Dept of Biology, Aarhus Univ., Aarhus C, Denmark. – G. Kluth and I. Reinhardt (<https://orcid.org/0000-0003-4314-3362>), LUPUS – German Inst. for Wolf Monitoring and Research, Spreewitz, Germany. – I. Kwiatkowska (<https://orcid.org/0000-0002-5618-6196>) and R. W. Mysłajek (<https://orcid.org/0000-0001-9619-2868>), Dept of Ecology, Inst. of Functional Biology and Ecology, Faculty of Biology, Biological and Chemical Research Centre, Univ. of Warsaw, Warszawa, Poland. – K. Lubińska, 'Bory Tucholskie' National Park, Charzykowy, Poland. – J. Michaux (<https://orcid.org/0000-0003-4644-9244>), Conservation Genetics Laboratory, Univ. of Liège, Liège, Belgium. – K. Olsen (<https://orcid.org/0000-0002-5624-128X>), Natural History Museum Aarhus, Aarhus C, Denmark. – M. Romański, Wigry National Park, Suwałki, Poland. – L. Schley (<https://orcid.org/0000-0001-7681-6143>), Administration de la Nature et des Forêts, Diekirch, Luxembourg. – S. Smith (<https://orcid.org/0000-0002-1318-0018>), Konrad Lorenz Inst. of Ethology, Dept of Integrative Biology and Evolution, Univ. of Veterinary Medicine, Vienna, Austria. – R. Špinkytė-Bačkaitienė, Vytautas Magnus Univ., Kaunas, Lithuania. – P. Stachyra, Roztocze National Park, Zwierzyniec, Poland. – K. M. Stępnia (<https://orcid.org/0000-0002-4506-2542>), Inst. of Genetics and Biotechnology, Faculty of Biology, Univ. of Warsaw, Warszawa, Poland. – P. Sunde (<https://orcid.org/0000-0002-7485-037X>), Dept of Bioscience, Aarhus Univ., Rønde, Denmark. – T. Zwijacz-Kozica (<https://orcid.org/0000-0002-7488-975X>), Tatra National Park, Zakopane, Poland.

The gray wolf *Canis lupus* range in central Europe is dynamically expanding, reconnecting previously isolated populations. Thus, a recent paper has proposed to merge the current Baltic and Central European (CE) wolf management units, which are no longer isolated by distance. However, recent genetic findings indicate that these two populations are not genetically homogenous. Here we review the most recent data on wolf genetic structure in central Europe and show that even though the CE and Baltic wolves represent the same phylogeographic lineage, their demographic history has resulted in significant genetic structure between these two populations. While the groups are interconnected by moderate gene flow, it is not high

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

enough to reduce the strong founder signal observed in the CE population, suggesting that population dynamics within the CE wolf range are largely independent from those of its source (Baltic) population. Consequently, a management unit combining the CE and Baltic wolves would not form a demographically coherent entity. Thus, we recommend that conservation management units maintain their separate status.

Keywords: gray wolf, *Canis lupus*, population management units, genetic structure, recolonisation

The recent recovery of large carnivores in Europe (Chapron et al. 2014) has led to range expansion and reconnection of previously isolated populations. The delineation of populations as units for conservation management is difficult, especially in species with dynamic ranges and propensities to disperse, such as European large carnivores in general and wolves in particular (Linnell et al. 2005, Blanco and Cortes 2007, Fabbri et al. 2007, Kojola et al. 2009, Andersen et al. 2015, Nowak and Mysłajek 2016, Ražen et al. 2016, Reinhardt et al. 2019). The current wolf population subdivision in Europe is based on the ‘Guidelines for population level management plans’ (Linnell et al. 2008) of the Large Carnivore Initiative for Europe (LCIE), a working group of the Species Survival Commission of the International Union for Conservation of Nature. These guidelines were developed in the context of the EU Habitats Directive and the need to manage large carnivores as entire biological units, i.e. at a population level rather than within the boundaries of single member states or even smaller administrative units. European large carnivore populations were delineated by Linnell et al. (2008), with continuity in distribution being a key discriminating factor. As pointed out by Linnell et al. (2008), population borders ‘need to be reassessed as carnivore populations expand and contract, and more fine scaled data become available’.

