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LETTER

Where have all the young wolves gone? Traffic and cryptic mortality create a wolf population sink in Denmark and northernmost Germany

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Abstract

Large carnivores are currently recolonizing Europe following legal protection, but increased mortality in landscapes highly impacted by humans may limit further population expansion. We analyzed mortality and disappearance rates of 35 wolves (of which three emigrated, nine died and 14 disappeared by 1 January 2020) by genetic monitoring in the heavily cultivated and densely populated Jutland peninsula (Denmark and Schleswig-Holstein, Germany). Annual traffic kill rate estimates ranged from 0.37 (95% CI: 0.11–0.85) to 0.78 (0.51–0.96) in the German part, equivalent to 0.08 (0.02–0.29)–0.25 (0.13–0.46) for the entire region, in the absence of any registered Danish roadkills. In Denmark, annual mortality rate estimates ranged from 0.46 (0.29–0.67) to 0.52 (0.35–0.71), predominantly from cryptic mortality. Despite successful reproductions, we conclude the region is a wolf population sink, primarily driven by cryptic mortality, most likely illegal killing. We hypothesize that frequent encounters between wolves and wolf-averse persecutors in cultivated landscapes may cause unsustainably high mortality rates despite the majority of hunters respecting protection laws.

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KEYWORDS

Canis lupus, Denmark, genetic wildlife monitoring, Germany, human–wildlife conflict, illegal killings, large carnivores, poaching, recolonization, roadkills, source–sink

1 | INTRODUCTION

European large carnivore populations have rebounded following implementation of legal protection (Chapron et al., 2014); for example, wolves (*Canis lupus* L.) in Germany rapidly expanded from one pack in 2000 to 68 in 2015 (Reinhardt et al., 2019), providing evidence for the effectiveness of legislation to restore populations. Behavioral flexibility and adaptability have enabled wolves to exploit habitats highly impacted by humans (Mech, 2017). However, human-induced mortality rates, a major cause of population regulation among large carnivores in habitats shared with humans (Chapron et al., 2014), may limit the future population expansion and ultimate distribution of wolves in the predominantly anthropogenic landscapes of Europe. Where wolves enjoy legal protection, traffic accidents and illegal killing contribute the majority of human-induced mortality. Where such anthropogenic mortality rates exceed reproductive success, the population of the habitats sinks, ultimately draining regional populations of individuals and inhibiting establishment in otherwise suitable habitats (Fahrig & Rytwinski, 2009; Recio et al., 2018). Illegal killing of large carnivores occurs globally, including in Germany and Denmark (Heurich et al., 2018; Reinhardt et al., 2019; Sonne et al., 2019), and may regulate wolf populations locally or regionally (Liberg et al., 2020; Suutarinen & Kojola, 2017; Treves et al., 2017). Sociopolitical factors driving the illegal killing of wolves are complex (Chapron & Treves, 2016; Liberg et al., 2020; Suutarinen & Kojola, 2018; von Essen et al., 2015; von Essen et al., 2018) as are their interactions with landscape conditions. For example, in Finland, rates of illegal killing among breeding GPS-collared wolves positively correlated with the frequency with which they crossed roads and hence be accessible to poachers (Suutarinen & Kojola, 2018). In Germany, survival of territorial wolves were higher inside military training areas, apparently because of reduced exposure to persecutors (Reinhardt et al., 2019). However, the extent to which wolf mortality in densely populated and cultivated landscapes of Western Europe exceeds the species' reproductive capabilities have remained unquantified.

Here, we analyze verified and apparent wolf mortality rates on the Jutland peninsula (46,208 km²) in Denmark and Schleswig-Holstein, Germany, an intensively cultivated region, where individual wolves are intensively monitored and emigration is limited, which has received

a steady flow of wolf immigrants from the Central European source population. Wolf population dynamics in this region may thus exemplify the situation in other parts of West and Central Europe where fates of individuals are less easy to monitor.

