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Research article

Reproductive success of the wood warbler *Phylloscopus sibilatrix* varies across Europe

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Differences in population trends across a species' breeding range are ultimately linked to variation in demographic rates. In small songbirds, demographic rates related to fecundity typically have strong effects on population trends. Populations of a forest songbird, the wood warbler *Phylloscopus sibilatrix*, have been declining in many but not all regions of the European breeding range. We investigated if clutch size, hatching rate, nest survival and number of fledglings vary across Europe, and if nest survival is related to differences in the regionally dominant nest predator class (birds versus mammals). From 2009 to 2020, we monitored 1896 nests and used cameras at a subsample of 645 nests in six study regions: the United Kingdom (mid-Wales, Dartmoor, the New Forest), Germany (Hessen), Switzerland (Jura mountains) and Poland (Białowieża National Park). Number of fledglings was lowest in the New Forest (1.43 ± 0.23), intermediate in Jura (2.41 ± 0.31) and Białowieża (2.26 ± 0.24) and highest in mid-Wales (3.02 ± 0.48) and Dartmoor (2.92 ± 0.32). The reason for low reproductive success in the New Forest, Jura and Białowieża was low nest survival, and large clutch sizes in Białowieża did not compensate for high nest losses. High reproductive success in mid-Wales and Dartmoor was due to high nest survival and large clutch sizes. Overall predation rates were similar everywhere despite variation between the regions in the dominant nest predator class. Unsuccessful nests in mid-Wales were mainly predated by birds; in Dartmoor, the New Forest, Hessen and Jura similarly by birds and mammals; and in Białowieża exclusively by mammals. Regional reproductive success does not match the population trends recently reported for the wood warbler in the six study regions (i.e. high reproduction \neq positive trend). Annual survival may be a decisive factor, but it is difficult to quantify for a nomadic species such as the wood warbler that rarely returns to the same breeding locations.

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Introduction

Identifying a species' demographic rates (e.g. survival or reproduction) that are responsible for variation in population size is important to understand regional differences in population change (Robinson et al. 2014). Recent studies have suggested that declines of some Afro-Palearctic migratory birds may be related to changes in conditions at non-breeding and stopover sites (Thaxter et al. 2010, Ockendon et al. 2012), suggesting that decreasing survival rates may be implicated. However, declines of migratory birds are not occurring uniformly across their European breeding ranges (Keller et al. 2020), suggesting that conditions in the breeding grounds, and hence reproductive rates, may also be important (Roodbergen et al. 2012, Robinson et al. 2014, Morrison et al. 2016). Important reproductive components are clutch size, hatching rate, nest survival and number of produced fledglings. While the influence of nest survival on populations is studied often (Newton 1998, Shaffer 2004), the influence of the other components is assessed less frequently (Macdonald and Bolton 2008), and even less so across a species' breeding range.

Spatial variation in these reproductive components can influence regional population trends (Newton 1998, Morrison et al. 2016). In altricial birds, the number of fledglings (in our case quantified directly by observation) is directly correlated with clutch size (Moreau 1944, Price and Liou 1989), which has been shown to vary with maternal condition and age, timing of egg laying, local food resources, intraspecific competition and latitude, and is often strongly density dependent (Nicholson 1933, Lack 1947, Ashmole 1963, Foster 1974, Martin 1987, Haywood and Perrins 1992). Hatching success (i.e. hatching rate = eggs hatched/eggs laid) can be influenced by fertilisation rate, incubation behaviour, nest site selection and ambient temperature (Ricklefs 1969, Koenig 1982, Webb 1987, DuRant et al. 2013). Nest survival from egg laying to fledging (i.e. at least one chick survives per nest) is strongly affected by predation, which may depend on landscape fragmentation and farming practices, and can have important implications for avian populations (Nice 1957, Ricklefs 1969, Newton 1998, Roodbergen et al. 2012).

Ground-nesting birds are particularly vulnerable to predators, and increased nest predation has been linked to population declines in a range of species, especially waders (Macdonald and Bolton 2008) but also forest songbirds (Schmidt 2003). However, predator diversity can vary considerably across a species' breeding range (Kurki et al. 1997, Wilson and Arcese 2006, Thompson 2007). As different predators exert different rates of nest predation (Benson et al. 2010), the identity of regionally dominant predator species may strongly influence rates of local nest survival (Rodewald and Kearns 2011, DeGregorio et al. 2014). Hence, spatial variation in dominant nest predators may lead to variation in nest survival and regional differences in population dynamics.

In addition to predation, the timing of failure during the breeding season or nesting cycle may affect demographic rates and consequently population persistence. Failing late during the breeding season (Arnold et al. 2010, Pakanen et al. 2014) or nesting cycle (Grüebler et al. 2015) reduces the chances of re-nesting in the same season and could thereby reduce net reproductive output. This effect may be strongest in birds constrained to short breeding seasons and limited to one or two broods per season (e.g. whinchat *Saxicola rubetra*) (Grüebler et al. 2015). In addition to the reproductive deficit, reproductive costs (e.g. reduced body condition and survival) may be higher if nests fail late during the nesting cycle compared to early failures because parents invest in both incubation and feeding (Brown and Brown 1999, Brinkhof et al. 2002). As the detectability of nests by predators typically increases at the chick stage (i.e. late during the nesting cycle) due to increased adult provisioning activity (Fontaine and Martin 2006, Benson et al. 2010, Weidinger 2010) and chick begging calls (Redondo and De Reyna 1988, Haskell 1994, Martin et al. 2000), regional differences in the relative proportion of predation compared to other nest failures (e.g. desertion) could lead to regional differences in population trends.

We explored patterns of reproduction in an Afro-Palearctic migrant, the wood warbler *Phylloscopus sibilatrix*, across six regions of Europe with different population trends. In general, populations have been declining in northwestern and western Europe since 1980, e.g. in the United Kingdom, Germany and Switzerland (Harris et al. 2020, Knaus et al. 2021), but have remained stable or experienced only slight declines in central and eastern Europe, e.g. in Poland (Keller et al. 2020, Wardecki et al. 2021). However, recent regional population trends (~15 years) suggest that populations in Wales (UK) and Hessen (Germany) are currently stable, while negative in Białowieża National Park (Poland, Table 1).

The wood warbler is a small (10 g), ground-nesting woodland songbird that experiences high rates of nest predation during the spring breeding season in Europe (Wesołowski and Maziarz 2009, Mallord et al. 2012a, Grendelmeier et al. 2015, Bellamy et al. 2018). Females often re-nest following failed attempts within the same breeding season, but subsequent broods appear to be rare after a successful breeding attempt (Glutz von Blotzheim and Bauer 1991). While many different species have been shown to predate wood warbler nests (Mallord et al. 2012a, Grendelmeier et al. 2015, Bellamy et al. 2018, Maziarz et al. 2018, 2019), no range-wide comparison of the relationship between nest survival and predator identity has been made, with a range-wide comparison of reproductive success also lacking.

