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Odours of caterpillar-infested trees increase testosterone concentrations in male great tits

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ABSTRACT

Trees release Herbivore-Induced Plant Volatiles (HIPVs) into the air in response to damage inflicted by insects. It is known that songbirds use those compounds to locate their prey, but more recently the idea emerged that songbirds could also use those odours as cues in their reproductive decisions, as early spring HIPVs may contain information about the seasonal timing and abundance of insects. We exposed pre-breeding great tits (*Parus major*) to the odours of caterpillar-infested trees under controlled conditions, and monitored reproduction (timing of egg laying, number of eggs, egg size) and two of its main hormonal drivers (testosterone and 17 β -estradiol in males and females, respectively). We found that females exposed to HIPVs did not advance their laying dates, nor laid larger clutches, or larger eggs compared to control females. 17 β -estradiol concentrations in females were also similar between experimental and control birds. However, males exposed to HIPVs had higher testosterone concentrations during the egg-laying period. Our study supports the hypothesis that insectivorous songbirds are able to detect minute amounts of plant odours. The sole manipulation of plant scents was not sufficient to lure females into a higher reproductive investment, but males increased their reproductive effort in response to a novel source of information for seasonal breeding birds.

1. Introduction

The timing of reproduction of most animal species is tightly linked to the phenology of other organisms (Durant et al., 2005; Post and Forchhammer, 2008). Consequently, many species try to adjust their reproductive decisions to the surge of resources they need to feed their offspring (Dias and Blondel, 1996; Maillard and Fournier, 2004; van Asch et al., 2010; Cadby et al., 2010; Dunn et al., 2011; Ljungström et al., 2015; Neuheimer et al., 2018; Peláez et al., 2020). Breeding mismatched to the optimal timing relative to food abundance may have negative effects on fitness, with offspring potentially experiencing reduced growth or survival rates (Thomas et al., 2001; Reed et al., 2013; Renner and Zohner, 2018). In the case of predators, they need to predict the date at which their prey will reach a peak of biomass to initiate their breeding at the appropriate time, which is often weeks before this peak. They therefore need to use cues present early in their environment to predict the annual phenology of the lower trophic levels (Wingfield and Moore, 1987; Di Bitetti and Janson, 2000; Rubenstein and Wikelski, 2003; Visser et al., 2004; Grant et al., 2009; Visser et al., 2009).

In seasonally reproducing species, photoperiod has been shown to be

the primary cue used by organisms to orchestrate their breeding phenology (Nelson, 1985; McAllan and Dickman, 1986; Nelson, 1986; Dawson, 2008; Rani and Kumar, 2014; Nakane and Yoshimura, 2019). Changes in photoperiod are, however, the same every year, meaning that photoperiod alone cannot predict yearly variation in the optimal timing of breeding. These species, as well as non-seasonal organisms (Porton et al., 1987; Hart et al., 2006; Frederick et al., 2012), must therefore rely on additional cues to decide when exactly to reproduce (Cumming and Bernard, 1997; Voigt et al., 2011; Ngalameno et al., 2017). Temperature, for example, has been shown to exert an influence on the timing of reproduction (Gorman et al., 1981; Crick et al., 1997; Visser et al., 2009; Schaper et al., 2012; Chambers et al., 2013; Williams et al., 2015; Wegge and Rolstad, 2017). However, several studies failed to show such a causal link with phenology and its underlying physiological mechanisms (Dawson, 2005; Perfito et al., 2005; Visser et al., 2011; Caro et al., 2013; Verhagen et al., 2020).

In the well-studied tree-caterpillar-passerine food chains (Perrins, 1970; Visser et al., 1998; Both et al., 2009), nestling growth and survival of several insectivorous bird species almost exclusively depend on the availability of a few caterpillar species (mainly the winter moth -

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Operophtera brumata, and the green oak tortrix - *Tortrix viridana*) (Dias and Blondel, 1996; Naef-Daenzer and Keller, 1999; Thomas et al., 2001; Gienapp and Visser, 2006). Caterpillars on the other hand entirely depend on the leafing of a few tree species for their development (Du Merle and Mazet, 1983; Buse and Good, 1996; van Asch and Visser, 2007; van Asch et al., 2012). Plant phenology has therefore been suggested to be one of the supplementary cues that birds could use to predict the phenology of their food source, and thereby their timing of reproduction. Many studies have indeed found correlations between tree phenology and laying dates in wild populations of insectivorous birds (Nilsson and Källander, 2006; Bourgault et al., 2010; Cole et al., 2015; Hinks et al., 2015; Szulkin et al., 2015), but whether there is a causal relationship between the two, and through which sensory path this relationship could come about, is not well understood yet (Visser et al., 2002; Schaper et al., 2011; Voigt et al., 2011).