The wolf range in central Europe is expanding dynamically (Nowak and Mysłajek 2016, Nowak et al. 2017, Hulva et al. 2018, Reinhardt et al. 2019, Szewczyk et al. 2019), justifying a re-evaluation of the geographic borders between the currently defined populations. Gula et al. (2020) recently addressed this issue in a paper that concluded the Baltic and Central European (hereinafter CE) wolf populations should no longer be treated as different populations. We welcome their paper’s contribution to the ongoing debate and value its new insights on landscape connectivity. While we agree with Gula et al. (2020) that distance no longer isolates the CE wolf population from the Baltic wolf population, we disagree that they form a continuum in terms of genetic structure. Their conclusions are not supported by recent genetic findings (Lesniak et al. 2017, Szewczyk et al. 2019) and represent a biased interpretation of previous studies on the genetic structure of wolves in central Europe. Gula et al. (2020) stated that ‘there is an urgent need to provide accurate and up-to-date information on the species population structure’, and we here focus on the most recent data, which show significant genetic structure between these two populations. We also dispute some of their interpretations of earlier molecular genetic studies and analyses of data on wolf presence and distribution in western Poland before and after 2000. Additionally, we briefly discuss other factors – mainly

socio-political – that support the current delineation of wolf management units in central Europe.

Recent molecular genetic data support the distinctiveness of the Central European wolf population

The claim of Gula et al. (2020) that there is no genetic structuring in wolves across the Polish lowlands is based on a brief review of three papers: a mtDNA-based phylogeographic study by Pilot et al. (2010), a Europe-wide analysis using a large SNP panel (Stronen et al. 2013), and a paper focused on wolf population structure within Poland (Czarnomska et al. 2013). We argue that Gula et al.’s (2020) reasoning has several flaws. Firstly, the authors make a series of questionable assumptions, as genetic connectivity is not necessarily equal to demographic connectivity (detailed discussion in the Supporting information). Secondly, as Pilot et al. (2010) and Stronen et al. (2013) included only a single sample from the area west of the Vistula River in Poland, we – including those of us who co-authored these papers – strongly caution against making inferences about genetic population structure in wolves from areas west and east of the Vistula River on the basis of these results. Finally, our interpretation of Czarnomska et al. (2013) differs from the conclusions of Gula et al. (2020), as discussed below. Furthermore, we highlight other recent studies – omitted by Gula et al. (2020) – that provide evidence for wolf population genetic structure within the lowland part of central Europe.

The first results indicating east–west structuring in the region were published by Lesniak et al. (2017) in a paper focussing on the endoparasite richness of wolves recolonizing Germany, which genotyped 13 microsatellite loci of 53 dead German wolves included in the parasitological analysis. Subsequent Bayesian clustering analyses that included reference genotypes from the Alpine, Carpathian and Baltic wolf populations showed nearly all German wolves formed a single, distinct CE wolf cluster, suggesting this newly established population is genetically separated from its source (presumably Baltic) population. Interestingly, out of 17 wolves sampled in Germany, but not assigned to any local pack (putative immigrants), only one clustered with the Baltic reference genotypes, 13 were grouped with the CE cluster and three showed intermediate genotypes. This indicated that 1) the geographic range of the CE genetic group extends east of the German border and 2) a contact zone exists between the CE and Baltic genetic groups, likely in Poland. However, the contact zone and the rate and patterns of gene flow between the two genetically separated groups remained unknown.

