

ARTICLE

Wood warbler population dynamics in response to mast seeding regimes in Europe

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Abstract

Mast seeding is the episodic, massive production of plant seeds synchronized over large areas. The resulting superabundance of seeds represents a resource pulse that can profoundly affect animal populations across trophic levels. Following years of high seed production, the abundance of both seed consumers and their predators increase. Higher predator abundance leads to increased predation pressure across the trophic web, impacting nonseed consumers such as the wood warbler *Phylloscopus sibilatrix* through increased nest predation after tree mast years. Over the past 30 years, the frequency of tree seed masts has increased, while wood warbler populations have declined in several regions of Europe. We hypothesized that increasing mast frequencies may have contributed to the observed population declines by creating suboptimal breeding conditions in years after masting. We measured reproductive output in four study areas in central Europe, which was between 0.61 and 1.24 fledglings lower in the years following masting than nonmasting. For each study area, we used matrix population models to predict population trends based on the estimated reproductive output and the

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local mast frequencies. We then compared the predicted with the observed population trends to assess if the frequency of mast years had contributed to the population dynamics. In Wielkopolska National Park (PL) and Hessen (DE), masting occurred on average only every 4 years and populations were stable or nearly so, whereas in Jura (CH) and Białowieża National Park (PL), masting occurred every 2 and 2.5 years, respectively, and populations were declining. The simple matrix population models predicted the relative difference among local population trends over the past 10–20 years well, suggesting that the masting frequency may partly explain regional variation in population trends. Simulations suggest that further increases in mast frequency will lead to further declines in wood warbler populations. We show that changes in a natural process, such as mast seeding, may contribute to the decline in animal populations through cascading effects.

KEYWORDS

Afro-Palearctic migrant, birds, deciduous forest, fecundity, masting, matrix population model, Passeriformes, population trends, productivity, trophic interaction

INTRODUCTION

Most tree species in temperate zones reproduce by mast seeding (or masting), which is a spatially synchronous year-to-year variation in seed production (Fernández-Martínez et al., 2017; Kelly, 1994). While seed production has been found to increase with tree and forest stand age (Minor & Kobe, 2017, 2019; Pesendorfer et al., 2020), seed production is also correlated with annual variation in weather (Koenig et al., 2016; Vacchiano et al., 2017), which renders masting in trees and other plants sensitive to climate change (Bogdziewicz, 2022; Bogdziewicz et al., 2020; Koenig et al., 2016; Monks et al., 2016). Although some studies forecasted no changes in mast seeding as a consequence of climate change (Kelly et al., 2013), most studies predicted increases in average seed production (Bogdziewicz et al., 2020; Callahan et al., 2008; Hilton, and Packham, 2003), increased frequency of mast years (McKone et al., 1998; Övergaard et al., 2007), and/or lower spatial synchrony of seed production (Bogdziewicz et al., 2020; Pesendorfer et al., 2020).

Mast seeding can have cascading effects on multiple ecosystem processes, such as population dynamics of seed consumers, resource-consumer or predator–prey interactions (Czeszczewik et al., 2020; Kelly et al., 2008; Ostfeld & Keesing, 2000; Yang et al., 2008). Many seed-consuming vertebrate species are affected by mast seeding, particularly small mammals (e.g., rodents *Rodentia*), whose reproduction and overwinter survival increase in mast years, leading to large populations in the following year (Bogdziewicz et al., 2016; Pucek et al., 1993). Numerical increases of seed consumers

(primary consumers) attract predators such as carnivorous mammals or raptors (secondary consumers), which in turn increase the predation pressure on other prey species in the ecosystem (Ostfeld & Keesing, 2000). For instance, in Białowieża forest, Poland, increased rodent numbers after mast years attracted predators such as pine martens *Martes martes* and tawny owls *Strix aluco*, which not only hunt rodents, but also birds and amphibians (Jędrzejewska & Jędrzejewski, 1998). In Eastern North America, mast-related rodent outbreaks in oak forests attracted mammalian carnivores (e.g., raccoon *Procyon lotor*, striped skunk *Mephitis mephitis*), which increased nest predation of various bird species, particularly ground nesters (Leimgruber et al., 1994; McShea, 2000).

Ground-nesting birds are especially vulnerable to predators and nest predation can have important implications for their populations (Newton, 1998; Schmidt, 2003). It is therefore conceivable that changes in mast seeding frequency and the associated changes in the abundance of primary consumers (seed predators) and secondary consumers (bird predators) affect the reproductive output and, consequently, the dynamics of bird populations. Avian population dynamics can also be influenced by changes in other demographic rates, including annual survival (Robinson et al., 2014) and immigration (Schaub & Ullrich, 2021). In some migratory birds, population fluctuations have been related to changes in environmental conditions at nonbreeding and stopover sites (Ockendon et al., 2012; Thaxter et al., 2010; Woodworth et al., 2017). However, declines of some migratory species are not occurring uniformly across their European breeding ranges (Keller et al., 2020), suggesting that

conditions in the breeding grounds, and hence reproductive output, may be important for explaining spatial variation in population trends (Morrison et al., 2016; Roodbergen et al., 2012).

Wood warblers *Phylloscopus sibilatrix* are Afro-Palearctic migrants that breed in European forests characterized by mast seeding (Glutz von Blotzheim & Bauer, 1991; Keller et al., 2020). They are small, ground-nesting passerines that experience nest losses from 43% up to 87%, with nest predation being the most common cause of loss (60%–95%, depending on year and region; Maag et al., 2022; Wesolowski & Maziarz, 2009). The most common nest predators are Eurasian jay *Garrulus glandarius*, common buzzard *Buteo buteo*, Eurasian sparrowhawk *Accipiter nisus*, pine marten, red fox *Vulpes vulpes*, and European badger *Meles meles* (Maag et al., 2022). With a few exceptions at the western edge of their breeding range (i.e., the UK and the Netherlands), wood warbler populations fluctuate in relation to rodent outbreaks following masting events, for example in Belgium (Herremans, 1993), Switzerland (Grendelmeier et al., 2018), Germany (Grendelmeier et al., 2019), and Poland (Szymkowiak & Kuczyński, 2015; Wesolowski et al., 2009). Wood warblers are nomadic and rarely return to the same breeding location, likely to avoid increased nest predation pressure associated with high rodent numbers in years after masting (Szymkowiak & Kuczyński, 2015; Wesolowski et al., 2009). In Switzerland and Poland, wood warbler nest survival was lower in years with high rodent numbers (and increased nest predation) than in years with low rodent numbers (Grendelmeier et al., 2018; Wesolowski et al., 2009). This suggests that the reproductive output of wood warblers may be affected by variation in mast seeding, with potential implications for their population dynamics.

