

Supplementary Information

Science-based solutions to foster connectivity of wolf populations are limited by available data

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Table S1: PRISMA checklist (Page et al., 2021).

Section and Topic	Item	Checklist item	Reported on page #
TITLE			
Title	1	Identify the report as a systematic review.	7
ABSTRACT			
Abstract	2	See the PRISMA 2020 for Abstracts checklist.	1
INTRODUCTION			
Rationale	3	Describe the rationale for the review in the context of existing knowledge.	1-5
Objectives	4	Provide an explicit statement of the objective(s) or question(s) the review addresses.	4
METHODS			
Eligibility criteria	5	Specify the inclusion and exclusion criteria for the review and how studies were grouped for the syntheses.	5
Information sources	6	Specify all databases, registers, websites, organisations, reference lists and other sources searched or consulted to identify studies. Specify the date when each source was last searched or consulted.	Fig. S1
Search strategy	7	Present the full search strategies for all databases, registers and websites, including any filters and limits used.	5
Selection process	8	Specify the methods used to decide whether a study met the inclusion criteria of the review, including how many reviewers screened each record and each report retrieved, whether they worked independently, and if applicable, details of automation tools used in the process.	N/A
Data collection process	9	Specify the methods used to collect data from reports, including how many reviewers collected data from each report, whether they worked independently, any processes for obtaining or confirming data from study investigators, and if applicable, details of automation tools used in the process.	N/A
Data items	10a	List and define all outcomes for which data were sought. Specify whether all results that were compatible with each outcome domain in each study were sought (e.g. for all measures, time points, analyses), and if not, the methods used to decide which results to collect.	5
	10b	List and define all other variables for which data were sought (e.g. participant and intervention characteristics, funding sources). Describe any assumptions made about any missing or unclear information.	N/A
Study risk of bias assessment	11	Specify the methods used to assess risk of bias in the included studies, including details of the tool(s) used, how many reviewers assessed each study and whether they worked independently, and if applicable, details of automation tools used in the process.	N/A
Effect measures	12	Specify for each outcome the effect measure(s) (e.g. risk ratio, mean difference) used in the synthesis or presentation of results.	N/A
Synthesis methods	13a	Describe the processes used to decide which studies were eligible for each synthesis (e.g. tabulating the study intervention characteristics and comparing against the planned groups for each synthesis (item 5)).	Fig S1
	13b	Describe any methods required to prepare the data for presentation or synthesis, such as handling of missing summary statistics, or data conversions.	N/A
	13c	Describe any methods used to tabulate or visually display results of individual studies and syntheses.	N/A
	13d	Describe any methods used to synthesize results and provide a rationale for the choice(s). If meta-analysis was performed, describe the model(s), method(s) to identify the presence and extent of statistical heterogeneity, and software package(s) used.	8-10
	13e	Describe any methods used to explore possible causes of heterogeneity among study results (e.g. subgroup analysis, meta-regression).	N/A
	13f	Describe any sensitivity analyses conducted to assess robustness of the synthesized results.	N/A
Reporting bias assessment	14	Describe any methods used to assess risk of bias due to missing results in a synthesis (arising from reporting biases).	N/A
Certainty assessment	15	Describe any methods used to assess certainty (or confidence) in the body of evidence for an outcome.	N/A

Supplementary Information**Science-based solutions to foster connectivity of wolf populations are limited by available data**

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Table S1: (continued) PRISMA checklist (Page et al., 2021).

Section and Topic	Item	Checklist item	Reported on page #
RESULTS			
Study selection	16a	Describe the results of the search and selection process, from the number of records identified in the search to the number of studies included in the review, ideally using a flow diagram.	11 + Fig S1
	16b	Cite studies that might appear to meet the inclusion criteria, but which were excluded, and explain why they were excluded.	N/A
Study characteristics	17	Cite each included study and present its characteristics.	11-14, Fig 1-3, Table S2
Risk of bias in studies	18	Present assessments of risk of bias for each included study.	N/A
Results of individual studies	19	For all outcomes, present, for each study: (a) summary statistics for each group (where appropriate) and (b) an effect estimate and its precision (e.g. confidence/credible interval), ideally using structured tables or plots.	N/A
Results of syntheses	20a	For each synthesis, briefly summarise the characteristics and risk of bias among contributing studies.	Table S2
	20b	Present results of all statistical syntheses conducted. If meta-analysis was done, present for each the summary estimate and its precision (e.g. confidence/credible interval) and measures of statistical heterogeneity. If comparing groups, describe the direction of the effect.	13-14
	20c	Present results of all investigations of possible causes of heterogeneity among study results.	N/A
	20d	Present results of all sensitivity analyses conducted to assess the robustness of the synthesized results.	N/A
Reporting biases	21	Present assessments of risk of bias due to missing results (arising from reporting biases) for each synthesis assessed.	N/A
Certainty of evidence	22	Present assessments of certainty (or confidence) in the body of evidence for each outcome assessed.	14-17
DISCUSSION			
Discussion	23a	Provide a general interpretation of the results in the context of other evidence.	14-17
	23b	Discuss any limitations of the evidence included in the review.	14-17
	23c	Discuss any limitations of the review processes used.	N/A
	23d	Discuss implications of the results for practice, policy, and future research.	14-18
OTHER INFORMATION			
Registration and protocol	24a	Provide registration information for the review, including register name and registration number, or state that the review was not registered.	N/A
	24b	Indicate where the review protocol can be accessed, or state that a protocol was not prepared.	5 + Fig S1
	24c	Describe and explain any amendments to information provided at registration or in the protocol.	N/A
Support	25	Describe sources of financial or non-financial support for the review, and the role of the funders or sponsors in the review.	Acknowledgements
Competing interests	26	Declare any competing interests of review authors.	N/A
Availability of data, code and other materials	27	Report which of the following are publicly available and where they can be found: template data collection forms; data extracted from included studies; data used for all analyses; analytic code; any other materials used in the review.	Data extracted from included studies: Tables S3, S4. Data used for all analyses: Table S4.

