

## Research article

# Habitat and density effects on the demography of an expanding wolf population in Central Europe

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Demographic parameters are key to understanding population dynamics. Here, we analyse the survival and reproduction of the German wolf population in the 20 years following recolonization. Specifically, we analysed the effects of environmental, ecological and individual characteristics on 1) survival probability of the population; 2) annual survival rates of age classes; 3) reproduction probability; and 4) reproductive output, measured as the number of detected pups/juveniles. Using Cox proportional hazards model, we estimated a median survival time of circa three years for wolves. Annual survival probabilities were found to be 0.75 for juveniles, 0.75 for subadults and 0.88 for adults. Survival was lower for juveniles in winter and for subadult males in summer, probably associated with dispersal events. Low habitat suitability was clearly associated with lower survival in juveniles and subadults, but not in adults. Local territory density was related to increased survival. Reproduction probability within a territory was 0.88, but explanatory variables had no effect. Reproductive output was four pups/juveniles on average, positively related to habitat suitability and female experience, but negatively related to territory density. Survival values were very high for the species when compared to other regions. We hypothesize that carrying capacity has not been reached in the study area, thus the survival may decrease in the future if the landscape becomes saturated. Furthermore, our results highlight a spatial pattern in survival and reproduction, with area of better habitat suitability favouring faster population growth. Thus, targeting conservation measures to low habitat suitability areas will have a strong population effect on the short term by boosting survival and reproduction of the individuals, while long-term viability should be carefully planned with high suitability areas in mind, as those contain the territories with higher survival and reproduction potential.

Keywords: *Canis lupus*, carnivore conservation, carnivore ecology, large carnivores, population dynamics, reproduction, survival



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## Introduction

Demographic parameters are the cornerstone to understanding wildlife population dynamics, determining if a population grows, remains stable or shrinks (Sibly and Hone 2002). They indicate the ability of a species to subsist in human-dominated landscapes (Lamb et al. 2020). Thus, understanding the effects of environmental and ecological conditions on individual fitness parameters and, consequently, on the demography of a species becomes a priority for conservation and ecological research. However, obtaining long-term data for long-lived species is challenging, as they usually obtain large spatial scales and monitoring efforts are huge (Di Marco et al. 2014).

In recent years, we have observed a unique comeback of large carnivores in the human-dominated landscapes of Central Europe (Chapron et al. 2014, Cimatti et al. 2021). A prime example is the grey wolf (*Canis lupus*; hereafter: wolf). After 20 years of wolf recolonization in Central Europe (Marucco and McIntire 2010, Nowak et al. 2017, Louvrier et al. 2018, Reinhardt et al. 2021), analysing the demographic parameters including environmental information to fully comprehend the species expansion and future perspective is timely, especially regarding increasing numbers of livestock kills, a decreasing tolerance of certain stakeholder groups and loud voices for active population management (Arbieu et al. 2019, König et al. 2020, Khorozyan and Heurich 2022).

So far, legal protection of the population after the European Habitats Directive and changes in human attitudes have favoured the wolf comeback to many regions (Boitani and Ciucci 2009, Cimatti et al. 2021), including densely populated areas like Germany (Reinhardt et al. 2019, Jarausch et al. 2021). Despite the risks that the species face in many areas, such as poaching and traffic collisions (Liberg et al. 2012, Sunde et al. 2021), wolves found patches of available habitat and managed to spread and increase their numbers not only in Germany but also to neighbouring areas in Denmark and the Netherlands (Large Carnivore Initiative for Europe 2022). This quick recovery shows the flexibility of the species and its ability to recover even in landscapes with intensive human use (López-Bao et al. 2015).

Population growth can be driven by a high survival of the individuals, a high reproduction rate or both. However, both parameters should be taken into account together to determine population dynamics (Johnson et al. 2020). Thus, the prediction of future scenarios requires knowing the exact demographic values associated with the individuals and the drivers of these values, as management actions might have completely different consequences depending on population characteristics, such as age class distribution (Rauset et al. 2015). Additionally, spatial or temporal effects might modify the demographic parameters. Temporal effects are usually related to seasonal effects or harvest effects in survival rates (Hebblewhite and Whittington 2020, Barber-Meyer et al. 2021). Environmental conditions associated with individual location, like the existence of wilderness refuges

(Barber-Meyer et al. 2021) or remains of natural vegetation, together with human density effects (Cimatti et al. 2021, Nakamura et al. 2021), play an important role on individual survival and reproduction. The combination of these spatial effects, summarised as habitat suitability, not only determines the minimum threshold for population establishment but also will create different spatial patterns in the demographic parameters (O'Neil et al. 2017). Furthermore, species density might modulate the effects of environmental parameters and affect demographics. On one hand, high conspecific density competition can limit the survival of individuals (Mech and Boitani 2003, Cubaynes et al. 2014, O'Neil et al. 2017). On the opposite side of the spectrum, at very low densities reproduction might be hindered due to Allee effects (Courchamp et al. 1999). Thus, neglecting to account for the variation in demographic parameters due to changes in habitat quality or population abundance will lead to under- or overestimation of the population growth.

Lastly, individual characteristics may also influence survival and reproduction, playing crucial roles in individual fitness. While sex has little effect (Barber-Meyer et al. 2021, Chakrabarti et al. 2022), survival is clearly affected by age class, e.g. adult wolves in Yellowstone (Smith et al. 2020) or dispersing young in Minnesota (Barber-Meyer et al. 2021) present the relative higher mortalities for their areas. Regarding reproduction, individual experience with previous reproduction events is related to higher success rates (Bernardo 1996, Wikenros et al. 2021). Understanding these demographic parameters in the expanding population in Central Europe and their drivers becomes, thus, a priority for their future conservation.