2 | MATERIALS AND METHODS

2.1 | Study area

Schleswig-Holstein with Hamburg (SH; 16,430 km², 4.47 million people, 272 km⁻²: 10% developed, 68% farmland, 11% forest) and the Danish part of Jutland (DK; 29,778 km², 2.58 million people, 87 km⁻²: 12% developed, 61% farmland, 13% forest, 10% heathland) constitute the 470-km long Jutland peninsula (Figure 1). Jutland is connected to the Central European mainland (CE) by a 60-km wide stretch of land between Hamburg (1.83 million people) and the Baltic Sea. Most of its human population resides in the southern district of SH that borders on Niedersachsen and Mecklenburg-Vorpommern.

2.2 | Wolf monitoring in Germany and Denmark

Wolves in Germany and Denmark belong to the Central European Lowland population (Andersen et al., 2015) centered in Western Poland and Eastern Germany, with single breeding pairs in Denmark, The Netherlands, Belgium, and Czech Republic. These countries monitor the population genetically based on 13 microsatellite markers using joint standards agreed by the CEWolf consortium (www.senckenberg.de/CEWolf), enabling genotyped individuals to be tracked throughout the entire population area (for further details, see Appendix S1).

In DK and SH, governmental agencies systematically sample DNA from scats, dead wolves, and wolf-killed livestock. In SH (where sheep farming is widespread and until recently not adapted to wolf presence), livestock killings have contributed with most genotype identifications. In DK, wolves kill livestock less frequently, so monitoring is primarily undertaken by DNA retrieval from scats (obtained by active search) (Appendix S1).

