RESEARCH PAPER

ethology | WILEY

Does acoustically simulated predation risk affect settlement and reproduction of a migratory passerine?

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Abstract

Nest predation is one of the most important drivers of avian life history evolution and population dynamics. Increasing evidence suggests that birds are able to assess nest predation risk and avoid settling in high-risk areas to increase their reproductive performance. However, the cues used for settlement decisions are poorly known in most species. Population sizes of the migratory wood warbler *Phylloscopus sibilatrix* are characterized by strong annual fluctuations, which are negatively correlated with the number of forest rodents. Wood warblers might avoid rodent-rich areas to reduce predation risk arising either from rodents, from rodent-hunting predators attracted to such areas or from predators not linked to rodents. To evaluate these hypotheses, we conducted a large-scale field experiment to test whether wood warblers avoided settling in plots with high predation risk simulated by broadcasting vocalizations of rodents or predators. Moreover, we tested whether reproductive performance varied in relation to simulated predation risk. Settlement patterns did not differ between plots with rodent, predator and noise control treatments. Likewise, measures of reproductive performance did not seem to differ across treatments. Thus, the broadcasted vocalizations of rodents and predators did not seem to be perceived as threat by wood warblers. Alternatively, the species might use other cues than those presented here, either other acoustic cues, visual and/or olfactory cues or a combination of cue types during settlement. Further experimental investigations to pin point cues and senses relevant for settlement decisions in wood warblers and birds in general are needed to better understand their life history and population dynamics.

KEYWORDS
acoustic cues, information use, *Phylloscopus sibilatrix*, playback experiment, predator–prey, wood warbler

1 | INTRODUCTION

Many ecosystems around the world are characterized by intermittent events resulting in pulsed dynamics of population sizes and ecological processes (Yang, Bastow, Spence, & Wright, 2008). For many organisms, resource pulses imply unpredictable variation of environmental conditions. However, uncertainty about environmental conditions can be reduced by gathering information (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Schmidt, Dall, & van Gils, 2010; Seppänen, Forsman, Mönkkönen, & Thomson, 2007), which requires an animal's ability to perceive distinct environmental characteristics and adjust its behavior accordingly. Therefore, it can be expected that animals only invest in gathering information if the

benefits of doing so outweigh the costs (Stamps, Krishnan, & Reid, 2005).

In birds, fitness and life history are considered to be strongly affected by predation (Lima, 2009; Martin, 1995; Newton, 1998; Thompson, 2007). There is ample evidence that birds are able to assess local predation risk for their nests and for themselves and accordingly adjust their breeding behavior (reviewed in Lima, 2009). In response to predation or predation risk, birds have been found to exhibit breeding dispersal (Dow & Fredga, 1983) and nest site shifts (Eggers, Griesser, Nystrand, & Ekman, 2006; Emmering & Schmidt, 2011; Marzluff, 1988; Peluc, Sillett, Rotenberry, & Ghalambor, 2008), decrease local densities (Emmering & Schmidt, 2011; Fontaine & Martin, 2006b; Forsman, Mönkkönen, Korpimäki, & Thomson, 2013) and adjust community structure (Hua, Fletcher, Sieving, & Dorazio, 2013). Moreover, birds have shown reduced feeding rate (Dudeck, Clinchy, Allen, & Zanette, 2018; Peluc et al., 2008), clutch size (Eggers et al., 2006; Zanette, White, Allen, & Clinchy, 2011), number of offspring and nest survival (Zanette et al., 2011), increased body mass (Walters et al., 2017) and have altered various aspects of parental investment (Eggers, Griesser, & Ekman, 2005; Fontaine & Martin, 2006a) and behavior (Abbey-Lee, Kaiser, Mouchet, & Dingemanse, 2016; Walters et al., 2017), when faced with increased predation or predation risk. Nonetheless, proactive avoidance of breeding sites with high predator occurrence is still quite weakly examined, even though it is probably widespread (Lima, 2009). Cues allowing especially long-distance migratory bird species to assess predation risk and habitat quality in general are of special interest here, as migrating species have little time available between the arrival at their breeding grounds and the start of breeding activity.

One such long-distance migratory species is the wood warbler *Phylloscopus sibilatrix*. In its European breeding range, population sizes are characterized by strong annual fluctuations (Glutz von Blotzheim & Bauer, 1991; Wesołowski, Rowiński, & Maziarz, 2009). In the wood warbler, settlement at the territory scale (Pasinelli, Grendelmeier, Gerber, & Arlettaz, 2016), abundance at the forest stand scale (Jędrzejewska & Jędrzejewski, 1998; Wesołowski et al., 2009) and population size at the landscape scale (Grendelmeier, Flade, & Pasinelli, 2019; Szymkowiak & Kuczyñski, 2015) are negatively correlated with the number of rodents (especially *Apodemus* spp. and *Myodes glareolus*). Based on these findings, it can be hypothesized that wood warblers actively avoid breeding sites with high rodent densities. However, because the proportion of wood warbler nests depredated by rodents is very small (Grendelmeier, Arlettaz, Gerber, & Pasinelli, 2015; Mallord et al., 2012; Maziarz, et al., 2018; Maziarz, Piggott, & Burgess, 2018), it is unclear whether wood warblers actually avoid rodents per se or rather some factor correlated with rodents. One such factor may be the presence of rodent-hunting predators, for which numerical increases in response to high rodent numbers have been shown (e.g., Grendelmeier, Arlettaz, & Pasinelli, 2018; Jędrzejewski, Jędrzejewska, & Szymura, 1995; Schmidt & Ostfeld, 2003). Indeed, rodent-hunting predators such as marten (*Martes* spp.), red fox (*Vulpes vulpes*) and tawny owl (*Strix aluco*) throughout the species' range, and non-rodent-hunting Eurasian jay (*Garrulus glandarius*, hereafter jay) in Western Europe are the most important predators of wood warbler nests (Bellamy et al., 2018; Grendelmeier et al., 2015; Mallord et al., 2012; Maziarz, Grendelmeier, et al., 2018; Maziarz, Piggott, et al., 2018), and nest survival is lower in years with high rodent abundance compared to other years (Grendelmeier et al., 2018). Thus, like other ground- or bush-nesting passerines in seasonal forests (Clotfelter et al., 2007), wood warblers face strongly differing densities of small rodents and predators around their nests from year to year (Grendelmeier et al., 2018). For these reasons, wood warblers are an ideal model species

TABLE 1 Expected responses of wood warblers during settlement and reproduction in relation to the vocalizations played back