Here, we present the first analysis of survival and reproduction rates of the German wolf population, using all available data since the arrival of the first individuals in 2000 until the end of the monitoring year 2020. We aimed at analysing and understanding the factors affecting survival and reproduction of wolves in Germany during the population expansion phase. Specifically, we analysed 1) how age, sex, season habitat suitability and local territory density affected wolf survival; 2) how these variables impacted the annual survival of juveniles, subadults and adults; and 3) how reproduction probability and number of pups per reproduction event were affected by the experience of the reproductive female, habitat suitability and local territory density. We believe these new insights on the demographic parameters will help researchers, wildlife managers and conservationists to understand dynamics of spreading populations and contribute to a better understanding of European wolf populations.

## Material and methods

### Study area

Germany represents a highly human-dominated Central European landscape, with a population of ~ 83 million inhabitants (2018) in an area of 358 000 km<sup>2</sup>, resulting in an average

density of 232 people km<sup>-2</sup>. However, population distribution is uneven with higher densities in the West and around large cities, like Berlin or Hamburg, and lower densities in forested areas or large agricultural areas of the East ([www.destatis.de](http://www.destatis.de)). Although the total forested area in the country represents about 30% of the land surface, the 16 National Parks only cover 0.6% of the German terrestrial area (Federal Agency for Nature Conservation – BfN, [www.bfn.de/nationalparke](http://www.bfn.de/nationalparke)). Additionally, intensive agriculture covers around 50% of the terrestrial area and about 14.2% of the country's surface is occupied by settlements and roads, with a total length of 13 000 km of motorways and 125 000 km of interstate and main roads (Statistisches Bundesamt, [www.destatis.de](http://www.destatis.de)).

In Germany, all wolf monitoring activities are conducted in all of the 16 federal states, following the German monitoring standards for large carnivores (Reinhardt et al. 2015). Due to the decentralised local responsibilities, monitoring intensity and strategies may vary in space and time. However, genetic samples are regularly collected in all federal states with occasional or regular wolf presence (Jarausch et al. 2021) and the common main goal of the monitoring is to identify all territorial wolves and their status (single territorial wolf, territorial pair or pack) every year, as well as whether reproduction occurred.

### Wolf data

Wolf individual and territory data (below) was provided by the Federal Documentation and Consultation Centre on Wolves (DBBW, [www.dbb-wolf.de](http://www.dbb-wolf.de)), which compiles the wolf monitoring data of all the German federal states and reports them to the public, and by the Senckenberg Centre for Wildlife Genetics, which serves as genetic reference laboratory for wolves in Germany. In addition, all dead wolves reported by citizens to the nature conservation authorities were collected and examined for their age, sex and reason of death and their information added to the monitoring reports. Information about individuals and territories were grouped into monitoring or wolf years, respectively. A monitoring year starts the 1 May of the reference year and ends 30 April of the next calendar year, i.e. monitoring year 2010 starts on the 1 May 2010 and ends 30 April 2011. Therefore, the year used in the statistical analysis refers to the monitoring year, not the calendar year.

The monitoring program followed the annual development of the wolf population in Germany from the first confirmed territory established in 2000, providing annual territory numbers and their centroid locations. The first genetic sample was obtained in 2001, and since then genetic samples were regularly collected during sign surveys within the frame of the annual monitoring (faeces, urine, hair) as well as after suspected attacks to livestock (saliva samples). In addition, all wolves that were found dead were genetically sampled (Jarausch et al. 2021). This detailed genetic data collected consecutively allowed for individual recognition and close monitoring of individual fate, as well as the assignment of individuals to wolf packs and territories.

The genetic data were used for the survival analyses and contained, for each individual sampled, the year of birth, sex, parental information, territory association, date of consecutive times the individual was verified via genetics, and death date if the corpse was found. For our analysis, we standardized all birth dates as the 1 May of the year the pup was born, as assigning the exact birth date is almost impossible and giving birth is assumed to happen at the beginning of the wolf year. The date of death was assumed to be within a week of finding the corpse to assign a standardized date of death. Although some individuals had multiple detections, the data comes from opportunistic observations and thus, it was not possible to estimate reliable detectability or observation histories for the individuals due the lack of information on sampling effort or detections. For this reason, we decided to use the reliable information and simplified the data to the first and last detection of each individual. The genetic data was limited from the monitoring year 2001–2020 (April 2021). For the survival analysis, the original dataset was filtered to retain only reliable information on the lifespan of the animals. Thus, individuals with NA ('not available') in the variables 'sex' or 'date of birth' as well as individuals born or died outside the German border were removed, as the environmental data included in the demographic analyses were only available for Germany. Consequently, the status of the individuals (dead, alive) was assessed until April 2021. The age classes were defined as juveniles including pups (0–12 months), subadults (13–24 months) and adults (> 24 months) (Mech and Boitani 2003). The final dataset contained a total of 1054 individuals (Table 1).

Reproduction data was analysed at the territory level. The dataset contained information on the identity of the territory, the type of territory (pair or pack; single territories

Table 1. Number of observations for the survival models per age class, divided by sex, classified as censored or dead for each model. Censored observations correspond to individuals that either disappeared during the monitoring or were alive at the end of the maximum time of the respective age class. Note that the total number of subadults also includes the number of juveniles still alive at the end of the juvenile period, as only the alive juveniles become subadults. The same applies to adults and subadults. The number of censored juveniles (first row) is higher than the total number of censored individuals (last row) as the individuals that went missing as subadults also count as censored in the juvenile data, and the same issue happens for individuals that went missing as adults.