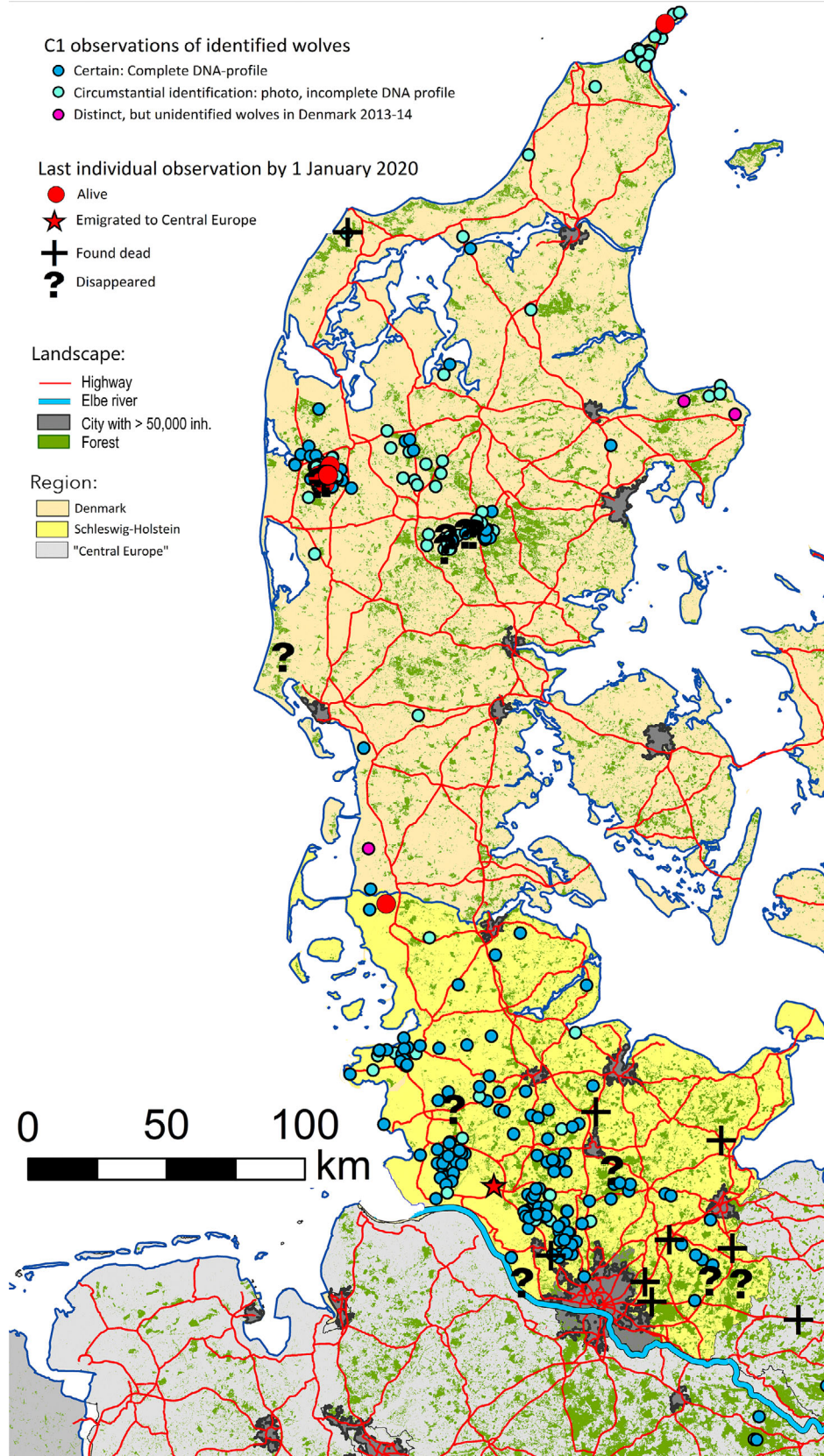


FIGURE 1 Map of the Jutland peninsula, with verified (C1) observations of genotyped wolves, 2007 to January 1, 2020. The last known observation in the region of each individual before January 1, 2020 is indicated by fate (a cross outside the region indicates the location of death of a wolf that emigrated out of the region is also shown on the map)

We also included GPS data from a vagrant male wolf (GW1172m) that immigrated to SH from Sachsen-Anhalt in April 2019, remaining there for 2 weeks before emigrating through Mecklenburg-Vorpommern to Poland (Appendix S1).

2.3 | Estimation of observation frequencies and probability of local persistence

We created two georeferenced observation datasets of identified individuals from the wolf registration databases in DK and SH, respectively, as of April 14, 2020. The first dataset (A: rigorous) consisted of full genotype profile identifications. The second data set (B: pragmatic) also included verified wolf observations that could be assigned with a high level of confidence to an individual of known genotype (e.g., photo documentation or incomplete DNA profiles). Incomplete DNA profiles were accepted when based upon a minimum of nine loci with ≥ 2 amplifications of a heterozygote and ≥ 3 amplifications of a homozygote locus or where individual assignment could be attained with high probability due to multiple sampling of an individual within a highly restricted temporal and geographic context (Appendix S1).

We estimated an individual's daily observation probability as $r_{\text{day}} = (n - 1)/x$, where n is the number of observation days and x is the number of days between the first and last observation. Hence, if an individual was registered on 11 different dates over a 100-day period, $r_{\text{day}} = (11 - 1)/100 = 0.1 \text{ day}^{-1}$.

From r_{day} , we derived the probability that a wolf would not be detected within a time period of z days since its last observation $(1 - r_z)$ as $(1 - r_{\text{day}})^z$. Individuals that had an $(1 - r_z) < 0.01$ were scored as disappeared. We estimated the probable date of disappearance as the last date of observation + the mean number of days between consecutive observations before it disappeared. At the population level, we modeled r_{day} and the mean number of days between consecutive observations ($1/r_{\text{day}}$) an interactive function of country (SH or DK) and year as fixed effects with wolf identity as random effect (Appendix S1). If a wolf was only observed once, its disappearance date was estimated by adding the population mean observation interval in the country and the year it was observed to the date of the last observation.

2.4 | Mortality analysis

We analyzed cause-specific mortality and/or disappearance rates as the number of verified deaths and/or

disappearance events per exposure day. We estimated cause-specific death and disappearance rates as (i) traffic, (ii) disappearances + verified illegal killings, and (iii) total (all verified deaths + disappearances).