Using matrix population models (Caswell, 2001), we tested the hypothesis that wood warbler population growth rates are lower in regions with higher mast seeding frequencies than in regions with lower mast seeding frequencies. We estimated the average reproductive output (i.e., fecundity, defined as the number of fledglings per female per year) in years after masts (representing years with bad conditions for breeding) and in years after nonmasts (good conditions for breeding) in four study areas in central Europe. The study areas were characterized by different mast seeding frequencies and, therefore, by different relative occurrences of good and bad breeding conditions for the wood warbler. We compared population projections obtained from our matrix models to the observed, local wood warbler abundance in the study areas to assess how well variation in reproduction arising from variation in mast frequency predicted local wood warbler population trends. While numerous studies have shown the trophic consequences of masting on avian

reproduction (Czeszczewik et al., 2020; Grendelmeier et al., 2018; McShea, 2000; Schmidt & Ostfeld, 2003; Sherry et al., 2015), this is the first study to quantitatively link mast seeding, reproductive output, and avian population dynamics across multiple populations.

METHODS

Study areas

We monitored 1803 wood warbler nests over multiple years in four study areas across Europe (Appendix S1: Figure S1): the Jura mountains, Switzerland (47°23' N, 7°34' E, 2010–2015 and 2017–2020, $n = 324$ nests); Hessen, Germany (50°56' N, 8°53' E, 2007, 2014–2015 and 2020, $n = 298$); and Wielkopolska (WNP, 52°16' N, 16°48' E, 2013–2020, $n = 229$) and Białowieża (BNP, 52°44' N, 23°53' E, 2003–2012 and 2015–2020, $n = 952$) National Parks, Poland. Nests were studied in broadleaved or mixed broadleaved–conifer forests with closed canopy and sparse understory, that is, in the main types of preferred wood warbler habitat (Glutz von Blotzheim & Bauer, 1991). The Jura and Hessen study areas consisted of medium to large forest areas (~10–700 km²) of mostly common beech (*Fagus sylvatica*) (Maag et al., 2022); WNP of one relatively large forest area (~46 km²) of mostly pedunculate oak (*Quercus robur*), sessile oak (*Q. petraea*), and Scots pine (*Pinus sylvestris*) (Szymkowiak & Thomson, 2019); and BNP of a large, protected forest area (~105 km², Polish part of BNP) of mostly hornbeam (*Carpinus betulus*), lime (*Tilia cordata*), and pedunculate oak (Wesolowski et al., 2022).

Nest monitoring

Surveys to locate singing wood warbler 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 every 1–6 days (Grendelmeier et al., 2015; Wesolowski & Maziarz, 2009) to estimate the number of fledglings. Successful fledging was inferred if at least one fledgling, fresh droppings, or adults carrying food were found near the empty nest. The number of fledglings was assumed to equal the number of nestlings found at the last visit prior to fledging, which was usually 7–9 days after hatching (i.e., 4–6 days prior to fledging, which occurs 13 days after hatching). Nest failure (i.e., number of fledglings = 0) was inferred if nesting material was torn apart, remnants of eggs, chicks and/or an adult were found, an intact nest was empty at a time when eggs or nestlings should have been present (predation), a nest

was deserted with its contents intact, or signs of trampling were evident (Maziarz et al., 2019). Nests that were abandoned before egg laying (i.e., during nest building) were not included in the analysis.

Abundance of wood warbler populations

In all study areas, abundance was measured by territory mapping. In Jura, observed abundances were provided by the national monitoring scheme of the Swiss Ornithological Institute (Knaus et al., 2021); in Hessen, by the national monitoring scheme of the Dachverband Deutscher Avifaunisten DDA (Wahl et al., 2020); and in WNP and BNP, respectively, by established monitoring in the study areas (Szymkowiak & Thomson, 2019; Wesolowski et al., 2022). In Jura and Hessen, the relative abundance per year was calculated in percentage of the mean yearly abundance (=100%) from 1990 to 2021 and in percentage of the abundance in the reference year of 2006, respectively; in WNP and BNP, abundances are territories per 1 km².

Mast seeding

Mast seeding has generally been found to increase rodent numbers in the year following a mast (for oaks: Grendelmeier et al., 2019; Ostfeld et al., 1996; for both oaks and hornbeam together: Czeszczewik et al., 2020; Pucek et al., 1993; for common beech: Jensen, 1982; Zwolak et al., 2016). For each study area, we used mast seeding data of locally dominant deciduous tree species because they have the largest influence on rodents and wood warbler abundance. By focusing on the dominant tree species per study area, we took into account that the biomass of produced seeds can strongly vary across tree species and thus the differentiation between mast and nonmast years depends on tree species as well. In the Jura and Hessen study areas, common beech is most abundant and, in the Jura, rodent outbreaks most strongly correlate with mast peaks of beech, which are also linked to year-to-year variation in wood warbler nest survival and abundance (Grendelmeier et al., 2018). In WNP, wood warblers mainly inhabit the oak-dominated parts of the forest, and fluctuations in wood warbler abundance negatively correlate with acorn production of both sessile and pedunculate oak (Szymkowiak & Kuczyński, 2015; Szymkowiak & Thomson, 2019). In BNP, rodent outbreaks correlate primarily with mast peaks of pedunculate oak and hornbeam (Czeszczewik et al., 2020; Pucek et al., 1993), with rodent numbers explaining fluctuations in wood warbler abundance (Wesolowski et al., 2009). Hence, in Jura and Hessen, we used seed production of common beech; in WNP, the combined

seed production of sessile and pedunculate oak; and in BNP, the combined seed production of pedunculate oak and hornbeam (Figure 1).