We tested if 1) clutch size, hatching success, nest survival and/or number of produced fledglings varied between six study regions in western and central Europe, 2) region-specific nest survival was related to regional variation in the predator class (avian versus mammalian) predominantly

Table 1. Description of the six study regions. Population trends refer to the past 15 years, the same period during which data for this study were collected.

Region	Latitude	Longitude	Forest type	Landscape fragmentation	Population	References
Mid-Wales	52°8'N	−3°45'W	Canopy: mostly sessile oak <i>Quercus petraea</i> , few birch <i>Betula pendula</i> and rowan <i>Sorbus aucuparia</i> . Understory: e.g. hazel <i>Corylus avellana</i> , holly <i>Ilex aquifolium</i> , rowan <i>Sorbus aucuparia</i> .	High: Small and scattered forest patches (5–43 ha) within a landscape of pastures, moorland and coniferous plantations.	Stable	Mallord et al. 2012, Bellamy et al. 2018
Dartmoor	50°34'N	−3°47'W	Canopy: mostly sessile and pedunculate oak <i>Quercus robur</i> , few birch, beech <i>Fagus sylvatica</i> and sycamore <i>Acer pseudoplatanus</i> . Understory: e.g. hazel, holly, rowan.	High: Continuous small forest patches along three river valleys (5–11 km) within a grazed open upland landscape.	Negative	Bellamy et al. 2018, Castelló and Burgess 2019
New Forest	50°52'N	−1°38'W	Canopy: birch, beech, ash <i>Fraxinus excelsior</i> , larch <i>Larix</i> sp. and Douglas fir <i>Pseudotsuga menziesii</i> . Understory: e.g. hazel, holly, rowan.	High: One continuous forest patch (11 km ²) with open areas, i.e. grazed wood pastures and lowland heath.	Negative	Ward and Wynn 2012, Bellamy et al. 2018, pers. obs. M. Ward and T. Davis
Hessen	50°57'N	8°55'E	Canopy: mostly beech, interspersed with spruce <i>Picea abies</i> . Understory: e.g. beech and field maple <i>Acer campestre</i> .	Medium: Three continuous forest patches (10–30 km ²) surrounded by agriculture and pastures.	Positive	Gerlach et al. 2019, Stelbrink et al. 2019, pers. comm. S. Trautmann
Jura	47°23'N	7°35'E	Canopy: mostly beech, some sessile and pedunculate oak, few pine <i>Pinus sylvestris</i> , spruce and fir <i>Abies alba</i> . Understory: e.g. beech, field maple, rowan.	Medium: Large but discontinuous forest area (460 km ²) interspersed by agriculture and pastures.	Negative	Pasinelli et al. 2016, Knaus et al. 2021
Białowieża	52°44'N	23°53'E	Canopy: mostly pedunculate oak, hornbeam <i>Carpinus betulus</i> and lime <i>Tilia cordata</i> , with Norway maple <i>Acer platanoides</i> and spruce. Structural diversity: tree species at different ages. Understory: mainly hazel and young canopy trees.	Low: Strictly protected fragment of a large continuous forest area (550 km ² ; Polish part), retaining primeval character. Bordered in the south by agriculture and pastures.	Negative	Wesołowski et al. 2015, pers. comm. G. Neubauer

predating wood warbler nests and 3) nest survival and nest predation were lower at the egg than the chick stage.

Materials and methods

Study sites

The fates of 1896 wood warbler nests were monitored over multiple years in six study regions across Europe (Supporting information): Mid-Wales (MW, n=168, 2009–2011), Dartmoor (DM, n=364, 2009–2019) and the New Forest (NF, n=105, 2011–2013) in the UK; Hessen in Germany (HE, n=207, 2014–2015 and 2020); Jura mountains in Switzerland (JR, n=326, 2010–2015 and 2017–2020); and Białowieża National Park (hereafter 'Białowieża') in Poland (BW, n=720, 2009–2012 and 2015–2020). These regions

represent the western and central parts of the wood warbler breeding range. At 645 of 1896 nests, camera traps were deployed to identify nest predators (MW=73, DM=65, NF=45, HE=89, JR=289, BW=84; see Supporting information for detailed sample sizes). The observations were carried out in the main types of preferred wood warbler habitat, in broadleaved or mixed broadleaved–conifer forests with closed canopy and sparse understory. Detailed habitat descriptions of the six study regions can be found in Table 1.

Nest monitoring

Surveys to locate wood warbler territories (i.e. singing males) lasted from male arrival in mid-April to the end of the breeding season in mid-July. Once males were paired, females were closely observed to locate nests. Nests were thereafter visited regularly, usually every 1–6 days

(Wesołowski and Maziarz 2009, Mallord et al. 2012a, Grendelmeier et al. 2015), to estimate first egg laying date, clutch size, egg hatching date, number of hatchlings, date of failure or fledging and number of fledglings. Nests that were abandoned before egg laying (i.e. during nest building) were not included in the analysis. First egg laying dates were determined either directly for nests found before or during egg laying ($n=1333$) or, for nests found later, by back-calculating based on the hatching date or developmental stage of the chicks ($n=563$) (Wesołowski and Maziarz 2009, Mallord et al. 2012a, Grendelmeier et al. 2015). If hatching or fledging took place between two visits, we used the median date between the visits immediately before and after hatching or fledging, respectively. The number of fledglings was assumed to equal the number of nestlings found at the previous visit (approx. $n=700$ nests out of 1896). Hatching date was used to define the stage during the nestling cycle when nest failure occurred, i.e. egg or chick stage. On average, the egg stage was 19 days (= 6 days of egg laying + 13 days of incubation) and the chick stage 14 days (= 1 day of hatching + 13 days nestling period), with fledging taking place 33 days after the date of first egg laying. Our estimates are consistent with those reported in the literature (Glutz von Blotzheim and Bauer 1991).

To identify nest predators, most cameras were deployed at a subsample of nests found during the nest-building or egg stage, and then redeployed at other nests at any stage to maximise the number of nests monitored by cameras. Depending on the deployment date, the first egg laying date, clutch size, hatching date, number of hatchlings, date of failure or fledging and number of fledglings could be determined from camera footage. Cameras used in the UK (MW, DM, NF) were custom-built (Bolton et al. 2007) and deployed at 0.5–1.5 m from the nests (Mallord et al. 2012a, Bellamy et al. 2018, Maziarz et al. 2018). In Hessen, Jura and Białowieża, Reconyx trail cameras (Reconyx Inc., Holmen, WI, USA) were used and deployed at 1–2 m from nests (Grendelmeier et al. 2015, Maziarz et al. 2019). Nest failure included predation and non-predation causes (e.g. desertion, trampling), the latter being hereafter referred to as ‘other failure’. All nests from which at least one young fledged were categorised as successful nests, including partially predated nests. We grouped predator species into mammalian, avian and unknown predators for the predation probability analysis (see Statistical analysis). We assigned domestic cats and dogs to the mammal category, as these show similar hunting behaviour to other mammals (Chalfoun et al. 2002). A detailed list of all detected predator species is provided in the Supporting information.