	Playback vocalization		
Response variable	Rodents	Predators	Rodents & Predators
Settlement pattern	RT > PT, CT	PT > RT, CT	RT & PT > CT
Settlement probability	RT < PT, CT	PT < RT, CT	RT & PT < CT
Distance of territories	RT > PT, CT	PT > RT, CT	RT & PT > CT
Number of territories	RT < PT, CT	PT < RT, CT	RT & PT < CT
Reproductive performance	RT < PT, CT	PT < RT, CT	RT & PT < CT

Note: RT = rodent treatment (vocalization of rodents played back), PT = predator treatment (vocalization of predators), CT = control treatment (vocalizations of wood pigeons). Settlement pattern refers to the temporal pattern of wood warbler settlement and is measured for each treatment type as the number of plots occupied by at least one territory per visit; settlement probability is the probability that a plot was occupied by at least one wood warbler territory over the course of the breeding season; distance of territories is the distance between playback sets and the center of the nearest wood warbler territories (which could be beyond an experimental plot); number of territories is the number of wood warbler territories within experimental plots (circle with 100 m radius); reproductive performance was measured through clutch size, number of fledglings and nest survival probability on experimental plots. Reading example: If wood warblers avoid rodent vocalizations, then settlement on rodent treatment plots should occur later in the season than on the other treatment plots.

to investigate how predation risk affects settlement behavior and reproduction.

In this study, we experimentally tested whether wood warblers considered rodent presence, predator presence or both during settlement. A number of studies revealed that birds assess predator presence by eavesdropping on predator vocalizations (e.g., Eggers et al., 2006; Emmering & Schmidt, 2011; Zanette et al., 2011). Additionally, by moving and filling space, sound is a good "transmitter of fear" (Clinchy et al., 2011). Hence, we established experimental plots with acoustically simulated increased presence of rodents and predators, as well as plots with noise control treatment (see Methods), among which we compared the settlement behavior and reproductive performance of wood warblers. Based on the findings cited above, we evaluated a priori predictions summarized in Table 1.

2 | METHODS

2.1 | Study area and species

The study took place at three sites in Hesse, Germany: Wollenberg (N 50.87°, E 8.68°; 395 m asl), Kellerwald (N 51.03, E 9.13; 310 m asl) and Gilsa (N 50.98, E 9.18; 427 m asl; see Appendix S1, Figure S1). All study sites are situated on southwestern, wooded hillsides with deciduous forests dominated by beech (*Fagus sylvatica*), interspersed with spruce (*Picea abies*) plantations.

The wood warbler is a ground-breeding, forest-dwelling, migratory passerine, wintering in sub-Saharan Africa and breeding from France and Britain to Scandinavia in the west to the Ural and Caucasian mountains in the east (BirdLife International, 2017). In the study area, males arrive in mid-April, followed by females who lay the first eggs at the end of April or early May (Bauer, Bezzel, & Fiedler, 2012). In most wood warbler populations, both breeding philopatry and natal philopatry seem to be remarkably low (reviewed in Wesołowski et al., 2009). This apparently nomadic behavior may explain the strong local population fluctuations from year to year, which in this magnitude seems to be unique among European

insectivorous passerines (Wesołowski & Tomialojc, 1997). Despite low philopatry, wood warbler territories are found in similar locations between years, a pattern most likely attributable to suitable habitat (Huber, Kienast, Ginzler, & Pasinelli, 2016; Pasinelli et al., 2016).

2.2 | Playback experiment

Centered at individual wood warbler nests of the preceding breeding season (based on each nest's coordinates), we established 45 experimental plots prior to the breeding season in 2015. Nests had to be at least 200 m apart to be selected as experimental plot centers. Using information on occupied habitat in 2014 helped assuring that wood warbler responses were linked to experimental treatment and not to variation in habitat conditions. As no single study site contained enough previously occupied habitat to accommodate the entire experiment, we set up 27 experimental plots at study site Wollenberg and nine plots each at study sites Kellerwald and Gilsa (Appendix S1, Figure S1). In each study site, the number of treatments was balanced (e.g., at Gilsa, there were three plots with predator treatment, three plots with rodent treatment and three plots with noise control treatment). To further control for possible habitat effects, we assigned treatments to plots randomly.

Experimental plots, in which we measured wood warbler responses, were defined as circular areas with a radius of 100 m around playback sets (Figure 1), equaling 3.14 ha for each plot. Territory size of the wood warbler spans 0.12–3 ha (Glutz von Blotzheim & Bauer, 1991), allowing thus from 1–26 territories to be potentially established on an experimental plot. Each experimental plot was equipped with one playback set consisting of one lead–acid battery (12V, 18Ah, FG21803 from FIAMM), one battery guard (M148A from Kemo), one voltage converter (20UA1 from KREE; battery to mp3 player), one mp3 player (Transcend MP350 from Transcend), one pair of speakers (MX SP 209 from Maxxtro), one 3.5-mm jack/jack cable (mp3 player to speaker), one voltage converter 12V to 9V (battery to speakers) and a 12V timer switch (Gutkes Elektro Vertriebs GmbH). To protect

FIGURE 1 Schematic drawing of an experimental plot. Wood warbler responses were measured in relation to the playback set (black triangle, e.g., "distance between playback set and closest wood warbler territory) or in a circular area of radius 100 m around the playback set (e.g., "number of territories per plot"). Locations of the twelve 50 m² squares on a 50 m by 50 m grid used to map habitat variables are shown within the circle. The inset shows the location of the five 1 m² squares within one 50 m² square and the location where track plates for the assessment of rodent density were placed (black point)
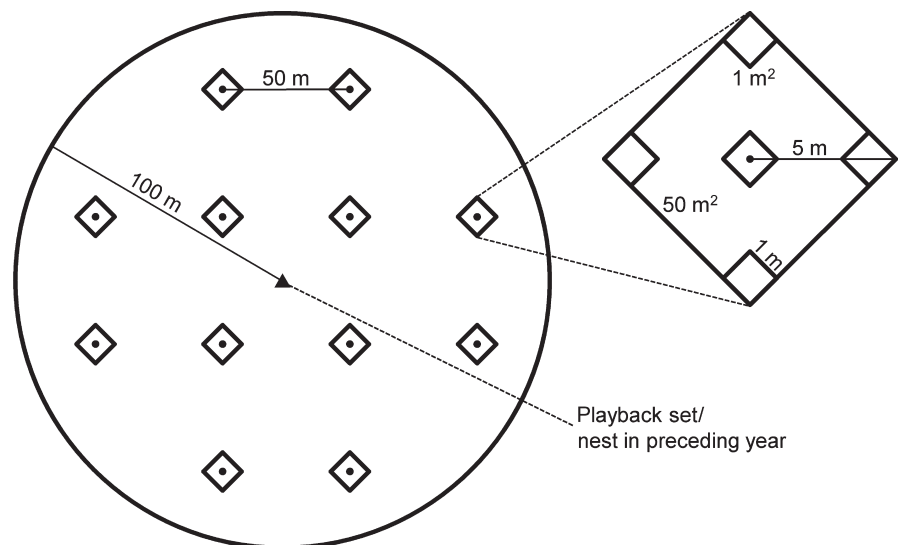
the playback sets from weather and dirt, we placed the speakers inside a thin plastic bag and the remaining equipment inside a plastic box, which was additionally wrapped into a plastic bag. The two speakers, placed about 20 cm above ground to facilitate handling of the equipment, were oriented horizontally and in opposite directions. The volume of the playback sets was standardized to 85 dB at one meter in front of the speakers. This applied to vocalizations of all species to allow the emitted sound to fill areas as similar in size as possible, irrespective of species vocalizations played back, and to avoid potential effects of species vocalizations on wood warbler settlement to be confounded by differences in volume among species.