Supplementary Information**Science-based solutions to foster connectivity of wolf populations are limited by available data**

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Table S2: Reviewed papers regarding their biological input data and methodological approaches used to identify barriers, with mention of the original sample size (no. of sampled and/or collared individuals, or # of observations) and summary of each approach.

Study	Wolf population	Biological input data	Methodological approach	Sample size	Summary
Aspi et al. (2006)	Finnish-Karelian	Genetics	Expert opinion	118 sampled	Territoriality and human pressure reported as possible causes of low levels of migration between Finnish and Russian wolves.
Aspi et al. (2009)	Finnish-Karelian	Genetics	Expert opinion	43 sampled (Russian) 118 sampled (Finnish)	Reduced gene flow between Finnish and Russian wolves hypothesised to be due to the occurrence of fences and territoriality.
Blanco and Cortes (2007)	Iberian	Movement	Empirical	14 collared	Analysed dispersal patterns, social structure, and mortality of wolves in agricultural areas.
Blanco et al. (2005)	Iberian	Movement	Empirical	11 collared	Assessed permeability of two barriers to individual wolf movements and population expansion through crossing frequencies.
Ciucci et al. (2009)	Italian	Movement	Empirical	1 collared	Documented long-distance dispersal (and dispersal success) of one wolf through several barriers.
Czarnomska et al. (2013)	Baltic, Carpathian	Genetics	Expert opinion	457 sampled	Hypothesised that the genetic structure among wolves might reflect landscape fragmentation and ecological differences by hindered gene flow.
Djan et al. (2014)	Dinaric-Balkan	Genetics	Expert opinion	87 sampled	Hypothesised that genetic differences between subpopulations of Dinaric-Balkan wolves might reflect different demographic histories or hunting pressures.
Fabbri et al. (2007)	Italian	Genetics	Expert opinion	435 sampled	Limited gene flow between Italian sub-populations hypothesised to be due to past bottleneck and current landscape fragmentation by highways and other infrastructures crossing a dispersal barrier.
Grilo et al. (2019)	Iberian	Detection	Expert opinion	Census data (numbers not provided)	Evaluated habitat suitability and concluded that suitable areas outside the current range indicated that other factors (e.g. persecution, anthropogenic mortality) may be hampering wolf expansion.
Gula et al. (2009)	Carpathian	Movement; Genetics	Empirical	1 collared	39 sampled Calculated landscape fragmentation from several indices (e.g. splitting index, effective mesh size). Used Mantel test and global spatial autocorrelation to detect and locate genetic discontinuities and correlate them with landscape features. Also calculated major road crossing frequencies from fieldwork.
Gurarie et al. (2011)	Finnish-Karelian	Movement	Expert opinion	2 collared	Respected habitat selection and avoidance, but did not integrate results in a resistance surface or least-cost path. Reported crossings of primary road, but did not evaluate frequency or success.
Hindrikson et al. (2013)	Baltic	Genetics	Empirical	166 sampled	DResD analysis (landscape genetics) identified geographic regions where genetic distance between individuals differs, mapping migration barriers.
Huck et al. (2011)	Baltic, Carpathian	Detection	Empirical	15,670 observations from census	Ecological Niche Factor Analysis -> suitability map and marginality values -> habitat type cost values derived from marginality values -> cost grid -> LCPs -> statistical comparison.
Hulva et al. (2018)	Baltic, Carpathian, Finnish-Karelian	Genetics;	Empirical	250 sampled	Compared distribution of genetic clusters with topographic, environmental, and anthropogenic features in a landscape genetics approach.
Jansson et al. (2012)	Finnish-Karelian, European	Genetics	Expert opinion	2110 sampled (Finnish)	37 sampled (Russian) Low gene flow between Finnish and Russian wolves hypothesised to be due to increased wolf mortality in the area.
Jedrzejewski et al. (2005)	Carpathian	Detection	Expert opinion	Census data (numbers not provided)	Used habitat selection model to identify possible barriers, but did not integrate results in a resistance surface or least-cost path.
Jedrzejewski et al. (2004)	Baltic	Detection	Expert opinion	Census data (numbers not provided)	Used habitat selection model to identify possible barriers, but did not integrate results in a resistance surface or least-cost path.
Kojola et al. (2006)	Finnish-Karelian	Movement	Empirical	60 collared	Examined direction, distance, and success of dispersal.
Kojola et al. (2009)	Finnish-Karelian	Movement	Empirical	35 collared	Examined direction, distance, and success of dispersal.
Kusak et al. (2005)	Dinaric-Balkan	Movement	Expert opinion	3 collared	Home ranges and distance to anthropogenic features were calculated. Resource use (e.g., use of roads and water sources) was not applied to any empirical analysis.
Kusak et al. (2009)	Dinaric-Balkan	Movement;	Detection Empirical	3 collared	2 camera-trapped Estimated permeability of a highway for large and medium-sized mammals. Calculated crossing frequencies.

Supplementary Information**Science-based solutions to foster connectivity of wolf populations are limited by available data**

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Table S2: (*continued*) Reviewed papers regarding their biological input data and methodological approaches used to identify barriers, with mention of the original sample size (no. of sampled and/or collared individuals, or # of observations) and summary of each approach.

