



Nest predator avoidance during habitat selection of a songbird varies with mast peaks and troughs

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Received: 23 January 2019 / Revised: 14 May 2019 / Accepted: 24 May 2019 / Published online: 13 June 2019
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Abstract

Predation risk is vital in determining habitat quality. But landscapes of fear are complex and dynamic, such as temperate deciduous forests characterized by intermittent, synchronized production of large seed crops (mast peaks). These “resource pulses” elevate the magnitude of predation risk via direct or indirect effects, possibly altering also predator avoidance strategies of a prey. Yet, how animals manage predation risk via informed habitat selection and how this depends on ecological context remains poorly explored. We studied risk-sensitive settlement behavior of wood warbler *Phylloscopus sibilatrix*. We tested the hypothesis that warblers flexibly avoid predators (Eurasian jays *Garrulus glandarius*) during habitat selection but that their interactions are mediated by mast seeding, which is known to elevate the overall nest predation risk for warblers through its cascading effects on population dynamics of rodents and generalist predators. We used a playback experiment to manipulate warblers’ perceived risk of nest predation by jays. We replicated the experiment in two consecutive years, followed by high or low seed crop. In the spring following mast trough, risky jay plots featured low abundance, late settlement, and poor pairing success compared to other treatments. In contrast, no response differences were found in the spring following mast seeding. Our results suggest that the way wood warblers adjust habitat choices to jay predation risk is indirectly mediated by mast seeding. This highlights plasticity in predator avoidance during prey habitat selection in complex and dynamic landscapes of fear, and the potential effects of mast seeding on animal behavior via indirect interactions.

Significance statement

Avoiding places with high nest predation risk during settlement decisions is believed to be widespread in birds. However, the mechanistic understanding of how birds acquire and use information about ambient nest predation risk to fine-tune settlement decisions is still limited. Using a playback experiment, we show that wood warblers eavesdrop on predator calls and avoid settling at sites with high perceived risk of nest predation by Eurasian jays. However, the way warblers adjust habitat choices to the nest predation risk posed by jays appears to be affected by tree mast seeding. This is potentially due to cascading effects of masting on the population dynamics of rodents and generalist predators, creating temporal peaks of elevated nest predation risk for wood warblers. Our study highlights plasticity in predator avoidance during prey settlement behavior in temporally variable, pulsed-resources ecosystems.

Communicated by P. A. Bednekoff

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00265-019-2702-z>) contains supplementary material, which is available to authorized users.

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Keywords Anti-predator behavior · Apparent competition · Information use · Interceptive eavesdropping · Habitat selection · Mast seeding

Introduction

Many animals are temporally bound to a specific location—a territory, in which a nest is placed and offspring are raised. These breeding site–selection decisions have far-reaching consequences for survival and reproductive success (Cody 1985; Fuller 2012). But individuals face uncertainty regarding habitat quality at potential breeding sites, due to spatial

heterogeneity in environmental conditions. This uncertainty can be reduced by gathering information about ambient conditions prior to making a territory choice (Dall et al. 2005; Seppänen et al. 2007; Schmidt et al. 2010; Szymkowiak 2013). Thus, information gathering and use provides a selective advantage that facilitates decision-making and allows for better choices, and is at the core of animal–environment interactions. Examining how animals use various cues for settlement decisions is needed for understanding complex habitat selection strategies.

Predation risk is a vital component determining habitat quality. Even the mere exposure to the risk of predation can have pronounced negative effects on prey fitness (reviewed in Lima 1998, 2009; Cresswell 2008; Clinchy et al. 2013). Individuals breeding under elevated predation risk often reduce reproductive investment, leading to reduced numbers of offspring and/or lower offspring quality (Korpimäki et al. 1994; Fontaine and Martin 2006; Sheriff et al. 2009; Zanette et al. 2011; Dudeck et al. 2018), which may in turn suffer physiological costs or lower immune activity (Saino et al. 2005; Meylan et al. 2010; Coslovsky and Richner 2011; McGhee et al. 2012). Managing the risk of predation via informed habitat selection decisions may thus be a frontline anti-predator defense, but our understanding of this phenomenon is still limited.

Predators and prey within a community are embedded in a complex network of ecological interactions. Natural systems are characterized by multiple predator species coexisting in the same habitat and differing in diet, hunting strategies, or sensory capabilities. From the preys' perspective, all enemies are not equal but pose different levels of risk (Lima 1992; Sih et al. 1998; Morosinotto et al. 2010). Furthermore, predators often kill a range of prey species which leads to a variety of indirect interactions among prey species linked in a food web by shared natural enemies. Such indirect links may affect the magnitude of predation risk experienced by prey. For example, an increase in abundance of one prey species may trigger a numerical response of a predator, which in turn will cause temporal peaks in predation risk to the other prey species of that predator—a phenomenon called apparent competition (Holt 1977; Holt and Bonsall 2017). This indirect interaction is ubiquitous in temporally variable, pulsed-resources ecosystems (cf Ostfeld and Keesing 2000; Schmidt and Ostfeld 2008), making these complex and dynamic landscapes of fear (Laundrè et al. 2001; Gaynor et al. 2019) where settlement behavior needs to be adjusted to predation risk varying in space and time, and with ecological context. This sets the stage for the use of flexible predator avoidance strategies, adopted by individuals in a context-dependent manner to fine-tune decision-making to the perceived risk. Such strategies, however, remain poorly understood.

In birds, nest predation is a key selective pressure; it is the most important cause of reproductive failures (Martin 1995).