Trees respond to insect grazing by releasing Herbivore Induced Plant Volatiles (HIPVs) (Dicke and van Loon, 2000; Arimura et al., 2005; Dicke and Baldwin, 2010) that carnivorous arthropods and parasitoids use to locate their insect prey (Turlings et al., 1990; Kugimiya et al., 2010; Fontana et al., 2011; Giunti et al., 2016). By attracting predators of insects feeding on the plants, HIPV release provides indirect protection to the plant (Kessler and Baldwin, 2001; Kant et al., 2009; McCormick et al., 2012). Although birds have been considered anosmic for a long time, it has been shown that foraging birds can discriminate between caterpillar-infested and uninfested trees only by smell (Amo et al., 2013; Mrazova et al., 2019; Graham et al., 2021; Sam et al., 2021), and can recognise and orient to an artificial odour mimicking HIPVs (Mäntylä et al., 2014; Rubene et al., 2022). In a recent study using artificial HIPVs, the authors found an innate attraction to those odours in blue tits (*Cyanistes caeruleus*), and birds increased their reproductive investment by producing more nestlings when artificial HIPVs were added in their breeding territories (Delaitre et al., in prep.). HIPVs thus represent a promising cue that birds could use to infer the phenology of their prey and modulate their reproductive investment accordingly. However, whether those volatile compounds influence the reproductive physiology and behaviour of birds has not been explored yet.

Sexual behaviours and reproductive control result from a cascade of physiological reactions involving steroid hormones produced by the gonads (Wingfield, 1994; Ball and Balthazart, 2009). In males, increases in testosterone (T) concentrations is an important indicator that they are preparing to breed (Kempnaers et al., 2008; Zhang et al., 2017), as it stimulates territorial defence (Silverin, 1980; Chandler et al., 1994), aggressive behaviour (Wingfield et al., 1987; Beletsky et al., 1990), as well as courtship and mating behaviours (Silverin, 1980; Ketterson et al., 1992; Enstrom et al., 1997; Hill, 1999). In females, oestrogens promote courtship behaviour. For example, the removal of the ovary in ring doves leads to the disappearance of wing flipping that are normally shown by females in response to male courtship (Cheng and Lehrman, 1975), but treating those females with oestrogens restore their normal sexual behaviours (Adkins and Alder, 1972). Moreover, estradiol is a good predictor of laying, as it stimulates the production of yolk precursors and peaks just prior females lay their first egg (Bluhm et al., 1983; Rehder et al., 1986; Sockman and Schwabl, 1999; Williams, 2012).

If HIPVs exert an effect on bird reproduction, we should observe effects of this olfactory signal on the mechanisms coordinating reproduction, i.e. on their reproductive hormone levels. Supporting this hypothesis, Graham et al. (2021) recently found that blue tit males with higher testosterone concentrations spent more time close to a tree infested with caterpillars compared to an uninfested tree. Gonads, which produce sex steroids, also developed faster in more exploratory (a personality trait) female blue tits exposed to HIPVs (Caro et al., 2023). Since HIPV emissions reflect the timing of emergence and the abundance of caterpillars in the environment (Horiuchi et al., 2003; Girling et al., 2011; McCormick et al., 2012; Miresmailli et al., 2012), by detecting HIPVs in early spring, songbirds could adjust their onset of breeding to

synchronize the feeding period of their chicks with the timing of maximal caterpillar biomass (Marciniak et al., 2007), and adjust their clutch size to match the predicted food availability in their breeding territory (Hussel and Quinney, 1985; Marciniak et al., 2007).

The purpose of this study was to determine experimentally if HIPVs emitted by caterpillar-infested oak buds induce behavioural and hormonal responses in an insectivorous songbird in terms of reproductive physiology, timing and investment. For this, we used 36 pairs of great tits housed in climate-controlled aviaries and induced the release of HIPVs by infesting oak buds (*Quercus robur*) with freshly hatched winter moth caterpillars. We hypothesized that birds exposed to HIPVs would advance and increase their reproductive hormone concentrations (i.e. testosterone and 17 β -estradiol), advance their laying date, and increase their reproductive investment (i.e., clutch size and/or egg size), compared to control birds.