Study	Wolf population	Biological input data	Methodological approach	Sample size	Summary
Louvrier et al. (2018)	Alpine	Detection	Expert opinion	Numbers not provided	Determined main drivers of wolf recolonization in France using dynamic site-occupancy models. Hypothesised a natural barrier and/or wolf hunting slow down dispersal, but did not base this on resistance surfaces, least-cost path analysis, or other empirical method.
Milanesi et al. (2018)	Italian	Genetics	Empirical	923 sampled	Used ecological niche models to relate each habitat type and features with genetic clusters in a landscape genetics approach.
Ordiz et al. (2015)	Scandinavian	Detection; Movement;	Move- Expert opinion	142 different wolf pairs = 284 individuals	Used habitat selection model to identify factors influencing wolf population expansion, but did not integrate results in a resistance surface or least-cost path.
Ražen et al. (2016)	Dinaric-Balkan	Genetics	Empirical	1 collared	Documented long-distance dispersal (and dispersal success) of one wolf through several barriers.
Rio-Maior et al. (2019)	Iberian	Movement	Empirical	15 collared	Habitat selection model (point selection) was used to build conductance maps, to then derive LCI
Rodríguez-Freire and Crecente-Maseda (2007)	Iberian	Detection	Expert opinion	Numbers not provided	Suitability values for each land use were assigned based on expert opinion (high value to uses associated with high vegetation cover / low human impact, low values to uses associated with modified habitats) and tested whether wolves' avoidance of areas with human activity changed over time, but did not include their results in a resistance surface analysis or least-cost-path to identify barriers.
Romberg et al. (2017)	Central European	Detection	Expert opinion	557 confirmed observations Data from hunter's wildlife survey (numbers not provided)	Hypothesised that the genetic differentiation between local sub-populations of Italian wolves might reflect long-range dispersal, territoriality, and high mortality of young wolves.
Scandura et al. (2011)	Italian	Genetics	Expert opinion	714 sampled	Hypothesised that the genetic structuring of central European wolves might be shaped by anthropogenic
Szewczyk et al. (2019)	Baltic, Carpathian, Central European	Genetics	Expert opinion	881 sampled	Absence of a barrier effect of high human activities was based on the sole presence of wolves in a highly disturbed anthropogenic area.
Valière et al. (2003)	Central European	Genetics	Expert opinion	99 sampled	Analysed dispersal distances and success.
Wabakken et al. (2007)	Scandinavian	Movement	Empirical	1 collared	

Supplementary Information

Science-based solutions to foster connectivity of wolf populations are limited by available data

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Table S3: Predictor variables used in the analysis of drivers of barriers to wolf connectivity

Variables	Variable codes	Definition (unit)	Categories	Classification
Geographical features	<i>Geo</i>	Geographical features identified as potential barriers in the study area (binary)	-	Rivers, mountains, large bodies of water (gulfs and bays).
Ecological factors	<i>Eco</i>	Ecological factors identified as potential barriers in the study area (binary)	-	Forest fragmentation, territoriality.
Land cover	<i>LandCover</i>	Predominant land cover in the study area	<i>CONIF</i> <i>BROAD</i> <i>AGRIC</i> <i>MOSAIC</i> <i>MOSALP</i>	Forests where coniferous species predominate. Forests where broad-leaved species predominate. Non-irrigated arable land, annual crops, pastures, and agroforestry areas. Mosaic landscape of two or more of the following: mixed forests, forest steppe, agricultural systems, human settlements. Mosaic landscape in alpine regions with glaciers or perpetual snow and sparsely
Main prey	<i>MainPrey</i>	Wolf preferred prey in the study area	Large wild ungulates (<i>LWU</i> , 240-457 kg) Medium-sized wild ungulates (<i>MWU</i> ; 20-130 kg) Domestic ungulates Carrion	Moose <i>Alces alces</i> Red deer <i>Cervus elaphus</i> Chamois <i>Rupicapra rupicapra</i> ; Mouflon <i>Ovis aries</i> ; Roe deer <i>Capreolus capreolus</i> ; Reindeer <i>Rangifer tarandus</i> ; Ibex <i>Capra ibex</i> ; Wild boar <i>Sus scrofa</i> Cattle <i>Bos sp</i> ; Horse <i>Equus sp</i> ; Sheep <i>Ovis sp</i> ; Goat <i>Capra sp</i> Livestock carrion
Prey species richness	<i>PreySp_Richness</i>	Wild prey species richness in the study area (no. of species), subsequently standardised for the analysis	-	-
Wild prey density	<i>WildPrey_density</i>	Wild prey density in the study area (no. individuals/km ²), subsequently standardised for the analysis	-	-
Domestic prey density	<i>DomPrey_density</i>	Domestic prey density in the study area (no. individuals/km ²), subsequently standardised for the analysis	-	-
Wolf populations	<i>Wolf-pop</i>	Wolf population group analysed in each study	Baltic, Carpathian, Dinaric-Balkan, Finnish-Karelian, Iberian, Italian, and Scandinavian.	-
Wolf population size	<i>Pop_size</i>	Wolf population size in the study area (no. of individuals), subsequently standardised for the analysis	-	-
Human density	<i>Human_density</i>	Mean human density in the study area (people/km ²), subsequently standardised for the analysis	-	-
Road density	<i>Road_density</i>	Mean main road density in the study area (km/km ²), subsequently standardised for the analysis	-	-
Anthropogenic structures	<i>Antr_Stru</i>	Anthropogenic structures identified as potential barriers in the study area (binary)	-	Main roads, highways, railways, windfarms, dams, fences.
Anthropogenic landscapes	<i>Antr_Land</i>	Anthropogenic landscapes identified as potential barriers in the study area (binary)	-	Agricultural and forestry areas; Settlements and urban areas.
Wolf hunting	<i>Hunt</i>	Wolf persecution identified as potential barriers in the study area (binary)	-	Poaching and legal wolf hunting.