An individual's exposure period started when its genetic profile was initially registered in the region and lasted until it was verified as dead or emigrated, estimated to have disappeared, or to January 1, 2020 if alive in the region by that date (Figure 2). In April 2021, we made a final check of our databases to confirm that no wolves categorized as disappeared had reappeared (last DNA-profile sampled February 5, 2021). Wolves born in the region entered the analysis on the first date their genetic profile was detected after 1 November in the year they were born. For wolves moving between DK and SH, we divided the exposure days for observation intervals involving border crossings between DK and SH relative to the ratio between mean observation frequencies in the two states, hence allocating the majority of the exposure days for trans-boundary intervals to DK (Table 1).

For the entire SH–DK region as well as for SH and DK individually, we estimated cause-specific event rates after three different data selection criteria. Using the first, most rigorous method (method 1), individual exposure intervals were calculated from data set A (strictly DNA-verified observations). Disappearance events were allocated to DK or SH depending on where the wolf was last observed. Individuals registered dead as the first record did not enter the analysis. Using the second, more pragmatic method (method 2), we calculated individual exposure intervals from data set B (including probable identifications). Since most immigrants to SH from CE dispersed further into DK within few weeks (Figure 2) and mean observation intervals in DK before 2016 were substantially longer than in SH (and later on in DK; Table 1), three disappeared individuals last observed in SH, 2012–2015 (Figure 2) were treated as emigrated to DK and disappeared there. Other criteria were similar to method 1. Method 3 was similar to method 2, but included five individuals reported killed by cars as their only registration. While we accept that inclusion of individuals killed at their first registration is not analytically rigorous (because they are drawn from an unknown population of undetected individuals), we consider that it is justified in this case, as they represented the majority of traffic deaths and probably represented individuals killed shortly after entering SH from CE. To compensate for exposure time before registration, we arbitrarily added 30 exposure days to each roadkill not previously registered in the SH–DK region, which was six times the mean observation interval in SH in 2019 (Table 1).

