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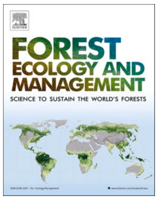

Response of cavity nesting birds to *Lymantria dispar* (Lepidoptera) and aerial spraying – An experimental approach

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ABSTRACT

Eruptive population dynamics of forest insect species regularly attract the interest of ecologists but also often evoke debates among stakeholders concerning impacts that outbreaks or pest control activities have on forest communities including insectivorous birds. *Lymantria dispar* is the most serious native defoliator in mixed oak-broadleaf forests in Central Europe. To investigate the treatment effects of *L. dispar* density, aerial application of the insecticide Mimic (tebufenozide) and nest box accessibility for *L. dispar* caterpillars on nest box success of cavity nesting birds, we deployed 352 nest boxes in a full factorial experimental design with 11 replicates. *L. dispar* density was predicted by egg mass counts made in the year before the study. The accessibility of nest boxes for *L. dispar* caterpillars was manipulated in all study sites by placing nest boxes on trunks for easy access to caterpillars and on branches for more difficult access. Successful nest boxes (binary metric that combines failed breeding attempt and empty nest box) and nest productivity (number of fledged chicks in successful boxes) were monitored in the peak year of a *L. dispar* outbreak, during which half of the plots were treated with Mimic, as well as in the following year when *L. dispar* populations had widely collapsed, and no further treatments were applied. *L. dispar* and non-target caterpillar biomass was sampled by canopy fogging to quantify prey abundance. Caterpillar biomass was significantly reduced by Mimic in the treatment year and remained low in the post-treatment year. Despite the reduction of caterpillars, our zero-inflation model found no effect of any tested variables on nest box success of the early brood. However, in the late broods the number of successful nest boxes was reduced in Mimic treated plots in the first year by 42%, while unaffected by initial *L. dispar* density. The number of successful nest boxes in the second year was lower in areas with initially high *L. dispar* densities and there was a marginal carry-over effect of insecticide treatment. *L. dispar* caterpillars entered nest boxes on the trunk in higher numbers than boxes on the branch, but nest box position had no effect on nest box success of birds.

We conclude that despite its strong negative impact on caterpillar prey, aerial application of Mimic targeting *L. dispar* caused an increase in the number of failed boxes in late broods in sprayed plots, particularly in the year of application and to some extent in the year after. We presume this delayed effect of Mimic only on late broods to be caused by Mimic-induced caterpillar shortages during first broods leading to an increased parental effort and a subsequent reduced number of second broods. The generally limited impact of Mimic might be explained by the overall extensive availability of alternate prey in oak forests in May during first broods and the ability of tits to increase their parental effort in times of caterpillar shortage. In unsprayed sites, *L. dispar* densities can create legacies of impact in following years, but caterpillars do not directly affect birds nest box success despite entering cavities.

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1. Introduction

Historically, most research on forest insects has focused on damaging pest species. However, more recently, there has been growing recognition of the value of non-pest species which comprise the majority of insect species in forests. These species represent an important component of the world's biodiversity and provide important ecosystem services. European mixed oak forests host a great diversity of insects, including many host specialists (Brändle and Brandl 2001, Kennedy and Southwood 1984, Leidinger et al. 2019, Southwood et al. 2004, Vogel et al. 2021). Among all phytophagous insects present in oak canopies, Lepidoptera typically account for the largest proportion of species (Brändle and Brandl 2001) including several species of high conservation value such as *Euphydryas maturna* and *Eriogaster catax* (Dolek et al. 2018, Hacker and Müller 2006).

1.1. Consequences of outbreaking Lymantria dispar

In contrast, other Lepidopteran species sometimes reach outbreak densities, resulting in intense defoliation of oaks. *Lymantria dispar L.* (Erebidae), formerly referred to as the "gypsy moth", is one of the most common defoliators of mixed oak forests in its native Eurasian range and in North America where it was accidentally introduced in the late 19th century. Its ability to defoliate large, forested areas during periodic outbreaks occurring every-five to 13 years in the US and Europe (Hlásny et al. 2016, Johnson et al. 2006) threatens various ecosystem services such as timber production, nutrient cycling and recreation. Major adverse effects include reduced tree growth (Muzika and Liebhold 1999), increased tree mortality (Davidson et al. 1999), altered nitrogen dynamics (Lovett et al. 2002), loss of landscape visual quality (Sheppard and Picard 2006) and even health effects associated with cutaneous reactions (Hossler 2010). Unlike for Europe, impacts of *L. dispar* have been extensively reported in its North American invasive range with annual expenditures of US$50 million for local government alone (Aukema et al. 2011). In the US, $283 million were spent in suppression treatments from 1980 to 2020 (USDA Forest Service 2021). Climate change is expected to alter frequency of outbreaks and range expansion of pest species (Logan et al. 2003, Netherer and Schopf 2010, Seidl et al. 2011, Thackeray et al. 2016). Concerning *L. dispar*, the area of climatic suitability is expected to increase or shift, posing an ongoing challenge to management of this pest species (Logan 2007, Régnière et al. 2009, Williams and Liebhold 1995). In the face of the rising awareness of the importance of insect biodiversity and the alarming state of forest health (Trumbore et al. 2015), the search for a trade-off between supporters and opponents of *L. dispar* control by pesticides is likely to continue (Carson 1962, White et al. 1981).

1.2. L. Dispar management and pest control

As part of programs to manage local *L. dispar* densities, forest managers in Germany implement a monitoring system during winter months that is used to guide decision-making for the airborne application of an insecticide to prevent heavy defoliation. During the 1980 s moulting inhibitors, in particularly diflubenzuron (Dimilin), were preferred insecticides for management programs. In recent years in the US the less effective but lepidopteran-specific microbial insecticide *Btk* (*Bacillus thuringiensis* var *kurstaki*), hereinafter called BT-product, became the most used treatment for *L. dispar* population suppression (Liebhold et al. 2021, Liebhold and McManus 1999). In Germany, the registration of Dimilin for forest-use expired in 2014, leading to its replacement by Mimic in 2018 (Umweltbundesamt 2018), used originally to control lepidopterous pests in viticulture (Irwin et al. 2003). Mimic with the active component tebufenozide is an ecdysone agonist that kills caterpillars by triggering a premature lethal moult. It has a very low acute toxicity to vertebrates and aquatic organisms and is highly selective to Lepidoptera among arthropods (Carlson 2000, Dhadialla et al. 1998). Mimic is persistent in the environment for weeks to months following application (Umweltbundesamt 2018) and has been shown to negatively affect populations of non-target Lepidoptera across multiple families (Butler et al. 1997, Leroy et al. 2019, Umweltbundesamt 2018).

Since widespread insecticide use has been implicated as a driver of biodiversity loss (Sánchez-Bayo and Wyckhuys 2019), the use of insecticides in highly diverse and natural ecosystems such as mixed-oak forests must be critically evaluated. Insecticides used to control lepidopteran defoliators can increase mortality in non-target lepidoptera (Leroy et al. 2019) and indirectly affect predators like birds by reducing the availability of insect prey or by direct toxicity (Blus and Henny 1997, Rodenhouse and Holmes 1992).