These questions were recently addressed by Szweczyk et al. (2019). This study was the first to cover the whole wolf range in Poland, including all recently recolonized areas. It also included reference samples from the whole of Lithuania and most of Slovakia, and several from Belarus, Ukraine and the Czech Republic. Microsatellite genotypes based on the panel from Lesniak et al. (2017) were analysed using spatial and non-spatial Bayesian clustering and multivariate discriminant analysis of principal components (DAPC). All results were congruent, showing clear separation of three genetic clusters, corresponding to the CE, Baltic and Carpathian wolf populations. The spatial distribution of the identified genetic groups was roughly concordant with the current wolf

populations as defined by Linnell et al. (2008) for this area (Fig. 1). One region in northern Poland east of the Vistula River was assigned to the CE wolf population by GENELAND software, whereas in DAPC and STRUCTURE analyses it was identified as an intermediary population. Another admixture hotspot was identified in south-central Poland (west of the Vistula River), in a contact zone of the CE, Baltic and Carpathian populations. In other regions admixture was relatively low, with the vast majority of individuals from western Poland assigned to the CE cluster, and > 90% of wolves from Lithuania, Belarus and the easternmost Polish regions assigned to the Baltic cluster. These results are concordant with gene flow estimates, which indicated nearly

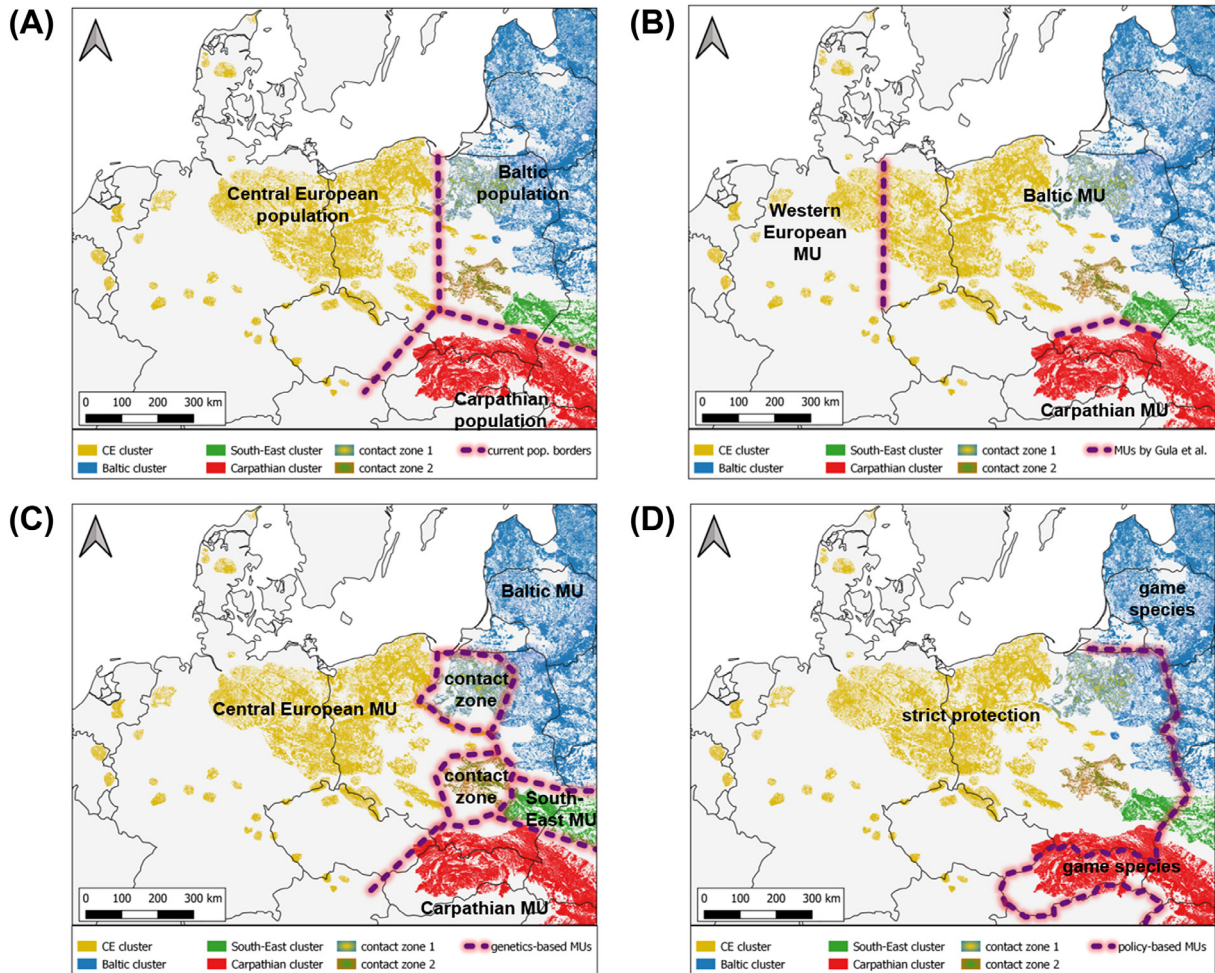


Figure 1. Current distribution of the Central European grey wolf population, adjacent populations in eastern Europe and possible scenarios of wolf management unit (MU) delineation in central Europe in the context of spatial distribution of identified genetic clusters and management policy. (A) Current wolf populations (following Linnell et al. 2008, Chapron et al. 2014, Diserens et al. 2017, Boitani 2018). (B) Re-evaluated MUs according to the proposal of Gula et al. (2020) N.B.: The line between the Central European and Baltic management units is indicative, as Gula et al. (2020) make no clear suggestion, but simply state that the border 'should be moved west'. (C) Hypothetical MUs strictly following genetic divisions. (D) Wolf management policies in CE countries. Apart from in