In some cases, fledging was not recorded on the camera traps, or nest predators could not be identified. In these cases, nest fate was based on the state of nests and their surroundings. Successful fledging was inferred if at least one fledgling, fresh droppings or adults carrying food were found near the empty nest. Predation was inferred from signs such as torn-apart nesting material or remnants of eggs, chicks and/or an adult, or an intact nest empty at a time when eggs or nestlings should have been present. If a nest was deserted with its

contents intact, or signs of trampling were evident, the nest was treated as other failure (Maziarz et al. 2019).

In Hessen (2015 and 2020), 62 nests included in this study were exposed to predator playbacks (red fox *Vulpes vulpes*, pine marten *Martes martes*, stone marten *M. foina*, tawny owl *Strix aluco*, common buzzard *Buteo buteo*, Eurasian sparrowhawk *Accipiter nisus* and Eurasian jay *Garrulus glandarius*) to test if simulated predation risk affected wood warbler reproduction. In Jura (2013, 2014, 2017 and 2018), 43 nests were exposed to playback of conspecific songs to test if a simulated increase in density affected reproduction. Neither predator nor conspecific treatments affected the reproductive performance of wood warblers (Grendelmeier et al. 2017, Stelbrink et al. 2019, Riess 2021), and so we considered them valid for inclusion in the current study.

Statistical analysis

Number of fledglings

We analysed the number of fledglings observed per nest ($n=1859$) with a zero-inflated Poisson mixed effects model using the R (<www.r-project.org>) library *glmmTMB* (Brooks et al. 2017). We included a six-level categorical variable *region* (MW, DM, NF, HE, JR, BW) to investigate differences in the number of fledglings produced between study regions. We used the random terms *year* and *region-year* to account for both overall annual variation (i.e. 2009, 2010, etc.) and region-specific annual variation (i.e. MW-2009, MW-2010, etc.; DM-2009, DM-2010, etc.) in wood warbler reproduction.

Clutch size

We analysed clutch size observed per nest ($n=1565$) with a linear mixed effects model using the R library *lme4* (Bates et al. 2014). We included *region* and a continuous variable *first egg* laying date to account for declining trends of clutch size during a breeding season (Winkler and Allen 1996). Here, we only used the random term *region-year* due to model-convergence issues when including both *year* and *region-year*. We decided to include *region-year* rather than *year* because in the other models within-region year variance was larger than among-region year variance (Table 2, 4 and 5).

Hatching rate

We analysed the proportion of chicks hatched per clutch (eggs hatched/clutch size, $n=737$) with a binomial mixed effects model weighted by clutch size using the R library *lme4*. We included *region* and the random terms *year* and *region-year*. The sample size was lower than in the above analyses because we only included successful nests for which both clutch size and number of hatchlings were known.

Nest survival

We quantified the daily nest failure rate of all nests ($n=1896$) by comparing lost (predation and other failure combined) to successful nests, using a Cox proportional hazard model with mixed effects in the R library *coxme* (Therneau 2018). Sample

Table 2. Top: Model output of number of fledglings per nest in relation to region. The model estimate (Est), standard error (SE) and significance (p) are reported for each variable of a zero-inflated Poisson mixed effects model. The model consisted of two parts, a Poisson part estimating the number of fledglings in successful nests and a zero-inflation part estimating the proportion of lost nests (binomial). p-values are valid only for the comparison to the baseline level (i.e. *regionBiałowieża*). See Supporting information for comparisons between other pairs of regions. Middle: Variance (Var) and standard deviation (SD) of random effects. Bottom: Model predictions (Pred) and 95% confidence intervals (CI) of, and contribution of Poisson (Poi) and zero-inflation (Zi) parts to the number of fledglings in each region. Predictions are the product of the two model parts: $Pred = Poi \times (1 - Zi)$.

Variable	Est	SE	p		
Poisson fixed effects					
intercept	1.73	0.03	0.000		
regionJura	−0.17	0.04	0.000		
regionHessen	−0.09	0.05	0.061		
regionNew Forest	−0.26	0.09	0.003		
regionDartmoor	−0.10	0.04	0.015		
regionMid-Wales	−0.07	0.05	0.166		
Variable	Est	SE	p		
Zero-inflation fixed effects					
intercept	0.41	0.08	0.000		
regionJura	−0.43	0.14	0.002		
regionHessen	−0.45	0.16	0.005		
regionNew Forest	0.31	0.22	0.169		
regionDartmoor	−0.69	0.13	0.000		
regionMid-Wales	−0.71	0.18	0.000		
Variable	Var		SD		
Random effects					
year	6.48e ^{−11}		8.05e ^{−6}		
region-year	2.64e ^{−10}		1.63e ^{−5}		
Region	Pred	2.5 CI	97.5 CI	Poi	Zi
Model predictions					
Białowieża	2.26	2.02	2.49	5.66	0.60
Jura	2.41	2.10	2.72	4.76	0.49
Hessen	2.62	2.21	3.04	5.14	0.49
New Forest	1.43	0.98	1.88	4.36	0.67
Dartmoor	2.92	2.61	3.24	5.12	0.43
Mid-Wales	3.02	2.55	3.50	5.26	0.43

size was higher compared to the above analyses because, for some nests, the number of fledglings ($n=31$) or clutch size ($n=325$) was unknown. In our analysis, the hazard ratio $h[t]$ represents the ratio of hazard (i.e. nest failure) between two groups (e.g. regions or nest stages) for a given time step and was calculated at daily intervals. The hazard ratio is interpreted as the instantaneous rate of occurrence of nest failure in nests remaining at risk. The coefficients reported in the Cox model can be interpreted as the multiplicative effect of each explanatory variable on the hazard ratio, i.e. the relative influence of a variable on the daily nest failure rate (Therneau 2018). We assigned separate starting dates (i.e. day zero) to the egg and chick stage, with the egg stage starting at laying of the first egg and the chick stage starting at hatching. We left-censored nests found after first egg laying and hatching, respectively, by including them only from the day they were found. We right-censored nests that hatched/fledged successfully by labelling them as 'still alive' on the day of hatching/fledging (Fox and Weisberg 2011).

We included *region*, a two-level categorical variable nest *stage* to compare nest survival between the egg and chick stage, a two-level categorical variable *camera* (present versus

absent) to control for potentially disturbing effects, and an interaction term between *region* and *stage* to account for region-specific differences in nest survival between the egg and chick stage. We used the random terms *year* and *region-year*, and *nest* identity to account for multiple data points (one point for each day) contributed by each nest. In all the above analyses, we tested a priori hypotheses at the significance level of 5% ($p=0.05$) based on Wald statistics. To identify significant differences between each pair of study regions (i.e. factor levels of the region variable), we assigned the base level (i.e. intercept) to each of the six study regions in turn (pairwise p-values in Supporting information).