Age class	Censored	Dead	Total
Juveniles	756	298	1054
Females	352	128	580
Males	404	170	574
Subadults	363	111	474
Females	193	49	142
Males	170	62	232
Adults	158	57	215
Females	90	32	122
Males	68	25	93
Total	588	466	1054
Females	271	209	480
Males	317	257	574

were excluded as no reproduction can happen), the proof of reproduction (pups) or reproduction signs (i.e. lactating female) in a territory for every monitoring year, the identities of the individuals in the breeding pair, and the number of pups detected in each territory. The reproduction data were obtained during the standard monitoring surveys in each German region, with no specific approach to obtain the total number of pups per breeding pair, but counting all information on detected pups during the whole monitoring year. However, most data on pups and pup numbers were collected in summer or autumn when they are juveniles and can be easily identified on pictures and assigned to a natal pack. In some cases, however, pups were assigned to packs later in the year by genetic information of ancestry. Hence, as the number of juvenile counts might be less than the actual number of pups born, we define this variable as 'minimum reproductive output'. Territories with more than 10 observed pups/ juveniles were removed from analyses to account for the fact that such a high number of pups might stem from a double reproduction and thus belong to one or more females ( $n = 4$ ). In addition, territories from the first year of pair formation were removed ( $n = 227$ ), because pairs typically form shortly before or during the breeding season (in autumn or winter) and therefore, there is no opportunity for reproduction in the months prior to the pair formation, which would correspond to the reproduction in the first year in the dataset. The final dataset consisted of 723 entries comprising 205 different territories with data from 1–16 years per territory.

## Explanatory variables

We analysed survival and reproduction of wolves in relation to environmental and ecological conditions and individual characteristics. For the survival analysis, we used as environmental conditions a wolf habitat suitability map for Germany (Planillo et al. 2024a) that accounts for the different land use types and human disturbance effects (e.g. forested areas, distance to roads or human density), and as ecological conditions the annual density of wolf territories around the focal territory and the season of the year. The original habitat suitability values represented the relative quality of the landscape for wolf territory establishment, with an average value of  $0.386 \pm 0.107$  in the observed territories until 2020 (Planillo et al. 2024a). Due to little changes in the German landscape during the study time window, the habitat suitability map was taken as a static map for all the study years. For survival analyses, environmental and ecological characteristics were extracted at both, natal and final individual locations or territories and the season was extracted at each recapture date. Habitat suitability values were extracted as the mean value in an 8 km radius of the territory centroid representing an area of approx. 200 km<sup>2</sup>, the average territory size of wolves in Germany (Reinhardt and Kluth 2016). In order to properly represent the increase of the wolf population in some regions, wolf local territory density was extracted for each year. Local territory density was obtained based on the count of territories in a 50 km radius around the wolf

natal territory or final territory centroids and standardized to a density of territories per 100 km<sup>2</sup>. For individuals with unknown natal or final locations, the first and last known locations were taken as a reference for calculating the habitat suitability and local territory density according to the procedure described above. For the calculation of the number of territories in the border regions of Germany, we assumed a mirrored situation in neighbouring countries, given the territory numbers and distribution in the last known years (e.g. Poland, see Nowak and Mysłajek 2016). Season was defined based on wolf biology and divided into two classes: summer (May–October) when small pups remain with the pack, and winter (November–April) associated with dispersal events and mating season (Mech and Boitani 2003). As individual characteristics, we used sex and age, with the latter being classified as age classes (below).

For the reproduction analysis, environmental and ecological conditions were described by habitat suitability values and local territory density around each breeding territory, calculated as described above. As individual characteristics we included the experience of the reproductive female in the models, measured sequentially as the number of years the same breeding female had reproduced, i.e. the first year that the female reproduced was considered year 1, the second year 2, and so forth.

## Data analysis

### Survival analysis

We analysed survival with two complementary approaches. First, we estimated the effects of the explanatory variables on the overall population survival ('overall population model') across the study period and obtained the median survival time for the population. Then, we analysed the effects of the explanatory variables on the annual survival probabilities of four different groups based on age class ('age class models'): all individuals pooled together, juveniles, subadults, adults. In all cases, we used the same initial set of explanatory variables, therefore assessing whether different variables were relevant for different age classes.

Survival probabilities were estimated using a Cox proportional hazards (CPH) regression model (Therneau and Grambsch 2000) to assess the effects of the explanatory variables described above on wolf mortality risk. In addition to the regression coefficients and the survival curve for the overall population, CPH models estimate the hazard ratios (HR) of the variables. A HR of 1 means no effect, while higher or lower values indicate an increase or decrease in the hazard risk associated with the variable, respectively.

Cox models use the time to the event of interest as response variable and are able to correct the estimates of the probability of an event incorporating the information of individuals that go missing during the trial time (Therneau and Grambsch 2000). For the survival analyses, the event of interest was the death of the individual. One of the main advantages of these models is that they can correct the estimates using the information of individuals that

are followed during the study but disappear. In our case, some individuals were known to be alive for some time but they are no longer found after that. These are considered censored observations and are used in the model to correct over- or underestimations of survival. For example, if an individual is confirmed alive for 10 weeks and then no longer found, that individual will be censored at 10 weeks and only accounted for in the survival estimates for the first 10 weeks, then it is removed from the pool of remaining individuals.

In our models we used as response variable the number of weeks until death for confirmed dead individuals or the number of weeks that the individual was alive for censored individuals. As explanatory variables we used individual sex, season of death, habitat suitability of the natal and the final territories, and local territory density around the natal and final locations (above). When individual's fate was undetermined, we right-censored individuals at their last known location and time. Numerical explanatory variables – habitat suitability and territory density – were tested for multicollinearity using Pearson's product moment correlation coefficient  $r$  (Supporting information). When they correlated ( $|r| > 0.7$ ), only the variable that had the best adjustment to the response based on AICc values of univariate CPH models was included in the final model. As a result, the local territory density around the natal territory was dropped for the overall population model, the annual survival of the population and the annual survival for subadult individuals (Supporting information). For the estimation of the annual survival in the age class models we decided to only use the environmental characteristics related to the natal territory for juveniles, and only those related to the final territory for adults, as we were interested in the characteristics affecting the individuals during the respective age classes. For subadults, as well as for all the individuals pooled together, we used both natal and final territory characteristics, when uncorrelated, as individuals in this age class typically disperse, thus their fate could be affected by both, natal and final territories. We included an interaction between sex and season to account for riskier lifestyles of the sexes related to for example onset of dispersal.