We used four study area-specific mast seeding indices, depending on the type of local data available. For Jura, Hessen, and WNP, we used mast seeding data provided by nationwide monitoring programs and collected in regions corresponding to our study areas, that is, northwestern Switzerland for Jura, central Germany for Hessen, and Poznań Regional Forest Directorate for WNP. For BNP, mast seeding data were collected in the same study area where wood warbler reproduction was measured. In Jura, we combined data from MastWeb ("MastWeb", 2021) and MASTREE (Ascoli et al., 2017). The two datasets use different ordinal indices to quantify seed production (MastWeb: classes ranging from 0 = very poor to 3 = full mast; MASTREE: classes ranging from 1 = very poor to 5 = full mast). We adapted the MastWeb to the MASTREE index by changing MastWeb-class 0 to MASTREE-class 1, MastWeb-class 1 to MASTREE-class 2, MastWeb-class 2 to MASTREE-class 3, and MastWeb-class 3 to MASTREE-class 5 (Ascoli et al., 2017). In Hessen, we used data from the Federal Office for Agriculture and Food ("Bundesanstalt für Landwirtschaft und Ernährung", 2021), in which seed production for state-certified beech stands was quantified as total beech nut mass in kilograms (Konnert et al., 2016). In WNP, we used data on the percentage of fruiting trees each year, which strongly correlated ($r > 0.80$) with the mass of seeds collected from the forest floor and seed traps (Bogdziewicz et al., 2017; Kantorowicz, 2000). In BNP, we counted the number of hornbeam infructescences on 1-m sections of 10 branches per tree and the number of acorns on an area of 1 m² under a tree, respectively, for 30 permanent monitoring trees and additional random trees of each species distributed across the study area (Wesolowski et al., 2015). The mean number of infructescences across 10 branches and the number of acorns per tree, respectively, were categorized into an ordinal index of five classes: 0 = none, 1 = 1–5, 2 = 6–10, 3 = 11–20, and 4 = more than 20. The definition of a mast year was that the annual seed production in the study area was $\geq 50\%$ of the local mast seeding index, which was three in Jura, 8000 kg in Hessen, 20 in WNP, and two in BNP (dashed lines in Figure 1).

Temperature and rainfall

Reproductive success in birds may also be influenced by weather factors. Low temperatures and high amounts of rainfall just before and during nesting can affect food resources and the provisioning of nestlings by the parents, potentially leading to a decreased number

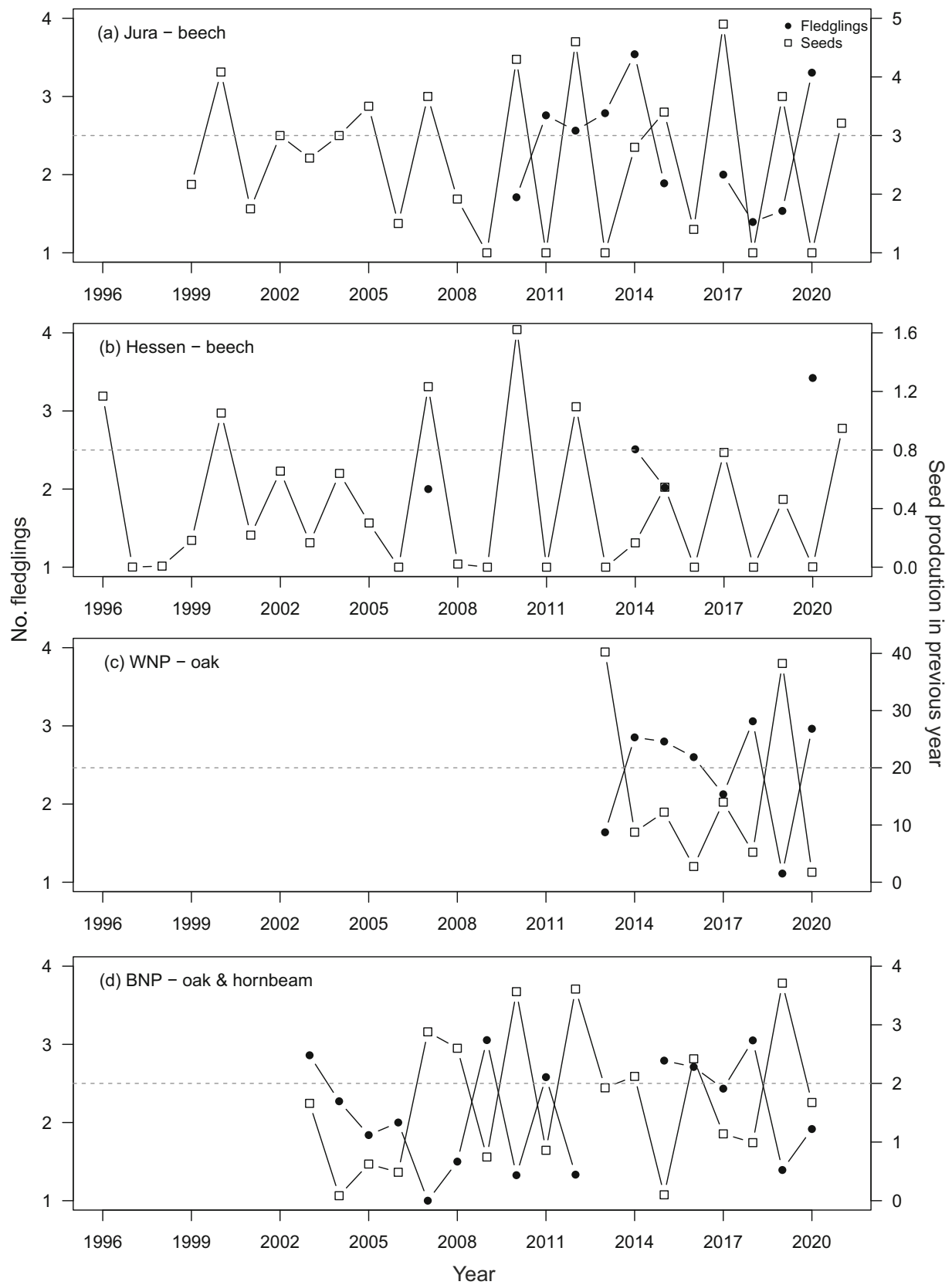


FIGURE 1 Legend on next page.

of fledglings (Arlettaz et al., 2010; Rodríguez & Bustamante, 2003). We obtained daily temperature estimates from the National Oceanic and Atmospheric Administration's (NOAA's) Climate Prediction Center ("NOAA CPC", 2022) and monthly rainfall data from NOAA's Global Precipitation Climatology Project ("NOAA GPCP", 2022). We used the mean temperature of the coldest 5-day period (calculated with a moving average of 5 days) and the total rainfall in the month with the highest rainfall between April and June of the current year because extraordinarily cold periods and heavy, long-lasting rainfall may diminish breeding success.