Predation probability by predator class

We quantified the probability of failed nests being predated by different predator classes or lost due to other reasons. In this analysis we only used unsuccessful nests with cameras ($n=335$ nests of 645 nests with cameras, Supporting information). We used a Bayesian multinomial mixed effects model with a four-level response variable (avian, mammalian, unknown predator, other failure) and default priors implemented in the R library *brms* (Bürkner 2017).

Table 3. Top: Model output of clutch size in relation to region and first egg laying date. The model estimate (Est), standard error (SE) and significance (p) are reported for each variable of a linear mixed effects model. For the variable *region*, p-values are valid only for the comparison to the baseline level (i.e. *regionBiałowieża*). See Fig. 2 and Supporting information for comparisons between other pairs of regions. Middle: Variance (Var) and standard deviation (SD) of the random effect. Bottom: Model predictions (Pred) and 95% confidence intervals (CI) of clutch size in each region.

Variable	Est	SE	p
Fixed effects			
intercept	11.66	0.22	0.000
regionJura	−0.41	0.10	0.000
regionHessen	−0.49	0.13	0.001
regionNew Forest	−0.50	0.14	0.001
regionDartmoor	−0.23	0.10	0.025
regionMid-Wales	−0.15	0.13	0.261
first egg	−0.04	0.00	0.000
Variable	Var	SD	
Random effects			
region-year	0.0307	0.1751	
Region	Pred	2.5 CI	97.5 CI
Model predictions			
Białowieża	6.15	6.02	6.28
Jura	5.74	5.60	5.88
Hessen	5.66	5.42	5.89
New Forest	5.65	5.40	5.90
Dartmoor	5.92	5.78	6.06
Mid-Wales	6.00	5.76	6.23

Non-mammalian/non-avian predators accounted for only four predation events (two European adders *Vipera berus* and two slugs *Arion* sp., Supporting information), so we included them with unknown predators ($n = 42$) to improve the model fit. As our focus was on the difference between mammalian ($n = 136$) and avian ($n = 107$) predators, pooling did not interfere with testing of our hypothesis. Owing to the small sample size, we here replaced the six-level variable *region* with a four-level variable *country*, including the UK (pooling MW, DM and NF), Germany (= HE), Switzerland (= JR) and Poland (BW). We further included nest *stage* and an interaction between *country* and *stage*, and the random term *region-year*. We tested a priori hypotheses based on 95% credibility intervals (2.5 CrI, 97.5 CrI) derived from the posterior distributions. Significant results are defined by credibility intervals not overlapping with zero.

Results

Number of fledglings

The mean number of fledglings produced per nest was significantly lower in the New Forest than in all other study regions (Fig. 1). In addition, the number of fledglings was higher in mid-Wales and Dartmoor than in Jura and Białowieża (Fig. 1). The model predictions shown in Fig. 1 are the product of the Poisson (Poi; non-zero nests; fledgling count ≥ 1) and zero-inflation (Zi; zero versus non-zero nests;

Table 4. Top: Model output of hatching rate in relation to region. The model estimate (Est), standard error (SE) and significance (p) are reported for each variable of a binomial mixed effects model. P-values are valid only for the comparison to the baseline level (i.e. *regionBiałowieża*). See Fig. 3 and Supporting information for comparisons between other pairs of regions. Middle: Variance (Var) and standard deviation (SD) of random effects. Bottom: Model predictions (Pred) and 95% confidence intervals (CI) of hatching rate in each region.

Variable	Est	SE	p
Fixed effects			
intercept	2.68	0.13	0.000
regionJura	−0.30	0.19	0.115
regionHessen	−0.40	0.24	0.088
regionNew Forest	−0.61	0.32	0.054
regionDartmoor	−0.58	0.18	0.001
regionMid-Wales	−0.51	0.24	0.032
Variable	Var	SD	
Random effects			
region-year	0.0245	0.1566	
year	0.0260	0.1611	
Region	Pred	2.5 CI	97.5 CI
Model predictions			
Białowieża	0.94	0.92	0.95
Jura	0.92	0.89	0.94
Hessen	0.91	0.87	0.94
New Forest	0.89	0.83	0.94
Dartmoor	0.89	0.87	0.92
Mid-Wales	0.90	0.86	0.93

binomial) parts of the zero-inflated Poisson mixed effects model (Table 2; $\text{Pred} = \text{Poi} \times (1 - \text{Zi})$). The contributions by each model part are presented separately in Table 2. While p-values are provided for differences between study regions in the separate model parts (Table 2, Supporting information), differences in the combined estimate ($\text{Pred} = \text{Poi} \times (1 - \text{Zi})$) are significant if the confidence interval of one region does not overlap the mean of another region (Fig. 1, Table 2).

Two study regions may vary significantly in both the number of fledglings produced in live nests (Poi) and the proportion of nests that were lost (Zi), but not in the combined estimate because the two effects can cancel each other out. For example, the number of fledglings produced in live nests in Jura (4.76) was significantly lower than in Białowieża (5.66), but the proportion of lost nests in Białowieża (0.60) was significantly higher than in Jura (0.49), resulting in a similar total production of fledglings (Białowieża = 2.26, Jura = 2.41, Table 2). Comparisons between predicted model averages and distribution of the raw data are provided in the Supporting information (a, number of fledglings; b, clutch size; c, hatching rate).

Clutch size

Mean clutch size was significantly higher in Białowieża than in the other study regions except mid-Wales (Fig. 2, Table 3). Clutch size was marginally higher in mid-Wales and Dartmoor than in the New Forest, Hessen and Jura (i.e.

Table 5. Top: Model output of daily nest failure rate in relation to region, nest stage and presence of camera. The hazard ratio ($h[t]$), coefficient (Coef), standard error (SE) and significance (p) are reported for each variable of a Cox mixed effects model. An $h[t] < 1$ indicates a reduced hazard of nest failure, an $h[t] > 1$ indicates an increased hazard of nest failure. A positive Coef denotes a positive effect on the nest failure rate, but a negative effect on the survival rate. For the variable region, p -values are valid only for the comparison to the baseline level (i.e. *regionBiałowieża*). See Fig. 4 and Supporting information for comparisons between other pairs of regions. Middle: Variance (Var) and standard deviation (SD) of random effects. Bottom: Model predictions (Pred) and 95% confidence intervals (CI) of nest survival to 33 days (days 0–33) in each region.