the genetic contact zones shown on the maps (mixed colour; based on Szweczyk et al. 2019), smaller admixture hotspots and enclaves of wolves of lowland origin have been identified in Slovakia, within the Carpathian MU (Hulva et al. 2018), which are beyond the resolution of the figure. In scenario C, we assumed that identified contact zones/admixture hotspots should be managed separately until it can be determined whether they have evolved into distinct subpopulations or merged with one of the source populations. Genetic divisions were based mainly on clustering results from Szweczyk et al. (2019), but also synthesized information from earlier works of Pilot et al. (2006, 2010), Czarnomska et al. (2013), Stronen et al. (2013), Lesniak et al. (2017) and Hulva et al. (2018). Sources of wolf distribution data are listed in the Supporting information. Distribution in Belarus, Russia and Ukraine is approximate and may not include fine-scale distribution gaps and possible recent range reductions. Distributions of the Alpine, Dinaric-Balkan and Scandinavian wolf populations, which are beyond the scope of this paper, are not shown on the maps.

unhampered dispersal within the CE wolf population and high immigration levels in the 'contact zones', but a relatively low rate of long-distance gene flow between western Poland and the Baltic wolf population (Szewczyk et al. 2019). Accordingly, the results from Szewczyk et al. (2019) suggest that population dynamics within the CE wolf range are largely independent from those in the Baltic wolf population.

The genetic distinctiveness of CE wolves has been attributed to a strong founder effect and allele surfing (Szewczyk et al. 2019), as both, mtDNA haplotypes and patterns of microsatellite diversity (e.g. lack of private alleles) confirmed that the CE wolves originate from the Baltic wolf population, in line with the earlier findings of Czarnomska et al. (2013). However, the founder event strongly altered microsatellite allele frequencies, leading to divergence of the CE cluster (Szewczyk et al. 2019). A similar event occurred when wolves recolonized the Alps, which involved a significant founder effect, resulting in clear genetic separation of Alpine wolves from their Apennine ancestors (Fabbri et al. 2007). Therefore, Alpine wolves are now considered a separate population (Boitani 2018).