1.3. Pest control and food shortage on birds

In early spring, which corresponds to the typical time for application of *L. dispar* suppression treatments, leaf-chewing caterpillars comprise the vast majority of insect biomass in European deciduous oak canopies (Brändle and Brandl 2001, Southwood et al. 2004). Insectivorous birds such as great tits (*Parus major*) rely almost entirely on caterpillars as food source for their nestlings and therefore synchronize their breeding with the timing of tree budburst and peak caterpillar biomass in May (Buse et al. 1999, Perrins 1991). A reduction of live caterpillar biomass following an application of Dimilin was shown to have detrimental effects on forest bird breeding success and was associated with reduction of the caterpillar fraction in the diet of great and blue tit nestlings in treated areas (Cooper et al. 1990, Sample et al. 1993, Schönfeld 2009). Besides insecticide effects, outbreaking *L. dispar* populations may adversely impact other species of forest Lepidoptera by reducing leaf biomass, increasing the production of plant defence compounds and increasing the number of generalist parasitoids (Manderino et al. 2014, Redman and Scriber 2000, Timms and Smith 2011). These processes may lead to reductions of prey availability for breeding birds considering that non-hairy caterpillars are preferred by most bird species despite their ability to handle caterpillars with urticating setae like *L. dispar* (Barbaro and Battisti 2011, Turcek 1948, Whelan et al. 1989). Although tits are very common in deciduous forests, data concerning their predation on *L. dispar* is scarce. Ceia et al. (2016) observed great and blue tits preying on *L. dispar* caterpillars and adults with an intake of 4.8 % of *L. dispar* caterpillars among all prey items. Turcek's (1949) list of bird species that feed on *L. dispar* caterpillars included great and other tits as well as nuthatches. Besides, *L. dispar* caterpillars may interfere with breeding by colonizing nest boxes. Late instars *L. dispar* larvae are night feeding and vacate the canopy during daytime to take shelter in concealed habitats such as tree holes, bark crevices (Campbell and Sloan 1976) and conceivably nest boxes.

Birds are important top-down control agents of herbivorous insects (Böhm et al. 2011, Marquis and Whelan 1994, Mols and Visser 2002, Şekercioğlu 2006). Birds are known to be important predators of *L. dispar* egg masses (Higashiura 1989, Mcmanus and Csóka 2007, Turcani et al. 2001). By contrast, only a few studies have examined predation by bird species on *L. dispar* caterpillars (but see Ceia et al. 2016, Forbush and Fernald 1896, Grushecky et al. 1998, Smith 1985, Whelan et al. 1989). Several studies (Campbell and Sloan 1977, Holmes 1990) suggest that birds contribute to the maintenance of *L. dispar* populations at low densities in non-outbreak times. However, there are a few bird species (e. g., some cuckoos and woodpeckers) known to positively respond to the resource pulse of outbreaking *L. dispar* populations (Gale et al. 2001, Koenig et al. 2011) by aggregating in forest stands with outbreaks.

To date, studies disentangling the effects of both high caterpillar densities and insecticide spraying in well-replicated designs are lacking. Here we investigated how *L. dispar* densities and airborne spraying with Mimic affect the breeding of birds in the year of a *L. dispar* outbreak and the subsequent post-outbreak year. Specifically, we hypothesize that (1) spraying reduces avian nest box success due to a lack of insect prey, (2) superabundant *L. dispar* caterpillars reduce avian nest box success based on the assumption that competition with other Lepidoptera larvae leads to reductions in preferred food availability, (3) Nest box colonization by *L. dispar* caterpillars impedes nest box success.

2. Material and methods

2.1. Study area and experimental design

The experiment was conducted in mixed oak forests in Southern

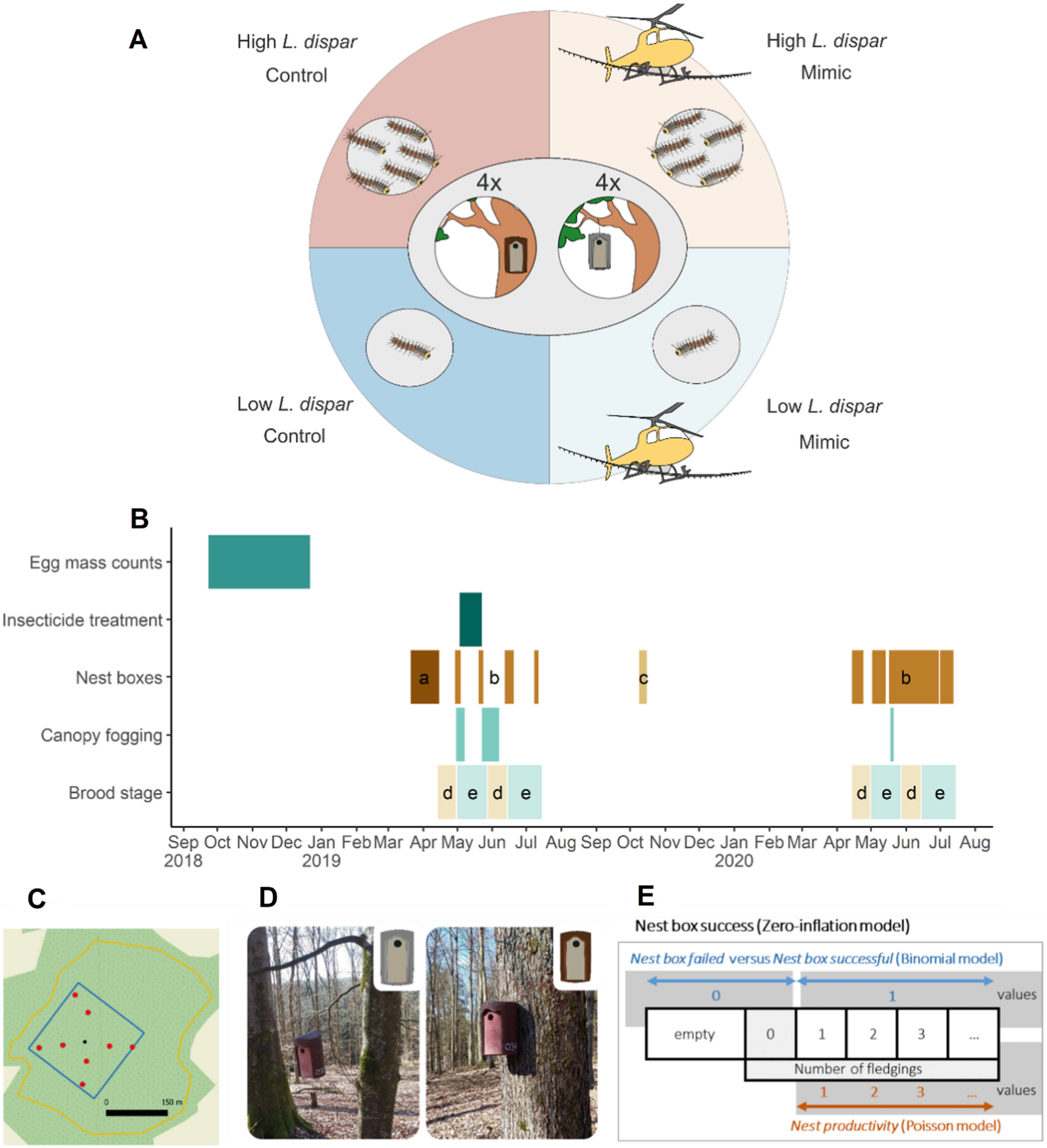

Fig. 1. A) Study design. There were 11 blocks, each containing four plots that were assigned one of four treatment categories: high *L. dispar* density - control (upper left), high density - Mimic (upper right), low densities - control (lower left) and low densities - Mimic (lower right). B) Timetable of egg mass counts, insecticide treatment, (a) nest box set up, (b) nest box survey rounds (early and late broods), (c) nest box cleaning, canopy fogging and mean brood stage of offspring in nestboxes; (d) egg stage and (e) nestling stage. C) In each plot, eight nest boxes in two different positions (branch, trunk) were set up on trees in the form of a cross around the centroid (dark dot) in the plot (rectangle). D) Photographs of the two types of nest box positions on trees: light nest box symbol depicts boxes hanging from a branch and dark nest box depicts boxes attached to an oak trunk. E) Schematic representation of the zero-inflation model used to study nest box success. The model combines a binomial model with 0 indicating 'nest box failed' for every box that remained empty or had no fledged nestlings and 1 indicating 'nest box successful' for boxes that contained broods with at least one fledged nestling and a poisson model, using the number of fledged nestlings in successful boxes as a measurement for nest productivity.