Variable	h[t]	Coef	SE	p
Fixed effects				
regionJura	0.91	−0.09	0.21	0.660
regionHessen	0.73	−0.31	0.25	0.210
regionNew Forest	1.21	0.19	0.30	0.530
regionDartmoor	0.69	−0.37	0.21	0.077
regionMid-Wales	0.68	−0.39	0.29	0.180
nest_stageChick	3.19	1.16	0.11	0.000
camera	1.02	0.02	0.10	0.840
regionJura:stageChick	0.91	−0.09	0.20	0.640
regionHessen:stageChick	1.00	0.00	0.22	0.990
regionNew Forest:stageChick	1.20	0.19	0.29	0.520
regionDartmoor:stageChick	0.89	−0.12	0.20	0.550
regionMid-Wales:stageChick	0.94	−0.06	0.28	0.830
Variable			Var	SD
Random effects				
year			0.0004	0.0203
region-year			0.0631	0.2512
nestID			0.0004	0.0198
Region		Pred	2.5 CI	97.5 CI
Model predictions				
Białowieża		0.37	0.34	0.41
Jura		0.41	0.35	0.48
Hessen		0.45	0.38	0.53
New Forest		0.23	0.15	0.33
Dartmoor		0.49	0.44	0.55
Mid-Wales		0.51	0.43	0.60

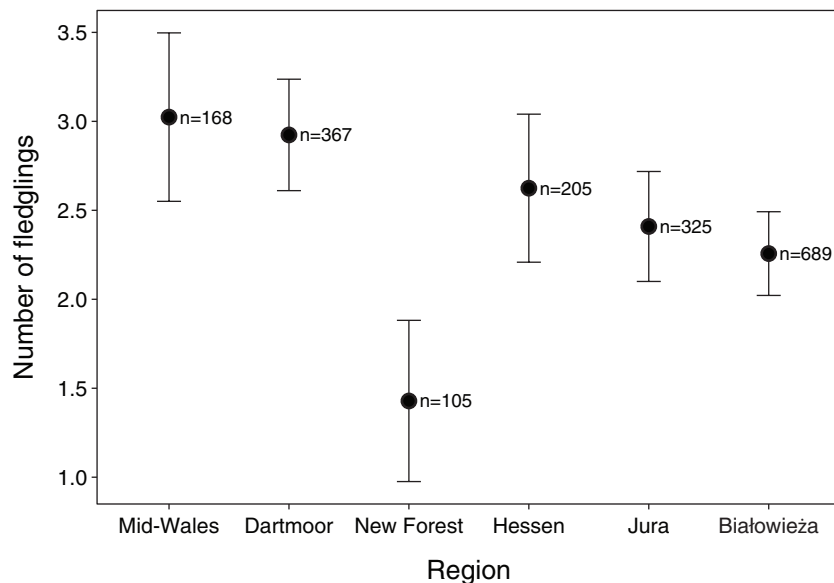


Figure 1. Mean number of wood warbler fledglings per nest in six study regions. Shown are model predictions and 95% confidence intervals of a zero-inflated Poisson mixed effects model. Two populations are significantly different from another if means and confidence intervals do not overlap.

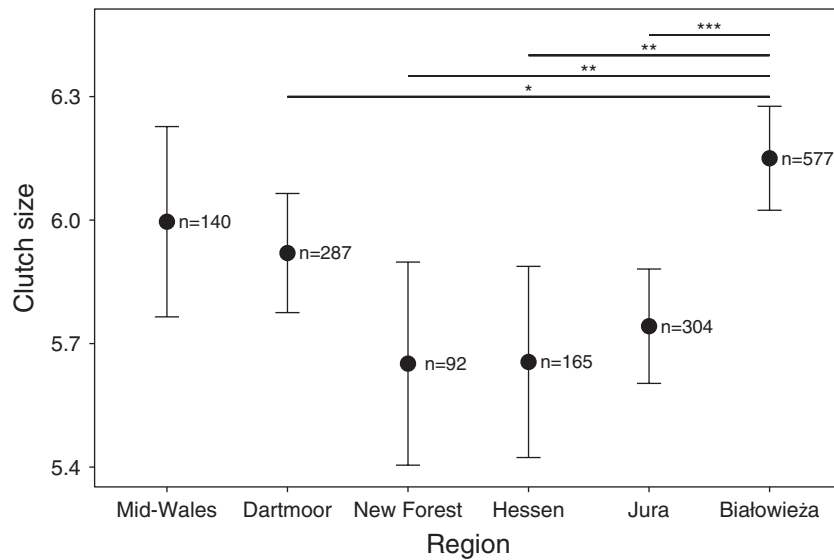


Figure 2. Mean wood warbler clutch size in six study regions. Shown are model predictions and 95% confidence intervals of a linear mixed effects model. Significant differences between population means (at end point of lines) are indicated by (*) $p < 0.05$, (**) $p < 0.01$ and (***) $p < 0.001$.

at the 10% significance level, Supporting information). In all study regions, clutch size decreased with increasing egg laying date (Table 3), with the peak of egg laying occurring earlier in Białowieża than in the other regions (Supporting information).

Hatching rate

The proportion of eggs hatched was significantly higher in Białowieża than in mid-Wales and Dartmoor (Fig. 3, Table 4), and marginally higher than in the New Forest and Hessen (Table 4).

Nest survival

The daily hazard of nest failure was not significantly different between the study regions (Fig. 4, Table 5, Supporting information). However, the small but non-significant differences in daily nest failure rates led to significant differences in overall nest survival (i.e. survival to 33 days after egg laying) between some study regions: lower in the New Forest than elsewhere, lower in Białowieża than mid-Wales, Dartmoor and Hessen, and lower in Jura than mid-Wales and Dartmoor (Table 5, no overlap between prediction means and confidence intervals). In summary, mid-Wales had the highest

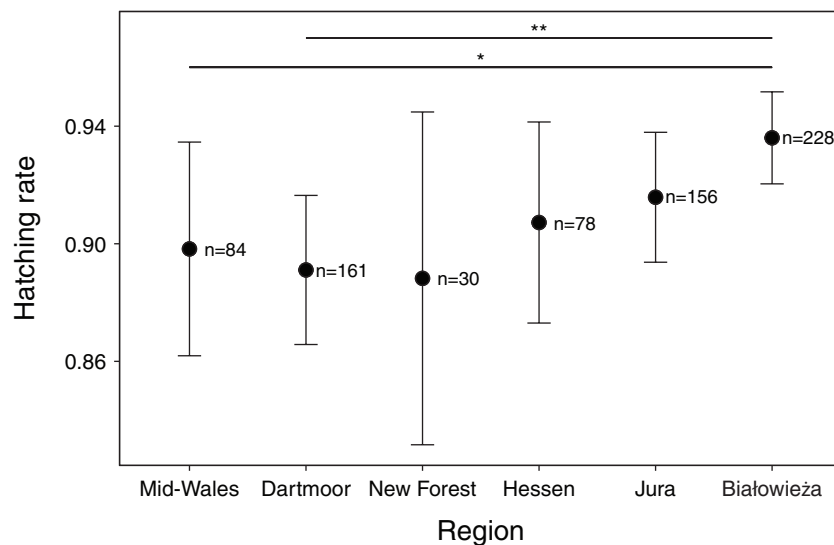


Figure 3. Mean wood warbler hatching rate in six study regions. Shown are model predictions and 95% confidence intervals of a binomial mixed effects model. Significant differences between population means (at end point of lines) are indicated by (*) $p < 0.05$, (**) $p < 0.01$ and (***) $p < 0.001$.