2.3 | Vocalizations

Recordings were kindly provided by the Tierstimmenarchiv, Berlin (TSA), the British Library, London (BL) and several people working actively on bioacoustic recordings, providing these on xeno-canto (XC, www.xeno-canto.org) or in personal sound archives (PSA). In addition, we used recordings from different commercially available media (Appendix S2, Table S2). The original recordings were partly cropped and/or repeated to yield a sound file of 1 min length each. All 1-min files were brought to standardized amplitude (cf. Zanette et al., 2011).

For rodent treatments, vocalizations of yellow-necked mouse *Apodemus flavicollis*, bank vole *M. glareolus* and common shrew *Sorex araneus* (hereafter referred to as "rodent" despite not being one) were played back. Together with the wood mouse *A. sylvaticus*, for which no recordings were available, these species are the characteristic ground-living small mammals and the typical prey of generalist predators in central European mixed deciduous forest ecosystems (Braun & Dieterlen, 2005). Furthermore, *A. sylvaticus* and *M. glareolus* were the principal small mammal species detected in wood warbler territories in Switzerland (A. Grendelmeier, unpublished data).

For predator treatments, vocalizations of seven species were played back: red fox, stone marten *Martes foina*, pine marten *M. martes*, tawny owl, common buzzard *Buteo buteo*, sparrowhawk *Accipiter nisus* and jay. Using camera traps, these species have been identified as main predators of wood warbler nests in Western Europe (Grendelmeier et al., 2015; Mallord et al., 2012; Maziarz, Piggott, et al., 2018).

To ensure that potential responses of wood warblers were not due to unspecific noise emitted by speakers, we included a noise control treatment with vocalizations of wood pigeons (*Columba palumbus*). The wood pigeon is a common species in wood warbler habitats and does not compete for breeding sites or diet of the wood warbler (Bauer et al., 2012). A silent control treatment was not used as a previous study found no difference in wood warbler response between noise control and silent control, and strong positive responses to conspecific song (Grendelmeier, Arlettaz, Olano-Marin, & Pasinelli, 2017).

To avoid pseudo-replication, we used vocalization recordings of at least four individuals per species (only one recording was available for *A. flavicollis*; Appendix S2, Table S2). Altogether we used 71

recordings from seven predator species, 11 recordings from three rodent species and 15 recordings from wood pigeons, respectively (Appendix S2, Table S2). All playback stations of a particular treatment type consisted of the same set of species, but a unique combination of the available vocalizations of these species.

Vocalizations of mainly diurnal species were played back between 06:00 and 21:00, those of mainly nocturnal species between 21:00 and 06:00 (for details see below). Within these timeframes, the order of species vocalizations was arranged randomly, with 1 min of vocalization of a single species being followed by 4 min of silence, succeeded by the next randomly selected species vocalization of 1 min and so on. The random order of playing back species vocalizations and the rather low ratio of sound to silence were used to prevent habituation of birds to playbacks. Furthermore, this strictly standardized procedure was chosen to avoid possible effects of playing back species' vocalizations at different time intervals.

For predator treatments, vocalizations of *G. glandarius*, *B. buteo* and *A. nisus* were played back only during the day (06:00–21:00), while vocalizations of *S. aluco* were played back only during the night (21:00–06:00). Vocalizations of mammalian predator species *V. vulpes*, *M. foina* and *M. martes* were played back during the night and occasionally during the day. In detail, during the day a total of 180 5-min files (1-min vocalization followed by 4 min of silence) were played back. These playbacks consisted of 45 5-min files each for *G. glandarius*, *B. buteo* and *A. nisus* and 15 5-min files each for *V. vulpes*, *M. foina* and *M. martes*. During the night, a total of 108 5-min files were played back, with 27 5-min files each for *S. aluco*, *V. vulpes*, *M. foina* and *M. martes*.

Activity of rodent species *A. flavicollis* and *M. glareolus* peaks at dusk, night and dawn; however, reduced activity occurs during the day as well (see Braun & Dieterlen, 2005). Hence, for rodent treatments, vocalizations of all rodents were played back during the day and night. Thus, a total of 96 5-min files each for *A. flavicollis*, *M. glareolus* and *S. araneus* were played back (i.e., 288 5-min files in total).

Vocalizations of *C. palumbus* for noise control treatments were played back during the day only. Hence, 180 5-min files (1-min vocalization followed by 4 min of silence) were played back.

To prevent habituation of wood warblers to vocalizations, playbacks were turned off on Thursdays and Sundays. The playback experiment started on April 6th before the first wood warblers typically arrive (Bauer et al., 2012) and ran until June 30th. This period covers the entire settlement phase, which is unusually long and dynamic owing to extensive movements on the breeding grounds in the wood warbler compared to other songbirds (Riedinger, 1995; S. Lüpold pers. comm.), and much of the phase of first nests and replacement nests (owing to the substantial nest losses due to predation).

All editing of recordings was conducted using software "Audacity" and the R package "tuneR" (Ligges, Krey, Mersmann, & Schnackenberg, 2016) applying sound file format ".wav," mono, 32bit, 44,100 Hz. The file order was arranged randomly for all treatments, with the default setting of one recording being played back consecutively a maximum of four times.

2.4 | Wood warbler response

Wood warbler settlement in relation to the simulated presence of rodents and/or predators was measured with (a) the distance between a playback set and the center of the nearest wood warbler territory (which could be beyond the 100-m circle, see below), (b) the number of wood warbler territories within experimental plots (circle with 100 m radius) and (c) settlement probability per plot (i.e., whether a plot was occupied by at least one territory over the course of the breeding season). Further, we considered the temporal pattern of settlement for each treatment type, measured by the number of plots occupied by at least one territory per visit. All study sites were visited at least every 5 days during settlement and breeding of wood warblers from early April to mid-July. All wood warblers observed or singing were mapped using a GPS device ("Garmin eTrex 30" and "Garmin eTrex Vista HCx"). Nests were searched and mapped in the same manner. To reduce inaccuracy of GPS data, GPS points of nest sites as well as playback sets were taken at every visit (at least 4) and their barycentres used for all analyses.