Germany, Northern Bavaria in a temperate climate. 37 % of Bavaria is covered by forest with a forest area of 2.61 million hectares (BMEL 2018). Study sites had no recent spray history with records of zero to three years with insecticide treatment in the years between 1997 and 2011. The elevation of our study area ranged between 185 and 465 m above sea level. A map showing the study region and design can be found in the supplement (S1).

In the winter 2018/2019, 11 forest experimental blocks were established in Franconian oak dominated forests (*Quercus robur* L. and *Quercus petraea* Mattuschka) (Leroy et al. 2021). The blocks were spread across an area of approximately 2400 km^2. Each block consisted of four comparable forest plots with an area of at least 4.5 ha each. Distance between the centre of the different treatment plots within a block ranged between 231 m and 10.7 km.

Based on egg masses surveys in the autumn 2018 (Fig. 1B) following a standardized protocol, two plots of each block exhibited a high defoliation risk index (DRI > 1) and two plots a low index (DRI < 0.5). DRI was calculated as the quotient of the average number of egg masses per stem up to two meters (counted in a transect of ten trees per plot) and the predefined critical egg mass density threshold (for a more detailed description of DRI see Leroy et al. 2021). Hereafter, high and low defoliation risk plots will be referred to as high and low predicted *L. dispar* density. Within each high and low density pair, one forest plot was randomly selected for treatment with the insecticide Mimic® (active ingredient [a.i.] tebufenozide, Spiess-Urania Chemicals, Hamburg, Germany; 240 g/L) at the maximal legal rate of 750 mL diluted in 50 L of water per ha and applied by helicopter between 3 and 23 May 2019, whereas the other two plots remained untreated as control. Thus, there were four different treatment categories with 11 replicates each: low density - Mimic, low density - control, high density - Mimic and high density – control (Fig. 1A). In the subsequent year, 2020, *L. dispar* populations collapsed in high density - control plots, and no further spraying was conducted.

2.2. Caterpillar biomass

To quantify prey abundance, caterpillars dwelling in the forest canopy were sampled by pyrethrum knockdown using a 2.5 % pyrethrum – petroleum oil solution vaporized into tree crowns with Swingfog sN-50 fogging machines (Swingtec, Isny, Germany). In each of the 44 plots, three areas were selected, and each used for fogging at three different sessions: pre-spray (30 April – 8 May 2019), post-spray acute phase (i.e. the period with the expected strongest effect of Mimic on Lepidoptera population, i.e. 23 May – 7 June 2019) and post-spray recovery phase (i.e. one year after treatment application, 18 – 21 May 2020) (Fig. 1B). Four 3 m × 5 m tarpaulin sheets were placed on the forest floor and tree crowns were fogged for 3 to 25 min, for a total sampled canopy area of 60 m^2 per plot and sampling session. All arthropods falling onto the sheets during a 30 min period started at the end of the fogging were collected and stored at −18 °C. Caterpillars were later separated from the by-catch and identified as either *L. dispar* or other (non-target) species. We measured the fresh weight of both fractions to a precision of 1 mg with an analytical balance (Mettler Toledo AB265-S; Mettler Toledo, Greifensee, Switzerland).

2.3. Installation of nest boxes

Nest boxes are a well-established research tool for quantifying breeding performance in cavity nesting passerine birds (Lambrechts et al. 2010). We used wood-concrete composite nest boxes with a front door opening. The 12-cm-diameter nest chamber can be accessed by birds via a 32-mm-diameter entrance hole. No predator prevention devices were attached. In contrast to natural cavities or wooden nest boxes, boxes of wood-concrete offer good protection from predatory mammals or birds like woodpeckers (Kaliński et al. 2009, McCleerly et al. 1996). At each of the 44 forest plots, we set up eight nest boxes between 21 March and 26 April 2019 (Fig. 1B). Four boxes were placed against the trunk of oaks with a minimum diameter at breast height (DBH) of 40 cm (i.e. easy access for *L. dispar* caterpillars) and four further boxes were hung freely from a low branch of various tree species (i.e. difficult access for caterpillars) (Fig. 1D). All nest boxes were set at about 1.50 m height. Nest boxes were arranged along four cross-shaped transects (about 150 m each) intersecting plot centres (Fig. 1C). Along each transect, two nest boxes were set up with alternating positions (trunk vs branch) (Fig. 1C). With a distance between 30 and 90 m between nest boxes in our study, a satiation of breeding density can be assumed from nest boxes alone as territories of great tits range from 40 to 50 m between nests (Krebs 1971). We positioned the nest boxes such that the entrance holes faced southeast whenever possible, as birds prefer nest-cavities with holes not oriented in direction of rain and wind (Goodenough et al. 2008).

Under ideal conditions, nest boxes should be set prior to the breeding season of potential occupying species which falls between mid-April to mid-May for nuthatches and great tits (Matthysen 1989, Perrins and McCleery 1989) whereas flycatchers migrate to Europe during April and start breeding later than nuthatches and tits around mid-May (Both et al. 2005). In our study, the set-up of nest boxes was delayed by logistical issues but their high occupancy (>90 %) confirmed their functional utility in measuring brood performance. During autumn 2019, the inside of all nest boxes was cleaned using a brush and the nest boxes remained in place for use during the 2020 breeding season (Fig. 1B).

In total, $44 \times 8 = 352$ nest boxes were installed with very few complications. In 2019, one nest box was missing and replaced after the breeding season. The classification of another nest box had to be changed from Mimic to control retroactively due to discrepancies with the boundary of insecticide treatment. Another nest box was removed from a branch and set on a trunk.

2.4. Nest box success

Starting at the end of April in 2019 and mid-April in 2020, nest boxes were checked four times throughout the breeding season that ended in mid-July similar to Schönfeld (2007). Nest box surveys were conducted regularly about every-three weeks (Fig. 1B). In 2019, one survey round of all boxes was conducted during four to eight consecutive days, while in 2020 the survey was spread over ten to 27 days (Fig. 1B). Survey rounds in 2020 were longer than in 2019 because nest boxes were accessible to birds throughout the winter and early spring and breeding could have started earlier than 2019. In order to avoid missing early broods, the first survey round was started in mid-April 2020, but spread over more than a week because in the beginning, birds were only in the nest-building or egg-laying stage. Due to the use of many replicates across a large area, we were not able to check weekly as has been done in other studies (Bodey et al. 2021, Kight et al. 2012). Here the challenge is similar to point counts of breeding birds distributed over large areas which have to be restricted to a few visits (Hutto et al. 1986). However, our survey protocol still enabled us to successfully record our target variables by timing the checks so that we were there ideally once after incubation was started, once at a time with older nestlings and again when nestlings had fledged and remaining dead eggs and nestlings could be counted (sometimes remaining individuals had to be counted while second brood was already started in the nest box). In the case of great tits, which occupied most boxes, about 13 days pass from the start of incubation (recognizable by the warmth of the eggs) until the nestlings hatch. Then the nestlings are about 18 days in the nest until they fledge (Van Balen 1973). Therefore, our approach appears sufficient to capture the variability in our breeding measures and it specifically provides a large number of true replicates.