Statistical analysis

For each study area, we analyzed the number of fledglings per nest (ranging from 0 to 8, $n = 1803$ nests) with a Gaussian linear mixed effects model (LMM) using the package *lme4* (Bates et al., 2014) in R software, version 4.1.2 (R Core Team, 2021). We included mast seeding as a binary fixed effect to estimate the mean number of fledglings produced after mast versus nonmast events. We assigned wood warbler nests to these two categories depending on whether the previous year was a mast or nonmast year. We included temperature and rainfall in spring as continuous fixed effects and used year as a random term in all models. We calculated variance inflation factors (VIF) for all model variables to examine collinearity among them (Belsley et al., 2005). In WNP, mast seeding in the fall and temperature in the following spring were correlated ($VIF = 8.34$), and we made a separate model to test the influence of weather. In Hessen, the sample size was too small to include all three variables in the same model, and we also made a separate model for weather. However, the partial correlations of fledgling numbers with temperature and rainfall were low (Appendix S1: Table S1) and we considered them to be negligible for the population model.

Population model

To calculate wood warbler population dynamics in each study area, we parameterized study area-specific matrix

population models with the estimated reproductive output (i.e., mean number of fledglings per nest; Figure 2) for years after mast and nonmast events. Because wood warblers rarely produce a second brood after a successful nesting attempt (Glutz von Blotzheim & Bauer, 1991) and we could not identify potential second broods, the number of fledglings per nest was considered equivalent to the number of fledglings per female per year, that is, fecundity. As the annual survival of both juvenile and adults could not be estimated for the wood warbler due to extremely low return rates (Wesołowski et al., 2009), we borrowed an apparent survival rate estimate from the willow warbler *Phylloscopus trochilus*, a closely related species that is very similar with respect to body mass and migration behavior (Keller et al., 2020). Adult apparent survival of willow warblers ranges from 0.41 to 0.47 (Morrison et al., 2016; Pratt & Peach, 1991; Tiainen, 1983) and we assumed an adult survival of 0.44 for the wood warbler. For juvenile apparent survival (i.e., survival of first calendar-year birds to their second calendar year), we chose 0.22 because in small passerines, juvenile survival is approximately half of the adult survival (Dybala et al., 2013; Fay et al., 2021; Sæther & Bakke, 2000). From the simple life cycle (Appendix S1: Figure S2) we derived a female-based prebreeding census matrix population model (Caswell, 2001):

$$\begin{bmatrix} N_{1,t+1} \\ N_{2+,t+1} \end{bmatrix} = \begin{bmatrix} \frac{F_t}{2} S_{\text{juv}} & \frac{F_t}{2} S_{\text{juv}} \\ S_{\text{ad}} & S_{\text{ad}} \end{bmatrix} \times \begin{bmatrix} N_{1,t} \\ N_{2+,t} \end{bmatrix} \quad (1)$$

where F_t is fecundity in year t (i.e., number of fledglings per female, divided by 2 to consider only female offspring), S_{juv} is annual juvenile survival, S_{ad} is annual adult survival, N_1 is the number of 1-year-old females, and N_{2+} is the number of adult females older than 1 year. To get initial values for N_1 and N_{2+} , we calculated the stable stage distribution (Appendix S1: Table S2) from the observed wood warbler abundances in the first year (Jura = 148 breeding pairs, Hessen = 205, WNP = 17, BNP = 50). For each study area, we built two matrices, one for years after mast and one for years after nonmast events, each including the respective estimate of fecundity. With the population model, we projected age-specific population sizes

FIGURE 1 Wood warbler reproduction (black circles) and seed production in the previous year (open squares) across time. The number of years for which wood warbler data was available varied between study areas: (a) Jura = 10 years, (b) Hessen = 4, (c) WNP = 8, (d) BNP = 16. Periods for which seed production and wood warbler abundance data were available and for which predictions on population trends were made are shown. Dashed lines mark 50% of the local seed index, which we used to group years in mast ($\geq 50\%$ of the local seed index) and nonmast years ($< 50\%$). The seed indices had following units of measurement/values: (a) ordinal values ranging from 1 = very poor seed production to 5 = full mast, (b) beech nut mass in kilogram times 10^4 , (c) percentage of fruiting trees, and (d) ordinal values ranging from 0 = no infructescence/acorns to 4 = mean number of infructescences and acorns > 20 .

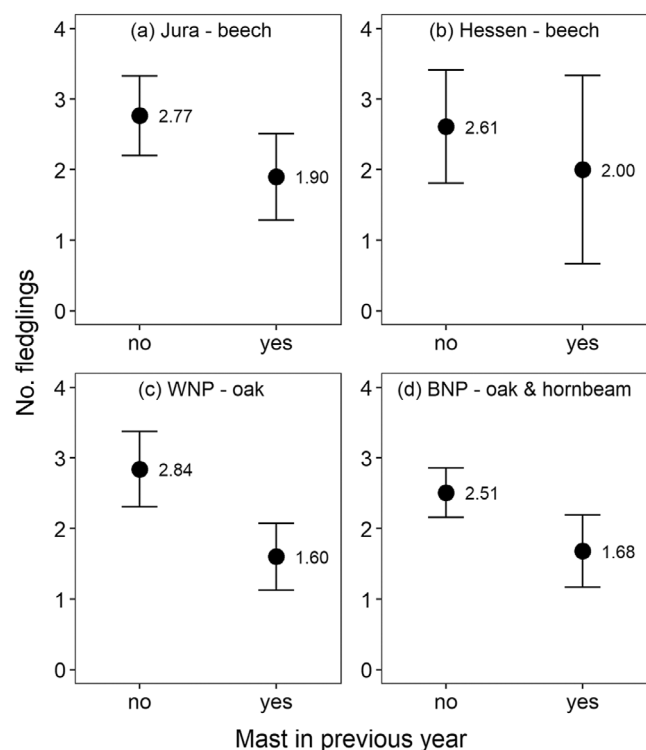


FIGURE 2 Wood warbler reproductive output (average number of fledglings per female) in years after mast and nonmast events in the four study areas (a–d). Model predictions and 95% CI of linear mixed effects models are shown. Sample sizes and statistics: (a) $n_{\text{Jura}} = 324$ nests sampled in 10 years, estimate = -0.87 , SE = 0.42 , $p = 0.073$; (b) $n_{\text{Hessen}} = 298$ nests in 4 years, estimate = -0.61 , SE = 0.79 , $p = 0.532$; (c) $n_{\text{WNP}} = 229$ in 8 years, estimate = -1.24 , SE = 0.36 , $p = 0.001$; (d) $n_{\text{BNP}} = 952$ nests in 16 years, estimate = -0.82 , SE = 0.32 , $p = 0.020$.