Do the recent findings of Szewczyk et al. (2019) contradict those of Czarnomska et al. (2013)? In our view these two studies offer separate temporal perspectives on the development of the CE population (Supporting information), and we interpret the findings of Czarnomska et al. (2013) differently to Gula et al. (2020). Firstly, we are puzzled by the statement of Gula et al. (2020) that 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'. The opposite is true: Czarnomska et al. (2013) reported clear microsatellite and mitochondrial DNA substructuring within the lowland region. Secondly, Czarnomska et al. (2013) analysed samples collected from 2001 to 2009, when wolves in western Poland and Germany occurred in discontinuous, mostly small or even ephemeral subpopulations or single packs (Nowak and Mysłajek 2016, Reinhardt et al. 2019). Thus, at this relatively early stage of the CE population's growth and expansion, the founder signal may have been much less pronounced. Still, Czarnomska et al. (2013) reported moderate, statistically significant pairwise F_{ST} values between western Poland and most of the eastern lowland regions, with the exception of the area Szewczyk et al. (2019) later identified as the contact zone of the CE and Baltic wolves.

Notably, Szewczyk et al. (2019) also detected a subdivision within the Baltic cluster, whereby wolves from the south-eastern Polish lowlands ('Roztocze' region) formed a fourth genetic group, probably representing the westernmost extent of the so-called 'Ukrainian Steppe' or 'Pontic' population identified in earlier phylogeographic studies (Pilot et al. 2006, 2010, Stronen et al. 2013). Concordantly, this cluster was also identified in spatially explicit SAMOVA and GENELAND analyses by Czarnomska et al. (2013). Thus, from a genetic point of view, these wolves also qualify as a separate population.

It is interesting to note that the reasons for the existence of genetically well-separated wolf populations within Europe is still unknown, given the species' high capacity to disperse across long-distances and adapt its behaviour to a wide range

of habitats. There are indications that long distance dispersers are less successful in reproducing than wolves that stay in the vicinity of their natal territory. Liberg et al. (2010) showed that most long distance dispersers did not successfully reproduce. Reinhardt et al. (2019) assumed that during the early stage of population recovery in Germany, only the long distance dispersers that happened to establish their territory on active military training areas survived and reproduced successfully. Therefore the ability to disperse over long distances does not necessarily translate proportionately into genetic connectivity. This is supported by the studies of Hulva et al. (2018) and Szewczyk et al. (2019), which showed few admixed genotypes between the Central European and Carpathian populations. Their results therefore support the population delineation by Linnell et al. (2008). In future, to track the dynamics of wolf population boundaries, the population status of European wolves should be assessed with genetic monitoring using a method harmonized across regions and studies targeting adaptive processes.

Other arguments favouring separate management of the CE and Baltic populations

Ideally, population management units consist of demographically coherent entities: management in one region should not counter management efforts in another region that is demographically connected, nor should management plans assume that local management actions are balanced in demographically disconnected areas (Mills 2007). The best approximation for demographic entities in the gray wolf are population genetic clusters. However, the current division in Europe is not based on genetics. The population subdivision according to the guidelines of Linnell et al. (2008) is pragmatic and often based on distribution gaps and geographical features. At first sight, the present geographical proximity of the CE and Baltic populations and their connection via dispersal corridors seem to justify considering them as a single continuous population. However, as has been shown by genetic analyses, this connection does not automatically translate into high levels of gene flow (Szewczyk et al. 2019), and therefore does not translate into demographic continuity. Moreover, appropriate management should not only be based on demographic and geographical factors, but should also consider, for example, that the functional role of large carnivores can vary across landscape environmental gradients (Kuijper et al. 2016, 2019). In central Europe, there are notable differences in environmental and anthropogenic features between eastern Poland and the CE population range (western Poland and Germany), e.g. in topography, climate, forest structure and ownership, transport infrastructure and urbanization, to list only the most important (Eurostat 2020). These factors, and especially the anthropogenic aspects, have a growing impact on the spatial distribution, reproduction success and mortality of CE wolves (Nowak and Mysłajek 2016, Reinhardt et al. 2019).