During each nest box inspection, the number of live and dead eggs and nestlings were recorded, along with the breeding bird species. For this purpose, eggs and nestlings were gently removed from the nest by hand and put back immediately after counting in order to avoid changing the micro-climate or chemical environment within the nest

(Lambrechts et al. 2010). The number of eggs in a single brood is subsequently referred to as clutch size. Nest boxes were considered occupied when at least one egg was laid. Eggs were recorded as dead when they turned a dark colour, smelled rotten, were damaged or when they were cold for at least two survey rounds. We assumed that the nestlings had fledged when nests with previously incubated eggs or nestlings were empty and at least 14 days had passed since potential hatching. Blue and great tits have fully developed plumage after two weeks and may already be able to fledge, although they normally stay in the nest box longer (Matthysen et al. 2011, Maziarz et al. 2016) whereas the nestling period of pied flycatchers is two weeks (Järvinen 1990). The number of fledged nestlings was calculated by subtracting the number of dead eggs or nestlings from the clutch size following the example of Schönfeld (2007). Broods found during the first two survey rounds were assigned to the early brood, while any brood detected after the second round was assigned to the late brood. In total, there were four survey rounds of nest boxes, two for the early brood and two for the late brood. It is possible that parent birds raised both, the early and the late brood in one nest box, however we did not collect this information. During the third and fourth survey round, the number of *L. dispar* caterpillars inside the nest box were counted (or estimated when present in large numbers) without removing them from the box.

To quantify the *nest box success,* we structured information as follows: First, we distinguished between *failed* nest boxes (boxes never occupied by birds and boxes with nests that fail to produce fledglings) and boxes with *fledglings* (Fig. 1E). In a second step, we counted the number of fledglings in successful boxes as measure of nest productivity. The first we focused on because previous studies have shown that response to pesticides is often in form of a lack of second broods (Schönfeld et al. 2007). This approach allowed us to quantify the breeding response at each level of decision a bird makes, starting from no breeding to the number of fledglings in one model (see below). Great tits also nested in natural cavities on our study site, but the high number of occupied nest boxes in our study makes the information on the number of failed nests particularly meaningful. The combination of this information in a single measure has only one small handicap. It does not distinguish between zeros caused by empty boxes and zeros caused by no successful fledglings (Fig. 1E). Therefore, and in order to allow comparison with previous studies as well as to provide a more classical approach including only active/occupied nests, the ‘number of fledged nestlings’ of all active nests and nest box occupation by birds (yes/no) were analysed and results can be found in the supplement (S3).

2.5. *Data analysis*

To test the impact of *L. dispar* outbreak and Mimic on availability of caterpillar prey, we fitted a generalized additive model (package mgcv) (Wood 2017) to caterpillar biomass (negative binomial distribution), separately for *L. dispar* and non-target species. We used predicted *L. dispar* density (high/low) and insecticide treatment (Mimic/control) as fixed effects in interaction with the sampling period (pre-spray/acute phase 2019/recovery phase 2020).

To test for impacts of *L. dispar* and Mimic as well as caterpillar access (nest box position) on the nest box success, we used a generalized additive zero-inflation model. This approach integrates the question about successful versus failed nest boxes as we defined it (by using a binomial model) and about nest productivity (by a poisson model for count data) (Fig. 1E) in one model as required by statistical assumptions. Insecticide treatment (Mimic/control), predicted initial *L. dispar* density (high/low) and nest box position (trunk/branch) were treated as fixed effects in interaction with a combination of year and brood phase (early/late). Species-specific differences could not be analysed due to a tit-dominated dataset with only minor observations of other species.

We fitted a similar model to test for the effect of insecticide treatment, *L. dispar* density and nest box position in both years and broods on numbers of *L. dispar* larvae and presence/absence in nest boxes.

Two additional generalized additive models were fitted to provide a more classical approach of nest box occupation (binomial) over all boxes and the number of fledged nestlings (poisson) with a subset of our data including only occupied nests. However, because this approach violates assumptions in statistics that testing one data set is allowed only ones, we present the outputs of the models only in the supplement (S3).

To account for the spatial arrangement of plots and for replicated measurements we estimated a correlated plot-specific intercept (geographical position of the plot) by a smooth factor in all models (Uhler et al. 2021). All analyses were conducted using the statistical software R version 4.0.5 (R Core Team 2021) and the script can be found in the supplement (S5).

3. Results

3.1. *Caterpillar biomass*

Before spraying, the fresh biomass of *L. dispar* caterpillars in the canopy of high predicted density plots was 9.3-fold higher than in low predicted density plots (Fig. 2A, Table 1). For non-target species, the difference of 1.7-fold higher biomass in high versus low density plots was not significant (Table 3). Mimic treatments suppressed caterpillar populations, with total caterpillar biomass below 250 mg per 60 m^2 in treated plots regardless of their predicted *L. dispar* density.

By contrast, *L. dispar* biomass increased exponentially in control plots, with an average of 22.9 and 4.3 g per 60 m^2 in high- and low predicted density plots, which corresponds approximately to 71 times the caterpillar biomass collected in the treated plots (Fig. 2A, Table 1). The biomass of other species was although strongly reduced by Mimic but did not differ between high- and low predicted *L. dispar* density plots, with an average of 3.7 g per 60 m^2 in control plots versus 114.4 mg per 60 m^2 in treated plots. One-year post-spray, the impact of Mimic was still visible, with 12.2- and 2.6-fold the caterpillar biomass of control plots for *L. dispar* and non-target species, respectively. *L. dispar* caterpillar biomass in former high density plots was lower, however not significantly, than in former low density plots, with 0.4 and 1.3 g per 60 m^2. For comparison of observed data and model predictions see supplement figure S4.

3.2. *Nest box success*

In 2019, 90 % of all nest boxes were occupied by breeding birds during the early brood, and 21 % were occupied during the late brood. In 2020, 95 % were occupied in the early brood and 18 % in the late (Supplement S1). Across $352 \times 2(\mathit{broods}) \times 2(\mathit{years}) = 1408$ nest box periods, 477 were occupied by great tit (*Parus major*), 254 by the blue tit (*Cyanistes caeruleus*), 35 by flycatchers (*Ficedula spec*.), 12 by nuthatches (*Sitta europea*) and 9 by tits that could not be assigned to a species. 621 box periods were unoccupied. Great tits had the majority of late broods (76 %). Clutch sizes over all species ranged from one to 22 eggs with a mean of 9 ± 0.1 (mean ± standard error (SE)) eggs per occupied nest box. More detailed information of clutch size and other breeding parameters within our design can be found in the supplement (S2).

In early broods of both years from total of 704 boxes (352 boxes × two years), we found 543 boxes with one or more successfully fledged chicks and 107 broods with a fatality of 100 %. Only 54 nest boxes were not occupied by early broods. In late broods, the number of unoccupied nest boxes was ten times greater than in early broods with 567 boxes of 704 without a brood. We counted 121 broods with successfully fledged chicks and only 16 broods with total fatality in late broods.