using the two matrices in the same order as mast and nonmast years occurred in the study areas (Figure 1). To account for the estimation uncertainty in fecundity (Figure 2), we generated a reproductive value for each year from a normal distribution with the fecundity estimates as the mean and its standard error as the standard deviation. We then repeated the population trajectories 1000 times to propagate the uncertainties in the fecundity estimates to the population trajectories. We summed N_1 and N_{2+} to get the population size in every given year.

To evaluate the explanatory power of our population models, we compared the simulated population projections with observed wood warbler abundances in each study area. We calculated the average population growth rates (λ) of the projected and observed wood warbler abundances across the considered time periods as the exponent of the slope of the linear regression of the logarithms of the abundances on year.

Stochastic population growth rates and elasticities

To estimate mean stochastic population growth rates and elasticities, we performed simulations across 5,000,000 years. Because the dominant eigenvalue of the projection matrix has a closed symbolic solution, we directly used it for the calculation of the annual population growth rates:

$$\lambda_t = S_{\text{ad}} + S_{\text{juv}} \frac{F_{z(t)}}{2} \quad (2)$$

where z is a state variable indicating years after mast and nonmast events, generated at random from the observed proportion of mast years (P) in the study areas (Jura = 0.48, Hessen = 0.23, WNP = 0.25, BNP = 0.39). The mean stochastic population growth rate (λ_s) was calculated as the geometric mean of the annual population growth rates. To evaluate the relative effect of each model parameter—that is, P , F_z , S_{juv} , and S_{ad} —on the stochastic population growth rate λ_s , we computed stochastic elasticities. We calculated them by increasing one model parameter by 1% at the time while holding the other parameters at their true value, and then subtracting the original values of λ_s from the resulting λ_s .

RESULTS

Wood warbler reproduction

In all study areas, the number of fledglings produced in years after masting was between 0.61 (Hessen: SE = 0.79) and 1.24 (WNP: SE = 0.36) fledglings lower than in years after nonmasting (Figure 2). In Jura and Hessen, statistical uncertainty was high (Figure 2) most likely due to mast seeding data not being collected directly in the study area and low sample size, respectively. However, point estimates (\pm SE) of Jura ($F_{\text{after nonmast}} = 2.77 \pm 0.29$, $F_{\text{after mast}} = 1.90 \pm 0.31$) and Hessen ($F_{\text{after nonmast}} = 2.61 \pm 0.41$, $F_{\text{after mast}} = 2.00 \pm 0.79$) were consistent with the other study areas. Partial correlations of the number of fledglings with weather were low, except in WNP, where fecundity was positively correlated with temperature ($0.14 \pm$ SE 0.06; Appendix S1: Table S1).

Population model

Using apparent survival rates of the willow warbler, the predicted population growth rates of the wood warbler were much lower than the observed growth rates

(Table 1) and predicted population trajectories diverged substantially from observed trends (Figure 3). However, the relative differences among study areas in predicted and observed growth rates were similar: that is, both predicted and observed growth rates were highest in WNP, second highest in Hessen, second lowest in Jura, and lowest in BNP (Table 1).

Because predicted population trajectories were unrealistically low using the apparent survival rates of the willow warbler, we determined hypothetical survival rates (i.e., S_{juv} and S_{ad}) so these could maintain population trajectories similar to the observed trends. We estimated these hypothesized survival rates by entering the observed population growth rates in the matrix equation and solving the equation for S_{juv} (upper matrix row) and S_{ad} (lower matrix row). We then calculated the mean of each survival rate across study areas, which were $S_{juv} = 0.41$ and $S_{ad} = 0.49$ (see “hypothesized” in Table 1 and Figure 3), and used those rates in the matrix models instead of the willow warbler’s rates ($S_{juv} = 0.22$, $S_{ad} = 0.44$). These models, incorporating only the temporal variation in reproduction arising from variation in mast years and hypothesized but constant survival rates (i.e., the same survival rates were used in all study areas), explained the differences between local wood warbler population trends reasonably well. In WNP and Hessen, where mast peaks occurred on average only every 4 years, growth rates were larger than and almost 1 ($\lambda_{WNP} = 1.025$; $\lambda_{Hessen} = 0.996$), respectively, and thus indicated increasing and nearly stable populations, while in Jura and BNP, where mast peaks occurred on average every 2 and 2.5 years, respectively, growth rates were less than 1 ($\lambda_{Jura} = 0.969$; $\lambda_{BNP} = 0.923$), indicating population declines (Figure 4a).

Stochastic population growth rates and elasticities

The mean stochastic population growth rates were $\lambda_{s(WNP)} = 1.002$, $\lambda_{s(Hessen)} = 0.995$, $\lambda_{s(Jura)} = 0.968$, and

$\lambda_{s(BNP)} = 0.935$. In all study areas, population growth rates were sensitive to changes in survival rates, with a 1% change in juvenile or adult survival leading to a relative change in λ_s of ~ 0.5 (Figure 4b). Changes in reproduction after mast years ($F_{after\ mast}$) and reproduction after nonmast years ($F_{after\ nonmast}$), respectively, generally had smaller relative effects on λ_s (0.1–0.3; Figure 4b), except in WNP and Hessen, where changes of reproduction after nonmast years also had a relatively large effect on λ_s (~ 0.4 ; Figure 4b). The elasticities for mast year frequency (P) were negative, indicating that an increase in mast frequency leads to a decrease in λ_s . In absolute terms, the elasticities for mast year frequency and reproduction were similar and smaller than the elasticities for survival.