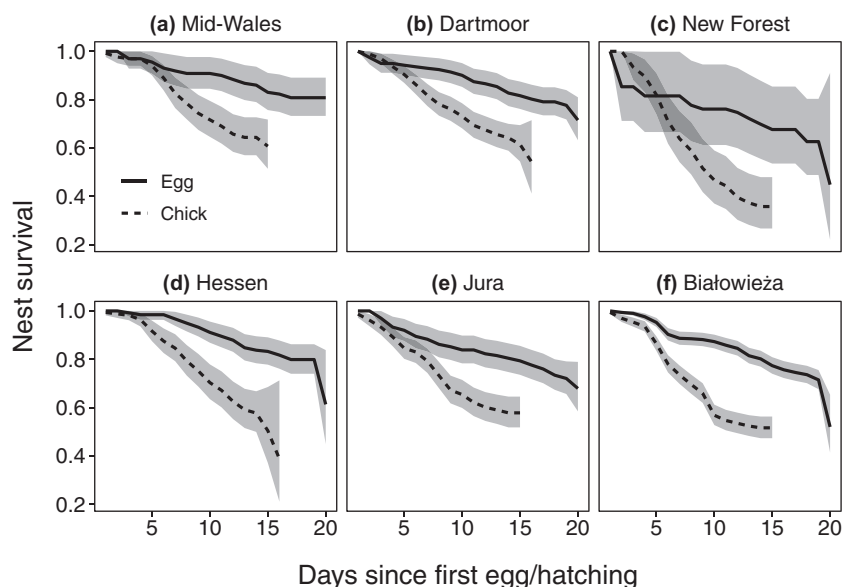


Figure 4. Daily survival rates of wood warbler nests in six study regions, starting on the day of first egg laying for the egg stage, and on the day of hatching for the chick stage. Survivorship curves and 95% confidence intervals were predicted by a Cox mixed effects model (MW = 168, DM = 365, NF = 105, HE = 207, JR = 326, BW = 720).

and the New Forest the lowest nest survival to 33 days. In all study regions, the daily rate of failure at the egg stage was significantly lower than at the chick stage (Fig. 4, Table 5). The interaction between region and nest stage was not significant (Table 5, Supporting information), confirming that the lower rate of nest failure at the egg than chick stage was consistent across regions. Raw data are provided in the Supporting information, which shows the number of censored nests on every given day.

Predation probability by predator class

The subsample of 335 unsuccessful nests with cameras showed that predation was the main cause of nest failure in all regions (Fig. 5). However, despite overall similar levels of predation, the probability of predation by either predator class varied among regions: nests in mid-Wales were mostly predated by avian predators (Fig. 5, Supporting information, total $n = 34$ failed nests), whereas nests in Białowieża were only known to be predated by mammals (Fig. 5, Supporting information, $n = 37$). Nests in Dartmoor ($n = 45$), the New Forest ($n = 33$), Hessen ($n = 46$) and Jura ($n = 140$) were predated by both avian and mammalian predators (Fig. 5, Supporting information).

Across both nest stages, avian predation probability was not significantly different among the UK (i.e. MW, DM, NF), Germany (i.e. HE) and Switzerland (i.e. JR), while mammalian predation probability was significantly higher in Poland (i.e. BW) and Switzerland than in the UK (Table 6). At the egg stage, predation (avian and mammalian) and other failures (e.g. desertion) occurred with similar probability, whereas, at the chick stage, predation was more likely than other failures (Fig. 6). At the chick stage, nests in the UK were more frequently predated by birds than mammals,

in Germany similarly by both, and in Switzerland more by mammals than birds (Fig. 6).

Jays were the avian predators most often recorded in mid-Wales, the New Forest, Hessen and Jura, and buzzards in Dartmoor (Supporting information). Pine martens were the mammalian predators most often recorded in Jura, foxes in Białowieża, European badgers *Meles meles* in Dartmoor and the New Forest, and raccoons *Procyon lotor* in Hessen (Supporting information).

Discussion

The number of fledglings produced from wood warbler nests was lowest in the New Forest, intermediate in Jura and Białowieża National Park, and greatest in mid-Wales and Dartmoor. Thus, in general, regional differences in population trends do not appear to track regional differences in reproduction, except for the New Forest and Białowieża, where reproductive success was low and population trends are declining (Supporting information). The low reproductive success in the New Forest, Jura and Białowieża was mainly due to low total nest survival (i.e. survival to 33 days). Although clutch sizes were large in Białowieża, this could not compensate for the low nest survival. The high reproductive success in mid-Wales and Dartmoor was due to higher nest survival and relatively large clutch sizes (marginal significance, Supporting information). The main cause of nest failure was predation in all countries, but the ratio of nest predators (birds versus mammals) varied among countries. In mid-Wales, nests were mainly predated by birds, while in Białowieża, nests were exclusively predated by mammals.

A possible explanation for larger clutch sizes in Białowieża, and to a lesser degree in mid-Wales and Dartmoor, is the