For the early brood in both years, neither insecticide treatment nor *L. dispar* density or nest box position affected nest box success (Table 4). In contrast, there were effects on the late brood. The number of successful boxes in late broods differed between insecticide treatment and control plots in 2019 with 24 % successful boxes in untreated plots compared to 14 % in treated plots. In 2020 insecticide treatment was

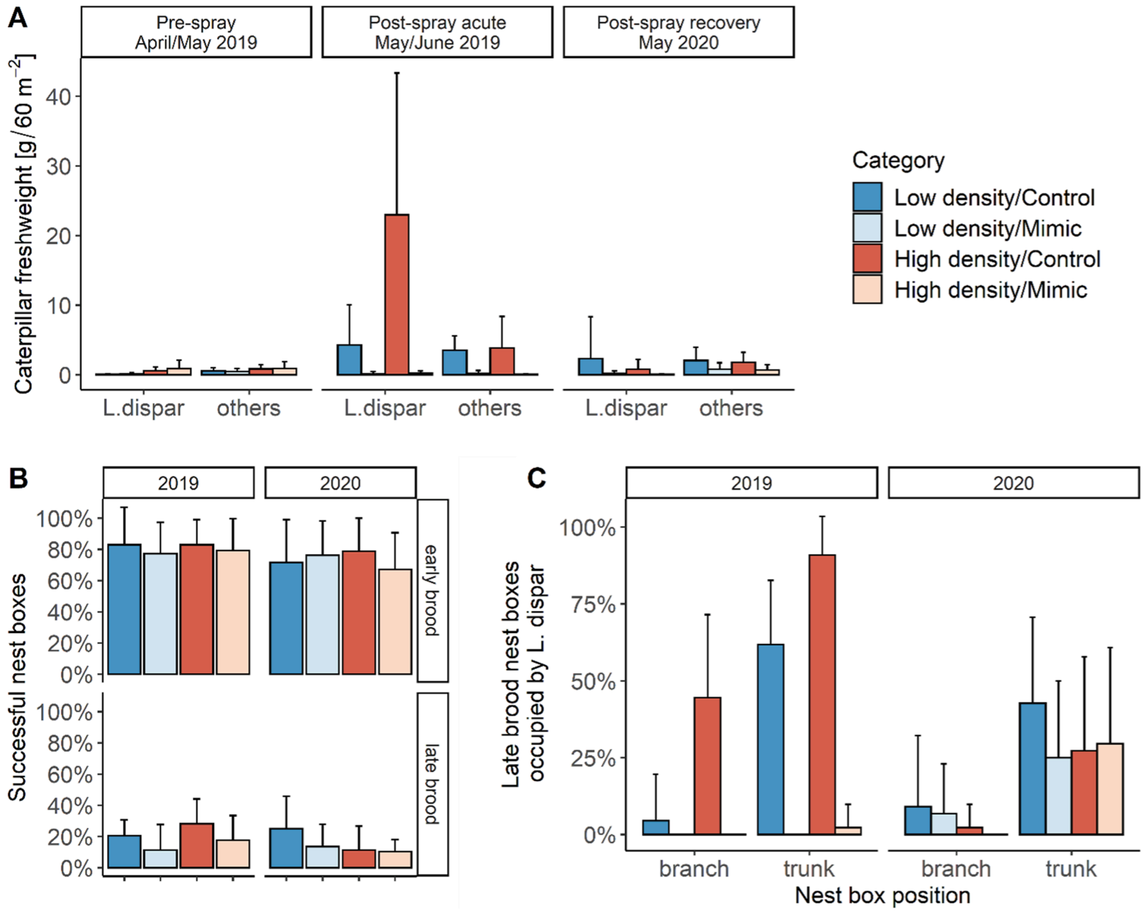

Fig. 2. Insect and bird responses to treatments. A) Biomass of *Lymantria dispar* and other caterpillars as a function of predicted *L. dispar* density (high/low) and insecticide treatment (control/Mimic) within each sampling period. B) Percentage of successful nest boxes per plot in the years 2019 and 2020 and separated in early and late broods as well as all four treatment categories (high/low density and control/Mimic treatment). C) Percentage of nest boxes occupied by *L. dispar* per plot during late broods in the years 2019 and 2020 for all four treatment categories (high/low density and control/Mimic treatment) and both nest box positions (branch/trunk). All figures display raw data. Bars indicate the mean, error bars indicate standard deviation.

only marginally significant with 18 % and 12 % successful boxes in untreated and treated plots, respectively (Fig. 2B, Table 2). The lower number of successful nest boxes was mainly due to the lower occupancy of the nest boxes with an occupation of 25 % and 22 % boxes in untreated plots in 2019 and 2020 and 15 % in treated plots in both years. While in 2019 there was no effect of *L. dispar* density on nest box success, in 2020 the number of successful boxes of late broods in originally low *L. dispar* density plots was with 19 %, significantly higher than the 11 % in high density plots (Fig. 2B). The position of nest boxes with easy or difficult access for *L. dispar* caterpillars showed no significant effect on nest box success.

Our additional models serving the classical approach (Supplement S3) are statistically less sound because of multiple comparisons using the same dataset but showed similar results. Additionally, the reduction of the number of fledglings in early broods was significant in 2020 (S3).

3.3. Occupancy of nest boxes by L. dispar caterpillars

We found 1800 *L. dispar* caterpillars in 154 boxes exclusively during the late brood across both years (Supplement S1). Of all nest boxes containing caterpillars, only 23 out of 154 boxes had signs of an active late brood with only four failed broods. *L. dispar* caterpillar occurrence and numbers were strongly affected by nest box position, pre-spray *L. dispar* density and Mimic treatment in 2019 (Table 4). With a mean of 20 (SE 2.2) larvae and 61 occupied boxes, caterpillars were found more often in boxes in plots with high *L. dispar* density (present in 35 %) compared to low density plots (present in 17 %, mean 14, SE 2.4, 30 boxes). We found *L. dispar* caterpillars in only one nest box in sprayed plots in 2019, whereas 51 % of boxes were occupied by caterpillars in control plots. Moreover, *L. dispar* caterpillars were more numerous (mean 20.2 larvae / box, SE 2.1) and found more often (present in 39 %) in boxes located on the trunk than in boxes hanging from a branch (mean 10.7 larvae / box, SE 1.9, present in 13 %) (Table 2, Fig. 2C, Supplement S1).

In 2020, the effects of initial *L. dispar* density and nest box position were generally weaker, but still there were more caterpillars in nest boxes on trunks and in plots of initial high *L. dispar* density (Table 2 and 4). However, in 2020 the former insecticide treatment did not have a significant impact on the colonization of nest boxes by *L. dispar* caterpillars. In high density plots, the number of *L. dispar* caterpillars in nest boxes was still significantly higher (mean 4 larvae/box, SE 1) than in low density plots (mean 3 larvae/ box, SE 0.6), but there was no difference in the number boxes with *L. dispar* present. With 31 % of boxes, more nest boxes on the trunk than boxes hanging from a branch (5 % of boxes) were occupied by *L. dispar* caterpillars in 2020 (Fig. 2C, Supplement S1).

4. Discussion

We found that aerial treatment with Mimic suppresses canopy caterpillar populations, effectively reducing food availability for breeding birds (Fig. 2a, Table 3). Based on this, our finding of a 42 % lower number of successful nest boxes in late brood in sprayed plots

(Fig. 2b, Table 4) supports our hypothesis 1 that spraying impedes nest box success for insectivorous birds. We found partial support for hypothesis 2 that high *L. dispar* densities also adversely affect avian nest box success. Finally, we could not confirm hypothesis 3, that *L. dispar* caterpillars invading nest boxes for shelter negatively affect nest box success.