If the frequencies of mast years in Hessen and WNP (where wood warbler populations are currently nearly stable and stable, respectively) increased from the current 0.23 and 0.25, respectively, to 0.5 (i.e., mast every other year such as in Jura and BNP), population growth rates would drop to 0.961 and 0.936, respectively (Figure 4c). Under this scenario, a 21% increase in reproduction after nonmast years or a 39% increase in reproduction after mast years would be required in WNP to compensate for the predicted increase in mast frequency. In Hessen, a 17% increase in reproduction after nonmast years or a 19% increase in reproduction after mast years would be required (Figure 4c), but the available local reproductive estimates may be less robust because these are based on only four breeding seasons (Figure 1). In Jura and BNP, where mast years are already occurring almost every second year and where populations are declining (Figure 4c), it would require 12% and 27% increases in $F_{after\ nonmast}$ or 18% and 32% increases in $F_{after\ mast}$, respectively, to reach stable population trends. With the current reproduction, λ of the Jura population would reach 1 if the frequency of mast years decreased to 0.3 (one mast every 3 years), while the population in BNP would continue to decline even if the frequency of mast years decreased to 0.1 (one mast every 10 years; Figure 4c).

TABLE 1 Population growth rates (λ) and associated 95% confidence intervals (CI) derived from the observed abundances, from the matrix model predictions based on the willow warbler’s survival rates, and from the matrix model predictions based on the hypothesized survival rates in the four study areas.

Study area	Observed		Willow warbler survival		Hypothesized survival	
	λ	CI	λ	CI	λ	CI
WNP ($n = 8$)	1.028	0.115	0.727	0.017	1.025	0.032
Hessen ($n = 4$)	0.987	0.024	0.712	0.014	0.996	0.024
Jura ($n = 10$)	0.951	0.012	0.698	0.011	0.969	0.020
BNP ($n = 16$)	0.930	0.055	0.672	0.009	0.923	0.017

Note: λ were calculated as the exponent of the slope of the linear regression of the logarithms of the abundances on year.

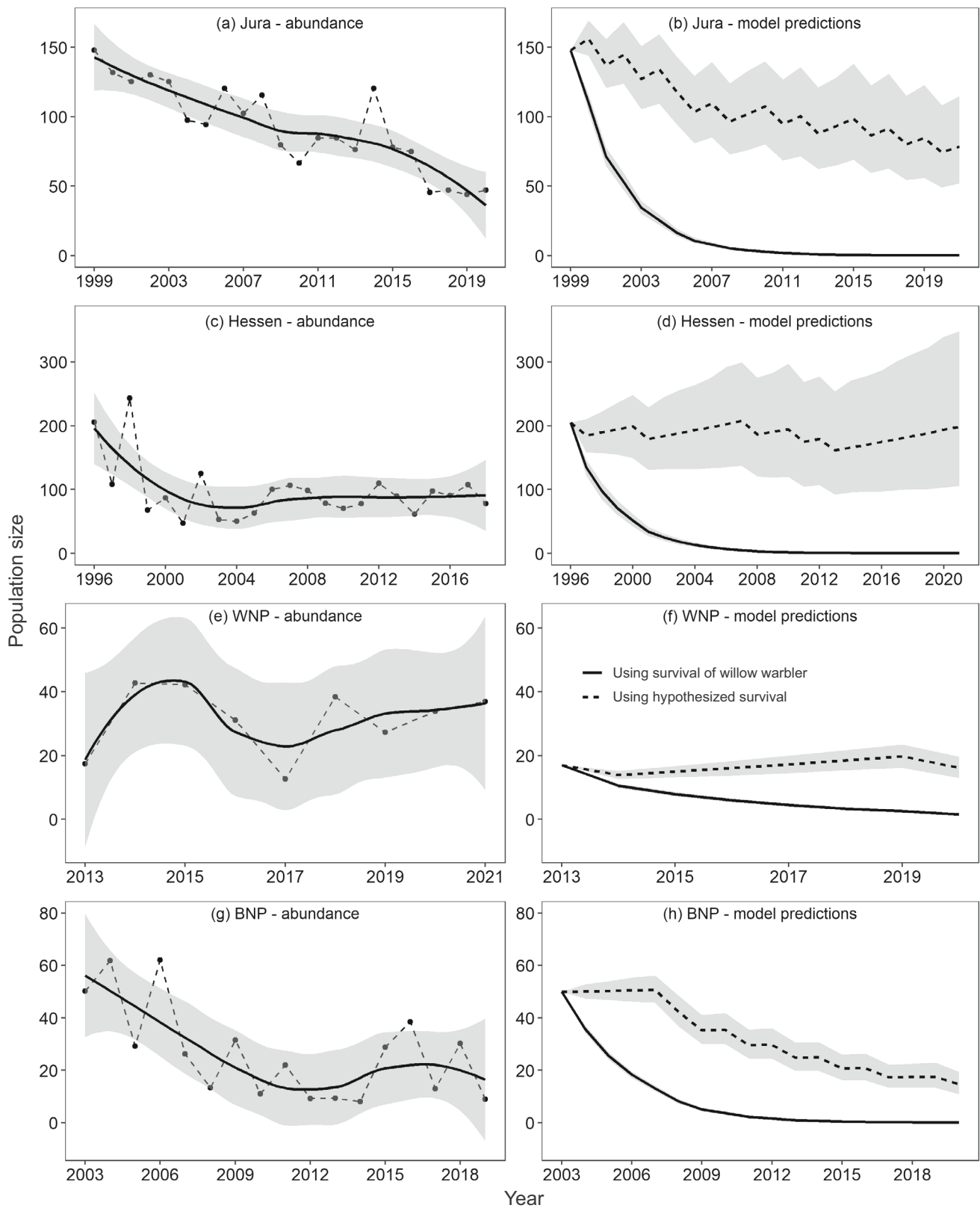
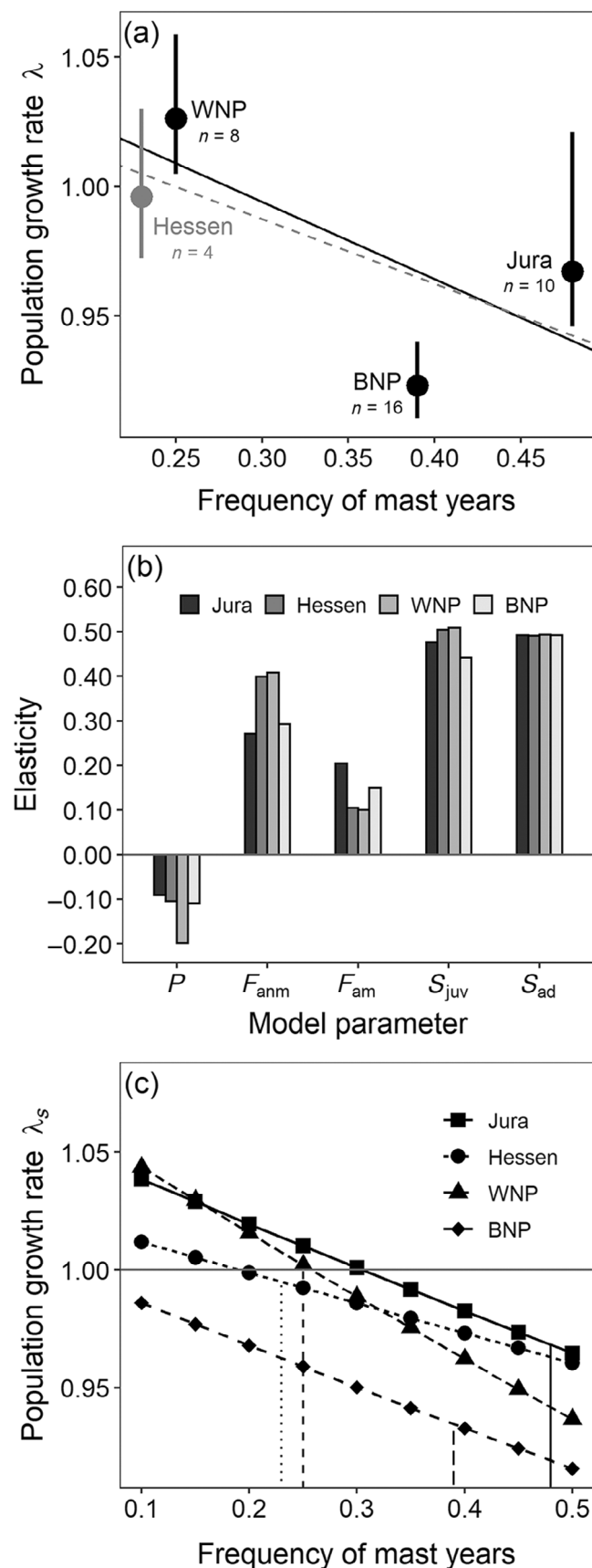