Within avian habitat selection research, perhaps the best documented anti-predator responses are changes in breeding location or nesting microhabitat following nest depredation (reviewed in Lima 2009; Ibáñez-Álamo et al. 2015). In contrast, avoidance of predators during settlement decisions, i.e., prior to a breeding attempt, has received much less research attention, even though it is believed to be widespread (Forstmeier and Weiss 2004; Eggers et al. 2006; Fontaine and Martin 2006; Thomson et al. 2006; Morosinotto et al. 2010; Emmering and Schmidt 2011; Hua et al. 2013). The mechanistic understanding of how birds acquire and use information about ambient nest predation risk to fine-tune settlement decisions is still limited and has received calls for increased research attention (Lima 2009; Ibáñez-Álamo et al. 2015).

We studied how wood warblers *Phylloscopus sibilatrix*—small, insectivorous songbirds, with breeding grounds spanning temperate Europe (Cramp et al. 1992)—manage the risk of nest predation during settlement decisions. Wood warblers inhabit deciduous forests, mainly dominated by oaks *Quercus* spp. or beech *Fagus sylvatica*, with light cover of herb layer. The domed nests of wood warblers are placed exclusively on the ground and exposed to an entire community of potential nest predators, e.g., martens *Martes* spp., foxes *Vulpes vulpes*, and Eurasian jays *Garrulus glandarius*, with predation accounting for up to 95% of nest failures (Wesołowski 1985; Wesołowski and Maziarz 2009; Mallord et al. 2012; Grendelmeier et al. 2015). Correlative evidence suggests that when deciding where to settle, wood warblers avoid habitat patches with high densities of Eurasian jays, common predators of their eggs and nestlings (Szymkowiak and Kuczyński 2015). However, wood warblers' predator avoidance strategies during settlement decisions were hypothesized to be indirectly mediated by tree mast seeding (Szymkowiak and Kuczyński 2015).

Mast seeding, i.e., highly synchronized and intermittent production of a large seed crop, is a key feature of temperate forests and occurs worldwide. It is well established that these “resource pulses” (Ostfeld et al. 1996; Ostfeld and Keesing 2000) temporally release seed-eating rodents from food limitation and they become superabundant in the following spring (Pucek et al. 1993; Ostfeld et al. 1996; Ostfeld and Keesing 2000; Bogdziewicz et al. 2016). Such rodent outbreaks extend over large spatial scales (Koenig and Knops 1998, 2000; Bogdziewicz et al. 2017) and have negative consequences for ground-nesting songbirds (Schmidt and Ostfeld 2003, 2008; Schmidt et al. 2008), including wood warblers (Wesołowski et al. 2009; Grendelmeier et al. 2018). Rodents per se are not a threat for wood warbler nests (cf Mallord et al. 2012; Grendelmeier et al. 2015); however, wood warblers and rodents are indirectly linked via shared enemies (apparent competition; Grendelmeier et al. 2018). It is well-documented that generalist predators, e.g., martens and foxes,

which are also important nest predators of wood warblers (Wesołowski 1985; Mallord et al. 2012; Grendelmeier et al. 2015), respond numerically and functionally to rodent outbreaks (Jędrzejewska and Jędrzejewski 1998; Ostfeld and Keesing 2000; Bogdziewicz et al. 2016). As a consequence, wood warblers suffer higher nest losses in years following mast seeding, and this is due to generalist predators (mainly marten and foxes) incidentally preying on warbler nests when hunting for rodents on the forest floor (Grendelmeier et al. 2018). Wood warbler densities and occurrence were found to be strongly negatively correlated with rodent abundance at a range of spatial scales (Wesołowski et al. 2009; Szymkowiak and Kuczyński 2015; Pasinelli et al. 2016). This suggests that wood warblers perceive this risk and avoid breeding in rodent outbreak areas (Wesołowski et al. 2009; Szymkowiak and Kuczyński 2015), even though some individuals take the risk and settle even in years following mast peaks (Szymkowiak and Kuczyński 2015).

We experimentally tested the hypothesis that wood warblers flexibly avoid predators during habitat selection and that their interactions with jays are indirectly mediated by oaks' mast seeding (Szymkowiak and Kuczyński 2015). We predicted that wood warblers will avoid settling in areas with high perceived risk of nest predation by jays in the year followed by mast trough (i.e., much lower acorn production compared to mast peak), thus featuring low rodent abundance in spring (e.g., Pucek et al. 1993). However, in the spring following mast peak, wood warbler settlement decisions will be unaffected by high perceived jay predation pressure (Szymkowiak and Kuczyński 2015), due to the response of generalist predators to rodent outbreak in turn resulting in temporal peak of nest predation risk for wood warblers (Grendelmeier et al. 2018). In contrast, wood warblers are assumed to perceive the elevated nest predation risk of numerous different predators and settle in low numbers irrespective of jay presence (cf Wesołowski et al. 2009; Szymkowiak and Kuczyński 2015).

Methods

Study site and species

The study was conducted in 2016 and 2017 in the Wielkopolska National Park (WNP), western Poland (52° 16' N, 16° 47' E). Forest habitats in WNP consist mainly of mixed-forests with pedunculate oak *Quercus robur*, sessile oak *Q. petraea*, and Scots pine *Pinus sylvestris*.

In the WNP, wood warblers inhabit mainly deciduous (oak-dominated) and mixed oak-pine forests with closed canopy cover and intermediate herb-layer cover (J Szymkowiak, unpublished data). Wood warblers are long-distance (Palearctic-Afrotropical) migrants showing very low breeding-site fidelity (0–5% return rates in Eastern Europe, Wesołowski et al.