4.1. Measurements of breeding performance and the effect of Mimic

In the literature there are a great number of different sampling designs, characteristics and terms used when working with nest boxes (Lambrechts et al. 2010). Statistical analyses are often only applied to

Table 1

Mean and SE (standard error) of the freshweight in [mg] of *L. dispar* caterpillars and caterpillars of other species sampled by canopy fogging of a canopy area of 60 m2 per plot. Data is shown for all three sampling sessions and the four treatment categories of this study: High predicted *L. dispar* density with (Mimic) and without insecticide treatment (Control) and low predicted *L. dispar* density with and without insecticide treatment.

		L. dispar caterpillar freshweight [mg]	Other caterpillar freshweight [mg]
Sampling session	Treatment	Mean ± SE	Mean ± SE
Pre-spray 2019	High-Control	595.22 ± 182.29	827.33 ± 209.59
	High-Mimic	862.89 ± 408.39	919.11 ± 319.73
	Low-Control	52.80 ± 13.94	537.10 ± 151.83
	Low-Mimic	104.30 ± 52.60	485.00 ± 130.60
Post-spray acute 2019	High-Control	22985.91 ± 6138.55	3866.73 ± 1363.69
	High-Mimic	226.09 ± 93.46	47.64 ± 15.11
	Low-Control	4257.82 ± 1742.49	3514.27 ± 624.59
	Low-Mimic	155.09 ± 89.78	181.09 ± 133.42
Post-spray recovery 2020	High-Control	805.36 ± 418.27	1779.00 ± 435.14
	High-Mimic	70.00 ± 13.87	684.09 ± 229.06
	Low-Control	2324.36 ± 1810.88	2059.91 ± 577.01
	Low-Mimic	186.82 ± 104.93	798.09 ± 275.20

Table 3

Z-scores for the generalized additive models testing for the impact of predicted *L. dispar* density, Mimic treatment nested within sampling period on caterpillar biomass in the forest canopy. Caterpillar biomass was quantified by fogging 60 m^2 of projected canopy area at three different periods: pre-spray (late April – early May 2019), post-spray acute phase (late May-early June 2019) and post-spray recovery phase (late May 2020).

Predictors	Sampling period	Z- scores, caterpillar biomass	
		L. dispar	others
High predicted density	Pre-spray – 2019	5.15***	1.46
	Acute phase – 2019	3.26**	−1.43
	Recovery phase – 2020	−1.03	−0.43
Mimic treatment	Pre-spray – 2019	1.59	0.33
	Acute phase – 2019	−10.74***	−13.15***
	Recovery phase – 2020	−5.88***	−2.93**

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Test values not followed by a symbol are not statistically significant.

Table 2

Nest box metrics shown for each year, brood (early and late) and the three design factors (high and low predicted *L. dispar*, Mimic and control treatment and nest box position on a trunk or branch). Percentage of successful nest boxes and of nest boxes occupied by *L. dispar* caterpillars were calculated as mean percentage and standard error (SE) within plots. Mean and standard error of the nest productivity (number of fledged nestlings from successful nests) and of *L. dispar* caterpillars in nest boxes are shown.

Brood	Year	Predicted *L. dispar* density	Insecticide treatment	Nest box position	% Successful nest boxes ± SE	Mean nest productivity ± SE	% Nest boxes occupied by *L. dispar* ± SE	Mean number of *L. dispar* in boxes ± SE
early	2019	low	control	branch	83.33 ± 7.11	7.64 ± 0.48		
				trunk	81.82 ± 8.32	7.65 ± 0.40		
			mimic	branch	75.00 ± 8.26	8.06 ± 0.48		
				trunk	79.55 ± 5.66	8.23 ± 0.47		
		high	control	branch	84.09 ± 6.10	8.66 ± 0.44		
				trunk	81.82 ± 6.82	7.94 ± 0.49		
			mimic	branch	81.82 ± 6.82	8.60 ± 0.58		
				trunk	77.27 ± 7.11	7.76 ± 0.49		
	2020	low	control	branch	73.48 ± 10.04	9.19 ± 0.35		
				trunk	68.64 ± 8.37	8.90 ± 0.37		
			mimic	branch	70.45 ± 8.80	8.19 ± 0.29		
				trunk	81.82 ± 7.61	8.44 ± 0.40		
		high	control	branch	85.00 ± 5.64	9.47 ± 0.43		
				trunk	72.73 ± 7.87	9.06 ± 0.47		
			mimic	branch	65.91 ± 9.09	9.10 ± 0.45		
				trunk	68.18 ± 7.61	8.93 ± 0.44		
late	2019	low	control	branch	18.18 ± 4.87	5.88 ± 0.72	4.55 ± 4.55	2.00 ± 0.00
				trunk	22.73 ± 6.27	5.80 ± 0.68	61.82 ± 6.30	15.11 ± 2.48
			mimic	branch	13.64 ± 7.81	6.83 ± 0.31	0	
				trunk	9.09 ± 3.80	4.75 ± 1.38	0	
		high	control	branch	30.91 ± 6.63	6.79 ± 0.45	44.55 ± 8.13	11.60 ± 1.96
				trunk	25.00 ± 5.84	5.27 ± 0.71	90.91 ± 3.80	24.15 ± 2.96
			mimic	branch	17.42 ± 6.20	6.00 ± 0.65	0	
				trunk	18.18 ± 4.87	5.63 ± 0.75	2.27 ± 2.27	2.00 ± NA
	2020	low	control	branch	22.73 ± 5.28	6.00 ± 0.33	9.09 ± 6.97	1.50 ± 0.29
				trunk	27.27 ± 9.20	6.50 ± 0.57	42.73 ± 8.43	3.58 ± 1.06
			mimic	branch	18.18 ± 5.93	5.75 ± 0.75	6.82 ± 4.87	1.00 ± 0.00
				trunk	9.09 ± 5.08	5.00 ± 0.82	25.00 ± 7.54	2.36 ± 0.66
		high	control	branch	11.36 ± 6.18	6.60 ± 0.87	2.27 ± 2.27	10.00 ± NA
				trunk	11.36 ± 3.94	7.20 ± 0.49	27.27 ± 9.20	4.42 ± 1.64
			mimic	branch	14.39 ± 4.22	5.33 ± 0.61	0	
				trunk	6.82 ± 3.52	6.67 ± 0.67	29.55 ± 9.43	3.85 ± 1.21

Table 4

Z-scores for the generalized additive models testing for the impact of predicted *L. dispar* density, nest box position and Mimic treatment on bird nest box success and nest box colonization by *L. dispar* caterpillars. Nest box success data was measured for early and late broods in two consecutive years. *L. dispar* colonization of nest boxes occurs only in early summer and was hence quantified only during the late brood.

Predictors	Brood	Year	Z-Scores, bird nest box success		Z- scores, *L. dispar* colonization of nest boxes	
			Nest productivity	Successful nest boxes	Abundance	Occurrence
High predicted *L. dispar* density	early	2019	1.15	−0.26		
		2020	1.25	−0.24		
	late	2019	−0.05	1.51	3.14**	4.90***
		2020	0.72	−2.32*	2.61**	−1.50
Trunk nest box position	early	2019	−1.07	−0.14		
		2020	−0.40	−0.40		
	late	2019	−1.64	−0.34	12.31***	6.89***
		2020	0.53	−0.77	1.65	5.56***
Mimic treatment	early	2019	0.52	−1.03		
		2020	−1.26	−0.82		
	late	2019	−0.09	−2.38*	−3.02**	−5.21***
		2020	−1.17	−1.67+	−1.43	−1.42

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Test values not followed by a symbol are not statistically significant.

data on nest boxes that were occupied by breeding birds, while empty boxes are excluded (Pascual and Peris 1992, Schönfeld 2007). In this context, 'nesting success' or 'breeding success' is mostly used as a binary metric to describe occupied nests with at least one hatched egg or fledged nestling (Evans et al. 2002, Mänd et al. 2005, Nagy and Smith 1997, Schönfeld 2007). In some studies, the term "success" is also used to describe the ratio of fledged to not fledged or hatched to not hatched individuals of an active nest (Bodey et al. 2021, Fokkema et al. 2018), whereas other studies focus on numbers of fledged nestlings, their mortality rates and weights (Barba et al. 2004, Maícas et al. 2012). However, important information is lost when only occupied boxes are included. Especially in the timeframe of second broods of great tits (here 'late brood'), nest box occupation is generally lower than in first broods which often leads to insufficient data and the exclusion of late broods in studies where empty boxes are excluded.