FIGURE 3 Observed wood warbler abundances from monitoring schemes (left: a, c, e, g) and matrix population model projections (right: b, d, f, h) in the four study areas. Left: Loess functions and 95% CI (solid line) derived from yearly abundance estimates (black circles). Right: Predictions and 95% CI of matrix models using the survival rates of the willow warbler (adult survival $S_{ad} = 0.44$, juvenile survival $S_{juv} = 0.22$) and those hypothesized for the wood warbler ($S_{ad} = 0.49$, $S_{juv} = 0.41$).



DISCUSSION

Many Afro-Palearctic migratory birds show different population trends in different parts of their breeding range (Morrison et al., 2013). Our results indicate that for one such Afro-Palearctic migratory species, the wood warbler, regional variation in mast seeding frequency in the breeding grounds is a possible explanation for divergent population trends. Our findings are especially intriguing because matrix population models based only on variation in reproduction in relation to the occurrence of masting (i.e., using the same, constant survival rates in all study areas) predicted the relative difference among observed population trends reasonably well. Hence, the observed variation in population trends may be at least partly attributed to regional variation in breeding conditions due to mast seeding events and the subsequent effects triggered by these resource pulses.

Masting frequency varies among regions and tree species, with potentially divergent consequences for regional wood warbler populations. In central Europe, beech mast frequency and year-to-year variability of annual beech nut production have increased in the last 30 years (Pesendorfer et al., 2020), while in the UK, year-to-year variability has decreased (i.e., full masts were less likely to occur; Bogdziewicz et al., 2020). In both regions, however, the average annual production of beech nuts has increased (Bogdziewicz et al., 2020; Pesendorfer et al., 2020). In both pedunculate and sessile oak, average seed production, mast frequency, and temporal variability of seed production have increased in Europe over the past 30 years (Pesendorfer et al., 2020). If nest predation

FIGURE 4 Population growth rates in relation to mast frequencies and to changes in model parameters in the four study areas. (a) Population growth rates λ and 95% CI predicted by the matrix population models using the hypothesized survival rates in relation to the frequency of mast years (e.g., mast occurs every 4 years = 0.25). If Hessen is omitted from the comparison (reproductive data only available from 4 years), the relationship between λ and mast frequency remains the same (including Hessen = dashed line, without Hessen = solid line). n = number of years with reproductive data. (b) Shown are elasticities expressing proportional changes in the stochastic population growth rates (λ_s) if the frequency of mast years (P), fecundity after nonmast years (F_{ann}), fecundity after mast years (F_{am}), juvenile survival (S_{juv}), or adult survival (S_{ad}) change by the same proportion. (c) Stochastic population growth rates λ_s in relation to changes in the frequency of mast years (in steps of 0.05); vertical lines show the observed average frequencies of mast years in the study areas.

rates increase due to increased average seed production or increased frequency of full mast events, wood warbler populations may (further) decline. However, if nest predation only increases in years after full masts (for which there is some indication, because in some study areas fecundity seems to decrease only after full mast years and not after years with medium seed production; see Appendix S1: Figure S3), and mast peaks are to be less pronounced in the future, wood warbler populations may be less affected.

The spatial scale of masting synchrony also varies between regions and tree species. For example, the area over which the beech mast is synchronized is decreasing in the UK (Bogdziewicz et al., 2020), but increasing in central Europe (Pesendorfer et al., 2020). Owing to their nomadic behavior, wood warblers may benefit from decreased among-site synchrony of masting because they would have to move less far to find better breeding conditions than under increased among-site synchrony. The example of the study areas Jura and Hessen shows that regions that are relatively close (i.e., northwest Switzerland and central Germany, ~440 km apart) can have divergent masting regimes (mast every 2 and 4 years, respectively) and wood warbler population growth rates ($\lambda_{\text{Jura}} = 0.969$ and $\lambda_{\text{Hessen}} = 0.996$). Hence, potential declines in the spatial extent of masting synchrony may mitigate the presumed negative effects of increased average seed production on wood warbler populations.