2009). In the WNP, male spring arrival and settlement usually start in mid-April, while females arrive approximately a week later (Szymkowiak et al. 2016, 2017).

Experimental design

We used a playback experiment to increase wood warbler perceived risk of nest predation by jays. Rodent outbreaks that follow mast years with a one-year time lag, or mast seeding per se, cannot be experimentally manipulated. However, we replicated the playback experiment in two consecutive years (2016 and 2017) which followed either mast failure in 2015 or mast peak in 2016 (see below). Hence, by taking the advantage of mast seeding that occurred naturally during the study, we were able to investigate its effects on wood warbler–jay interactions in a quasi-experimental setting.

Seed production monitoring

Acorn production in the WNP has been monitored since 2013 on permanent sampling points established in oak-hornbeam forest, as part of a long-term study on bird's responses to mast seeding. We monitored acorn production of sessile oaks, while there are also pedunculate oak present at our study site; however, both species have very similar biology and ecology, and their seed production is highly synchronized (Bogdziewicz et al. 2017). Each year, seed fall was measured using seed traps ($n = 12$ traps/year, 1 trap/tree) consisting of a fine-grained mesh supported on a frame made of PVC tubes, with an additional coarse-grained mesh mounted at the top of a trap allowing seeds to fall into a trap but preventing seed removal by seed predators (Online Resource 1: Fig. A1). Each trap had a collection area of 1 m². We calculated all acorns that fell into traps at least every two weeks from early-September (with peak of seed fall being in mid-October) to late-November until no additional acorns were retrieved from the traps. We used the total number of acorns per tree as an index of seed crop size for subsequent analyses.

Playback experiment

In each year, the experiment was conducted on 15 plots, each with an area of 9 ha (300 × 300 m). The size of the study plots was chosen to ensure appropriate spacing among plots and playback coverage (details below), but it would allow settlement of multiple wood warbler pairs (cf Szymkowiak et al. 2016, 2017). All plots were established within typical wood warbler habitats in the study area to reduce any confounding effects of vegetation quality on wood warbler responses to experimental manipulation (cf Szymkowiak et al. 2016, 2017). The median nearest-neighbor distance between plot centers was 630.4 m (range = 590.1–718.8 m). In 2016, we randomly assigned plots to one of three treatments ($n = 5$ plot

replicates/treatment): (i) “risky,” on which we increased the perceived risk of nest predation to wood warblers by broadcasting jay vocalizations; (ii) “sound-control,” on which we broadcast songs of chaffinch *Fringilla coelebs*, a forest songbird commonly occurring in the WNP and putatively neutral for wood warblers, to control for potential effects of playback equipment and sound broadcasting per se on wood warblers’ behavior; and (iii) “silent-control,” on which we did not broadcast any vocalizations nor deploy playback equipment. In the pre-treatment year (2015), wood warbler abundance on “risky” (mean no. of territories = 3.71, 95% CI 2.56–6.12), “sound-control” (mean = 3.27, 95% CI 1.87–5.14) and “silent-control” (mean = 4.13, 95% CI 2.20–5.66) plots did not differ (zero-truncated GLM, treatment effect: Wald $\chi^2 = 0.61$, $df = 2$, $P = 0.737$), and were well within typical wood warbler densities in preferred forest habitats (cf Wesołowski et al. 2010). In 2017, plots were randomly re-assigned to playback treatments, but ensuring that no plots received the same treatment in both years.

We placed one broadcast system at the center of each playback treatment plot to simulate the presence of either jays or chaffinches. Each broadcast system consisted of one tablet PC (GoClever Orion 70, Android 4.2. software) powered by two portable USB power banks (GP GL301, 10,400-mAh capacity) and placed in a plastic box that was buried in the ground. The tablet was wired to two Trust Remo 2.0 stereo speakers (frequency range 50–15,000 Hz) with built-in amplifier, which were mounted on trees 3–3.5 m above the ground, placed 30 m apart and pointed in opposite directions selected at random.

Playback vocalizations consisted either of series of typical jay calls (“kreeh!” and “kschaach!”) or songs of territorial chaffinch males. The vocalizations (10–15 s, i.e., ~5–8 jay calls or ~2–3 chaffinch songs) were interspersed with periods of silence (15–20 s) on repeat for 5 min. These 5-min bouts of vocalizations were interspersed by 5–8-min periods of silence; the exact time intervals were randomized (cf Zanette et al. 2011; Walters et al. 2017). We prepared 10 unique playbacks (one per plot), each based on recordings of three unique individuals (i.e., altogether we used vocalizations from 30 individuals). The vocalizations of the 30 individuals were obtained in the WNP in 2013–2015 using a Tascam DR-100MKII recorder connected to a Sennheiser ME67 shotgun microphone (sampling rate 44.1 kHz, resolution 16 bit) and from online bird sounds repository (www.xeno-canto.org). We processed the recordings to remove background noise and then compiled them into two-channel stereo files (mp3, bit rate = 320 kbps, sampling rate = 44.1 kHz). We used the same playback files in both years of the experiment. Playback preparation was performed in Adobe Audition CS6 software.

We broadcast playbacks from 6 April to 30 May, spanning the spring arrival, settlement, and mating phases of the wood warbler breeding season at the WNP (Szymkowiak et al.