Supplementary Information**Science-based solutions to foster connectivity of wolf populations are limited by available data**

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Table S4: Data sources consulted for each predictor, per study (n=14)

Study	Wolf pop	Wolf pop size	Main Prey	Prey sp. richness	Wild prey density	Domestic prey density	Human density	Road dens
Blanco and Cortes (2007)	Chapron et al. (2014): Iberian	Data retrieved from Llaneza and Blanco (2005) and calculated for the study area	Original study	Original study	Original study	Subdirección General de Estadística (2020)	Original study	Original stu
Blanco et al. (2005)	Chapron et al. (2014): Iberian	Data retrieved from Llaneza and Blanco (2005) and calculated for the study area	Original study	Original study	Original study	Subdirección General de Estadística (2020)	Data retrieved from City Population database (Thomas Brinkhoff: City Population, 2020a)	Data retrie Instituto Es Castilla y (2019) and lated in Q
Ciucci et al. (2009)	Chapron et al. (2014): Italian	Data retrieved from Galaverni et al. (2016) and calculated for the study area	Imbert et al. (2016)	Carnevali et al. (2009)	Carnevali et al. (2009)	Imbert et al. (2016)	Original study area	Original study
Gula et al. (2009)	Chapron et al. (2014): Carpathian	Kaczensky et al. (2013)	Jedrzejewski et al. (2012)	Jedrzejewski et al. (2012)	Gula (2008)	Musiał and Musiał (2019)	Original study	Original stu
Hindrikson et al. (2013)	Chapron et al. (2014): Baltic	Kaczensky et al. (2013)	Zunna et al. (2009)	Zunna et al. (2009)	Pittiglio et al. (2018) Anderson-Lilley et al. (2010)	Central Statistical Bureau of Latvia (2020)	Data retrieved from Worldometers database (Worldometers.info, 2020a) and calculated for the study area	Data retrie Knoema (Knoema, mean den Estonia and
Huck et al. (2011)	Chapron et al. (2014): Baltic, Carpathian	Kaczensky et al. (2013)	Jedrzejewski et al. (2012)	Jedrzejewski et al. (2012)	Gula (2008)	INIG (2014)	Data retrieved from Worldometers (Worldometers.info, 2020b) database and calculated for the study area	Original stu
Hulva et al. (2018)	Chapron et al. (2014): Baltic, Carpathian, Central European	Kaczensky et al. (2013)	Jedrzejewski et al. (2012)	Jedrzejewski et al. (2012)	Gula (2008)	Food and Agriculture Organization of the United Nations (2020)	Illés (2008)	Nowak et al
Kojola et al. (2006)	Chapron et al. (2014): Finnish-Karelian	Kaczensky et al. (2013)	Kojola et al. (2004)	Aspi et al. (2006)	Kojola et al. (2004)	Natural Resources Institute Finland (2020)	Original study	Data retrie Knoema (Knoema, for the stud
Kojola et al. (2009)	Chapron et al. (2014): Finnish-Karelian	Kaczensky et al. (2013)	Kojola et al. (2004)	Aspi et al. (2006)	Kojola et al. (2004)	Natural Resources Institute Finland (2020)	Original study	2004 retrie Knoema (Knoema, for the stud
Kusak et al. (2009)	Chapron et al. (2014): Dinaric-Balkan	Original study	Octenjak et al. (2020)	Original study	Octenjak et al. (2020)	Octenjak et al. (2020)	Original study	2006 Original stu

Supplementary Information**Science-based solutions to foster connectivity of wolf populations are limited by available data**

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Table S4: (*continued*) Data sources consulted for each predictor, per study (n=14)