Territory centers were defined as either the nest or, if no nest could be found, as the center of the minimum convex polygon connecting the outermost singing points (e.g., Kenward, 2007; Leonard, Taylor, & Warkentin, 2008), calculated in QGIS 2.8.1. In all analyses, we included only territories in which a nest was found or where singing males were present for at least 3 weeks to avoid counting singing males on migration. Applying these criteria, we found 44 territories with nests and 24 territories without nests at Wollenberg, 35 territories with nests and five territories without nests at Kellerwald, and 18 territories with nests and 14 territories without nests at Gilsa, giving 97 territories with nests and 43 territories without nest in all three study areas.

Duration of occupation of each territory was the number of days from arrival to departure. Date of arrival was defined as the middle date between the date of first detection of a singing male or a pair and the date of the previous visit of the respective area. Similarly, date of departure was defined as the middle date between the date of the last detection of territory occupancy (active nest or singing male) and the date of the subsequent visit of the respective area. Distances between playback sets and territory centers as well as number of territories within experimental plots were calculated using the R packages "rgdal" (Bivand, Keitt, & Rowlingson, 2015) and "geosphere" (Hijmans, 2015).

Reproductive performance was measured through clutch size, number of fledglings and nest survival (probability) on experimental plots (within 100 m of the playback set). For the analysis of clutch size, we used only clutches that were complete as judged from repeated nest checks. Number of fledglings per nest was analyzed including both all nests and successful nests only, the latter being nests producing at least one fledgling. We used the number of nestlings from the last visit before fledging, which was determined by camera traps placed at all nests in our experimental plots and at as many nests as possible outside of the plots (for details on nest camera use, see Grendelmeier et al., 2015 and Maziarz, Grendelmeier, et al., 2018; Maziarz, Piggott, et al., 2018). The analysis of nest survival was based on the time a nest was active, defined as the period from the initiation date (when the first egg was laid) until the end date (when the nestlings fledged or the nest failed). In the following, we refer to this period as exposure time in days. To determine exposure time, age of nests upon finding needs to be estimated to determine nest initiation date. We back-calculated nest initiation dates from nest age estimates obtained by assuming (a) one egg was laid per day, (b) an incubation period of 14 days beginning with the laying of the last egg, and a nestling period of 13 days (G. Pasinelli, unpublished data, Grendelmeier et al., 2015), and by determining (c) nestling age from nestling development with pictures of reference nestlings from nests where exact hatching dates were known (Grendelmeier et al., 2017). Details on the nest survival analysis are given in the section on statistical analyses below.

2.5 | Environmental variables

When analyzing wood warbler settlement behavior in relation to the simulated presence of rodents and predators, additional environmental conditions known to influence the species' territory selection were

TABLE 2 Environmental variables recorded in experimental plots

Variable	Description	Calculation for analyses
Rodent abundance index	Number of rodent traces on track plates laid down in the center of all twelve 50 m^2 squares for 3 days each	Sum
Number of grass tussocks	Number of grass and sedge tussocks within all sixty 1 m^2 squares	Sum
Number of trees	Number of trees with diameter at breast height > 8 cm within all twelve 50 m^2 squares	Sum
Ground cover	Visually estimated percentage of ground covered by vegetation smaller than 0.5 m within all sixty 1 m^2 squares	Median of means of each 50 m^2 square
Slope steepness	Slope (°) measured along a 1 m slat (direction of highest slope steepness) through the center points of all twelve 50 m^2 squares using the application "Clinometer + bubble level" (vers. 2.3 from plaincode^{TM}) on a Samsung S7710 smartphone.	Median

Note: Shown are descriptions of field recording methods within 50 m^2 and 1 m^2 squares (Figure 1) and calculations performed to obtain values for analyses.

accounted for: rodent abundance, number of grass tussocks, number of trees, ground cover and slope steepness (Pasinelli et al., 2016; Table 2). Environmental variables were recorded based on a 50 m by 50 m grid within experimental plots (Figure 1). Rodent abundance was assessed using track plates, a non-sophisticated and cheap, but reliable method for assessing an index of rodent abundance (Connors et al., 2005). We used white plastic plates (12.5 cm × 25 cm × 0.2 cm) covered with a dark gray graphite/oil mixture diluted with ethanol for application. To minimize disturbance to nesting wood warblers, environmental variables were assessed after nests had become inactive. Within each experimental plot, environmental variables were recorded in twelve 50 m^2 squares and sixty 1 m^2 squares, respectively (Table 2, Figure 1). Environmental variables were only assessed on the scale of experimental plots, but not on the scale of nests or territories.

2.6 | Statistical analysis

Despite using nest locations of the previous year as centers for each experimental plot to control for habitat, we tested whether the rodent abundance index, number of grass tussocks, number of trees, ground vegetation cover and slope steepness differed between experimental plots through multivariate analysis of variance (MANOVA).

We used a linear mixed effects model (LMM, package lme4; Bates, Maechler, Ben, & Steven, 2015) to model the relationships of distance between playback sets and the nearest territory (dependent variable, log_{10}-transformed) to treatment type as categorical variable and environmental variables (rodent abundance index, number of grass tussocks, number of trees, ground cover and slope steepness). Prior to the analyses, environmental variables were standardized ($\bar{x} = 0$, standard deviation = 1) to facilitate model convergence and to allow comparison of regression coefficients. Study site was included as random effect with random intercept to account for the dependencies of experimental plots within the same study site.

To test for an effect of treatment type on the number of territories per experimental plot, we used a generalized linear mixed effects model (GLMM, package lme4; Bates et al., 2015) assuming a Poisson distribution and a log link. Similarly to the LMM above, fixed effects were treatment type and standardized environmental variables. Study site was again included as random effect with random intercept. We also modeled settlement probability per plot (presence/absence of territories per experimental plot, modeled was presence = 1) in relation to treatment type and standardized environmental variables as fixed effects and study site as random effect using a GLMM with binomial distribution and logit link.

To test whether the temporal pattern of settlement differed between treatment types, we used the qbeta function implemented in R to calculate 95% credible intervals (CrI) of the proportion of occupied plots per treatment (Korner-Nievergelt et al., 2015). We evaluated whether 95% CrI of one treatment overlapped with the means of the other two treatments. More specifically, if the 95% CrI of one treatment (e.g., treatment 1) included the means of other treatments, treatment 1 was deemed to be not different from the other treatments.