2016, 2017). Playbacks were broadcast from dawn to dusk, matching the diurnal vocal activity of jays and chaffinches. Within a single broadcast system, the playback alternated between the two speakers every 5–8 min to simulate movements of a predator (or male chaffinch) and thereby reduce wood warbler habituation to playbacks (cf Szymkowiak et al. 2017). To further minimize the likelihood of habituation, we broadcast playbacks following a 2-day-on 2-day-off scheme (i.e., two days of silence after two days of broadcasting) and circulated playback files between plots within a given treatment at the beginning of each 2-day-on period (cf Zanette et al. 2011; Walters et al. 2017). Playbacks were broadcast at standardized volume of 85 (± 1.4) dB, measured at 1 m from the loudspeaker using a sound-level meter (CEM DT-8852, weighting level A, fast response); playbacks were audible 100–120 m away; thus, most of the area of each plot was covered by a playback.

Measuring response of wood warblers to perceived predation risk

We assessed plot-level abundance of wood warblers using the territory mapping method. Censuses were made weekly between 10 April and 30 June usually starting between 0600 and 0700 h. All plots were visited at the same frequency, with a total number of 12 censuses per plot per year. As a rule, a single survey on each plot lasted ca. 60 min. The observer walked along parallel transects 100 m apart and marked the exact locations of territorial individuals using a handheld GPS device (Garmin Oregon 450, 4 (± 1) m accuracy). A territory was classified as occupied when (i) a singing male was recorded at least three times in the same location, (ii) a pair was observed at least twice on subsequent visits, and (iii) a nest was found (cf Szymkowiak et al. 2016, 2017). Analogous methods were used to assess the abundance of jays on study plots, although with no attempt to find nests. It was not possible to record blind data because our study involved focal animals in the field.

During censuses, we noted the pairing status of each wood warbler male. This was assessed based on direct observation of a pair and an unambiguous change in males’ singing behavior. After pair formation, male wood warblers cease to sing their usual trill and whistle songs and instead sing distinct “short songs” near the nest until young fledge or the nest is lost (Temrin 1986). We also estimated the settlement date of each male, taken as the midpoint between the last census visit when a given territory was unoccupied and the first census visit when a male was found to occupy a territory. Moreover, to quantify fine-scale patterns of spacing of territories within study plots, we measured the Euclidean distance from a center of male’s territory to the center of a plot (i.e., from where playbacks were broadcast). Coordinates of territory centers were calculated by averaging coordinates of locations of an

individual male during territory mapping censuses. Spatial analyses were conducted using QuantumGIS 2.8.9 and R version 3.4.1 software.

Statistical analyses

To compare acorn production between years, we used generalized linear mixed-effects model with total number of seeds collected per tree as the response and year as a fixed effect. We included tree ID as random intercept to account for data dependency arising from measuring seed crop of the same individual trees over years. The model was fitted with negative binomial distribution and log link function to address overdispersion.

We used generalized estimating equations (GEE) to examine responses of wood warblers to experimental treatment. GEE allow accounting for data dependency and nested structure and are flexible, quasi-likelihood extensions of generalized linear models (Hardin and Hilbe 2003). However, instead of estimating subject-specific (conditional) effects, as mixed-effects models, GEE estimate population-specific (marginal) effects, providing more robust results when there are relatively few observations per subject (Hardin and Hilbe 2003; Pekár et al. 2017).

To test settlement responses of wood warblers to treatment at the plot level, we used GEE with number of territories (abundance) as a response variable, assuming Poisson distribution and log link function, and included plot ID as clustering term to account for using the same study plots in two consecutive years. When analyzing effects of treatment on timing of settlement, territory spacing, and pairing probability, a territorial male was the sampling unit. For testing treatment effects on timing of settlement, we used GEE with male settlement date (expressed as April days, i.e., days since the 1st of April) as a response and gamma distribution with inverse link function. To analyze the differences in fine-scale patterns of spacing of territories within study plots and effect of treatment on pairing probability, we fitted GEE with distance from a territory to plot center (Gaussian distribution, identity link) and male's pairing status (binomial distribution, logit link) as response variables, respectively. In these models, we included plot ID nested within a year as a clustering term to account for data dependency arising from using multiple observations from the same study plot in each year. In all models, we included treatment (risky, sound-control, silent-control), year (2016 vs 2017), and interaction between both variables as fixed effects, which allowed testing whether wood warbler responses to experimental treatment differed between years. We included the abundance of jays as a covariate. Preliminary data exploration revealed that jay's abundance on study plots was either zero or one; hence, this variable was included as a two-level factor (absence/presence).

To test whether the jay presence was affected by playback treatments, we fitted GEE with jay occurrence (absence/presence) as a response (binomial distribution, logit link) and treatment, year, and interaction between both variables as fixed effects. This was done to test if jay responses to treatments could explain wood warbler responses to treatment. Plot ID was included as clustering term to account for using the same study plots in two consecutive years.

We tested significance of model terms using Wald's χ^2 test and compared pairwise contrasts of least-squares means to test for differences in wood warbler responses to treatments, using the R package *lsmeans* (Lenth 2016).

Results

Acorn production differed strongly between the two years of study and consistently across all oak individuals measured (Fig. 1). Specifically, oak seed crop in 2015 was low (mean no. of acorns (95% CI) = 10.8 (6.9–17.0), $n = 12$ trees), while 2016 was a mast year with high acorn production (mean = 548.7 (361.4–833.0), $n = 12$ trees; Wald $\chi^2 = 156.73$, $df = 12$, $P < 0.001$).

The plot-level probability of jay occurrence did not differ between years or between treatments (2016, silent-control: mean = 0.17 (0.02–0.64), sound-control: mean = 0.18 (0.02–0.67), jay treatment: mean = 0.43 (0.10–0.83); 2017, silent-control: mean = 0.4 (0.08–0.83), sound-control: 0.33 (0.05–0.82), jay treatment: mean = 0.33 (0.05–0.82), $n = 5$ plots per treatment per year; Table 1e).