Regarding socio-political aspects, Gula et al. (2020) state that wolves inhabiting the lowlands on both sides of the Vistula River have similar conservation statuses, management regimes and conflicts with humans. However, while

this is somewhat true at the Polish national level (despite e.g. a significant deficiency in the Natura 2000 coverage of the wolf range in western Poland, as reported by Diserens et al. 2017), it is not the case for the Gula et al.'s (2020) proposed Baltic management unit as a whole, which would reach from Estonia, Belarus and Russia to eastern Germany, spanning very different management regimes (Trouwborst 2018, Fig. 1). Wolf management in Poland (legal protection) is similar to that in Germany, the Czech Republic and the recently recolonized countries in the western part of central Europe (Fig. 1D), which differs markedly from management in the Baltic states (game species, heavy harvest) and especially Belarus and Russia (persecution; Jędrzejewski 2010). Moreover, countries inhabited by CE wolves have similar policies on wolf–dog hybridization (WDH) management (monitoring and lethal removal of hybrids identified genetically). However, in Belarus and Ukraine WDH is not managed (Salvatori et al. 2020), what may explain elevated introgression rates in some regions of eastern Europe (Pilot et al. 2018). Thus, from a conservation management perspective, we regard there to be no practical basis for Gula et al.'s (2020) proposal that 'the border between the current central European and Baltic management units should be moved west [how far west was not stated by the authors] (...) while wolves occupying western Poland and possibly eastern Germany should be incorporated into the Baltic unit', which could in fact impede the effective long-term conservation of wolves and their ecological function in the region.

Historical and current wolf occurrence in western Poland

Historical wolf occurrence data for western Poland (reviewed by Nowak and Mysłajek 2017) contradict Gula et al.'s (2020) statements that this species was permanently present and regularly reproducing in western Poland since 1971, and that the recovery of wolves in this area began in the early 1980s. In our opinion Gula et al. (2020) should clearly differentiate between permanent and sporadic wolf occurrence following established standards (Chapron et al. 2014). Chapron et al. (2014) treated cells of reference grid maps of the European Environmental Agency as permanently occupied by wolves if they were occupied by the species at least 50% of the time over three years or more and/or where there was either confirmed reproduction or the presence of resident adult females. On the other hand, cells with occasional presence of wolves (e.g. dispersers) and/or no reproduction were defined as 'sporadic occurrence'. Nowak and Mysłajek (2017) applied Chapron et al.'s (2014) standards to the same occurrence data as used in Gula et al. (2020), and found that from 1975 to 1997, under hunting exploitation, wolf presence was sporadic in western Poland, despite very good quality habitats and high densities of wild ungulates. Only solitary individuals or single small ephemeral wolf groups were present in just one to maximum four forest tracts per year. Most of these wolves were harvested before their first reproduction. Longer persistence including reproduction (from 2 to 8 years) was recorded in only three packs inhabiting three different forest tracts, but finally all were shot (Fig. 2 in Nowak and Mysłajek 2017). According to Nowak and

Mysłajek (2017) the simplified forest structure and a regular, dense network of sandy forest roads in western Poland allowed hunters to easily detect and shoot wolves. This hunting activity prevented wolf recovery across western Poland.

The scarcity of wolves in western Poland before and just after 2000 was confirmed during the first national wolf and lynx census (Jędrzejewski et al. 2002) and in studies on wolf recovery in western Poland in 2001–2016 (Nowak and Mysłajek 2016, Nowak et al. 2017). These studies were performed by experienced wolf researchers and used year-round wolf tracking, detection of scent-marks and remains of wolf prey, howling stimulation, wolf genetics and camera trapping. These data were then analysed according to the international standards detailed in Reinhardt et al. (2015). These occurrence data used the so-called categories C1 and C2, which reflect either undeniable proof (photographic or genetic evidence, C1) or observations (visual, scat, tracks, C2) validated by a professional researcher (Molinari-Jobin et al. 2012, Reinhardt et al. 2015). Gula et al. (2020), in their analysis of wolf range changes in western Poland in 2001–2017 (Fig. 1, 2 and Table 1 in Gula et al. 2020), mostly used data from questionnaires filled by hunters and foresters, and records in the Atlas of Polish Mammals provided by various observers (most of whom were not wolf experts). Given the lack of expert verification and validation, such data should be categorized as C3 (unconfirmed observation), thus being less reliable (Molinari-Jobin et al. 2012, Reinhardt et al. 2015). Hence, the recent wolf distribution in different regions of Poland as well as wolf range changes presented by Gula et al. (2020) are questionable.