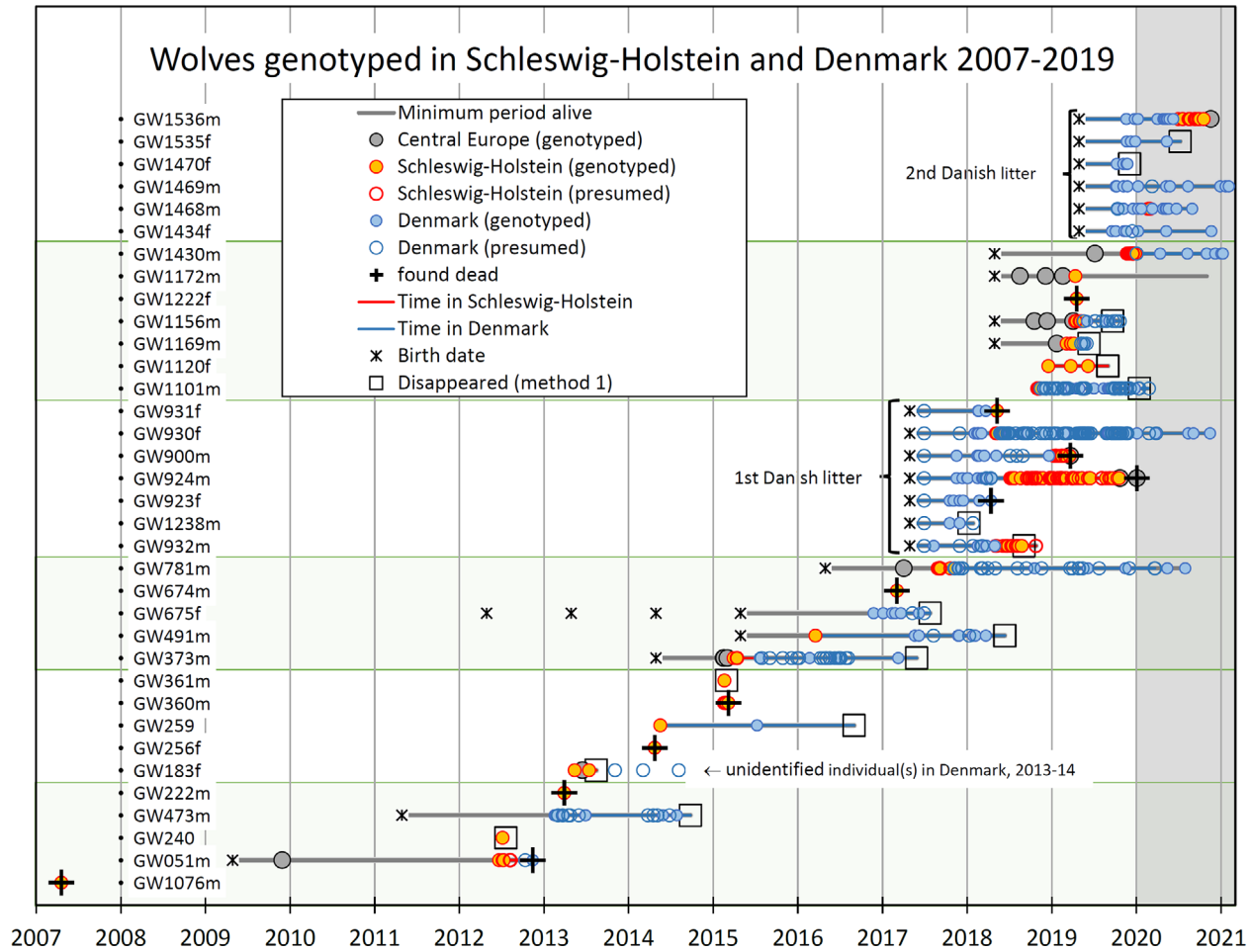


FIGURE 2 Observation timelines of the 35 genotyped wolves registered in Schleswig-Holstein and Denmark, 2007–2019. Data obtained after January 1, 2020 was not included in the mortality analysis, hence indicated with gray shaded background. Accordingly, GW1101m and GW1535f (estimated disappeared c. January 17, 2020 and July 10, 2020 by method 1) was coded as alive in the analysis. Multiple possible birth dates of GW675m are the breeding seasons when it could potentially have been born based on pedigree analysis in relation to its parents (it is most likely it was born in the last of these years)

TABLE 1 Mean observation intervals for wolves in Denmark (DK) and Schleswig-Holstein (SH), as predicted from Generalized Linear Mixed models (observation unit = observation intervals, response variable: 1/length [days] of the observation interval; link = logit; binomially distributed errors with variance inflation factors differentiated to state and period [2012–15 vs. 2016–19])

Year	DNA-verified observations				All observations			
	Mean observation intervals (days)			1 - r _{year} (%)	Mean observation intervals (days)			1 - r _{year} (%)
	DK (95%CL)	SH (95%CL)	DK:SH	DK (95%CL)	DK (95%CL)	SH (95%CL)	DK:SH	DK (95%CL)
2012	299 (21–4427)	14 (4–56)	21.4	43 (0–94)	98 (27–358)	18 (4–96)	5.4	8 (0–49)
2013	200 (21–1933)	12 (4–39)	16.7	28 (0–88)	72 (24–216)	15 (4–60)	4.8	3 (0–31)
2014	134 (21–847)	10 (4–27)	13.4	15 (0–74)	54 (22–131)	12 (4–38)	4.5	0.9 (0–14)
2015	90 (22–375)	9 (4–19)	10.0	6 (0–51)	40 (20–80)	10 (4–24)	4.0	0.2 (0–4.2)
2016	60 (22–169)	7 (4–13)	8.6	1.5 (0–22)	29 (17–50)	8 (4–16)	3.6	0 (0–0.6)
2017	40 (20–80)	6 (4–10)	6.7	0.2 (0–4)	22 (15–32)	7 (4–11)	3.1	0 (0–0)
2018	27 (17–44)	5 (4–8)	5.4	0.0 (0–0.3)	16 (11–23)	5 (4–8)	3.2	0 (0–0)
2019	18 (10–34)	5 (3–8)	3.6	0.0 (0–0.1)	12 (8–18)	4 (3–7)	3.0	0 (0–0)

DK:SH indicate the ratio between mean observation lengths in DK and SH. (1 - r_{year}) is the estimated percentage probability that a wolf will escape detection for 365 days (only shown for DK as all estimates for SH were <0.1 %).