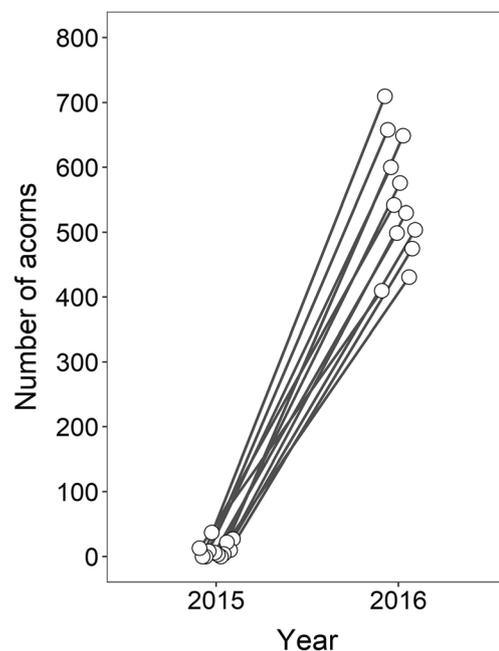


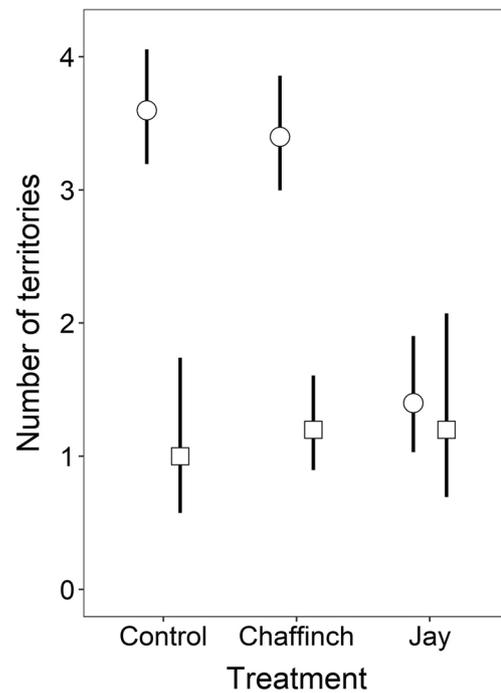
Fig. 1 Acorn production in 2015 and 2016 in the Wielkopolska National Park. Each point represents an individual oak tree

Table 1 Results of generalized estimating equations models examining the responses of wood warblers to experimental treatment (a–d) and comparing probability of jay occurrence (e) among treatments

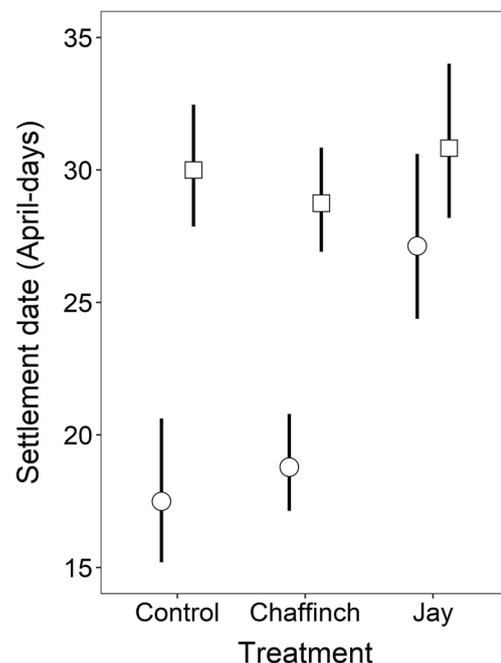
Fixed effect	Wald χ^2	df	<i>P</i>
(a) Number of territories			
Treatment	9.05	2	0.011
Year	35.75	1	< 0.001
Jay (presence/absence)	0.26	1	0.610
Treatment \times year	7.35	2	0.025
(b) Timing of settlement			
Treatment	18.41	2	< 0.001
Year	35.09	1	< 0.001
Jay (presence/absence)	0.93	1	0.335
Treatment \times year	19.95	2	< 0.001
(c) Distance from territory to plot center			
Treatment	30.09	2	< 0.001
Year	0.01	1	0.906
Jay (presence/absence)	0.01	1	0.941
Treatment \times year	0.55	2	0.758
(d) Probability of pairing			
Treatment	12.28	2	0.002
Year	12.78	1	< 0.001
Jay (presence/absence)	0.95	1	0.330
Treatment \times year	6.61	2	0.037
(e) Probability of jay occurrence			
Treatment	0.75	2	0.687
Year	0.40	1	0.529
Treatment \times year	0.62	2	0.735

We found a negative effect of the “risky” jay treatment on plot-level wood warbler abundance, but this effect depended on year (Table 1a, Fig. 2). In the spring following mast trough (2016), the number of wood warbler territories on plots with simulated jay presence (mean = 1.4 (1.03–1.90), $n = 5$ plots) was lower relative to silent-control plots (mean = 3.6 (3.20–4.06), $n = 5$ plots; post hoc test: $z = -5.63$, $P < 0.001$) and sound-control plots (mean = 3.4 (3.00–3.86), $n = 5$ plots; $z = -5.24$, $P < 0.001$). However, in the spring following mast peak (2017), wood warbler abundance on jay treatment (mean = 1.2 (0.70–2.07), $n = 5$ plots), sound-control (mean = 1.2 (0.90–1.61), $n = 5$ plots), and silent-control plots (mean = 1.0 (0.57–1.74), $n = 5$ plots) did not differ (all $P \geq 0.836$) and were similar to “risky” treatment in 2016 (Fig. 2).