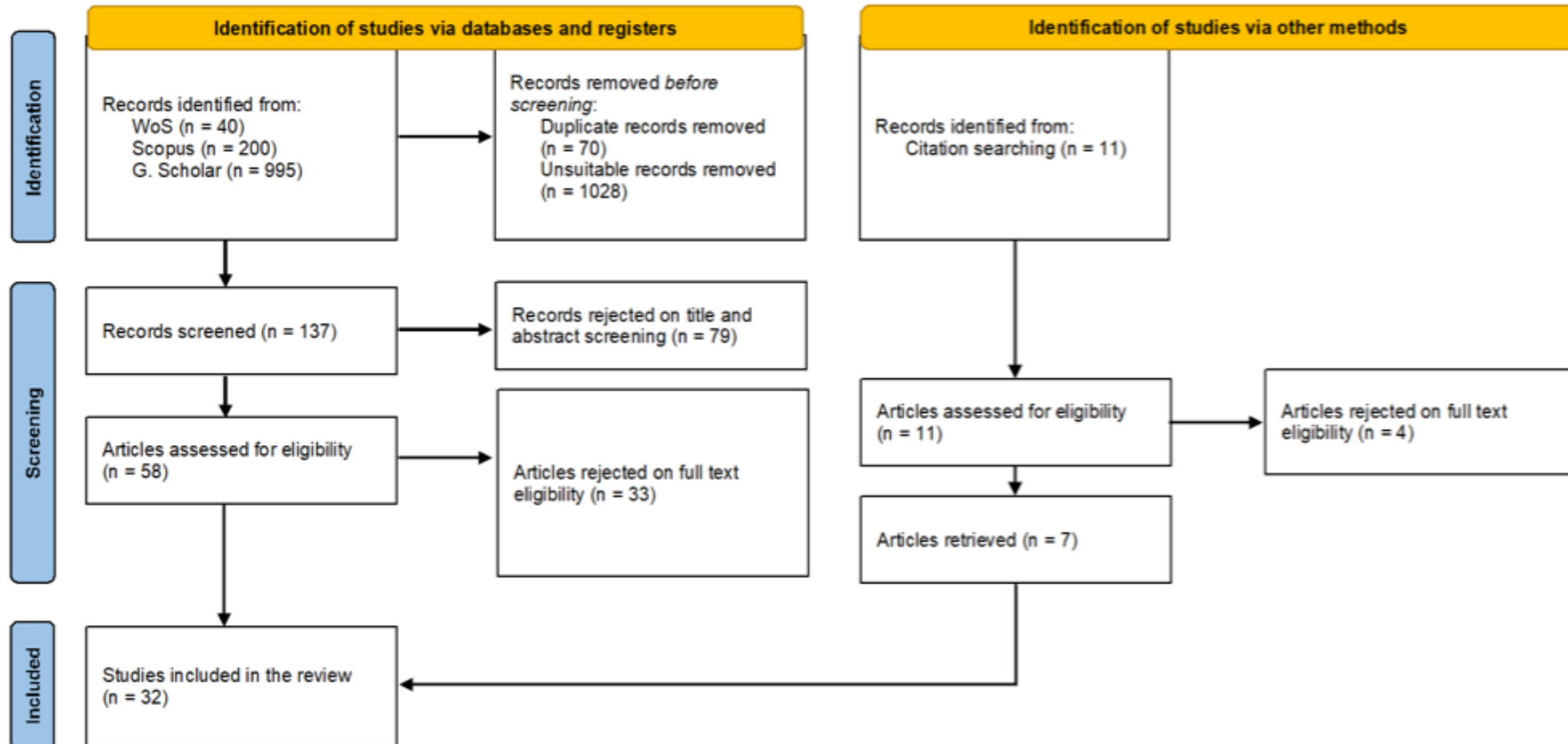
Study	Wolf pop	Wolf pop size	Main Prey	Prey sp. richness	Wild prey density	Domestic prey density	Human density	Road density
Milanesi et al. (2018)	Chapron et al. (2014): Italian	Data retrieved from Galaverni et al. (2016) and calculated for the study	Meriggi et al. (2011)	Carnevali et al. (2009)	Gazzola et al. (2005) Ståhlberg et al. (2017)	Imbert et al. (2016)	Schuler et al. (2004)	Ciucci et al. (2009)
Ražen et al. (2016)	Chapron et al. (2014): Dinaric-Balkan	Kaczensky et al. (2013)	Original study	Original study	Carnevali et al. (2009) Ramanzin et al. (2007)	Alpine Convention (2017)	Schuler et al. (2004)	Kurzweil and Ibesich (2010)
Rio-Maior et al. (2019)	Chapron et al. (2014): Iberian	Pimenta et al. (2005)	Original study	Original study	Original study Bosch et al. (2012)	Instituto Nacional de Estatística (2020)	Original study	Original study
Wabakken et al. (2007)	Chapron et al. (2014): Scandinavian	Kaczensky et al. (2013)	Original study	Original study	Karlsson et al. (2007)	Wojan and Elofsson (2018)	Original study	Data retrieved from Knoema database (Knoema, 2020c), mean density for Norway, Sweden and Finland in 2005

Supplementary Information

Science-based solutions to foster connectivity of wolf populations are limited by available data

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Figure S5: PRISMA flow chart showing the exclusion process Moher et al. (2009)



Supplementary Information

Science-based solutions to foster connectivity of wolf populations are limited by available data

S. Lino, J. Carvalho, E. Ferreira, C. Fonseca, L.M. Rosalino

Bibliography

Alpine Convention, 2017. Mountain Agriculture, P.S.o.t.A. Convention, Alpine Signals 8, Innsbruck.

Andersone-Lilley Z., Balčiauskas L., Ozolins J., Randveer T., Tönisson J., 2010. Ungulates and their management in the Baltics (Estonia, Latvia and Lithuania). In: Apollonio M., Andersen R., Putman R. (Eds.) European ungulates and their management in the 21st century. Cambridge University Press. 103–128.

Aspi J., Roininen E., Ruokonen M., Kojola I., Vilà C., 2006. Genetic diversity, population structure, effective population size and demographic history of the Finnish wolf population. *Mol Ecol* 15: 1561–1576. <https://doi.org/10.1111/j.1365-294X.2006.02877.x>

Aspi J., Roininen E., Kiiskilä J., Ruokonen M., Kojola I., Bljudnik L., Danilov P., Heikkinen S., et al., 2009. Genetic structure of the northwestern Russian wolf populations and gene flow between Russia and Finland. *Conservation Genetics* 10: 815–826. <https://doi.org/10.1007/s10592-008-9642-x>

Blanco J.C., Cortés Y., Virgós E., 2005. Wolf response to two kinds of barriers in an agricultural habitat in Spain. *Canadian Journal of Zoology* 83: 312–323. <https://doi.org/10.1139/z05-016>

Blanco J.C., Cortés Y., 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. *Journal of Zoology* 273: 114–124. <https://doi.org/10.1111/j.1469-7998.2007.00305.x>

Bosch J., Peris S., Fonseca C., Martínez-Avilés M., De la Torre A., Martín I., Muñoz M., 2012. Distribution, abundance and density of the wild boar on the Iberian Peninsula, based on the CORINE program and hunting statistics. *Folia Zoologica* 61: 138–151. <https://doi.org/10.25225/fozo.v61.i2.a7.2012>

Carnevali L., Pedrotti L., Riga F., Toso S., 2009. Banca Dati Ungulati: Status, distribuzione, consistenza, gestione e prelievo venatorio delle popolazioni di Ungulati in Italia. Rapporto 2001-2005 [Italian-English text].

Central Statistical Bureau of Latvia, 2020. Agricultural Census 2010: Number of agricultural holding and livestock by statistical region. <https://www.csb.gov.lv/en/statistics/statistics-by-theme/agriculture/agricultural-census> [Accessed September 2020].