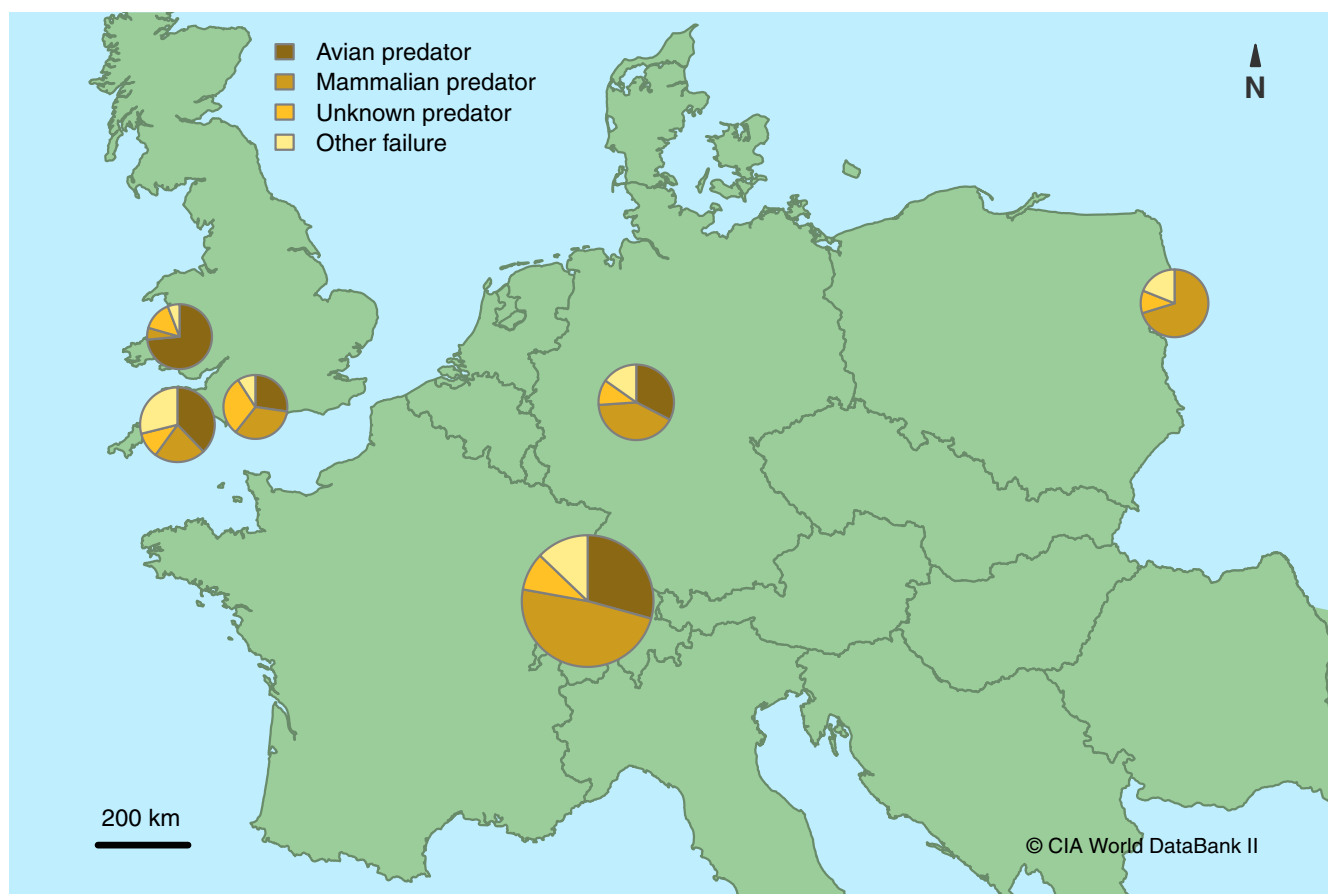


Figure 5. Causes of wood warbler nest failure in the study regions mid-Wales, Dartmoor, the New Forest, Hessen, Jura and Białowieża (from west to east). Diagrams show the proportion of avian, mammalian and unknown predators, and the proportion of other failures (e.g. desertion, trampling). Shown are raw data of 335 unsuccessful nests monitored with cameras (MW = 34, DM = 45, NF = 33, HE = 46, JR = 140, BW = 37).

more northern locations of these two study regions compared to the others (Supporting information). Clutch size typically increases with increasing latitude due to increased foraging hours owing to longer days (Lack 1947) and/or by a combination of high seasonal food availability and relatively low adult density (Ashmole 1963). Lack's (1947) hypothesis may be more applicable to wood warblers than Ashmole's (1963), as wood warbler densities are higher in Białowieża than in western regions (Wesołowski et al. 2006, Keller et al. 2020). However, large clutch sizes in Białowieża did not translate to stable or positive population trends (Supporting information), which may instead be related to annual survival and conditions faced on migration, at stopover areas, or in wintering grounds (Sanderson et al. 2006, Hewson and Noble 2009, Morrison et al. 2013). It should be noted though, that wood warblers exhibit low breeding site philopatry and are nomadic during the breeding season (Herremans 1993, Wesołowski et al. 2009), so conclusions about the effect of survival and reproduction for population dynamics are likely to require a large-scale perspective rather than a local one.

Although the low reproductive success in the New Forest and Białowieża was caused by low nest survival, the underlying cause of this low nest survival is difficult to explain. This

is especially true for the New Forest, where reproductive success and nest survival were particularly low, and where we could not statistically evaluate if predation rates were higher than elsewhere, owing to the small sample size (study regions of the UK were pooled for the predator analysis). The raw data indicate that predation was higher in the New Forest than anywhere else, with the proportion of unidentified predators being particularly high (17.8%, Supporting information). Since badgers preyed on nests relatively often in the New Forest (8.9%), and adders were observed only there (Supporting information), these two predators may also have accounted for some of the unknown predators, which could have had an impact on nest survival at this site. However, nest cameras were not deployed in all study years (Supporting information) and, therefore, the results shown in Supporting information have a limited explanatory power. The incomplete coverage by nest cameras also explains why the descriptive nest survival (Supporting information) in some cases varies from the estimate of the Cox hazard model, which included all study years (Table 5). An additional explanation for the high nest predation rates in the New Forest is a low cover of the field layer due to high grazing pressure (Bellamy et al. 2018), potentially reducing nest concealment.

Table 6. Top: Model output of predation probability by avian, mammalian and unknown predators, and failure due to other causes in relation to country and nest stage. The model estimate (Est) and 95% credibility interval (2.5% CrI, 97.5% CrI) are reported for each variable of a Bayesian multinomial mixed effects model. Unknown predators are the reference level of the multinomial response variable and complement all other levels (birds, mammals, other failures) to one. For the response variable *country*, CrI are valid only for the comparison to the baseline level (i.e. *countryUK*). See Fig. 6 for a visual comparison of all levels (response and explanatory). Because birds were not observed as nest predators in Poland, model uncertainties were high and results for birds in Poland should be ignored. Bottom: Estimate and 95% credibility interval of the random effect *region-year* for each level of the response variable.

Variable	Est	2.5 CrI	97.5 CrI
Fixed effects			
Bird			
intercept	−0.06	−1.58	1.48
countryPoland	−68.92	−294.64	−1.25
countryGermany	0.16	−2.72	3.01
countrySwitzerland	2.24	0.04	4.69
stageChick	1.30	−0.22	2.87
countryPoland:stageChick	17.71	−130.33	223.27
countryGermany:stageChick	0.34	−2.65	3.46
countrySwitzerland:stageChick	−2.57	−5.16	−0.29
Mammal			
intercept	−0.72	−2.51	0.90
countryPoland	3.38	0.44	7.19
countryGermany	1.58	−1.04	4.37
countrySwitzerland	3.19	0.94	5.77
stageChick	0.92	−0.73	2.71
countryPoland:stageChick	−1.60	−5.55	1.58
countryGermany:stageChick	−0.30	−3.21	2.46
countrySwitzerland:stageChick	−1.88	−4.53	0.48
Other failure			
intercept	0.34	−1.16	1.87
countryPoland	1.99	−1.16	5.88
countryGermany	1.30	−1.42	4.32
countrySwitzerland	1.33	−0.99	3.85
stageChick	−1.07	−2.68	0.46
countryPoland:stageChick	−3.22	−8.11	0.69
countryGermany:stageChick	−1.77	−5.85	1.68
countrySwitzerland:stageChick	−0.72	−3.37	1.74
Region-year			
	Est	2.5 CrI	97.5 CrI
Random effects			
interceptBird	0.50	0.03	1.16
interceptMammal	0.63	0.08	1.27
interceptFailure	0.94	0.27	1.78

As in many other ground-nesting bird species (Nice 1957, Ricklefs 1969), predation was the major cause of nest failure in wood warblers. However, while predation-related nest failures have been suggested to drive population changes in some bird species (Newton 1998), we found no evidence of regional variation in wood warbler nest predation rates. This finding is not completely surprising, as ground-nesting birds are typically adapted to high predation rates, and some ground-nesting woodland songbirds have been shown to have stable populations despite high nest failure rates resulting from predation (Schmidt 2003). For example, songbird populations in oak woods of southeastern England remained stable when populations of Eurasian sparrowhawk, an important nest predator able to consume large numbers of prey, increased as their numbers recovered after local extirpation (Newton 1998). Hence, bird populations may depend on compensatory reductions in other losses or improved reproduction in areas with high predation.