The jay treatment also affected timing of settlement of wood warblers, but again this effect was year-dependent (Table 1b, Fig. 3). Male wood warblers were later in establishing territories on jay treatment plots (mean settlement date = 27.14 (24.38–30.61), $n = 7$ males) relative to silent-control plots (mean = 17.50 (15.20–20.63), $n = 18$ males; $z = -4.14$, $P < 0.001$) and sound-control plots (mean = 18.79 (17.14–20.80), $n = 17$ males; $z = -4.85$, $P < 0.001$) but only in the

**Fig. 2** The effect of experimental treatment on the number of wood warbler territories in the year preceded by mast trough (2016, circles) and the year following mast peak (2017, squares). Points are estimated mean numbers of territories, while whiskers are 95% confidence intervals

spring following low acorn production (2016). In contrast, in the spring following mast peak (2017), male settlement dates on jay-treatment plots (mean = 30.83 (28.20–34.01), $n = 6$

**Fig. 3** The effect of experimental treatment on timing of settlement of wood warbler males in the year preceded by mast trough (2016, circles) and the year following mast peak (2017, squares). Points are estimated mean settlement dates expressed as April days (i.e., days since the 1st of April), while whiskers are 95% confidence intervals

males) did not differ relative to silent-control (mean = 30.00 (27.88–32.47), $n = 5$ males; $z = 0.45$, $P = 0.896$) and sound-control plots (mean = 28.75 (26.92–30.85), $n = 6$ males; $z = -1.20$, $P = 0.454$). Overall, settlement dates of wood warblers in the spring following mast peak (2017) were similar to “risky” treatment in 2016 (Fig. 3).

Our playback manipulation demonstrably affected wood warbler behavior in both years. Therefore, the lack of a treatment effect on the abundance and timing of settlement in 2016 was not due the wood warblers not attending to the playbacks. In particular, independently of the year, the jay treatment affected fine-scale spacing of wood warbler territories within study plots (Table 1c, Fig. 4). In 2016, wood warblers established territories further from plot centers on jay treatment plots (mean distance = 133.45 m (117.64–149.27), $n = 7$ males) than on silent-control (mean = 95.53 m (85.13–105.93), $n = 18$ males; $z = -3.93$, $P < 0.001$) or sound-control plots (mean = 97.98 m (85.96–109.99), $n = 17$ males; $z = 3.50$, $P = 0.001$). Similarly, in 2017, the average distance from a territory to plot center was greater on jay treatment plots (mean = 140.54 m (120.19–160.89), $n = 6$ males) than on silent-control (mean = 91.25 m (72.28–110.23), $n = 5$ males; $z = -3.47$, $P = 0.002$) and sound-control plots (mean = 94.56 m (79.98–109.14), $n = 6$ males; $z = 3.6$, $P < 0.001$).

We also found a negative, year-dependent effect of jay treatment on the probability of a male pairing (Table 1d, Fig. 5). In 2016, males that settled on jay treatment plots had a lower probability of pairing (mean = 0.14 (0.03–0.51), $n = 7$

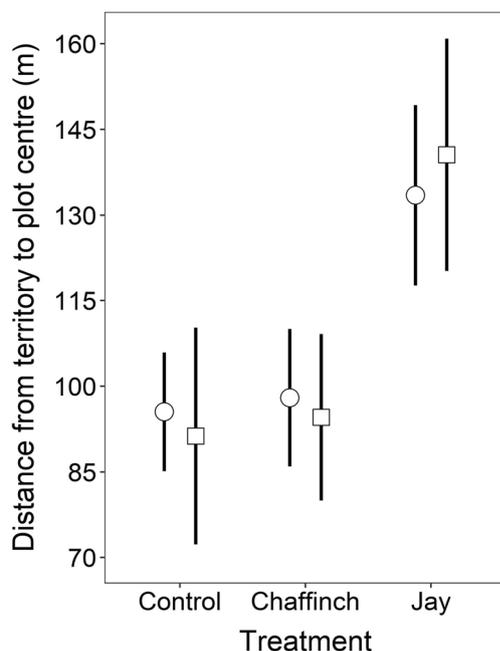


Fig. 4 The effect of experimental treatment on spacing of wood warbler territories in the year preceded by mast trough (2016, circles) and the year following mast peak (2017, squares). Points are estimated mean distances from a territory to plot center (m), while whiskers are 95% confidence intervals

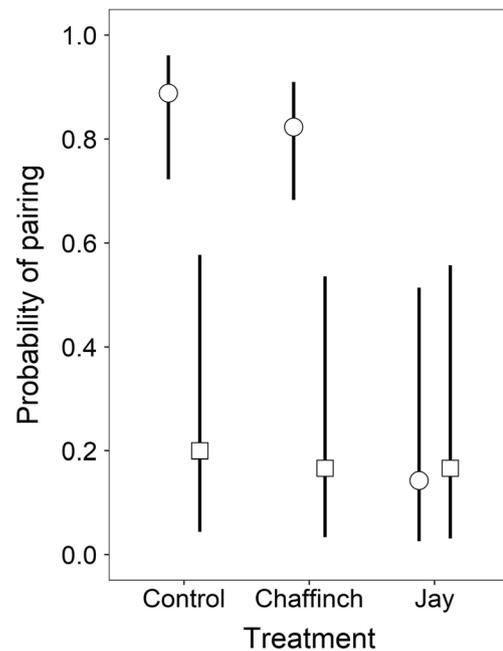


Fig. 5 The effect of experimental treatment on pairing probability in the year preceded by mast trough (2016, circles) and the year following mast peak (2017, squares). Points are estimated mean probabilities of pairing, while whiskers are 95% confidence intervals