'Successful nest box', as it is used in this study, combines two things, the fate of a breeding attempt and the important information of nest boxes being occupied or not, which is at least for great and blue tits, associated with their assessment of the box being located in a suitable breeding environment with suitable food availability (Goodenough et al. 2009, Mänd et al. 2005). We are aware, that with our approach we lose information of how many broods failed and how many boxes were empty because we value both scenarios as equivalent based on their net outcome in offspring. In late broods, the number of successful boxes is mainly driven by differences in box occupancy with only 16 of all 583 failed boxes found with active but failed broods. In studies on open-nesting passerines such as yellowhammers (*Emberiza citrinella*), unoccupied nests cannot be included easily because there is no defined number of suitable nesting habitats and nests have to be located by systematic search and observation of adults (Hart et al. 2006). A standardised design using nest boxes however allows us to directly address the net outcome of breeding birds in nest boxes like in our study. We can simply merge the information about nest box occupation and breeding success together by defining empty nest boxes as 'failed boxes'.

We evaluated both the nest productivity (of boxes with successful broods only) and the number of successful nest boxes (of all boxes) because both measurements provide different information. The binary variable 'successful nest box' provides more general but stable information by ignoring individual differences in breeding experience, competition and natural fluctuations in mortality of nestlings (Balen 1973, Martin 1987) while 'nest productivity' provides a more detailed information about the nestlings' fate.

4.2. *Successful nest boxes and nest productivity*

While the average nest productivity was lower in treated plots compared to controls, this difference was not significant (Table 4). However, we found a significant negative effect of insecticide treatment on the number of successful nest boxes but only during the timeframe of late broods.

The number of fledged nestlings of successful broods (nest productivity) provides key information about the fate of single chicks but may vary greatly between bird species and other variables such as clutch size (Järvinen 2020, Löhrl 1966, Nour et al. 1998). Density of breeding birds, both in terms of birds per nest box and numbers of nests across the home range of breeding birds, may further influence clutch size and therefore the reproductive output by interspecific and intraspecific competition (Bodey et al. 2021, Mänd et al. 2005, Møller et al. 2018). However, because we lack information about breeding densities in our plots, we were not able to correct reproductive rates for differences in conspecific density. Our findings indicate that whenever a brood was successful, the number of fledged nestlings (nest productivity) did not differ regardless of differences in caterpillar availability in treated and non-treated plots.

While nest abandonment is unlikely beyond the stage of egg laying, costly parental effort of first broods can limit the attempt and success of renesting (Pascual and Peris 1992, Martin 1987). Similar to our finding of unaltered nest productivity, a great range of other studies also observed no change in numbers of successfully fledged nestlings with differing prey densities (Howe et al. 1996, Martin et al. 1998, Shiao et al. 2019). However, those studies found a decrease in nestling body measurements, such as fledgling weight and growth rate of nestlings, with decreasing food availability (Hart et al. 2006). Fledgling weight is considered to be critical for post-fledge survival of chicks (Tinbergen and Boerlijst 1990) and therefore influences the condition of the future bird population. Apart from fledgling weight, reduced food availability can lead to an increased parental effort resulting in expanded foraging ranges and a prolonged post-fledging feeding of chicks (Seki and Takano 1998, Naef-Daenzer 1994, Powell 1984). Although we did not measure fledgling weight or parental effort in our study, increased parental effort following caterpillar density reduction, as a result of insecticide treatment during the early brood, is one plausible explanation for the increased number of failed nest boxes in late broods.

Our finding of insecticide treatment leading to an increase in failed (unused or unproductive used) nest boxes only in late broods with no significant difference in nest productivity across boxes with successful broods is supported by previous studies. Schönfeld (2007) reported a sixfold reduction in the occupancy of nest boxes in second broods of tits resulting in a tenfold reduction in breeding success of active nests after the application of diflubenzuron (Dimilin) in one oak forest located in our study region. In our replicated study, estimated reduction of successful nest boxes was slightly weaker and ranged from 42 % to 34 % in the year of insecticide treatment and the following year. Pascual and Peris (1992) found dose dependent differences in a study where pyrethroid was applied to European deciduous oak forests on the breeding success and number of fledged nestlings of blue tits. In this study, a high dosage of cypermethrin caused a near complete mortality of arthropods resulting in a decline in successfully fledged nestlings and successful broods in both early and late broods. Consistent with our results, a lower dosage killed only 90 % of the caterpillars, reducing the number of boxes with fledglings in late broods but not the numbers of fledged nestlings. Nestlings were affected in the low dosage sites only up to the age of one week (Pascual and Peris 1992). As in our study, when insecticide treatment was applied during the nestling stage of early broods, the majority of early broods were unaffected. In contrast with our findings, a study where treatment with Mimic and a BT-product was applied shortly before tennessee warblers (*Vermivora peregrina*) laid their eggs in a spruce budworm outbreak showed only a marginal negative effect of Mimic treatment during the egg-laying stage on nest success (Holmes 1998). However, it did cause female parents to make longer foraging trips. Red-eyed vireos (*Vireo olivaceus*) showed no decrease in breeding success after reduction of Lepidoptera by BT-products (Marshall et al. 2002). In the present study, the reduction of caterpillar biomass by Mimic persisted in the post-treatment year (Fig. 2). This long-lasting effect of Mimic on caterpillars can be associated with the observed marginal elevated number of failed boxes in treated plots one year after spraying. Nagy and Smith (1997) found reduced breeding success in hooded warblers (*Wilsonia citrina*) the year after application of BT-products for *L. dispar* control but concluded that the reduction was mostly caused by predation. Losses due to predation may increase if parent birds spend more time foraging due to reduced food availability, with the consequence that their nest attentiveness is reduced (Chalfoun and Martin 2007) and predators have a greater chance to steal nestlings. It has been shown that nest predation risk affects nest success and shapes habitat choice in migrating birds (Fontaine and Martin 2006). Based on the statistically nondifferent numbers of fledged nestlings and the reduction in successful nest boxes largely due to low occupancy rates in late broods rather than mortalities, we do not expect predation to be a major factor in our study. As a resident bird species, the great tit is not expected to abandon its territory and choose a new habitat for the second brood (Fontaine and Martin 2006). Nevertheless, the higher predation risk due to food reduction on migratory birds such as the pied flycatcher should be further investigated. Due to the material of our nest boxes made of wood concrete, the most common predator in our study area, the woodpecker, could be largely excluded (Kaliński et al. 2009, McCleery et al. 1996). However, predation may play a role in natural cavities in treated areas.