In both approaches, i.e. the overall population model and the annual survival models, we used a model selection procedure based on hypotheses to obtain the best survival model according to AICc values (Burnham and Anderson 2002). Therefore, we compared models based on the environmental and ecological effects, the individual effects or the combination of both. The interaction between sex and season was included only in the models where it improved the AICc values. Competing models for each approach are shown in the Supporting information (Supporting information). The CPH model for adults was based on recurrent annual observations of the individuals that survived for more than a year (Fieberg and Delgiudice 2009), therefore it also included a cluster term (individual ID) that was used to compute robust SEs (Therneau and Grambsch 2000), as the individual survival times were recalculated for each year and multiple rows per individual were added when necessary.

### Reproduction analysis

We studied wolf reproduction patterns focusing on two main aspects of reproduction: probability of reproduction in a territory and number of pups or juveniles, respectively, i.e., the minimum reproductive output per reproductive event. In both cases, data were analysed using generalised linear mixed-effects models (GLMMs) with binomial error distribution and logit link for reproduction probability and Poisson error distribution and log link for the reproductive output. Territory identity (*terrID*) was included as a random effect to account for repeated observations in the same territories over several years. The total number of years that a territory was monitored in the dataset was included as weighting variable to avoid an inflated effect of the territories observed only for one year. As explanatory variables, we included the mean habitat suitability of the territory (8 km radius around centroid, following the territory definition in the monitoring data, Planillo et al. 2024a), local territory density in a buffer of 50 km and the experience of the female as fixed effects. The experience of the female was included as a quadratic effect to account for a potential peak in reproductive age. In both cases, model assumptions were visually checked in the residuals of the full models.

As we did not find a correlation between explanatory variables ( $|r| < 0.7$ , Supporting information), all variables were included in the initial models. To identify the best model for each aspect of reproduction, we used a model selection approach similar to the survival analyses, based on several competing hypothesis-driven models and a null model. The best model was selected based on the lowest AICc value.

### Population growth

Finally, we used the values of survival and reproduction to estimate population growth ( $\lambda$ ) and contrast it with the observed data. This analysis serves as a validation for the obtained survival and reproduction parameters. We additionally used this approach to evaluate the effects of habitat suitability on population growth, within the observed range of habitat suitability values for the species. We developed a population matrix model using three age classes, based on obtained values of reproduction and annual survival for the age classes, and used the eigenvalue of the matrix as our  $\lambda$ . We explored the observed population growth values with respect to the effects of the minimum and maximum values of habitat suitability. To compute the lambda for the latter cases, we predicted survival of juveniles and subadults and number of pups per reproduction in areas with the lowest and highest observed values of habitat suitability. We kept all other variables as mean values for the prediction. We used a fixed value of adult survival (adult annual survival = 0.88) and fixed probability of reproduction (probability of reproduction = 0.88) in all cases, as the survival and reproduction analyses did not show an effect of habitat suitability on those variables.

All statistical analysis were ran in R 4.2.3 ([www.r-project.org](http://www.r-project.org)) using packages 'survival' for the survival analysis (Therneau 2023), 'lme4' for mixed models (Bates et al.

2015), and 'popbio' (Stubben and Milligan 2007). Data and code to run the analyses are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dncjsxm5m>, and from github repositories: [https://github.com/aplanillo/2024\\_WolfDemography\\_Germany](https://github.com/aplanillo/2024_WolfDemography_Germany) or [https://github.com/EcoDynIZW/Planillo\\_2024\\_WILD-BIOL](https://github.com/EcoDynIZW/Planillo_2024_WILD-BIOL).

## Results

### Survival

The survival dataset included the fate of 1054 wolves in Germany, of which 588 individuals were censored during the study as they were missing or still alive, including the 269 individuals still alive at the end of monitoring year 2020 (April 2021), and 466 observations belonged to dead individuals (Table 1). The maximum recorded age of a wolf was 662 weeks or 12.7 years. The average values of the explanatory variables across all individuals in the different age classes showed that adult individuals, i.e. those individuals that survived until adulthood, were born in territories with higher habitat suitability and lower local territory density than the average for all juveniles (Table 2).

The model selection for the overall population survival clearly yielded the full model that contained all variables and the interaction between sex and season as best model by AICc ( $\Delta AICc=8.82$  to the second model, Supporting information). This model estimated median survival time in the studied population to be 146 weeks (95% CI: 106–360 weeks), i.e. approximately three years (Fig. 1). All variables in the model were significant except for the single effect of season and the habitat suitability of the final territory ( $HR_{\text{season[winter]}}$ : 1.28, CI: 0.95–1.73,  $p=0.100$ ;  $HR_{\text{HSfinal}}$ : 0.91, CI: 0.82–1.02,  $p=0.099$ ). The hazard ratios showed an increasing risk for males ( $HR_{\text{sex[male]}}$ : 1.67, CI=1.20–2.33,  $p=0.002$ ) but mainly during summer ( $HR_{\text{sex[male]:season[winter]}}$ : 0.63, CI=0.42–0.93,  $p=0.021$ ), decreasing risk with increasing habitat suitability in the natal territory ( $HR_{\text{HSnatal}}$ : 0.84, CI=0.76–0.93,  $p=0.001$ ) and decreasing risk with increasing local territory density around the final territory ( $HR_{\text{TerrDensFinal}}$ : 0.87, CI=0.79–0.96,  $p=0.006$ ) (further model details in Supporting information).