Chapron G., Kaczensky P., Linnell J.D.C., von Arx M., Huber D., Andrén H., López-Bao J.V., Adamec M., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1517–1519. <https://doi.org/10.1126/science.1257553>

Ciucci P., Reggioni W., Maiorano L., Boitani L., 2009. Long-Distance dispersal of a rescued wolf from the Northern Apennines to the Western Alps. *Journal of Wildlife Management* 73: 1300–1306. <https://doi.org/10.2193/2008-510>

Czarnomska S.D., Jędrzejewska B., Borowik T., Niedziałkowska M., Stronen A.V., Nowak S., Mysłajek R.W., Okarma H., et al., 2013. Concordant mitochondrial and microsatellite DNA structuring between Polish lowland and Carpathian Mountain wolves. *Conservation Genetics* 14: 573–588. <https://doi.org/10.1007/s10592-013-0446-2>

Djan M., Maletić V., Trbojević I., Popović D., Veličković N., Burazerović J., Čirović D., 2014. Genetic diversity and structuring of the grey wolf population from the Central Balkans based on mitochondrial DNA variation. *Mammalian Biology* 79: 277–282. <https://doi.org/10.1016/j.mambio.2014.03.001>

Fabrizi E., Miquel C., Lucchini V., Santini A., Caniglia R., Duchamp C., Weber J.M., Lequette B., 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. <https://doi.org/10.1111/j.1365-294X.2007.03262.x>

Food and Agriculture Organization of the United Nations, 2020. Cattle, sheep and goat numbers in Slovakia 2014. <http://www.fao.org/faostat/en/data/QA> [Accessed September 2020].

Galaverni M., Caniglia R., Fabrizio E., Milanese P., Randi E., 2016. One, no one, or one hundred thousand: how many wolves are there currently in Italy? *Mammal Research* 61: 13–24. <https://doi.org/10.1007/s13364-015-0247-8>

Gazzola A., Bertelli I., Avanzinelli E., Tolosano A., Bertotto P., Apollonio M., 2005. Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *Journal of Zoology* 266: 205–213. <https://doi.org/10.1017/S0952836905006801>

- Grilo C., Lucas P.M., Fernández-Gil A., Seara M., Costa G., Roque S., Rio-Maior H., Nakamura M., et al., 2019. Refuge as major habitat driver for wolf presence in human-modified landscapes. *Animal Conservation* 22: 59–71. <https://doi.org/10.1111/acv.12435>
- Gula R., 2008. Wolf depredation on domestic animals in the Polish Carpathian mountains. *The Journal of Wildlife Management* 72: 283–289. <https://doi.org/10.2193/2006-368>
- Gula R., Hausknecht R., Kuehn R., 2009. Evidence of wolf dispersal in anthropogenic habitats of the Polish Carpathian mountains. *Biodiversity and Conservation* 18: 2173. <https://doi.org/10.1007/s10531-009-9581-y>
- Gurarie E., Suutarinen J., Kojola I., Ovaskainen O., 2011. Summer movements, predation and habitat use of wolves in human modified boreal forests. *Oecologia* 165: 891–903. <https://doi.org/10.1007/s00442-010-1883-y>
- Hindrikson M., Remm J., Männil P., Ozolins J., Tammeleht E., Saarma U., 2013. Spatial genetic analyses reveal cryptic population structure and migration patterns in a continuously harvested Grey Wolf (*Canis lupus*) population in North-Eastern Europe. *PLOS ONE* 8: e75765. <https://doi.org/10.1371/journal.pone.0075765>
- Huck M., Jedrzejewski W., Borowik T., Jedrzejewska B., Nowak S., Mysłajek R.W., 2011. Analyses of least cost paths for determining effects of habitat types on landscape permeability: wolves in Poland. *Acta Theriologica* 56: 91–101. <https://doi.org/10.1007/s13364-010-0006-9>
- Hulva P., Černá Bolfíková B., Woznicová V., Jindřichová M., Benešová M., Mysłajek R.W., Nowak S., Szewczyk M., et al., 2018. Wolves at the crossroad: Fission–fusion range biogeography in the Western Carpathians and Central Europe. *Diversity and Distributions* 24: 179–192. <https://doi.org/10.1111/ddi.12676>
- Illés I., 2008, The Carpathians: a European macroregion. In: Illés I., Gál Z., Rácz S. (Eds). *Socio-Economic Analysis of the Carpathian Area*, Pécs, Hungary.
- Imbert C., Caniglia R., Fabbri E., Milanese P., Randi E., Serafini M., Torretta E., Meriggi A., 2016. Why do wolves eat livestock?: Factors influencing wolf diet in northern Italy. *Biological Conservation* 195: 156–168. <https://doi.org/10.1016/j.biocon.2016.01.003>
- INIG, 2014. *Livestock Farms in Poland*, Oil and Gas Institute – National Research Institute Poland.
- Instituto Estadística Castilla y León, 2019. *Carreteras de Castilla y León: red viaria*, Spanish text. <https://idecyl.jcyl.es/geonetwork/srv/spa/catalog.search/metadata/SPAGOBCY> [Accessed May 2020].
- Instituto Nacional de Estatística, 2020. *Recenseamento Agrícola. Análise dos principais resultados: 2009*. [Portuguese text] <https://www.ine.pt/xurl/pub/119564579> [Accessed September 2020].
- Jansson E., Ruokonen M., Kojola I., Aspi J., 2012. Rise and fall of a wolf population: genetic diversity and structure during recovery, rapid expansion and drastic decline. *Molecular Ecology* 21: 5178–5193. <https://doi.org/10.1111/mec.12010>
- Jedrzejewski W., Niedziałkowska M., Mysłajek R.W., Nowak S., Jedrzejewska B., 2005. Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. *Acta Theriologica* 50: 417–428. <https://doi.org/10.1007/BF03192636>
- Jedrzejewski W., Niedziałkowska M., Hayward M.W., Goszczyński J., Jedrzejewska B., Borowik T., Bartoń K.A., Nowak S., et al., 2012. Prey choice and diet of wolves related to ungulate communities and wolf subpopulations in Poland. *Journal of Mammalogy* 93: 1480–1492. <https://doi.org/10.1644/10-mamm-a-132.1>
- Jedrzejewski W.N., Nowak S., Jedrzejewska B., 2004. Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. *Diversity and Distributions* 10: 225–233. <https://doi.org/10.1111/j.1366-9516.2004.00073.x>
- Kaczensky P., Chapron G., von Arx M., Huber D., Andrén H., Linnell J., 2013. Status, management and distribution of large carnivores – Bear, lynx, wolf and wolverine in Europe. Part 1. IUCN/SSC Large Carnivore Initiative for Europe.
- Karlsson J., Brøseth H., Sand H., Andrén H., 2007. Predicting occurrence of wolf territories in Scandinavia. *Journal of Zoology* 272: 276–283. <https://doi.org/10.1111/j.1469-7998.2006.00267.x>
- Knoema, 2020a. Estonia, Latvia Road Density, 1990-2020. <https://knoema.com/atlas/Estonia/topics/Transportation/Road-transport/Road-density>, <https://knoema.com/atlas/Latvia/Road-density> [Accessed May 2020].
- Knoema, 2020b. Finland Road Density, 1990-2020. <https://knoema.com/atlas/Finland/Road-density> [Accessed May 2020].