Conclusions

The current division of wolves in central Europe into the CE and Baltic populations was delineated 12 years ago (Linnell et al. 2008) based on non-genetic criteria. However, it reflects management strategies adopted by different European countries (Boitani 2018) quite well, and accords with genetic structure revealed on the basis of comprehensive genetic sampling across the range of both populations (Szewczyk et al. 2019, Fig. 1A). We encourage additional fine-scale studies on genetic structure and gene flow across the CE and Baltic management units, and inclusion of the subsequent genetic findings into future reassessments of population structure. Furthermore, to make sensible predictions about the demographic and genetic consequences of different management scenarios on the CE and Baltic wolf populations, robust and reliable spatially explicit predictive population models that integrate the aforementioned information should be developed.

Although the CE and Baltic wolves represent the same phylogeographic lineage, their recent demographic histories have resulted in clearly divergent allele frequencies (Szewczyk et al. 2019). The populations are connected by ecological corridors (Huck et al. 2011, Gula et al. 2020), but currently the gene flow between them, possibly hampered by sink-source dynamics created by lethal management in the Baltic states, Belarus and Russia (Kaliningrad), is not high enough to effectively reduce the strong founder signal observed in the CE population (Szewczyk et al. 2019). Consequently,

the groups are to a large extent demographically independent, suggesting that from a biogeographical perspective they should be considered as parapatric populations. In this sense, the groups qualify as distinct populations as defined by Waples and Gaggiotti (2006): 'A group of individuals of the same species living in close enough proximity that any member of the group can potentially mate with any other member', whereas a management unit combining CE and Baltic wolves would not fulfil this criterion. Hence, at least for the time being, it appears appropriate for conservation management to continue considering the Baltic and CE populations as separate management units, maintaining the current border between them.

Acknowledgements – RWM and IK were supported by the National Science Centre, Poland (grant no. 2019/35/O/NZ8/01550). TAD was supported by funding of the National Science Centre, Poland (grant no. 2017/25/B/NZ8/02466). The research was co-financed by the Forest Fund, as part of the agreement between the Polish State Forests National Forest Holding and the Wigry National Park (grant no. EZ.0290.1.20.2019), Roztocze National Park (grant no. EZ.0290.1.30.2017, EZ.0290.1.27.2018 and EZ.0290.1.15.2019), Tatra National Park (grant no. EZ.0290.1.32.2018) and 'Bory Tucholskie' National Park (grant no. EZ.0290.1.13.2020). Preparation of this manuscript was coordinated within the framework of the Central European Wolf (CEwolf) Consortium. MS, CN, PH, JM, BCB, AG, MMH, HJ, GK, IK, JRM, SN, KO, IR, LS, SS, PS, PFT and RWM are members of the Consortium.

References

Andersen, L. W. et al. 2015. Long-distance dispersal of a wolf, *Canis lupus*, in northwestern Europe. – *Mamm. Res.* 60: 163–168.

Blanco, J. and Cortes, Y. 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. – *J. Zool.* 273: 114–124.

Boitani, L. 2018. *Canis lupus* (errata version published in 2019). – 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.

Diserens, T. A. et al. 2017. Deficiencies in Natura 2000 for protecting recovering large carnivores: a spotlight on the wolf *Canis lupus* in Poland. – *PLoS One* 12: e0184144.

Eurostat. 2020. Statistical Atlas. Eurostat regional yearbook 2020. – <<https://ec.europa.eu/eurostat/statistical-atlas/gis/viewer/>>, accessed 28 September 2020.

Fabbri, E. et al. 2007. From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf *Canis lupus* population. – *Mol. Ecol.* 16: 1661–1671.

Gula, R. et al. 2020. Re-evaluation of the wolf population management units in central Europe. – *Wildl. Biol.* 2020: wlb.00505.

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.