3 | RESULTS

3.1 | Observation patterns

By January 1, 2020, 35 different wolves had been identified through genotyping in SH and DK, 22 immigrants from CE and 13 born in DK (Figure 2). Nine of the immigrants were first registered in SH and then in DK, two only in DK, and 11 only in SH (six killed, four disappeared, one returned to CE). Thirteen of 15 wolves known to have entered SH from independent data (nine of 11 immigrants registered in DK, three Danish-born wolves registered in CE, and one GPS-tagged individual; Figure 2) were registered genetically in SH, equating to a detection probability of 0.87 (95% CI: 0.59–0.97).

On average, immigrants from CE stayed for 38 days (SE = 4.8) in SH before leaving SH again (Kaplan–Meier analysis with 10 emigrations as events, one death, and four disappearances as censored cases, stay lengths estimated using method 1). Immigrants from DK on average stayed for 217 days (SE = 113) in SH before dispersing to CE or returning to DK. No immigrants to DK left the country upon entry (Figure 2).

From 2012 to 2019, the mean interval between consecutive genetic identifications in SH and DK reduced from 14 to 5 and from 299 to 18 days, respectively (Table 1).

3.2 | Cause-specific mortality and disappearance rates

As of January 1, 2020, of the 35 genotyped wolves, representing 22.1–23.9 exposure years (82% in DK, 18% in SH), nine were alive, nine were registered dead (seven traffic kills, one diseased, one shot illegally), three emigrated, and 14 had disappeared (Table 2).

All traffic deaths were registered in SH (Table 2). Depending on estimation method, annual road fatality rates ranged from 0.37 to 0.78 for SH and from 0.08 to 0.25 for the entire SH–DK region (Table 2).

In DK, the annual rate of illegal killings and disappearances ranged from 0.42 to 0.50 and the total death + disappearance rate from 0.46 to 0.52 (Table 2). For SH, total annual rates of deaths + disappearances varied from 0.61 to 0.85, with traffic deaths representing the most frequent event type and the only type of verified death (Table 2).

4 | DISCUSSION

With an 87% registration probability of wolves passing through SH and a mean observation frequency of less than 2 weeks, it is unlikely that a wolf in SH would avoid detec-

tion for more than a few months. The same also applies for DK since 2016–17, when the Danish wolf survey was established. Most immigrants from CE were transient in SH and moved on to DK from where they never returned. It should therefore be safe to conclude that all, or at least the vast majority, of wolves that disappeared in DK also died there. It is not possible to draw the same conclusion for SH, as wolves last observed in SH might have dispersed to DK or CE. At least one genetically unidentified wolf lived in DK during 2013–14 (Sunde & Olsen, 2018), so at least one and possibly all three wolves that disappeared from SH during 2012–15 potentially dispersed to DK and eventually died without ever being genotyped there. With respect to estimation of disappearance rates, method 1 is therefore conservative for DK and possibly inflated for SH, whereas method 2 might give a more accurate estimate for both DK and SH. Method 3 (which also included wolves registered first when killed by cars) was less rigorous, as an unknown number of wolves might have entered the urbanized southern part of SH and returned to CE without entering the analysis. It may nevertheless be realistic, as a total registration rate of 87% and >50% registration probability within 2 weeks indicate that the wolves not registered before they were killed had died few days after entering the urbanized southern part of SH from CE. Further support for using this method comes from the fact that despite our arbitrary setting of the number of exposure days of wolves killed at initial registration to 30 days (six times the mean observation interval in 2019, so unrealistically high), the 150 exposure days from the five cases comprised less than 9% of the total number of exposure days in the analysis for SH and less than 2% for SH + DK. Hence, the arbitrarily chosen number of exposure days per wolf killed at first encounter had little influence on mortality estimates generated from method 3 compared with the contribution of death events.