2. Methods

2.1. Ethical note

Ethical permits requested for this experiment were provided by the Animal Welfare Body of NIOO-KNAW (IVD - NIOO 20.09 AVD8010020209246/IVD 1556a).

2.2. Birds and experimental set-up

2.2.1. Birds

The experiment was carried out at the Netherlands Institute of Ecology (NIOO-KNAW) in Wageningen, the Netherlands. 72 great tits (36 females and 36 males) born in captivity in 2020 were used in this experiment. Birds were the second generation of a population originated from Boslust near Arnhem, the Netherlands, a 70 ha field site consisting of mixed pine-deciduous forest (van den Heuvel et al., 2022). Eggs were laid in captivity, and subsequently incubated and reared by foster parents in the wild, up to the age of 10 days. At this stage, chicks were brought back to the NIOO for hand-rearing, following the procedure described in a previous study (Drent et al., 2003; van den Heuvel et al., 2022). Adult birds were fed daily as described in Delaitre et al. (2023), with mixture of minced beef heart, canary egg food proteins and vitamins, dry food, apple and water for drinking and bathing.

2.2.2. Housing in climate-controlled aviaries

To enhance the chances that birds successfully breed in climate-controlled aviaries, a preference test to pair females with one of their preferred males was conducted. In short, females could visit six males in a carousel-shaped six-choice chamber for 90 min, and mate choice was inferred from the amount of time females spent close to each male (see Delaitre et al., 2023, for details). Time spent by the females in the choice zone of the male has been shown to predict courtship behaviours, pair formation and reproductive success in other studies (Balzer and Williams, 1998; Gonçalves and Oliveira, 2003; Witte, 2006; Zandberg et al., 2017). In zebra finches for example, the time females spent in front of a male correlates positively with the number of solicitation displays directed to that male, therefore, linking mate preference measured by courtship displays with preference measured through the time a female spends with a male (Witte, 2006). Similarly, in the above-mentioned study, we showed that female great tits paired with a male with which they spent more time, laid earlier (Delaitre et al., 2023).

From early February, birds were housed in opposite-sex pairs in 36 climate-controlled chambers (2 × 2 × 2.25 m) as described in Delaitre et al. (2023) (Fig. 1). Briefly, photoperiod and temperature were set to mimic natural conditions prevailing outside at the time of the experiment. Three 58 W high frequency fluorescent tube lights served as the main source of lighting. Before sunrise and after sunset, a second 7 W incandescent light bulb simulated dawn and nightfall for 5 min each. From a logistical point of view, it was not possible to adjust the aviary