When analysing the annual survival probability of all individuals pooled together, the full model had the lowest AICc value ( $\Delta AICc=18.10$ , Supporting information). In this model, the annual survival of the population was found to be 0.81 (95% CI: 0.76–0.85). Regarding the age specific analyses, the model selection process for the annual survival models for the three age classes selected the full model for juveniles, although with a similar value as the model without local territory density ( $\Delta AICc=0.05$ ), the full model for subadults ( $\Delta AICc=5.88$ ), and the model containing only the local territory density around the final territory for adults ( $\Delta AICc=3.39$ , all model selection tables are provided in the Supporting information). The annual survival probabilities by age class were 0.75 for juveniles (95% CI: 0.69–0.81), 0.75

for subadults (95% CI: 0.66–0.86) and 0.88 for adults (95% CI: 0.85–0.91). Juveniles and subadults were clearly the most vulnerable classes, affected by multiple explanatory variables, while adult survival was only related to a significant but small effect of local territory density (Fig. 2). For juveniles, sex or local territory density around the natal territory had no significant effect ( $HR_{\text{sex[male]}}$ : 1.19, CI: 0.95–1.50,  $p=0.130$ ;  $HR_{\text{TerrDensNatal}}$ : 1.09, CI: 0.97–1.22,  $p=0.148$ ), but higher risk was found in the winter season ( $HR$ : 1.38, CI: 1.05–1.81,  $p=0.019$ ) and in natal territories with lower habitat suitability ( $HR$ : 0.81, CI: 0.72–0.90,  $p < 0.001$ ). In the analysis of subadult annual survival, we found higher risk for males ( $HR$ : 2.29, CI: 1.30–4.03,  $p=0.004$ ), although only in the summer ( $HR$ : 0.44, CI: 0.20–0.94,  $p=0.034$ ), and lower risk in final territories with higher habitat suitability ( $HR$ : 0.80, CI: 0.65–0.99,  $p=0.043$ ) and higher local territory density ( $HR$ : 0.67, CI: 0.53–0.85,  $p < 0.001$ ). No significant effect of the habitat suitability of the natal territory was detected ( $HR$ : 0.88, CI: 0.71–1.07,  $p=0.204$ ). Finally, adult annual survival was associated with a lower risk with increasing local territory density ( $HR$ : 0.98, CI: 0.96–0.99,  $p < 0.009$ ).

	Juveniles	Subadults	Adults
Sex			
Males	574	232	93
Females	480	242	122
Season			
Summer	321	201	89
Winter	733	273	126
Habitat suitability – Natal territory			
Mean	0.376 ± 0.102	0.389 ± 0.102	0.406 ± 0.097
Min	0.071	0.071	0.147
Max	0.628	0.628	0.628
Habitat suitability – Final territory			
Mean	0.339 ± 0.107	0.337 ± 0.104	0.348 ± 0.104
Min	0.053	0.054	0.054
Max	0.651	0.651	0.553
Local territory density – Natal territory			
Mean	21.17 ± 14.75	19.78 ± 14.43	19.35 ± 14.36
Min	0	0	1.209
Max	58.881	53.889	53.889
Local territory density – Final territory			
Mean	21.65 ± 15.77	21.72 ± 16.17	24.63 ± 16.69
Min	0	0	0
Max	61.524	60.352	60.352

for subadults (95% CI: 0.66–0.86) and 0.88 for adults (95% CI: 0.85–0.91). Juveniles and subadults were clearly the most vulnerable classes, affected by multiple explanatory variables, while adult survival was only related to a significant but small effect of local territory density (Fig. 2). For juveniles, sex or local territory density around the natal territory had no significant effect ( $HR_{\text{sex[male]}}$ : 1.19, CI: 0.95–1.50,  $p=0.130$ ;  $HR_{\text{TerrDensNatal}}$ : 1.09, CI: 0.97–1.22,  $p=0.148$ ), but higher risk was found in the winter season ( $HR$ : 1.38, CI: 1.05–1.81,  $p=0.019$ ) and in natal territories with lower habitat suitability ( $HR$ : 0.81, CI: 0.72–0.90,  $p < 0.001$ ). In the analysis of subadult annual survival, we found higher risk for males ( $HR$ : 2.29, CI: 1.30–4.03,  $p=0.004$ ), although only in the summer ( $HR$ : 0.44, CI: 0.20–0.94,  $p=0.034$ ), and lower risk in final territories with higher habitat suitability ( $HR$ : 0.80, CI: 0.65–0.99,  $p=0.043$ ) and higher local territory density ( $HR$ : 0.67, CI: 0.53–0.85,  $p < 0.001$ ). No significant effect of the habitat suitability of the natal territory was detected ( $HR$ : 0.88, CI: 0.71–1.07,  $p=0.204$ ). Finally, adult annual survival was associated with a lower risk with increasing local territory density ( $HR$ : 0.98, CI: 0.96–0.99,  $p < 0.009$ ).

### Reproduction

We obtained reproduction data from 205 different territories in Germany until the monitoring year 2020. After removing territories with unknown breeding female identity, the

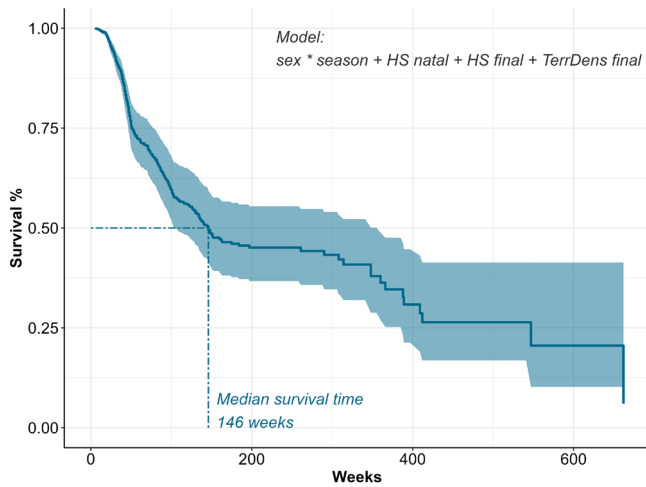


Figure 1. Survival curve obtained in the Cox regression model for the German wolf population. Dashed line indicates the median survival time (146 weeks). Estimates based on the best model for the general population, the full model (model formula in the top right). *HS*: Habitat suitability in 8 km radius, *TerrDens*: local territory density in 50 km buffer.