In addition to elevated parental foraging effort leading to a decreased number of initiated second broods, treatment effects on late broods may be related to seasonal changes in food availability. In previous studies, the lack of impact of food reduction on the reproductive success of birds is often explained by the existence of a food base threshold (Howe et al. 1996, Nagy and Smith 1997, Powell 1984). If the food base is not reduced below a biologically significant threshold, nestling growth and survival will be unaffected (Howe et al. 1996). Therefore, it can be assumed that during May, when caterpillar biomass peaks in deciduous oak forests (Southwood et al. 2004) and first broods are at the nestling stage, the insecticide treatment reduced the abundance of both *L. dispar* and non-target caterpillars, but not to a degree that is threatening nest box success. In this context, Pascual (1994) suggested to focus on the abundance of surviving arthropods rather than their mortality in the context of impacts on bird populations. During second broods however, prey biomass in oak forests is lower and the impact of insecticide treatment on prey abundance may increase with time. In a study on yellowhammer breeding on arable cropland, prey abundances at sites treated with pyrethroid insecticides remained depressed until the end of July, while numbers in control sites increased (Hart et al. 2006).

While it is known that the diet of nestlings becomes more diverse during late broods due to decreasing caterpillar numbers, it was shown that second brood nestlings of great tits are mostly fed adult moths (Barba et al. 2004). Therefore, it is possible that caterpillar reduction caused by insecticide treatment in this study reduced the availability of adult moths in June, which may have led to a higher number of failed nest boxes. Here it is important to note that by using nest boxes, we focused on common species like blue and great tits to assess the impact of *L. dispar* outbreaks and Mimic, because they were sufficiently abundant to be analysed. Broods of flycatchers and nuthatches comprised only 6 % of all broods and are therefore their responses are assumed to be dominated by the tits. Furthermore, collared (*Ficedula albicollis*) and pied flycatchers who are of high conservation value, are long-distance migrants and arrive later during the spring in oak forests. Their first brood lies between the first and the second brood period for the tits. They are more flexible in their food choice, but particular for oak forests the importance of high proportions of caterpillars for fledging performance has been shown (Burger et al. 2012) which might make them more vulnerable to impeded breeding conditions in the timeframe of tit's second broods.

4.3. Effect of L. dispar density on nest box success

In contrast to our hypothesis that high densities of *L. dispar* caterpillars reduce nest box success, there was no evidence of neither positive nor negative effect of the *L. dispar* outbreak on the nest box success of tits. Our hypothesis was based on the assumption that *L. dispar* outbreak phases provoke a reduction in quantity and quality of foliage, which may cause population declines of other folivorous insects (Manderino et al. 2014). As caterpillars compose more than half of the nestling diet in many bird species (Ceia et al. 2016, García-Navas et al. 2013, Nour et al. 1998, Pagani-Núñez et al. 2015, Seki and Takano 1998) and hairy caterpillars are less preferred food items (Whelan et al. 1989), a reduction of non-target caterpillar biomass in tree canopies could lead to nestling starvation and therefore a decreased reproductive output. However, in our study there was neither a reduction in the biomass of non-target canopy caterpillars, nor a reduction in nest box success in plots with high *L. dispar* densities. Also, we found no increase in breeding output of tits by capitalizing on the food pulse associated with outbreaking *L. dispar* caterpillars as it was shown for other hairy caterpillars (Pimentel and Nilsson 2007).

In our experiment, the *L. dispar* outbreak terminated in the summer 2019, with no significant defoliation reported in any of our plots in summer 2020. Interestingly, we detected a 42 % reduction in successful nest boxes of late broods in former high density plots (Fig. 2B), which by then had less *L. dispar* caterpillar biomass than the former low density plots (Fig. 2A). These results suggest, that although superabundant *L. dispar* caterpillars have no effect on nest box success, the drastic reduction of this formerly plentiful food source decreases attractiveness of nest boxes in this area for late broods. Especially during late broods when *L. dispar* are in their late larval stages or already imagines, they can be a valuable food source for nestlings while availability of other caterpillars declines (Southwood et al. 2004). Great tits (dominating late broods) are known to feed their late broods mostly with adult moths (Barba et al. 2004) and might therefore suffer from the almost complete collapse of *L. dispar* populations in former high density plots.

4.4. Effect of caterpillar nest occupancy on nest box success

By manipulation of caterpillar access to cavities (by altering nest box position), we showed that *L. dispar* caterpillars occupying nest boxes as hiding space during the day do not negatively affect broods. In fact, there seems to be a spatial and temporal segregation with *L. dispar* caterpillars occurring mostly in empty nest boxes after the breeding season. However, we were able to show that numbers of *L. dispar* were drastically lower in nest boxes located on branches (away from oak trunks), suggesting that it is very unlikely for *L. dispar* larvae to access those boxes. From the perspective of nest box maintenance (e.g., the yearly cleaning after the breeding season), the deployment of boxes on branches is more practical. Also, Lance & Barbosa (1982) observed longer presence of caterpillars on trees with preferred foliage like oak and availability of suitable resting sites. When nest boxes are placed on the trunk of large oaks with easy access for *L. dispar* caterpillars, high caterpillar presence of larvae in boxes can be anticipated. Due to our experiment, caterpillars occurred in high numbers only in the high *L. dispar* density – control plots, and only in year 2019 because *L. dispar* densities were generally very low in all plots 2020 (Leroy et al. 2021).

With our experiment, we cannot characterize harm caused by contact of *L. dispar* caterpillars to nestlings. To our knowledge, there are no studies about direct negative effects of urticating hairs on naked-skinned nestlings. There are reports of skin reactions following contact with the far more potent processionary moth setae, yet these reports only concern mammals (Battisti et al. 2017). As *L. dispar* caterpillars seem to mostly occupy empty nest boxes after the breeding season, possible reactions of naked nestlings to stinging setae are of minor importance for the nestling's survival.

5. Conclusion

With our well replicated experiment we were able to disentangle the effects of *L. dispar* densities and insecticide treatment on bird nest box success.

We could show that nest box success of early broods during peak caterpillar abundance was unaltered by insecticide treatment with Mimic, whereas we found negative effects on late broods in the treatment and post-treatment year. We presume that the observed shortage of prey availability in treated sites during early broods led to elevated parental effort (not measured in this study) and decreased the attempts of a second late brood. By affecting mid to late season bird broods, possible effects of *L. dispar* control with Mimic affecting the broods of late arriving long-distance migratory species, already under pressure by mistiming of caterpillar peaks and bird arrival (Burger et al. 2012, Both et al. 2006) should be carefully investigated further. Moreover, our results show that high densities of *L. dispar* did not affect birds nest box success in the year of outbreak, but when populations collapsed and *L. dispar* caterpillar biomass decreased drastically in the second year, the number of successful boxes in late broods was impaired. We found no negative effect of hairy *L. dispar* caterpillars entering nest boxes on breeding due to temporal and spatial segregation of larval presence and birds breeding in nest boxes. In summary, our study with Mimic showed consistent results with those of previous studies addressing the impacts of other insecticides on the reproductive performance of forest birds. However, we present novel findings of a treatment effect persistent for two years and a delayed effect of *L. dispar* outbreaks on late broods thanks to a replication level that has not been previously achieved in such studies. We contribute knowledge that allows informed decisions on management of *L. dispar* outbreaks, showing that breeding in birds can be affected when biomass of target and non-target canopy caterpillars are reduced by spraying. This information should be carefully considered, along with knowledge of other ecological interactions, when forming management decisions.

Author contribution

Conceptualization: JM, SH, WWW. Formal analysis: OM. Investigation: SH, BMLL, DR. Methodology: JM, SH. Visualization: SH. Writing – original draft: SH, JM, BMLL, AML. Writing – review & editing: OM, WWW, HP, TH, DR.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120520.

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