To test for an effect of treatment type on reproductive performance, we ran linear models with clutch size and number of fledglings as dependent variables, respectively, and treatment type as fixed effect. We also evaluated the same models using GLMM including study site as random effect, but the random effect had a variance of 0 ± 0 *SD*. Because of similar results, we only show results of the linear models. Moreover, to test for an effect of treatment type on wood warbler nest survival we ran survival analysis using the Cox mixed effect model function (R package coxme; Therneau, 2018). The Cox proportional hazard model is a semi-parametric regression model and belongs to a set of statistical methods often referred to as survival time analysis models (Austin, 2017; Hosmer Jr & Lemeshow, 1999; Kleinbaum & Klein, 2012; Nur, Holmes, & Geupel, 2004). The Cox model allows to simultaneously evaluate the effects of several covariates on survival and is expressed by the hazard rate $h(t)$. $h(t)$ is estimated by $h_0(t) \times \exp(b_1 x_1 + b_2 x_2 + ... + b_p x_p)$ where the hazard $h(t)$ can vary over time and h_0 is the baseline hazard, which is the hazard rate if all covariates equal zero. The impact of the covariates ($x_1, x_2, ..., x_p$) can be measured by their effect size $\exp(b_1, b_2, ..., b_p)$ (Cox, 1972). As with all time-to-event survival methods, Cox models can incorporate censored data, which can arise due to nests found at various ages (e.g., during the nestling stage; left-censored data) or due to nests that did not experience an event of interest (e.g., nest failure; right-censored data) (Kleinbaum & Klein, 2012; Nur et al., 2004). We modeled exposure time (see above under Wood warbler response) in relation to treatment type as fixed effect and study site as random effect. The proportional hazards assumption of the Cox model was tested following methods of Grambsch and Therneau (1994) implemented in the cox.zph function in R. Because this function does not work with output from a Cox model including random effects, we run a Cox model with the coxph function that included study site as a cluster variable accounting for the non-independence of observations from the same study sites (Kleinbaum & Klein, 2012). Both the test for treatment type levels (*p* values ranging from 0.132 to 0.305) and the global test were not significant (*p* = 0.213), indicating that the proportional hazards assumption was not violated.

Posterior distributions of the model parameters were obtained using Monte Carlo simulations as implemented in the function sim (R package arm, Gelman & Su, 2016, 5,000 iterations). The means of the posterior distributions were used as point estimates of the model parameters and the 2.5% and 97.5% quantiles as lower and upper limits, respectively, of the 95% credible intervals (CrIs). For parameters describing effect sizes, we calculated the proportion of the posterior distribution being positive. This proportion corresponds to the posterior probability of the hypothesis that the parameter value is larger or smaller than zero (Table 3). All statistical analyses were conducted in R version 3.5.2 (R Development Core Team, 2018).

2.7 | Permits

All procedures were performed according to the laws of Germany. Playback experiments were conducted with the permission no. P/21.10/2015-0001 by the department "Bauen, Wasser- und Naturschutz" of the Landkreis Marburg-Biedenkopf and

the permission no. 60.4-324563-03/2014 by the department "Bauaufsicht und Naturschutz" of the Schwalm-Eder-Kreis.

3 | RESULTS

3.1 | Difference in environmental factors among treatment groups

Based on the MANOVA (Wilk's λ = 0.81, $F_{2,42}$ = 0.83, p = 0.60), we did not find a difference between treatments for the rodent abundance index ($F_{2,42}$ = 0.74, p = 0.49), number of grass tussocks ($F_{2,42}$ = 0.40, p = 0.68), number of trees ($F_{2,42}$ = 0.43, p = 0.65), ground vegetation cover ($F_{2,42}$ = 0.36, p = 0.70) and slope steepness ($F_{2,42}$ = 1.95, p = 0.16).

3.2 | Settlement in relation to experimental treatments

The temporal pattern of settlement (i.e., the proportion of occupied plots over time) did not differ among treatments, as all 95% CrI overlapped all means for most of the observation period (Figure 2).

Deviations from this general pattern occurred during a few days in the first week of June (mean of the rodent treatment is not included in the upper 95% CrI of the other two treatments) and for a few days around June 15th (means of predator and control treatments are not included in the lower 95% CrI of the rodent treatment). Despite these minor deviations, the temporal pattern of settlement was very similar across treatment types (Figure 2).

Settlement probability per plot did not differ between treatment types (Figure 3a, Table 3a). Mean settlement probability per plot ($\pm SD$) was 0.73 ($\pm$0.46) for rodent treatments, 0.67 ($\pm$0.49) for predator treatments and 0.67 ($\pm$0.49) for noise control treatments. Of the 45 plots, 31 (68.9%) contained at least one territory.

The number of territories (n = 48) did not differ between treatment types (Figure 3b, Table 3b). The mean number of territories ($\pm SD$) was 1.4 ($\pm$1.3) for rodent treatments (n = 21 territories), 0.9 ($\pm$0.8) for predator treatments (n = 14) and 0.9 ($\pm$0.8) for noise control treatments (n = 13). The highest number of territories was found on two plots with rodent treatment (Figures 3b, 4 territories/plot ≈ 12 territories/10 ha). The number of territories on experimental plots was not significantly related to any of the environmental variables (Table 3b).

TABLE 3 Settlement responses of wood warblers to rodent treatment, predator treatment, noise control treatment (wood pigeon) and environmental variables

Source	(a) Settlement probability				(b) Number of territories				(c) Distance			
	β	2.5%	97.5%	Prob	β	2.5%	97.5%	Prob	β	2.5%	97.5%	Prob
Intercept	0.94	−0.25	2.19	0.93	−0.11	−0.66	0.44	0.66	1.87	1.67	2.07	1
Predator treat.	−0.29	−2.01	1.44	0.62	−0.05	−0.86	0.76	0.55	−0.04	−0.28	0.21	0.62
Rodent treat.	0.06	−1.58	1.75	0.52	0.42	−0.28	1.12	0.88	−0.05	−0.28	0.18	0.68
Rodent index	−0.05	−0.77	0.69	0.55	−0.02	−0.33	0.28	0.56	0.01	−0.09	0.11	0.60
No. of tussocks	0.12	−0.71	0.96	0.62	−0.19	−0.56	0.19	0.84	0.04	−0.07	0.15	0.75
Number of trees	−0.57	−1.35	0.20	0.93	−0.08	−0.53	0.17	0.84	−0.02	−0.14	0.09	0.65
Ground cover	−0.91	−1.84	0.00	0.97	−0.07	−0.43	0.30	0.64	0.04	−0.08	0.16	0.73
Slope steepness	−0.12	−0.86	0.63	0.62	−0.18	−0.51	0.15	0.86	−0.02	−0.13	0.09	0.65

Note: Shown are parameter estimates β for the experimental treatments and five environmental variables (z-standardized) on (a) settlement probability of experimental plots (based on a GLMM, n = 45, modeled was presence = 1), (b) the number of wood warbler territories on experimental plots (based on a GLMM, n = 45) and (c) $\log_{10}$ – transformed distance (m) between playback sets and the nearest wood warbler territory (based on a LMM, n = 45). Given are the mean β and the 2.5% and the 97.5% quantiles (95% CrI) of the posterior distribution, respectively, and the posterior probability Prob that the estimate is larger than zero [Prob(β > 0)] for positive estimates or smaller than zero [Prob(β < 0)] for negative estimates.