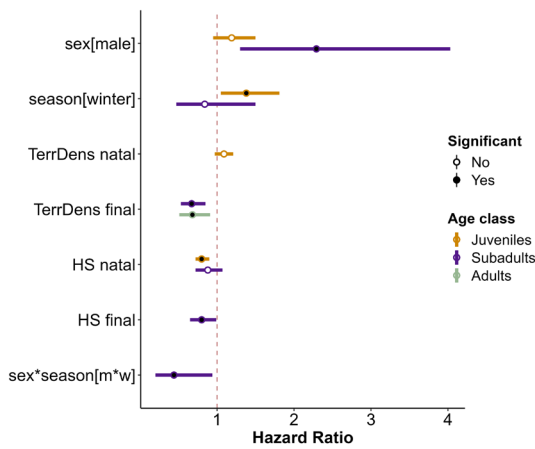


Figure 2. Comparison of the variables and their hazard ratios in the best models for each age class. Variables not depicted in the figure were not included in the best models of the respective age class. For example, the best survival model for adults only included the effects of local territory density, which decreased the risk ( $HR < 1$ ). The model for juveniles included the effects of sex, season, and habitat suitability and local territory density around the natal territory. The model for subadults included all variables except the local territory density around the natal territory. *HS natal*: habitat suitability value in natal territory, *HS final*: habitat suitability value in final territory, *TerrDens natal*: local territory density in 50 km buffer around the individual natal territory, *TerrDens final*: local territory density in 50 km buffer around the individual final territory. Sex [female] and season [summer] are reference levels for the categorical variables, thus the figure shows the contrast for males in winter in relation to these.

dataset consisted of 165 territories from 2002 to 2020, accounting for 201 different breeding females. On average, female experience was 2.81 years, ranging from 1 to 10 years. The observed reproduction probability per territory was  $0.88 \pm 0.045$  SD (Fig. 3). The average number of pups/juveniles representing the minimum reproductive outcome confirmed per reproductive event was 4.08 pups ( $\pm 2.03$  SD), resulting in an average of  $3.72 \pm 2.27$  pups in all reproductive territories when including the zeros.

The best model for probability of reproduction was the model based on territory density, although with AICc values very similar to the null model ( $\Delta AICc = 0.46$ , Supporting information), and with a non-significant effect of the local territory density ( $\beta_{TerrDens} = 0.735 \pm 0.521$ ,  $p = 0.158$ ). This result suggests that none of the analysed variables had a strong effect on the probability of reproduction.

Regarding the reproduction outcome, the best model was the full model containing the interactions between explanatory variables ( $\Delta AICc = 21.40$  with the second best model, Supporting information). This model showed a positive effect of habitat suitability ( $\beta_{HS} = 0.051 \pm 0.026$ ,  $p = 0.048$ ), a positive effect of the experience of the breeding female, which becomes stronger in areas of good habitat suitability during the initial years ( $\beta_{FemExp} = 0.155 \pm 0.038$ ,  $p < 0.001$ ;  $\beta_{FemExp2} = -0.088 \pm 0.039$ ,  $p = 0.024$ ,  $\beta_{HS:FemExp} = 0.153 \pm 0.039$ ,  $p < 0.001$ ;  $\beta_{HS:FemExp2} = -0.159 \pm 0.040$ ,  $p < 0.001$ ), and a negative effect of the local territory density ( $\beta_{TerrDens} = -0.105 \pm 0.019$ ,  $p < 0.001$ ), especially for areas with low suitability ( $\beta_{HS:TerrDens} = 0.044 \pm 0.017$ ,  $p = 0.009$ ) (Fig. 4). This means, for a given habitat suitability, the minimum reproductive output per territory will be smaller at higher territory densities, but this decrease of reproductive output is exacerbated in areas with low habitat suitability.

## Population growth

The observed population growth during the study period was estimated at  $\lambda = 1.32$  from the observed number of territories

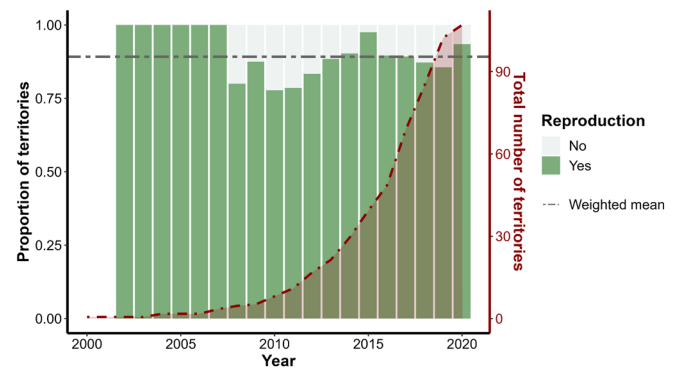


Figure 3. Proportion of wolf territories with and without detected reproduction events over the years. The grey dashed line represents the weighted mean proportion over the whole study period. The red shaded area represents the total number of territories over the years that could potentially reproduce (pack and pair territories from the second year onwards).

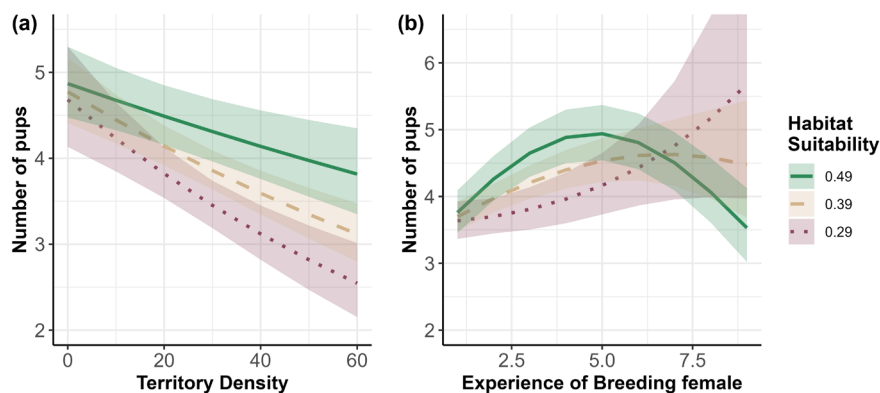


Figure 4. Effects of the Poisson generalized linear mixed model (GLMM) for number of pups in wolf territories. The shaded area represents the confidence zone for the coefficients: (a) Interaction between local territory density and habitat suitability, (b) Interaction between experience of the breeding female in years and habitat suitability. Habitat suitability values used for the effects are the mean (0.39) habitat suitability value observed in the territories with reproduction, and values with  $\pm 0.1$  habitat suitability values as comparison (Observed habitat suitability values ranged from 0.11 to 0.63).