males) than males on silent-control (mean = 0.89 (0.72–0.96), $n = 18$ males; $z = 3.51$, $P = 0.001$) and sound-control plots (mean = 0.82 (0.68–0.91), $n = 17$ males; $z = -3.26$, $P = 0.003$). However, in 2017 (i.e., the spring following mast peak), the probability of pairing for males on jay treatment (mean = 0.17 (0.03–0.56), $n = 6$ males) did not differ compared to silent-control (mean = 0.20 (0.04–0.58), $n = 5$ males; $z = 0.17$, $P = 0.983$) and sound-control plots (mean = 0.17 (0.03–0.54), $n = 6$ males; $z = 0$, $P = 1$), and was similar to that on “risky” treatment plots in 2016.

Discussion

Wood warblers appear to assess spatial heterogeneity in predation risk to their offspring and avoid settling on plots with simulated jay presence. However, the negative effects of jay presence on abundance and timing of settlement were apparent only in the spring following mast trough (2016), and completely vanished in the spring following mast peak (2017). In fact, the abundance and settlement timing in the spring following mast seeding were similar, regardless of treatment, to abundance and settlement dates on the “risky” jay treatment in 2016. Between-year differences in habitat selection responses of wood warblers to simulated presence of jays could not be attributed to variation in abundance of naturally occurring jays. Instead, our results support the hypothesis that wood warblers deciding where to settle avoid

nest predators in a context-dependent manner (Szymkowiak and Kuczyński 2015).

Male wood warblers adjusted fine-scale territory spacing to the perceived risk of nest predation by jays and consistently increased the distance between the putative location of a nest predator and their own territories. Thus, adult wood warblers appear to assess spatial heterogeneity in predation risk by jays to their offspring and use this information to fine-tune settlement decisions. Even relative to highly mobile predators, establishing territories 50 m further away may significantly decrease the risk of nest depredation or non-lethal costs associated with predator proximity. For example, a small difference in spatial territory selection relative to a breeding predator can considerably affect prey behavior and physiology, which may further translate into short-term reproductive output and long-term fitness consequences (Geer 1978; Thomson et al. 2006, 2010, 2012). Thus, the spatial adjustment in territory selection we observed in wood warblers could be biologically relevant and part of their predator avoidance strategy.

Wood warblers avoided settling in the spring following mast peak. We found that in the spring after mast peak, wood warblers settled later and at lower numbers across all study plots. This was presumably due to high rodent abundance, as rodents exhibit strong numerical response to mast seeding and become superabundant in the following spring (Pucek et al. 1993; Ostfeld et al. 1996; Ostfeld and Keesing 2000; Bogdziewicz et al. 2016). In turn, temporal peaks in rodent abundance following mast years elevate the risk of nest predation for wood warblers, due to numerical and behavioral responses of shared enemies, e.g., mustelids and foxes (Grendelmeier et al. 2018). Consequently, wood warblers suffer higher nest losses during rodent outbreaks due to overall increased predator activity on the forest floor (Wesołowski et al. 2009; Grendelmeier et al. 2018). Moreover, the proportion of wood warbler nests predated by rodent-hunting predators increases during rodent outbreaks, while the proportion of nests predated by jays appears independent on rodent numbers (Grendelmeier et al. 2018). Concurrently, mast seeding and the rodent outbreaks following mast events (and associated predation risk) are highly synchronized in time and space, spanning even over thousands of kilometers (Koenig and Knops 1998, 2000; Bogdziewicz et al. 2017). Thus, simple avoidance of jays would be an inefficient habitat selection strategy during rodent outbreaks that follow mast years (cf Wesołowski et al. 2009; Szymkowiak and Kuczyński 2015).

Wood warblers appear to perceive temporal peaks of elevated nest predation risk. To escape breeding under strong predator pressure, they switch habitat selection strategy and largely avoid settling in rodent outbreak areas, irrespective of jay presence (Wesołowski et al. 2009; Szymkowiak and Kuczyński 2015). The negative effects of jay presence on wood warblers abundance and timing of settlement vanished in the spring following high acorn crop. The decision-making pattern we

observed supports the hypothesis that wood warblers flexibly avoid predators during habitat selection and that their interactions with jays are indirectly mediated by oaks' mast seeding, likely due to its cascading effects on population dynamics of rodents and generalist predators (Szymkowiak and Kuczyński 2015). It remains a challenge for future studies to unravel further decision-making of birds refusing to settle in rodent outbreak areas. They could forgo breeding in rodent outbreak years, but currently there is no evidence for such predator-induced breeding suppression in relatively short-living songbirds (Lima 2009). Alternatively, wood warblers may search for safer breeding grounds and settle in areas where rodent abundance is low. These could be stands in which seed production in the previous year was low, which depending on the scale of mast seeding may require moving tens to several hundred kilometers (cf Bogdziewicz et al. 2019). However, at a finer spatial scale, wood warblers could settle in forests with higher proportion of conifers or stands dominated by other deciduous tree species that do not produce seeds in synchrony with oaks (e.g., beech: Bogdziewicz et al. 2017).