Hulva, P. et al. 2018. Wolves at the crossroad: fission–fusion range biogeography in the western Carpathians and central Europe. – *Divers. Distrib.* 24: 179–192.

Jędrzejewski, W. 2010. Synthesizing wolf ecology and management in eastern Europe: similarities and contrasts with North America. – In: Musiani, M. et al. (eds), *The world of wolves: new perspectives on ecology, behaviour and management*. – Univ. of Calgary Press, Calgary.

Jędrzejewski, W. et al. 2002. The wolf and the lynx in Poland – results of a census conducted in 2001. – *Kosmos* 51: 491–499, in Polish with English summary.

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

Kuijper, D. P. J. et al. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. – *Proc. R. Soc. B* 283: 20161625.

Kuijper, D. P. J. et al. 2019. Keep the wolf from the door: how to conserve wolves in Europe's human-dominated landscapes? – *Biol. Conserv.* 235: 102–111.

Lesniak, I. et al. 2017. Population expansion and individual age affect endoparasite richness and diversity in a recolonising large carnivore population. – *Sci. Rep.* 7: 41730.

Liberg, O. et al. 2010. Integrating research into management of a recolonizing wolf population – the Scandinavian model. – In: Musiani, M. et al. (eds), *The world of wolves: new perspectives on ecology, behaviour and policy*. Univ. of Calgary Press, p.182.

Linnell, J. D. C. 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). – Large Carnivore Initiative for Europe IUCN/SSC, Rome, <https://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/guidelines_for_population_level_management.pdf>.

Mills, L. S. 2007. Conservation of wildlife populations: demography, genetics and management. – Blackwell.

Molinari-Jobin, A. et al. 2012. Monitoring in the presence of species misidentification: the case of the Eurasian lynx in the Alps. – *Anim. Conserv.* 15: 266–273.

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. W. 2017. Response of the wolf (*Canis lupus* Linnaeus, 1758) population to various management regimes at the edge of its distribution range in western Poland, 1951–2012. – *Appl. Ecol. Environ. Res.* 15: 187–203.

Nowak, S. et al. 2017. Sedentary but not dispersing wolves *Canis lupus* recolonising western Poland (2001–2016) conform to the predictions of a habitat suitability model. – *Divers. Distrib.* 23: 1231–1364.

Pilot, M. et al. 2006. Ecological factors influence population genetic structure of European grey wolves. – *Mol. Ecol.* 15: 4533–4553.

Pilot, M. et al. 2010. Phylogeographic history of grey wolves in Europe. – *BMC Evol. Biol.* 10: 104.

Pilot, M. et al. 2018. Widespread, long-term admixture between grey wolves and domestic dogs across Eurasia and its implications for the conservation status of hybrids. – *Evol. Appl.* 11: 662–680.

Ražen, N. et al. 2016. Long-distance dispersal connects Dinaric-Balkan and Alpine grey wolf *Canis lupus* populations. – *Eur. J. Wildl. Res.* 62: 137–142.

Reinhardt, I. et al. 2015. Standards for the monitoring of the Central European wolf population in Germany and Poland. – Bundesamt für Naturschutz, Bonn.

Reinhardt, I. et al. 2019. Military training areas facilitate the recolonization of wolves in Germany. – *Conserv. Lett.* 12: e12635.

- Salvatori, V. et al. 2020. European agreements for nature conservation need to explicitly address wolf–dog hybridization. – *Biol. Conserv.* 248: 108525.
- Stronen, A. V. et al. 2013. North–south differentiation and a region of high diversity in European wolves *Canis lupus*. – *PLoS One* 8: e76454.
- Szewczyk, M. et al. 2019. Dynamic range expansion leads to establishment of a new, genetically distinct wolf population in central Europe. – *Sci. Rep.* 9: 19003.
- Trouwborst, A. 2018. Wolves not welcome? Zoning for large carnivore conservation and management under the Bern Convention and EU Habitats Directive. – *Rev. Eur. Comp. Int. Environ. Law* 27: 306–319.
- Waples, R. S. and Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. – *Mol. Ecol.* 15: 1419–1439.