(from 14 pair and pack territories in 2010 to 185 pair and pack territories in 2020). The population matrix model using the survival and reproduction parameters gave a  $\lambda = 1.36 \pm 0.05$  SD, being 4% points higher than the observed growth rate, but still less than one SD, thus validating the estimated parameters. When estimating population growth for low and high habitat suitability areas, we obtained values of 1.22 and 1.48, respectively, indicating the importance of habitat suitability for population development.

## Discussion

Here we present the first demographic analysis of the German wolf population, a recovered population that is rapidly expanding in human-dominated landscapes. Given the large sampling effort during the monitoring of the German wolf population, we could clearly identify the different drivers for survival of the age classes. We found that survival rates are quite high for all age classes of the population, as expected in an expanding population, but especially for adults, whose survival seems to be no longer affected by individual or environmental characteristics. On the other hand, although reproduction probability is high in all territories, individual characteristics, conspecific density and habitat suitability affect the number of pups in each reproductive territory, pointing to strong spatial patterns for demographic parameters in the population.

We found higher survival rates in German wolves than in other populations, probably related to the recent expansion of the species and most of the population being still formed by juvenile and subadult individuals. For example, the highest survival rates for adults observed in other non-hunted populations are around 0.78 in USA (Barber-Meyer et al. 2021) or 0.82 in alpine regions in Europe (Marucco et al. 2009), but well below the 0.88 obtained in this study. It is possible that the arrival of the wolf in a previously unoccupied landscape with high prey densities (Carpio et al. 2021)

and effective legal protection created an ideal combination for the species to thrive. In addition, the high survival values might indicate that the rates of undetected illegal persecution and other human-caused mortality in Germany are so far rather low compared to other regions in Europe (Liberg et al. 2012, Sunde et al. 2021). The official German record of detected illegal kills are given as approx. 10% of all non-natural deaths like road kills (DBBW 2022). In Denmark, on the other hand, annual survival rates range between 0.48–0.54 (Sunde et al. 2021), and the Danish wolf population only survives because it is supported by dispersing animals from Germany. In comparison, the mean survival probability across all age classes of the German wolf population is 0.81. Annual survival values with a calculated high rate of cryptic mortality (Liberg et al. 2012) equal 0.76 in Sweden (Liberg et al. 2020) and 0.24–0.60 in Finland (Suutarinen and Kojola 2017), which led to a population decline especially in Finland some years ago. As the German population expands further and will likely reach saturation in the future, however, we also expect a decrease in the observed survival rates, either due to intraspecific competition or by depletion of resources (Cubaynes et al. 2014). We cannot, however, rule out that we might have overestimated survival rates because cryptic deaths do not account as deaths in the analysis but as unobserved. Unfortunately, we do not have frequent recaptures of the wolf individuals, so we could not construct recapture histories and include detection probability in our analyses, as for example in capture–recapture studies or as in Sunde et al. (2021). Two counteracting biases might level each other out in the method we used: individuals that are alive for some time undetected will result in underestimation of the true survival, while individuals that die without being recorded as dead, e.g. cryptic deaths, will result in an overestimation of the survival rates. However, the CPH method was explicitly designed to account for the ‘disappearance’ of individuals during the study time and it adjusts the estimates at every step for only the existing data at that step, i.e. correcting for the removal of individuals from

the data at any step (Therneau and Grambsch 2000). The inverse fit of our estimates with a matrix model at the population level confirmed that our estimates were in a plausible range, depending on habitat quality and territory density (below). We have to bear in mind that survival rates might change over years, as the wolf population increases, human tolerance decreases and cryptic deaths might increase. Hence, our mean estimates might represent optimistic values.

The minimum reproductive outcome in the German population is low compared to other established populations, which is most likely an artefact of the monitoring. While the German monitoring aims at detecting whether reproduction has happened within packs or not, the number of pups is a non-systematic observation. Hence, reproductive values cannot directly be compared when monitoring methods and efforts are not standardized. Other populations reported higher average numbers of pups, with  $\sim 5$  pups in the Yukon area (Hayes and Harestad 2000), 5.6 pups in Alberta (Webb et al. 2011),  $\sim 6$  pups in Bialowieza (Jeódrzejewska et al. 1996) or  $\sim 4.7\text{--}7.0$  pups in Belarus (Sidorovich et al. 2007), although the differences might not be significant in all cases if there is high variability. However, the observed numbers are considerably higher than the  $\sim 2$  pups observed in the neighbouring central and western Polish population, which is the origin of the German wolves (Nowak et al. 2008). We hypothesize that the high juvenile survival rates (0.75) observed in our data already compensated for the relatively low reproduction output, because pup or juvenile survival is usually lower in other populations, with values  $\sim 0.5$  (Chapron et al. 2003, Bauduin et al. 2020). However, our value should be taken with care, as pups that died early in the season might be undetected, thus the real survival might be lower than the one estimated here.

Variation in survival and reproduction could affect population dynamics. Here, we showed a clear effect of habitat suitability in both survival of juveniles and reproduction. However, the estimated population growth was still above 1 for cases where habitat suitability was low. The population growth values we found corroborate previous growth calculations of the population (Reinhardt et al. 2019, Khorozyan and Heurich 2022). While ecological traps can never be discarded in human dominated landscapes (Bartín 2004, Gilroy and Sutherland 2007), the current German environmental conditions seem to favour wolf expansion. However, there are two caveats that the reader should bear in mind. First, our matrix model assumes an average value for the environmental conditions across Germany. While the survival and reproduction analyses were spatially explicit and depend on habitat quality and territory density, the population growth was estimated in a non-spatial way. Thus, the result only translates to the areas of Germany with those values and, for example, we know that most of Germany is below the average habitat suitability (Planillo et al. 2024a). Second, our analysis only included those individuals for which the birth date was known and for which we had a confirmed genetic identity. Undetected individuals or those that went missing from our dataset might be affected by cryptic mortality (Sunde et al.