- Knoema, 2020c. Norway, Sweden, Finland Road Density 1990-2020. <https://knoema.com/atlas/Norway/Road-density>, <https://knoema.com/atlas/Sweden/Road-density>, <https://knoema.com/atlas/Finland/Road-density> [Accessed May 2020].
- Kojola I., Huitu O., Toppinen K., Heikura K., Heikkinen S., Ronkainen S., 2004. Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. *Journal of Zoology* 263: 229–235. <https://doi.org/10.1017/S0952836904005084>
- Kojola I., Aspi J., Hakala A., Heikkinen S., Ilmoni C., Ronkainen S., 2006. Dispersal in an expanding wolf population in Finland. *Journal of Mammalogy* 87: 281–286. <https://doi.org/10.1644/05-mamm-a-061r2.1>
- Kojola I., Kaartinen S., Hakala A., Heikkinen S., Voipio H.-M., 2009. Dispersal behavior and the connectivity between wolf populations in Northern Europe. *Journal of Wildlife Management* 73: 309–313, 305. <https://doi.org/10.2193/2007-539>
- Kurzweil A., Ibesich N., 2007. Road infrastructure, permanent secretariat of the Alpine convention, transport and mobility in the Alps - 1st Report on the State of the Alps, Austria, www.alpconv.org
- Kusak J., Skrbinšek A.M., Huber D., 2005. Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *European Journal of Wildlife Research* 51: 254–262. <https://doi.org/10.1007/s10344-005-0111-2>
- Kusak J., Huber D., Gomerčić T., Schwaderer G., Gužvica G., 2009. The permeability of highway in Gorski kotar (Croatia) for large mammals. *European Journal of Wildlife Research* 55: 7–21. <https://doi.org/10.1007/s10344-008-0208-5>
- Llaneza L., Blanco J., 2005. Situación del lobo (*Canis lupus* L.) en Castilla y León en 2001. Evolución de sus poblaciones. *Galemys: Boletín informativo de la Sociedad Española para la conservación y estudio de los mamíferos* 17(1): 15–28.
- Louvrier J., Duchamp C., Lauret V., Marboutin E., Cubaynes S., Choquet R., Miquel C., Gimenez O., 2018. Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. *Ecography* 41: 647–660. <https://doi.org/10.1111/ecog.02874>
- Meriggi A., Brangi A., Schenone L., Signorelli D., Milanesi P., 2011. Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology Ecology & Evolution* 23: 195–210. <https://doi.org/10.1080/03949370.2011.577814>
- Milanesi P., Caniglia R., Fabbri E., Puopolo F., Galaverni M., Holderegger R., 2018. Combining Bayesian genetic clustering and ecological niche modeling: Insights into wolf intraspecific genetic structure. *Ecology and Evolution* 8: 11224–11234. <https://doi.org/10.1002/ece3.4594>
- Moher D., Liberati A., Tetzlaff J., Altman D.G., The P.G., 2009. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA Statement. *PLOS Medicine* 6: e1000097. <https://doi.org/10.1371/journal.pmed.1000097>
- Musiał W., Musiał K., 2019. Deanimalisation processes in the Polish Carpathians - Production, economic and ecological aspects. *Annals PAAAE XXI*: 331–340. <https://doi.org/10.5604/01.3001.0013.5912>
- Natural Resources Institute Finland, 2020. Agricultural statistics: Number of Livestock (Cattle, Sheep, Goats) by Municipality. <http://statdb.luke.fi/PXWeb/pxweb/en/LUKE/> [Accessed September 2020].
- Nowak S., Mysłajek R., Jedrzejewska B., 2008. Density and demography of wolf *Canis lupus* population in the western-most part of the Polish Carpathian Mountains, 1996-2003. *Folia Zool* 57: 392–402.
- Octenjak D., Paen L., Šilić V., Reljić S., Vukičević T.T., Kusak J., 2020. Wolf diet and prey selection in Croatia. *Mammal Research* 65: 647–654. <https://doi.org/10.1007/s13364-020-00517-8>
- Ordiz A., Milleret C., Kindberg J., Månsson J., Wabakken P., Swenson J.E., Sand H., 2015. Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere* 6: 1–14. <https://doi.org/10.1890/ES15-00243.1>
- Page M.J., McKenzie J.E., Bossuyt P.M., Boutron I., Hoffmann T.C., Mulrow C.D., Shamseer L., Tetzlaff J.M., et al., 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* 372: n71. <https://doi.org/10.1136/bmj.n71>
- Pimenta V., Barroso I., Álvares F., Correia J., Costa G., Moreira L., Nascimento J., Petrucci-Fonseca F., et al., 2005. Situação populacional do lobo em Portugal: resultados do censo nacional 2002/2003.