FIGURE 2 Temporal pattern of wood warbler settlement on experimental plots in relation to treatment type. Shown is the daily proportion of occupied rodent plots (n = 15), predator plots (n = 15) and noise control plots (n = 15) and 95% CrI
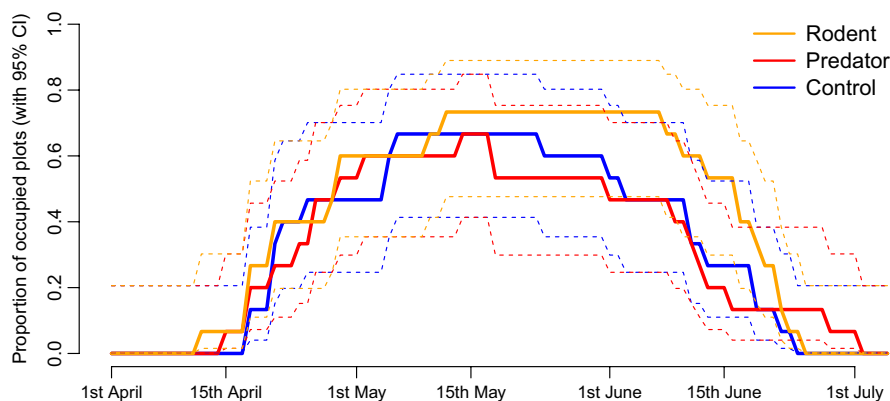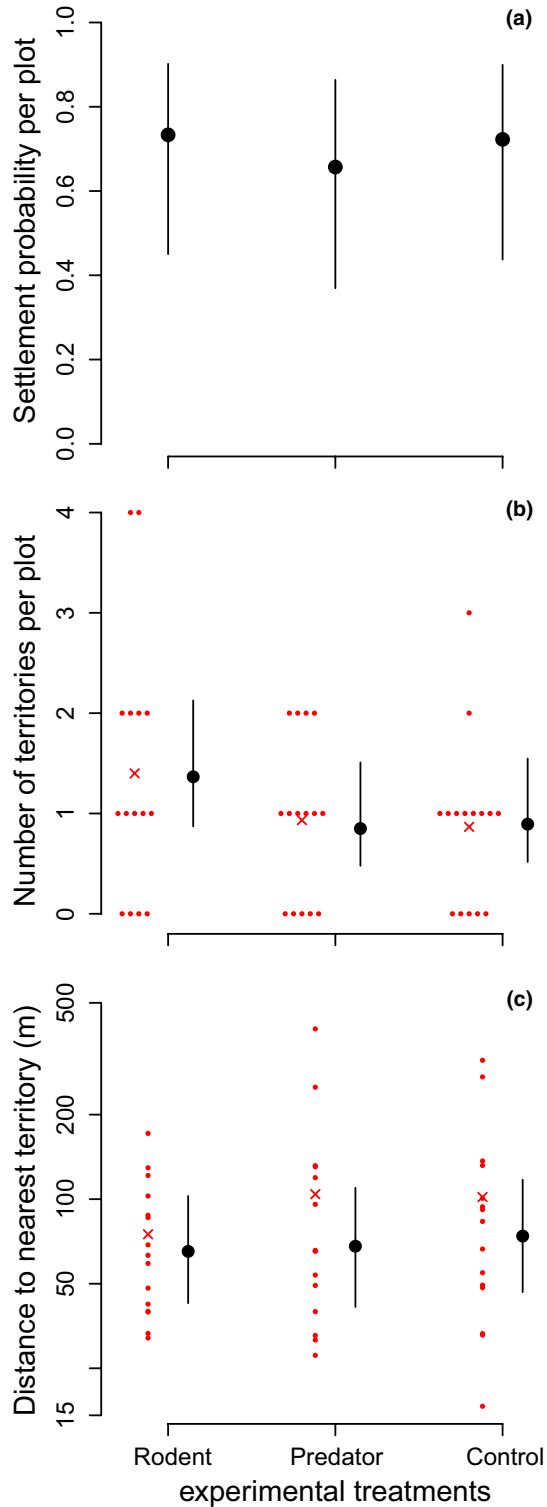
FIGURE 3 Settlement responses of wood warblers to rodent treatment, predator treatment and noise control treatment (wood pigeon). Shown are settlement probability per plot (panel a), number of territories per plot (panel b) and distances between playback sets and the nearest wood warbler territory (panel c) in relation to treatment type. Raw data (red points, panels b and c), means of raw data (red crosses, panels b and c) and means of model predictions (black points) with 95% CrI (black lines) are given. Each red point gives the number of territory on one plot in panel b. Note that distances were log_{10} – transformed for statistical analyses. $n = 15$ plots per treatment type
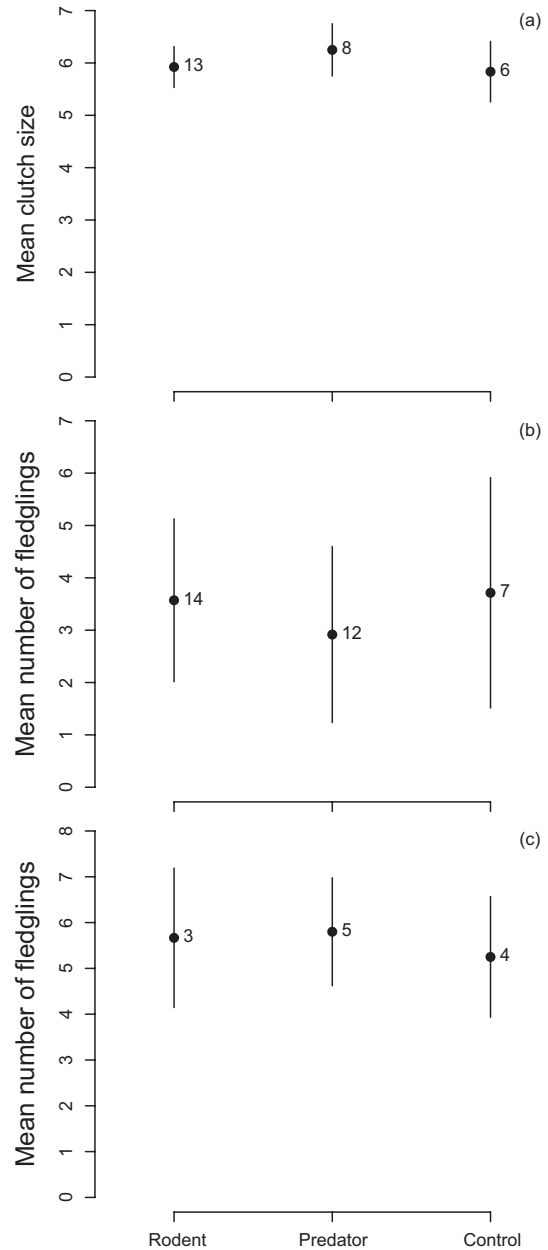
FIGURE 4 Reproductive performance of wood warblers in relation to rodent treatment, predator treatment and noise control treatment (wood pigeon). Shown are mean clutch size (panel a), mean number of fledglings of all nest (panel b) and of successful nests only (panel c) for the three treatment types. Given are model predictions (black points) with 95% CrI (black lines)