2021), and thus, mortality for the species might be higher than the reported one.

An unexpected result is the positive effect of local territory density on survival. Increased wolf density is expected to lower individual survival (Cubaynes et al. 2014, O'Neil et al. 2017). However, when the population is not yet saturated or the main mortality cause is human-related, intraspecific competition might not play a strong role (Hebblewhite and Whittington 2020). In our case, we believe the observed pattern is the result of two phenomena. First, it is likely that the population has not yet reached carrying capacity, as the number of territories in 2020 (197 territories, DBBW database, <https://www.dbb-wolf.de>) is quite far away from the total number of potential territories estimated for Germany ( $\sim 700\text{--}1400$  territories, Kramer-Schadt et al. 2020, Planillo et al. 2024a). Second, the areas with higher number of territories might also be related to areas with continuous, good habitat, thus representing large patches of good habitat that will promote individual survival. Therefore, this trend is susceptible to change in the future as the areas with high habitat suitability will reach carrying capacity and population growth will slow down due to saturation. Actually, the first indication of saturation could be already observed in the most recent monitoring data. The number of packs and territories in Germany grew by 10.7% from 2019 to 2020 (from 178 to 197), while the growth was only 5.9% from 2021 to 2022 (from 220 to 232; DBBW database, <https://www.dbb-wolf.de/home>).

The most vulnerable age class in our survival analyses was the subadult age class, which had the same survival rate as juveniles, but with larger variability. This supports the idea that the dispersing young individuals – mostly subadults – are the section of the population facing the highest risk (Mech and Boitani 2003). The lower survival of subadult males in summer also points in the same direction, as during the dispersing phase some males will move longer distances (Jarausch et al. 2021), thus encountering more risky areas than females staying closer to their natal territory. Regarding the adults, the lack of clear environmental or individual effects and the high annual survival probability are consistent with other studies (Barber-Meyer et al. 2021, Chakrabarti et al. 2022). Individuals surviving to adulthood have already proven their skills and at this stage they already survived most of the risks affecting the other age classes.

Density-dependent effects arise from the reproduction analysis, as also found in other populations (Sidorovich et al. 2007). The lower number of pups detected in areas with higher wolf density may be related to young pup numbers being limited by higher competition for prey with neighbouring packs during the breeding season. In high density areas, territory sizes might get smaller and thus, resource availability scarcer, to which wolves might react with decreasing litter sizes. As the number of pups was not systematically collected across the study area, there is a possibility that less pups were detected in areas with higher wolf density, as the monitoring effort had to be distributed across more territories, thus possibly creating a bias in the data that led to this outcome. Since

monitoring effort was not systematically recorded, we cannot test this hypothesis. On the other hand, habitat quality, although of limited relevance for reproduction in our analyses, was identified by Planillo et al. (2024a) as an important predictor for the total number of reproductions in a territory over the years. As we focused our analyses on a yearly basis, we were not able to detect long-term effects of habitat quality, but it is possible that territories in better habitats areas are more stable, thus accumulating more reproduction events over time.

Finally, experience of the breeding female had different effects depending on habitat quality. The quadratic effect of breeding female experience in good habitats has two potential explanations. On the one hand, females with increasing experience in good areas could be able to successfully raise larger number of pups (Bernardo 1996) or count on helpers that will have a positive impact on pup survival (Sparkman et al. 2011). On the other hand, as survival is higher in good habitats, this effect might arise if double reproduction happens in the territories with high habitat suitability, as the daughters might remain in the maternal territory for longer times and start reproducing in parallel to the main breeding female (unpubl.). In areas with low habitat quality, the increase of the number of pups with female experience occurred much more slowly and in a linear way. We interpret this result in such that the bad habitat is limiting reproduction regardless of female experience, and that the reproductive outcome, counted as number of pups, does not improve until there are enough helpers around the breeding female; the latter can be a result of juveniles from previous years surviving and staying in the pack. More exhaustive data collecting would be needed to separate those effects.

From a conservation perspective, our results highlight that any measure will have a stronger short-term impact on the population in low habitat suitability areas, although actions aiming at the long-term conservation of the species should protect the high suitability areas that could serve as sources for the population in the future.

## Conclusions

Our results provided strong evidence that the German wolf population had high survival and reproduction rates that explained the rapid expansion of the population within the human-dominated German landscapes. Although these rates are unlikely to continue in the future if the population approaches the carrying capacity, they situate the German population as one of the populations with highest recorded survival rates worldwide for the expansion phase. Habitat suitability seems to be the main driver of both demographic parameters, survival and reproduction. Areas with high suitability clearly benefit survival and reproduction, making them sources for the population. In contrast, the effects of low suitability values are less direct. While adults will still survive and establish territories in these areas, low juvenile

and subadult survival as well as reduced number of pups per reproduction will reduce the population growth, thus slowing the spread of the species.

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## Author contributions

**Aimara Planillo:** Conceptualization (equal); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ilka Reinhardt:** Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Gesa Kluth:** Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Sebastian Collet:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Gregor Rolshausen:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Carsten Nowak:** Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Katharina Steyer:** Methodology (equal); Project administration (equal); Writing – review and editing (equal). **Goetz Ellwanger:** Methodology (equal); Project administration (equal); Writing – review and editing (equal). **Stephanie Kramer-Schadt:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

## Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01246>.

## Data availability statement

Data and scripts are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dncjsxm5m> (Planillo et al. 2024b), as well as from the github repositories: [https://github.com/aplanillo/2024\\_WolfDemography\\_Germany](https://github.com/aplanillo/2024_WolfDemography_Germany) or [https://github.com/EcoDynIZW/Planillo\\_2024\\_WILDL-BIOL](https://github.com/EcoDynIZW/Planillo_2024_WILDL-BIOL).

## Supporting information

The Supporting information associated with this article is available with the online version.

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