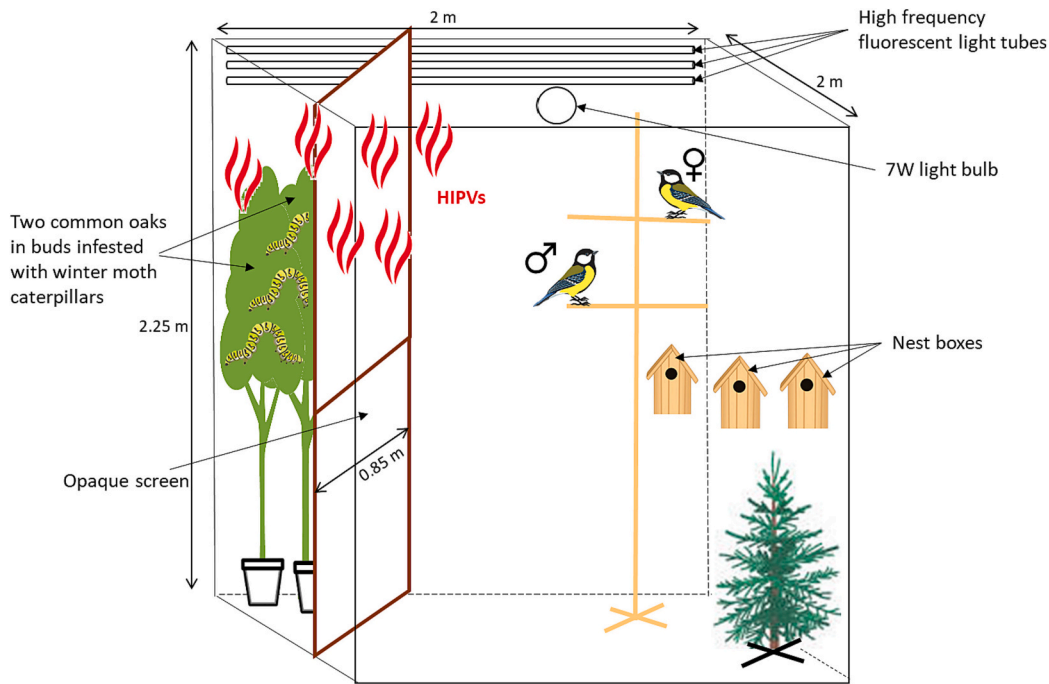


Fig. 1. Housing of birds in climate-controlled aviaries.

Each of the 36 opposite-sex pairs of great tits was housed in a climate-controlled aviary under an artificial light regime mimicking a natural daylight pattern using three 58 W tube lights and one 7 W light bulb. Temperatures were weekly set to mimic the outside temperatures of the week before. Birds had ad libitum access to food and water. Perches and an artificial tree were provided to the birds to perch and hide. Three nest boxes were installed in each aviary. An opaque screen was installed in the back-left corner to hide the two caterpillar-infested trees for the experimental group, or the two pots filled with soil for the control group. The experimental birds could thus only smell the HIPVs released by the trees but could not have access, or see the oak trees and caterpillars.

temperatures to match the outside temperatures on a daily basis. As a result, the simplest logistical solution was to set the temperatures of the next eight days in aviaries based on the temperatures of the previous eight days in the wild. Hourly temperatures were determined from The Royal Netherlands Meteorological Institute (KNMI) database. Perches, an artificial tree and three nest boxes, allowing females to select their breeding cavity, were available in each aviary. In order to hide the potted oak trees, a screen (0.85×2.25 m, Figs. 1, S1) made of an opaque white fabric was installed in the back-left corner of each aviary. No visual or acoustic interactions were possible between the pairs.

2.2.3. Oak trees

160 common oak trees (*Quercus robur*; approx. 2 m high, and 0.5 m of diameter) grown in pots were used as sources of odour. From early January, trees were maintained at different locations to spread out timing of bud burst over the season. A group was maintained in an open area fully exposed to sun ($n = 60$), one was placed in the corner of a building in the shade ($n = 45$), and the last group was kept on the east side of a building with partial exposure to sun ($n = 55$). Caterpillars being unable to perforate the protective scales of the oak tree buds (Du Merle and Mazet, 1983), the oaks were considered ready to use in the experiment when the buds began to elongate and to lose their scales (stage 4, Fig. S2). Out of the 160 trees, 108 were used in the experiment.

2.2.4. Caterpillars

The main caterpillar species infesting the common oak in the Netherlands is the winter moth (Visser et al., 2006). Adult winter moths were collected in Doorwerth, the Netherlands, between November and December. Adults were kept in 50 mL tubes with paper strips on which the females laid their eggs. Eggs were kept outdoor protected from rain and direct sunlight. Caterpillars and trees were thus experiencing similar temperature conditions.

2.2.5. Bud infestation

Once caterpillars began to hatch, oak trees with buds at an appropriate stage were infested with caterpillars using a small paintbrush (Graham et al., 2021). Two oak trees were placed behind the opaque screen in 18 experimental aviaries, whereas two pots filled with the same soil were placed behind the opaque screen in 18 control aviaries. Every week, one of the two trees was replaced by a new one with earlier bud stages than the one that had just been removed. When experimental aviaries were opened to change a tree, control aviaries were also opened to ensure all birds experienced similar disturbances. Between 20 and 50 caterpillars (depending on caterpillar availability, on average 36 caterpillars per tree) were placed across five branches with buds at stage 4 (bud elongated, swollen and green) to 6 (bud bursting, leaf shoots can be distinguished but are still intricate) (Fig. S2) (Du Merle and Mazet, 1983). During infestation, the experimenter observed the caterpillars for a few minutes to ensure they entered the buds. In addition, when a tree was removed from an aviary, it was examined for caterpillar damage on leaves to ensure that HIPVs had been released. A recent study by Graham and colleagues (Graham et al., 2023) has shown that oak buds emit HIPVs in early spring when they are grazed by freshly hatched caterpillars, and that HIPV emissions were proportional to the damages inflicted. Caro et al. (2023) also exposed blue tits kept in airtight compartments (terrariums) to air from enclosures containing caterpillar-infested oak trees and identified compounds known to be HIPVs in the air reaching the terrariums (Graham et al., 2023). First trees were introduced in the aviaries between 16th and 20th April. In total, seven tree changes were done for each experimental aviary until 24th May. When no more caterpillars and trees were available for new infestation, we stopped changing trees and let them progress in the aviaries until the final blood samples were taken (see details below).