Distances between playback sets and the nearest territory did not significantly differ between treatment types (Figure 3c, Table 3c) and were on average ($\pm SD$) 75 m ($\pm$41 m) for rodent treatments, 104 m ($\pm$101 m) for predator treatments, 102 m ($\pm$85 m) for noise control treatments. This result did not change when excluding territories that were located more than 100 m from playback sets (Appendix S3, Table S3). Distance between playback sets and the nearest territory was not significantly related to any of the environmental variables (Table 3c).

FIGURE 5 Probability of nest survival in relation to nest age for the three treatment types. Dashed lines give 95% CI
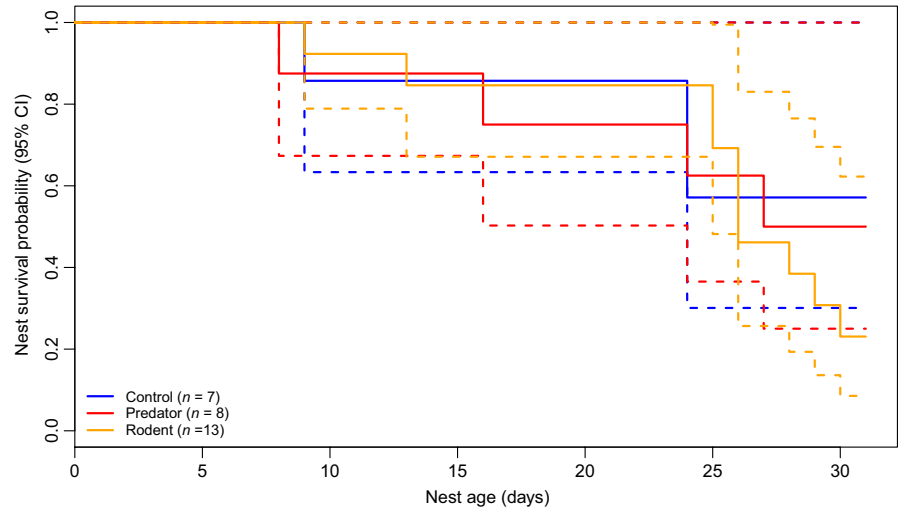

TABLE 4 Identified predators from 35 predation events out of 72 wood warbler nests monitored with cameras by study site

	Gilsa	Kellerwald	Wollenberg	Total
Birds				
Jay *Garrulus glandarius*	3	4	3	10
Common buzzard *Buteo buteo*	0	0	1	1
Great spotted woodpecker *Dendrocopos major*	0	1	0	1
Mammals				
Raccoon *Procyon lotor*	2	2	1	5
Badger *Meles meles*	0	1	2	3
Hedgehog *Erinaceus europaeus*	0	2	1	3
Fox *Vulpes vulpes*	0	2	0	2
Pine marten *Martes martes*	0	1	1	2
Mouse *Apodemus* sp.	0	2	0	2
Wild boar *Sus scrofa*	0	0	1	1
Other				
Unknown	0	2	3	5

Note: Includes nests both inside and outside the experimental plots.

3.3 | Reproductive performance in relation to experimental treatments

Clutch size ($F_{2,24}$ = 0.793, p = 0.464, n_{nests} = 27), number of fledglings from all nests ($F_{2,30}$ = 0.238, p = 0.790, n_{nests} = 33) and number of fledglings from successful nests ($F_{2,9}$ = 0.258, p = 0.778, n_{nests} = 12) did not differ between treatment types (Figure 4). Likewise, the probability of nests surviving over time did not vary among the treatments (likelihood ratio test, chi^2 = 1.11, df = 2, p = 0.575, Figure 5). Neither the predator treatment (hazard ratio [HR] = 1.188, 95% confidence interval [CI] = 0.266–5.313; regression coefficient [β] = 0.172, SE of β = 0.764, Wald statistic z = 0.226, p = 0.821) nor the rodent treatment (HR = 1.821, 95% CI = 0.499–6.652; β = 0.599, $SE(\beta)$ = 0.661, z = 0.907, p = 0.364) differed significantly from the baseline hazard (the noise control treatment, Figure 5). The probability of nests to survive the entire nesting period averaging 31 days in wood warblers (Grendelmeier et al., 2015, Maziarz, Grendelmeier, et

al., 2018; Maziarz, Piggott, et al., 2018) was 0.571 (95% CI = 0.301–1.0, n = 7) on control plots, 0.500 (0.250–1.0, n = 8) on predator plots, 0.231 (0.086–0.623, n = 13) on rodent plots and 0.414 (0.264–0.648, n = 28) across treatments.

Across study sites, nest predation occurred at 35 nests (Table 4) of 72 nests monitored by cameras inside and outside of experimental plots and was the main cause of nest failure accounting for 87.5% of all 40 nest losses. Additional losses occurred due to nest abandonment for unknown reasons (4) and incidental nest trampling by wild boars (1). Rates of nest losses were similar as found elsewhere (Grendelmeier et al., 2015; Wesołowski & Maziarz, 2009).

4 | DISCUSSION

This is the first study to experimentally test whether wood warbler settlement and reproduction are affected by predation risk.