Our results showed that predation by birds and mammals was the most important cause of nest failure at the chick stage, but not at the egg stage, where desertion (other failures) was as likely as predation. Although each separate cause of failure (birds, mammals and desertions) did not significantly differ between the egg and chick stages, overall predation was higher at the chick than egg stage, leading to lower nest survival at the chick stage. Similar patterns of nest predation have been found in different habitats, where raptors (Benson et al. 2010, Rodewald and Kearns 2011) and medium-sized mammals (Teunissen et al. 2008, Maziarz et al. 2019) were shown to predate chicks more often than eggs. Increased predation during the chick stage may lower the chances of producing another brood (Grüebler et al. 2015), which could reduce the net annual reproductive output and have a negative effect at the population level. In contrast, if nest failure occurs at the egg stage, parents do not have to invest in provisioning of young, which may improve parental survival and chances for another brood.

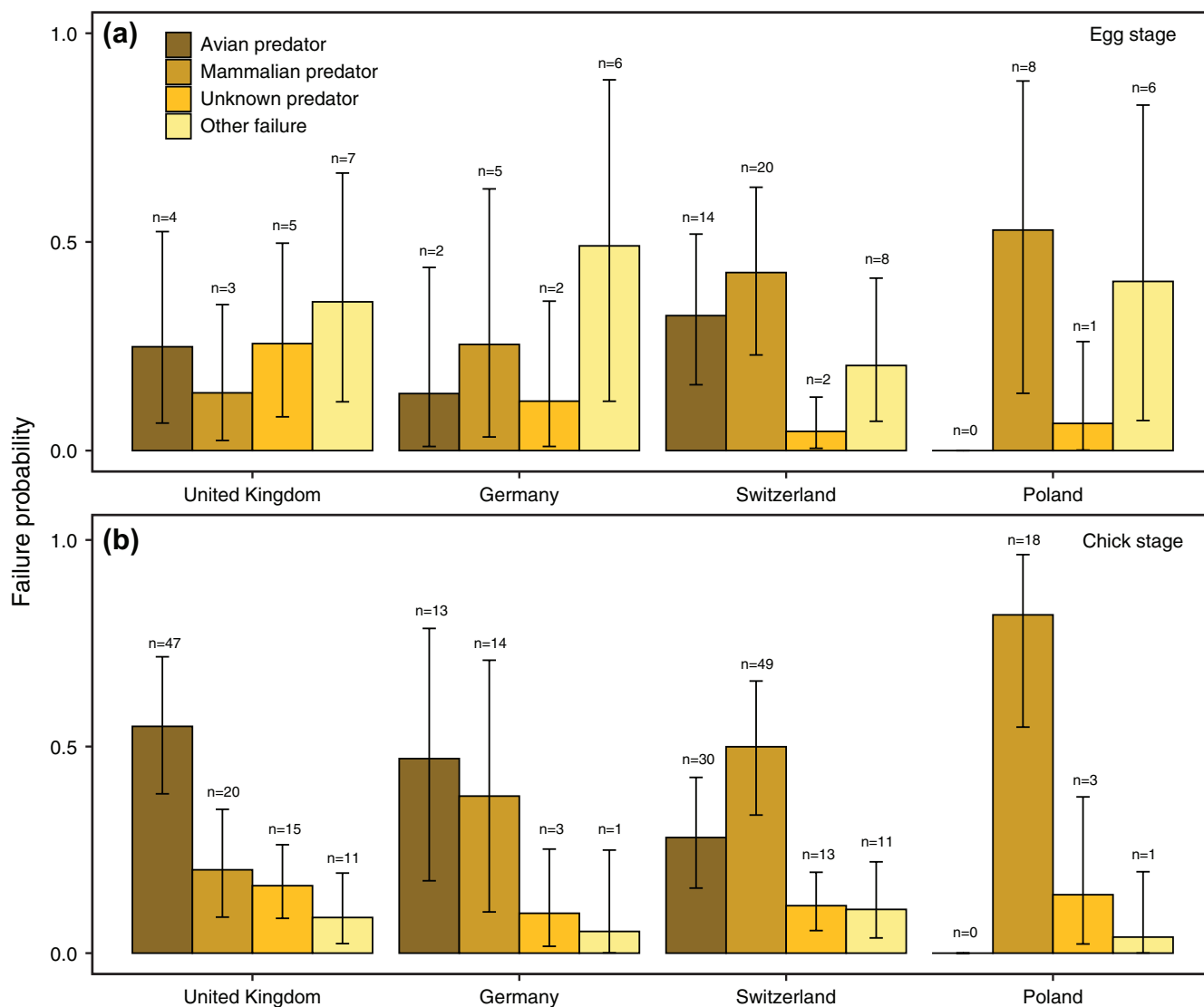


Figure 6. Predation probability of wood warbler (a) eggs and (b) chicks by avian, mammalian and unknown predators, and failure due to other causes in the UK, Germany, Switzerland and Poland. Shown are posterior estimates and 95% credibility intervals of a Bayesian multinomial mixed effects model.

Reasons that explain the varying numbers of avian and mammalian predations observed in the different study regions are unclear. As the range of potential nest predator species was the same, or greater, in Białowieża than in western regions (Tomialojc et al. 1984, Maziarsz et al. 2019), the predator species of wood warbler nests in Białowieża would be expected to be similar or more diverse than elsewhere. Based on camera recordings of potential nest predators visible at wood warbler nests but not preying on them, avian predators in Białowieża rarely explored the forest floor (Maziarsz et al. 2019). Possible explanations for this might include regional differences in predator density, varying availability of major or alternative prey species, and higher predation risk from mammalian predators (e.g. foxes) for avian predators like jays (Maziarsz et al. 2019). Further research would be valuable to

fully understand the intricate differences in predator–prey interactions across Europe, particularly in woodlands with varying levels of anthropogenic disturbance (human-transformed versus primeval).

The spatial variation in reproduction that we document here cannot conclusively explain the different population trends of wood warblers in central and western Europe. As long as information about regional patterns of annual survival is unavailable and results on reproductive output are limited to a few study regions, no clear inferences about the impact of reproduction on population dynamics can be made. Future work should include more study sites in central, eastern and northern Europe to improve our understanding of the demographic factors underlying wood warbler population dynamics.

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Data availability statement

Data supporting this manuscript are available in the vogelwarte.ch Open Repository and Archive: <<https://doi.org/10.5281/zenodo.6801204>>. Please contact the authors before using the dataset (Maag et al. 2022).

Supporting information

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

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