Our results show that the risk of nest predation is an important cue governing avian habitat selection. Several studies have experimentally manipulated predator cues and demonstrated their importance in driving birds' settlement behavior (e.g., Eggers et al. 2006; Fontaine and Martin 2006; Emmering and Schmidt 2011; Hua et al. 2013). Risk-sensitive habitat choices reduce the likelihood of predator encounters and minimize the non-lethal costs associated with breeding under high perceived predation risk (Lima 1998, 2009; Cresswell 2008; Clinchy et al. 2013). We found that males establishing territories under high predation risk had lower probability of attracting a female. This pattern could arise because either these males were lower quality or females perceived the elevated risk to offspring and refused to mate, irrespective of male quality. Predation risk effects on breeding-site quality may alter the spatial distribution of phenotypes within populations (Cody 1985; Fuller 2012), even at small spatial scales (Thomson et al. 2010, 2012). Fear-sensitive settlement behavior therefore brings several important ecological consequences (Lima 1998; Cresswell 2008). The ability of prey to exploit spatial refugia may reduce predator efficiency, which in turn will affect predator-prey dynamics (e.g., Goodwin et al. 2005; Schaubert et al. 2009). Our results together with past studies point towards potentially far-reaching role of predation risk in structuring breeding bird communities through individual-level informed habitat choices.

Our results suggest that the way wood warblers adjust habitat choices to ambient nest predation risk posed by jays is indirectly mediated by oaks' mast seeding. This highlights plasticity in predator avoidance during avian settlement decisions and provides understanding of prey habitat selection in complex and dynamic landscapes of fear. For prey living in dynamic landscapes of fear characterized by a multitude of coexisting predator species (Lima 1992, 2009; Sih et al.

1998), flexible predator avoidance strategies adopted in a context-dependent manner would be crucial. Analogous mechanisms may occur when assessing spatial heterogeneity in predation risk during habitat selection, but current evidence is limited (e.g., Forstmeier and Weiss 2004; Morosinotto et al. 2010). We suggest that context-dependent information use may be common and would allow fine-tuning settlement decisions to spatio-temporally variable conditions (Parejo et al. 2018), ultimately making an efficient, frontline anti-predator behavior.

Our results highlight the potential effects of mast seeding on birds' habitat selection behavior via indirect effects. Rodent outbreaks following mast years likely create temporal peaks of predation risk for many forest songbirds, especially ground-nesters (cf Jędrzejewska and Jędrzejewski 1998; Schmidt and Ostfeld 2003, 2008; Schmidt et al. 2008). These can arise either directly or indirectly, as increased rodent abundance may strengthen the magnitude of apparent competition between rodents and songbirds via responses of shared enemies. Predation risk for songbirds may also peak two years after mast year, when rodent population crashes and generalist predators switch to alternative prey (Schmidt and Ostfeld 2003, 2008; Schmidt et al. 2008). Behavioral flexibility during habitat selection in response to mast seeding and rodent outbreaks might be community-wide phenomena. Surprisingly, although mast seeding is a key feature of temperate forests and occurs worldwide (Ostfeld and Keesing 2000; Yang et al. 2010), its effects on avian habitat selection remain unexplored and almost exclusively refer to seed-eating birds aggregating in mast-rich habitats (cf Bogdziewicz et al. 2016). We suggest that researchers interested in avian habitat selection should be particularly aware of potential effects of mast seeding, as ignoring them may hinder full understanding of complex decision-making processes governing birds' settlement behavior.

We acknowledge that we explored effects of mast seeding on wood warbler settlement behavior over a short time frame. Theoretically, settlement patterns we observed could emerge due to some other factors differing between study years. This could be, for example, variation in weather, local production of young or survival, or conditions at wintering grounds and migratory routes, which in turn could affect wood warbler population abundance and settlement patterns differently in both years. In addition, the magnitude of non-consumptive effects of predators on prey is often mediated by resource dynamics (Preisser et al. 2009); thus, responses of wood warblers to perceived nest predation risk posed by jays could vary with food availability. However, numerical declines of wood warblers in years following mast peaks have been observed over long-term (30 years) trends and could not be attributed to variation in weather, food availability, local production of young, or survival (cf Wesolowski et al. 2009; Maziarz et al. 2018), which suggest that they emerge as a part of their habitat selection strategy.

We explored wood warbler–jay interactions in two extreme scenarios, i.e., in the spring following mast seeding or trough with very low acorn production. However, beyond mast and trough years, oaks may produce moderate seed crops (e.g., Bogdziewicz et al. 2017), resulting in more continuous fluctuations of rodent numbers over a longer time frame. In turn, this may result in non-linear interactions between acorns, rodents, jays, and wood warblers. Such non-linear effects of seed production and small mammal population dynamics on songbirds were shown in other mast-driven system (Schmidt and Ostfeld 2003, 2008). Exploring how wood warblers adjust predator avoidance strategies during settlement across a gradient of seed production and fluctuating rodent numbers would provide valuable insights into flexible information use strategies during avian habitat selection.

Acknowledgments We thank Peter A. Bednekoff, Michael Clinchy, and an anonymous reviewer for the valuable feedback upon the earlier draft of this text. We thank Lechosław Kuczyński for providing resources to build the seed traps. JS was supported by the Foundation for Polish Science (FNP) scholarship “Start.”

Authors' contributions JS conceived the study, designed the methodology, and collected and analyzed the data; JS and RLT interpreted the results and drafted the manuscript; RLT and JS revised the manuscript. Both authors gave final approval for publication.

Funding This work was supported by the National Science Centre in Poland (grant number 2012/07/N/NZ8/00129).

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The study complies with the current laws of Poland and was conducted under the permit no. 2B/2012 given by the Director of the Wielkopolska National Park.

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