The most conservative estimates of annual mortality rates in both SH (traffic: 0.37) and DK (deaths and disappearances: 0.46) exceeded natural and traffic-caused mortality rates in Sweden (0–0.06; Liberg et al., 2020) and Finland (natural: 0.03, traffic: <0.07; Suutarinen & Kojola, 2017). They also exceeded the maximum sustainable harvest rates (≤ 0.29) and total sustainable mortality rates (0.34) estimated for wolf populations (Adams et al., 2008; Fuller et al., 2003), suggesting that the Jutland peninsula constitutes a population sink.

Even though the traffic fatality rates exceeded sustainable harvest rates in SH, traffic mortality was not a population-regulating factor for the whole region, as no traffic deaths were registered in DK. The locations of the traffic kills (Figure 1) reveal that most traffic deaths occurred in a delimited “death zone” around Hamburg, affecting wolves that dispersed through the area. This

TABLE 2 Number of genotyped wolves registered in Schleswig-Holstein (SH) and Denmark (DK) by 1 January 2020, showing the cumulative number of exposure days and cause-specific event rates

Region	Method	Number of wolves according to fate categories as of January 1, 2020							Cause specific event rate per year (95% CI)			
		A	E	N	I	T	D	Total	Days	Traffic deaths	Illegal + disappeared	Deaths + disappeared
SH	1	1	13	0	0	2	5	21	1432	0.40 (0.12–0.87)	0.72 (0.41–0.95)	0.83 (0.57–0.98)
	2	0	17 ^a	0	0	2	2	21	1564	0.37 (0.11–0.85)	0.37 (0.11–0.84)	0.61 (0.30–0.92)
	3	0	17 ^a	0	0	7	2	26	1714	0.78 (0.51–0.96)		0.85 (0.63–0.98)
DK	1	8	4	1	1	0	9	23	6596	0.00 (0.00–0.17 ^b)	0.42 (0.26–0.64)	0.46 (0.29–0.67)
	2	9	4	1	1	0	12 ^a	27	6931	0.00 (0.00–0.16 ^b)	0.50 (0.33–0.69)	0.52 (0.35–0.71)
DK + SH	1	9	3	1	1	2	14	30	8028	0.09 (0.02–0.30)	0.49 (0.34–0.68)	0.56 (0.40–0.73)
	2	9	3	1	1	2	14	30	8495	0.08 (0.02–0.29)	0.48 (0.32–0.66)	0.54 (0.39–0.71)
	3	9	3	1	1	7	14	35	8692	0.25 (0.13–0.46)		0.62 (0.47–0.77)

Fates by January 1, 2020: A = alive, E = emigrated from region, N = natural death cause, I = illegal killing, T = traffic kill, D = disappeared.

Methods: 1: observations based only on full DNA-profiles; 2: observations of likely identifications included; 3: wolves killed by cars as the first ever registration in the region included, associated with 30 exposure days each (see text for full explanation).

^aIncludes three individuals last observed in SH (2013–15), presumed emigrated to DK and one individual (GW1430m) coded as emigrated to DK on 30 December 2019 based on a likely identification (therefore coded as alive in SH by method 1, but as alive in DK and emigrated from SH by method 2).

^bUpper confidence limit calculated by substituting 0 events/x days with 1 event/(2x) days.

emphasizes the potential importance of local areas with heavy traffic as regional population drains.

The reasons for the apparently unsustainably high mortality rate in DK are more subtle, as disappearances and one illegal killing accounted for nine of 10 presumed deaths (based on the most conservative estimate). The annual rate of DK disappearances and illegal killings (most conservative estimate: 0.42) exceeds the highest measured rates in Sweden (0.24) (Liberg et al., 2020) and equals the highest rates measured in Finland (0.31–0.43) (Suutarinen & Kojola, 2017), levels which, in both countries, resulted in population declines. Unreported car accidents are unlikely to contribute significantly to the high disappearance rates since most wolves disappeared from areas with relatively low traffic intensity (Figure 1) and because most motorists are aware of, and report, hitting a wolf. Eliminating all other explanations, illegal killing remains the only plausible reason behind most DK disappearances.

That illegal killing is the predominant cause of high wolf disappearance rates is not unexpected, given that acceptance of illegal killing to resolve wolf conflicts seem to be widespread amongst rural Jutland landowners (Højberg et al., 2017).