- Pittiglio C., Khomenko S., Beltran-Alcrudo D., 2018. Wild boar mapping using population-density statistics: From polygons to high resolution raster maps. *PLOS ONE* 13: e0193295. <https://doi.org/10.1371/journal.pone.0193295>
- Ramanzin M., Sturaro E., Zanon D., 2007. Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. *Canadian Journal of Zoology* 85: 280–289. <https://doi.org/10.1139/Z06-210>
- Ražen N., Brugnoli A., Castagna C., Groff C., Kaczensky P., Kljun F., Knauer F., Kos I., et al., 2016. Long-distance dispersal connects Dinaric-Balkan and Alpine grey wolf (*Canis lupus*) populations. *European Journal of Wildlife Research* 62: 137–142. <https://doi.org/10.1007/s10344-015-0971-z>
- Rio-Maior H., Nakamura M., Álvares F., Beja P., 2019. Designing the landscape of coexistence: Integrating risk avoidance, habitat selection and functional connectivity to inform large carnivore conservation. *Biological Conservation* 235: 178–188. <https://doi.org/10.1016/j.biocon.2019.04.021>
- Rodríguez-Freire M., Crecente-Maseda R., 2007. Directional connectivity of wolf (*Canis lupus*) populations in Northwest Spain and anthropogenic effects on dispersal patterns. *Environmental Modeling & Assessment* 13: 35. <https://doi.org/10.1007/s10666-006-9078-y>
- Ronnenberg K., Habbe B., Gräber R., Strauß E., Siebert U., 2017. Coexistence of wolves and humans in a densely populated region (Lower Saxony, Germany). *Basic and Applied Ecology* 25: 1–14. <https://doi.org/10.1016/j.baae.2017.08.006>
- Scandura M., Iacolina L., Capitani C., Gazzola A., Mattioli L., Apollonio M., 2011. Fine-scale genetic structure suggests low levels of short-range gene flow in a wolf population of the Italian Apennines. *European Journal of Wildlife Research* 57: 949–958. <https://doi.org/10.1007/s10344-011-0509-y>
- Schuler M., Stucki E., Roque O., Perlik M., 2004. The delineation of European mountain areas. In: Gløersen E., Price M., Aalbu H., Stucki E., Roque O., Schuler M., Perlik M. (Eds.) *Mountain Areas in Europe: Analysis of mountain areas in EU member states, acceding and other European countries - Final report*. Nordregio, Brussels. 19.
- Ståhlberg S., Bassi E., Viviani V., Apollonio M., 2017. Quantifying prey selection of Northern and Southern European wolves (*Canis lupus*). *Mammalian Biology* 83: 34–43. <https://doi.org/10.1016/j.mambio.2016.11.001>
- Subdirección General de Estadística, 2020. Encuestas Ganaderas 2002, Ganado Bovino, Ovino, Caprino en Castilla-Leon. [Spanish text] <https://www.mapa.gob.es/es/estadistica/temas/estadisticas-agrarias/ganaderia/encuestas-ganaderas/> [Accessed September 2020].
- Szewczyk M., Nowak S., Niedźwiecka N., Hulva P., Špinkytė-Bačkaitienė R., Demjanovičová K., Bolfíková B.Č., Antal V., et al., 2019. Dynamic range expansion leads to establishment of a new, genetically distinct wolf population in Central Europe. *Scientific Reports* 9: 19003. <https://doi.org/10.1038/s41598-019-55273-w>
- Thomas Brinkhoff: City Population, 2020a. Census data 2001 for Zamora and Valladolid. https://www.citypopulation.de/en/spain/admin/CLE__castilla_y_le%C3%B3n/ [Accessed May 2020].
- Thomas Brinkhoff: City Population, 2020b. Census data 2002 for Karelia and Arkhangelsk Oblast. <https://www.citypopulation.de/en/russia/karelija/>, <https://www.citypopulation.de/en/russia/archangelsk/> [Accessed May 2020].
- Valière N., Fumagalli L., Gielly L., Miquel C., Lequette B., Poulle M.-L., Weber J.-M., Arlettaz R., et al., 2003. Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. *Animal Conservation* 6: 83–92. <https://doi.org/10.1017/S1367943003003111>
- Wabakken P., Sand H., Kojola I., Zimmermann B., Arnemo J.M., Pedersen H.C., Liberg O., 2007. Multistage, long-range natal dispersal by a global positioning system-collared Scandinavian wolf. *The Journal of Wildlife Management* 71: 1631–1634. <https://doi.org/10.2193/2006-222>
- Widman M., Elofsson K., 2018. Costs of livestock depredation by large carnivores in Sweden 2001 to 2013. *Ecological Economics* 143: 188–198. <https://doi.org/10.1016/j.ecolecon.2017.07.008>
- Worldometers.info, 2020a. Population of Latvia and Estonia in 2010. <https://www.worldometers.info/world-population/latvia-population/>, <https://www.worldometers.info/world-population/estonia-population/> [Accessed May 2020].
- Worldometers.info, 2020b. Population of Poland in 2005. <https://www.worldometers.info/world-population/poland-population/> [Accessed May 2020].
- Zunna A., Ozolins J., Pupila A., 2009. Food habits of the wolf *Canis lupus* in Latvia based on stomach analyses. *Estonian Journal of Ecology* 58: 141. <https://doi.org/10.3176/eco.2009.2.07>