2.3. Reproduction monitoring

Nesting material (moss and dog hair) was provided from early

March. Reproduction was monitored as described in a previous study (Delaitre et al., 2023). Briefly, from mid-March, we monitored nest building and egg laying activities. We began to check the nest boxes once and then twice a week as birds were closer to lay (Dufva, 1996), and then daily until the last egg of the clutch had been laid. The pair laying date is defined as the date that the first egg was found. We weighed (to the nearest 0.01 mg with an electronic balance, Eidyer), and measured all eggs (to the nearest 0.05 mm using a calliper, Ecotone Measy DG) and calculated their volume (egg volume = $0.4673 \times \text{length} \times \text{breadth}^2 + 0.042$ (Dufva, 1996)). The clutch size was determined after birds laid their last egg. Nests and eggs were removed after at least five days of incubation, so that birds could start a new clutch. After removing 6 females that started laying before the first trees and caterpillars were introduced to aviaries, we were left with 30 pairs to use in analyses. As only three females (one in the control group, two in the treatment group) produced a second clutch, we only analyzed the first clutch laid.

2.4. Physiological measures

2.4.1. Blood samples

We followed the procedures described in Delaitre et al. (2023). Briefly, birds were caught in their aviary and transported to a laboratory room, where they were weighed and bled in the jugular vein using an insulin syringe (max. 150 μL). Blood was transferred to heparinised tubes, plasma was separated by centrifugation and stored in freezers (-80°C) until assayed for hormones. Birds were returned to their aviary after the sampling. Each bird was sampled every two weeks (18 aviaries per week (36 birds)) between 18th March (before first laying) and 17th June (seven blood samples per bird). Mean time between catching and blood sampling was 3 min 22 s \pm SD 46 s for females and 6 min 01 s \pm SD 1 min 10 s for males.

2.4.2. 17β -estradiol assay

The assay procedure used for 17β -estradiol assay is described in detail in Delaitre et al. (2023) and validated for blue and great tits (Caro et al., 2019). Concisely, plasma 17β -estradiol (E_2) was measured using a commercially available double-antibody ^{125}I - E_2 radioimmunoassay (DSL-4800, Ultra-sensitive Estradiol RIA, Beckman Coulter, Brea, CA, USA) modified to increase the sensitivity of the assay (Charlier et al., 2010; Caro et al., 2019). Steroids were extracted from 30 μL of plasma, dried under nitrogen gas at 40°C , and reconstituted overnight with PBSg (PBS with 0.1 % gelatin) containing 0.7 % ethanol (Caro et al., 2019). Recovery value after extraction was 91.5 %. Samples were then assayed in duplicate and counted on a gamma counter. Seven assays were needed to estimate the concentration of the 250 samples. The intra- and inter-assay coefficients of variation were 3.73 % and 4.10 %, respectively. Assay sensitivity was 0.65 pg/mL. E_2 was only assayed in females and not in males because we were not able to sample enough plasma to assay both testosterone and E_2 . E_2 would have been interesting to measure in males as well as it is a key determinant of male-typical behaviours, although this mostly results from local conversion of androgens by aromatase within the brain (Soma et al., 2003; Ball and Balthazart, 2004).

2.4.3. Testosterone assay

Plasma testosterone was measured using a commercially available double-antibody ^{125}I -testosterone radioimmunoassay (IM1087, RIA Testosterone, Beckman Coulter, Brea, CA, USA). Steroids were extracted from 50 μL of plasma using diethyl ether (DEE). First, 3 mL of DEE were added to the plasma. The tubes were dipped in a methanol and dry ice bath for 15 s and organic phase was poured in another tube. This step was repeated a second time with the aqueous phase and with 2 mL of DEE. The organic phase was then dried under nitrogen gas at 40°C . Finally, dried samples were resuspended in 120 μL of extraction assay buffer and shaken overnight at 4°C . Recovery value after extraction was estimated at 91 %. Concentrations were adjusted for samples that did