Increases in average seed production and mast frequency could affect many taxa, including birds (Ostfeld & Keesing, 2000). Although plasticity in nest placement may help some species avoid nest predation in years with high rodent abundance (Arheimer & Enemar, 1974), studies from various forest ecosystems demonstrate that birds suffer higher nest predation in years with increased rodent populations due to preceding mast events (Czeszczewik et al., 2020; McShea, 2000; Schmidt & Ostfeld, 2003; Sherry et al., 2015). McShea (2000) showed that predation rates of artificial nests increased after years of high acorn production due to an initial increase in mouse numbers followed by a pulse of carnivorous mammals. Schmidt and Ostfeld (2003, 2008) showed the same relationships for real nests in some thrush species, which were caused by numerical increases in rodents and other predators preying on bird nests. These examples also show that declines in some bird populations are correlated with mast-induced deficits in reproduction. Using population models, we extend these studies by presenting a mechanistic link between mast seeding, reproductive output, and population dynamics in a ground-nesting forest songbird.

However, reproduction is presumably not the only demographic rate of the wood warbler influenced by mast

seeding. Adult survival rates can covary with productivity because nest predators sometimes also kill adults incubating eggs or brooding nestlings (Low et al., 2010), and we have occasionally found remains of adult females near predated wood warbler nests (S. B. Luepold & M. Maziarz, personal observations; Wesolowski, 1985). Thus, while our results demonstrate an intriguing relationship between wood warbler population trends and masting frequency, reproductive output is probably not the sole driver of this pattern. Indeed, our elasticity analyses showed that wood warbler population growth rates were more sensitive to changes in juvenile and adult survival than to changes in reproduction. The situation is likely to be even more complex because apparent annual survival, which is the probability that an individual survives and returns to the original population, is confounded with emigration (which occurs frequently and over large spatial scales in nomadic species). Not accounting for immigration and emigration processes may also explain why our initial matrix population model, which was based on willow warbler apparent survival (Morrison et al., 2016; Pratt & Peach, 1991; Tiainen, 1983), resulted in substantial underestimation of population growth.

Finally, wood warbler population trends may be affected by factors unrelated to mast seeding. One example is the elevated nest predation rates in areas with reduced nest concealment due to high grazing pressure, such as in the New Forest in the UK (Bellamy et al., 2018). The weather during the nestling period might potentially be another factor (unrelated to mast seeding) influencing fecundity and thus population growth rate. However, we only found a moderate, positive relationship between fecundity and temperature in one of our study populations (WNP), and no relationships to rain in any of the study populations. The lack of clear weather effects on the fecundity of wood warblers is in line with previous studies (Grendelmeier et al., 2015; Maziarz et al., 2022). Furthermore, population trends of Afro-Palearctic migratory birds may be related to conditions faced during migration, at stopover areas, or in the wintering grounds (Halupka et al., 2017; Hewson & Noble, 2009; Pasinelli et al., 2011; Sanderson et al., 2006). The strong decline in observed wood warbler abundance in Hessen between 1996 and 2000, which was not captured by the matrix population model and can therefore not be attributed to mast seeding, may be the result of other factors operating during the breeding period or at different points in the annual cycle. Similar declines were observed at approximately the same time in the Netherlands (Bijlsma, 2012), Switzerland (Knaus et al., 2021), and Germany (Flade & Schwarz, 2004), but the reasons are unknown. Similarly, the relatively stable observed and modeled population trends in BNP from 2012 onwards, despite a moderate increase in mast seeding

frequency, points to additional factors influencing abundance. An indication of the involvement of changes in immigration is a contraction of the wood warbler breeding range in the northwest over the past 20–30 years, for example in the UK, Denmark, and Finland (Keller et al., 2020), which seems to be unrelated to reproductive output (Maag et al., 2022).

Our simulations suggest that wood warbler populations are at risk due to recent and projected increases in mast events (e.g., every second year instead of every third or fourth year). Although higher reproductive output in springs following nonmast years could hypothetically compensate for the increased occurrence of mast years, this is an unlikely scenario considering that nest predation rates in wood warblers are relatively high (Maag et al., 2022). In addition, the magnitude of the absolute percent difference in mean reproductive output across study areas $((2.19 - 2.57)/2.19 \times 100 = 17\%)$ is much lower than that of mast frequency $((0.23 - 0.48)/0.23 \times 100 = 109\%)$, suggesting that possible adaptations (e.g., increases in clutch size) cannot compensate for the increase in mast frequencies.

The wood warbler may thus offer an example of how changes in a natural process (seed masting) arising from global warming and/or increasing tree and forest stand age can potentially imperil a species by generating poor breeding habitat conditions, ultimately resulting in population decline. However, the nomadism of wood warblers may allow them to benefit from the decreasing among-site synchrony of beech and oak masts observed in recent decades, at least in some regions of Europe. A consequence of this nomadism is that a lower proportion of the overall, regional population will be affected by the increased predation pressure in years following a mast due to settling in regions with more favorable conditions for breeding. It is conceivable that other forest bird species may also respond to changes in average seed production and mast seeding frequency and the subsequent changes in predator abundances. Our findings highlight the need to study how demographic rates and population dynamics of animals may be linked to resource pulses altered by global change in other ecosystems.

AUTHOR CONTRIBUTIONS

Nino Maag and Gilberto Pasinelli conceived the study. Nino Maag curated data and wrote the manuscript. Nino Maag and Fränzi Korner-Nievergelt performed analyses. Fränzi Korner-Nievergelt wrote the population model. Jakub Szymkowiak, Natalia Hałas, Marta Maziarz, Grzegorz Neubauer, Shannon Buckley Luepold, Sandro Carlotti, Alex Grendelmeier, Michael Riess, and Pablo Stelbrink collected data. Michael Schaub wrote code for the elasticities. Martin Flade and Daniel Scherrer

provided mast seeding data. Gilberto Pasinelli led the editing of the writing and conducted the revisions. Fränzi Korner-Nievergelt, Jakub Szymkowiak, Natalia Hałas, Marta Maziarz, Grzegorz Neubauer, Shannon Buckley Luepold, Sandro Carlotti, Michael Schaub, Martin Flade, and Daniel Scherrer provided critical input on writing. All authors read and approved the final draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Maag et al., 2023) are available on the vogelwarte.ch Open Repository and Archive hosted by Zenodo at <https://doi.org/10.5281/zenodo.10082957>.

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SUPPORTING INFORMATION

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

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