However, in contrast to our expectations, wood warblers did not avoid settling in areas with acoustically simulated increased presences of rodents and predators. In addition, reproductive performance of wood warblers did not seem to be affected by simulated predation risk. In the following, we discuss possible explanations for these results.

Hearing is undoubtedly an important avian sense (e.g., Köppl, 2015). It is however possible that wood warblers do not have the sensory ability to perceive broadcasted vocalizations of rodents and predators. Yet, based on previous studies, this seems unlikely for the following reasons. Frequencies audible to mammals (rodents and carnivores; Braun & Dieterlen, 2005) and passerines (Köppl, 2015) have differential ranges, but overlap below 10 kHz. Recordings of carnivore vocalizations and rodent vocalizations used in this experiment contained frequencies in the range audible to passerines. Furthermore, birds are known to respond to playbacks of avian (Eggers et al., 2006; Zanette et al., 2011) and mammalian predators (Zanette et al., 2011), including rodents (Emmering & Schmidt, 2011). Even though we assume that wood warblers have the sensory ability to perceive our playbacks, the presented acoustic cues, aimed at simulating increased predation risk related to the presence of rodents and predators, may not correspond with the one considered by wood warblers during settlement. Whether or not other acoustic cues possibly related to rodent presence such as the rustling resulting from rodents moving through leaf litter may be important for settling wood warblers remains to be tested.

Alternatively or additionally, entirely different senses like vision (Güntürkün, 2000) and/or olfaction (Clark, Hagelin, & Werner, 2015; Steiger, Fidler, Valcu, & Kempenaers, 2008) might be used to assess predation risk. The importance of vision in predator recognition (Curio, 1975) has been shown in experimental studies exposing different passerine species (Peluc et al., 2008; Tilgar, Moks, & Saag, 2011), including wood warblers (Maziarz, Piggott, et al., 2018), to taxidermy mounts. It is therefore possible that wood warblers mainly respond to visual cues, such as movement or more specifically movement frequency of rodents and/or predators. Some bird species are also supposed to visually recognize UV active substances in mammalian excrements (Probst, Pavlicev, & Viitala, 2002; Viitala, Korpimäki, Palokangas, & Koivula, 1995). Aforementioned studies were however conducted in open farmland habitat and/or laboratory, where UV light reflectance is presumably stronger than in typical wood warbler habitats, which are characterized by closed forest canopies (Huber et al., 2016; Pasinelli et al., 2016). In addition, Lind, Mitkus, Olsson, and Kelber (2013) showed that vole urine added very little UV light reflectance to the already low reflectance of most natural substrates under natural conditions and concluded that vole urine unlikely provides a reliable visual cue. Detection of UV active substances in mammalian excrements may thus be of little importance to settling wood warblers (O. Lind, pers. comm.), but whether or not the low levels of UV light reflectance in forest habitats may still allow this cue to be used by settling wood warblers needs to be studied.

On the other hand, passerines have been shown to adjust habitat selection according to the presence/absence of excrements of mammalian nest predators (Forsman et al., 2013). Whether visual and/or olfactory cues were used by the passerines studied by Forsman et al. (2013), when selecting habitats, remained open. Olfactory capabilities of birds have presumably been underrated in the past (Clark et al., 2015; Steiger et al., 2008). Indeed, passerines have been found to respond to odor of mammalian predators with avoidance (Amo, Galván, Tomás, & Sanz, 2008; Roth, Cox, & Lima, 2008). It is currently unknown, if wood warblers determine predation risk based on olfactory cues.

The lack of a response to our experimental treatments might reflect the indifference of wood warblers to natural presences of rodents and predators. Although negative correlations between rodents and wood warblers have been found at various spatial scales (Grendelmeier et al., 2019; Pasinelli et al., 2016; Szymkowiak & Kuczyński, 2015; Wesołowski et al., 2009), there need not to be an underlying causality. It is well established that rodents respond positively to mast seeding (e.g., Pucek, Jedrzejewski, Jedrzejewska, & Pucek, 1993) and rodent hunters positively to increased rodent numbers (e.g., Grendelmeier et al., 2018; Schmidt & Ostfeld, 2003). Hence, wood warblers may use environmental cues related to mast seeding other than rodent or predator presence to decide where to settle.

According to state forestry agencies in Germany and Switzerland, the seed crop of beech and oak trees in 2014 was average, even though rodent abundance in 2015, based on similar track plate data from northern Switzerland (Grendelmeier et al., 2017) and own observations, was rather high. Hence, the effect of simulating increased rodent presence might have been weakened. Nevertheless, the rodent abundance index did not significantly differ between treatment types and hence natural rodent abundance did not seem to be affected by the treatments. Likewise, we assume that abundances of predators were not affected by our playbacks because of their much larger home ranges compared to rodents.

Aside from being responsible for nest losses, most of the predator species identified in this and other studies (Bellamy et al., 2018; Grendelmeier et al., 2015; Mallord et al., 2012; Maziarz, Grendelmeier, et al., 2018; Maziarz, Piggott, et al., 2018) are capable of taking adults at nests. This indicates that both nest survival and an adult's immediate survival should underlie the (costly) anti-predator responses mounted by adult wood warblers during settlement and throughout the breeding cycle.

Finally, acoustically simulated predation risk did not seem to affect reproductive performance either, as clutch size, number of fledglings and nest survival did not seem to differ between treatments. Predation risk has been shown to negatively affect reproductive output of birds (Eggers et al., 2006; Zanette et al., 2011), but these effects vary across species (LaManna & Martin, 2016). Again, as with settlement responses above, wood warblers may not have perceived playback vocalizations as a cue indicating predator presence and therefore did not adjust reproductive investment. Alternatively, wood warblers may be constrained in their ability to adjust reproductive efforts in relation to predation risk, resulting in the observed lack of response to the treatments. Finally, wood warblers may have responded to simulated predation risk, but low

sample sizes and hence large uncertainty levels (i.e., large confidence bands) might not have allowed statistically revealing existing differences among treatments.

To conclude, experimental studies showing that vocalizations of rodents and/or predators elicit a response in birds have recently increased in number. However, such vocalizations are not always the relevant cues used when birds determine where to settle, as evidenced in our study by the lack of response of wood warblers to acoustically simulated rodent and/or predator presences. Thus, further experimental studies on environmental cues relevant for individual wood warbler settlement decisions and the senses involved are needed. Insights into the relevant cues are important as they can help to better understand the dynamics of wood warbler population sizes in relation to resource pulses within their breeding ecosystems. More generally, such studies would increase knowledge on the timing, settlement and reproductive decisions of birds and thus on how birds optimize fitness in environments characterized by varying levels of predation risk.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

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