not have 50 μL of plasma available ($n = 32$ out of 237). Resuspended samples were then assayed in duplicate and tubes were counted on a gamma counter (Automatic Gamma Counter, Perkin Elmer, Waltham, MA, USA). Concentrations of testosterone were obtained using a linear regression with the log-transformed concentrations of the standards provided in the assay kit. The 237 plasma samples were run across six assays, and the intra- and inter-assay coefficients of variation, as estimated by assaying one high and one low concentration testosterone standard in duplicate, were 2.80 % and 7.48 %, respectively. Assay sensitivity was 0.075 ng/mL. It was defined as the highest point on the standard curve whose standard deviation did not overlap that of the blank standard (Wingfield and Farner, 1975). No sample was found to be below the detection limit. We validated the assay following the methods of Caro et al. (2019). Briefly, pooled plasma samples were spiked with exogenous testosterone and serially diluted. Percentages of tracer bound (B/B_0) from the serial dilutions were parallel to the standard curve (Fig. S3). As for E_2 in males, we could not assay plasma testosterone in females due to the limited quantity of plasma available. This could have been interesting given that female testosterone has sometimes been shown to enhance female aggression (Rosvall, 2013; Zysling et al., 2006; but see Elekonich and Wing, 2000; De Ridder et al., 2002), impair or delay onset of breeding (Clotfelter et al., 2004; Lahaye et al., 2015), reduce clutch size (Rutkowska et al., 2005; López-Rull and Gil, 2009), or influence maternal yolk and by extension chick phenotypes (Schwabl, 1993).

2.5. Statistical analyses

Analyses were performed in R version 1.3.1093 (R CoreTeam, 2019). The lme4 package (Bates et al., 2015) was used for linear mixed-effects and generalized linear mixed-effect models. Generalized additive models were conducted using the mgcv package (Wood, 2017). P -values of mixed-model analyses were obtained with the lmerTest package (Kuznetsova et al., 2017). Effect sizes were calculated using η^2 (Lenhard and Lenhard, 2016, https://www.psychometrica.de/effect_size.html). Plots were created with the ggplot2 package (Wickham, 2016).

2.5.1. Reproduction

We compared reproductive parameters between HIPV and control pairs by performing (i) a linear model on lay date, (ii) a generalized linear model with negative binomial distribution on clutch size; and (iii) a linear mixed-effect model on egg volume. For clutch size, we also tried a Poisson distribution, which is regularly used for analysing clutch sizes (e.g. Marini et al., 2017; Thornton et al., 2017; Eyck et al., 2020; Martay et al., 2023). Analysing clutch size with a Poisson distribution returned a p -value that was close to significance, with larger clutches under HIPVs ($z = 1.89$, $p = 0.057$, $\eta^2 = 0.12$; details of this statistical model not shown). In the linear mixed effect model for egg volume, female identification was added as a random intercept to account for the fact that each female laid several eggs. All models included treatment as explanatory variable.

2.5.2. Hormone level analyses

We tested whether the HIPV treatment played a role on plasma steroid levels in both sexes. Because we measured a different hormone in each sex, we ran separate models for males and females. None of the females were removed from the dataset but two males were: one male with only three blood samplings and one male for which all samples were below detection limit of the assay kit. We used generalized additive models (GAMs) because we did not want to impose any prior assumption on the shape of the relationship between hormone levels and time. We tested whether there was variation in E_2 and T concentrations over the course of the breeding season, whether steroids levels were impacted by the time spent between the catching and the bleeding of the birds, and whether E_2 and T levels differed between HIPV and control birds over the course of the breeding season. For this we fitted GAMs with date

(continuous variable, centred on first egg date, and ranging from -71 to 66) in a spline function, time between catching and bleeding (continuous variable, in seconds, ranging from 143 to 564 s for females, and from 270 to 890 s for males), time of day (continuous variable, in minutes; birds were usually sampled between 8:30 am and 2 pm), treatment (HIPVs vs Control) and the interaction between time (days from laying date) and treatment in a spline function as explanatory variables. The bird identification was added as a random intercept to take into account repeated hormone measures for each bird taken during the course of the breeding season. To identify if at some point, the hormone levels fitted by the GAM models were significantly different in the HIPV compared to the control groups, we used the “get_smooths_difference” function from the “tidymv” package (Coretta, 2022). This function calculates the difference between the mean control and the mean HIPV curves for each day and the corresponding 95 % confidence interval. When the confidence interval does not overlap zero, the hormone concentration between the control and the HIPV curves are considered significantly different.