The results from the Jutland peninsula contrast elsewhere in Germany where the population increased by 34% year⁻¹ during 2000–2015 (Reinhardt et al., 2019). Differing patterns of landscape and landownership, rather than attitudes, potentially explain this difference. Relative to the East-Central Germany and Western Poland source population area, forest areas in SH and DK are small, fragmented, and usually managed by multiple landowners. Accordingly, wolves in SH and DK may move between more properties, exposing themselves to greater numbers of potential persecutors than do wolves in the core population. Wolves establishing territories in German military training areas survived better than wolves in similar habitats outside the training areas (Reinhardt et al., 2019) implying that illegal killing are conditional on landownership and that hunting practice is also a population regulating factor elsewhere. If this is the case, the future distribution and abundance of European wolves may rather be more defined by (illegal) mortality driven source–sink dynamics than by habitat availability per se, as previously described for the Eurasian lynx (*Lynx lynx*) in Germany and the Czech Republic (Heurich et al., 2018).

We therefore suggest that such killings arise from random encounters between wolves and people willing and able to kill wolves when the opportunity occurs. Such illegal killing fundamentally differs from the common practice in the continuous forest landscapes in Fennoscandia where wolves are actively hunted through organized, communal efforts under snow-covered conditions (Suutarinen & Kojola, 2017). In Denmark, hunting is practiced

on >80% of the rural land surface (Primdahl et al., 2012). As a result, illegal killing on small estates is probably more feasible, “private,” and less subject to social control than that in Fennoscandia. In this situation, proportionally few active individuals could inflict unsustainably higher kill rates there compared with Fennoscandia, where the number of separate ownerships encompassed within a wolf’s activity range is low. If this explanation is true, local poaching rates should inversely correlate with mean estate size and be highest among the most mobile individuals, such as dispersing vagrants. In that case, the availability and spatial distribution of wolf habitats with low poaching risk of sufficient size to include breeding home ranges may be of crucial importance for regional persistence of wolves (see also Grilo et al., 2019). Ultimately, improved understanding of landscape-related mortality rates and the sociopolitical drivers causing violations to protective legislation are a prerequisite to predict better wolf colonization success in the densely populated landscapes of West-Central Europe.

In western countries, illegal carnivore persecution appears rooted in resource conflicts (game, livestock), committed in frustration with, or as acts of political resistance against, governmental policies (Liberg et al., 2020; Pohja-Mykra & Kurki, 2014; von Essen et al., 2015; von Essen et al., 2018). Therefore, mitigation initiatives are essential to increased acceptance of protective legislation to avoid illegal actions determining where wolf populations can and cannot become established in the future (Pohja-Mykrä, 2017; Sonne et al., 2019; Treves & Bruskotter, 2014).

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AUTHORS’ CONTRIBUTIONS

P.S. analyzed the data and led the writing of the paper. J.M. and B.S. were coordinating and conducting wolf monitoring in Schleswig-Holstein; K.O., C.S.V., and P.S. were responsible for the monitoring in Denmark. C.N. and S.C. were responsible for genetic analyses of samples from Germany and partly from Denmark and organized the register of genotyped wolves in Central Europe. M.M.H. and P.F.T. were responsible for genetic analyses in Denmark since 2017. F.W. provided GPS data on GW1172m. All authors provided input to the manuscript and its revised version.

ETHICS STATEMENT

The search for and sampling of genetic material from wolves involved nonintrusive methods that did not affect the sampled subjects. Active monitoring efforts at all times followed the stringent procedures and obligations imposed by the states' laws and regulations for activities on public and private land. The capture, handling, and GPS tagging of wolf GW1172m was licensed by the federal state of Sachsen-Anhalt (animal welfare permit: 42502-2-1513 HNEE, permit for tagging wild specially protected animals: WZI 01 20181019).

DATA ACCESSIBILITY STATEMENT

The data that support the findings of this study are openly available at <http://doi.org/10.13140/RG.2.2.19903.02723>

CONFLICT OF INTEREST

The authors declare no conflicts of interest

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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