3. Results

All the 30 pairs included in the analyses built a nest and only one female (from the control group) did not lay. We found no significant difference in laying date ($F_{1,27} = 1.26$, $p = 0.27$, $\eta^2 = 0.04$, Fig. 2A) or clutch size ($z = 1.055$, $p = 0.29$, $\eta^2 = 0.04$, Fig. 2B) between HIPV and control birds. Out of the 208 eggs measured, we did not find evidence for a significant effect of the odour treatment on egg volume ($F_{1,26.67} = 1.13$, $p = 0.29$, $\eta^2 = 0.004$, Fig. 2C). Analyses of the other data relating to egg size (length, breadth, weight) also showed no effect of the treatment (data not shown).

Individual variation in 17β -estradiol and testosterone over time is depicted at Fig. 3A and B, respectively. Both hormones varied significantly over time (E_2 : $F = 6.20$, $p < 0.001$, $\eta^2 = 0.03$, Fig. 3A, T: $F = 2.87$, $p = 0.05$, $\eta^2 = 0.02$, Fig. 3B) and were more elevated around laying. Time between catching and bleeding did not influence E_2 levels of females ($F = 0.66$, $p = 0.42$, $\eta^2 = 0.003$) but influenced T levels of males ($F = 4.12$, $p = 0.04$, $\eta^2 = 0.02$), with T levels decreasing when the time interval increased. The time at which the blood samples were taken influenced E_2 levels of females ($F = 13.64$, $p < 0.001$, $\eta^2 = 0.06$), and T levels of males ($F = 8.89$, $p < 0.01$, $\eta^2 = 0.05$), with E_2 levels decreasing, and T levels increasing, when the blood samples were taken later in the day.

The “get_smooths_difference” function, from which the curves in Fig. 3E and F originate, calculated the daily difference between the control and the HIPV curves of Fig. 3C and D, and the 95 % confidence interval. The confidence interval of these curves overlaps zero over the

entire breeding period for E_2 , meaning that E_2 concentrations in females were not significantly different between the control and HIPV groups over the course of the breeding season (Fig. 3E, Table S1A). In males, T concentrations were significantly different between control and HIPV birds around the laying period, from 11 days before laying until eight days after (Fig. 3F, Table S1B). An additional linear model including treatment and time between catching and bleeding, run on the period 11 days before laying to eight days after, confirmed that testosterone levels were higher in the HIPV group than in the control group for this time period ($F_{1,32} = 6.56$, $p = 0.02$, $\eta^2 = 0.17$, Fig. 3G).

4. Discussion

We found no evidence that great tits exposed to HIPVs, an olfactory cue released by trees in response to caterpillar infestation, advanced their laying date, laid larger clutches or produced larger eggs in captivity. We however found that males in the HIPV group had higher concentrations of testosterone than control males just before and during the female laying period. These results suggest that males, more than females, adjust their sexual behaviours in response to odorous alarm signals emitted by trees in spring.

One main finding of our study is that males exposed to HIPVs had higher testosterone (T) levels during the laying period than control males. Graham and colleagues (Graham et al., 2021) found a similar relationship between HIPVs detection and T levels in male blue tits. After having trained birds to associate the presence of HIPVs with that of food, they found a positive correlation between the time spent close to the HIPV-emitting trees and male T levels (Graham et al., 2021). Males could use HIPVs as an environmental signal indicating higher food abundance (Horiuchi et al., 2003; Girling et al., 2011; McCormick et al., 2012; Miresmailli et al., 2012) and upregulate their T levels accordingly, as it has been observed with other stimuli like the presence of a nest box in starlings (*Sturnus vulgaris*) (Gwinner et al., 2002) or food availability in zebra finches (*Taeniopygia guttata*) (Lynn et al., 2015). Since T concentrations in males are associated with courtship and mating behaviour (Silverin, 1980; Ketterson et al., 1992; Enstrom et al., 1997; Hill, 1999), males could have upregulated their hormonal status in response to HIPVs to stimulate their female to invest in reproduction.

Males reacted to HIPVs, but we did not find that females adjust their timing of laying, clutch size or egg size when exposed to the odorous treatment. This goes against our initial prediction of a higher investment of females following detection of HIPVs, but is in line with a recent study in which adding artificial HIPVs around nest boxes in the wild did not advance laying, nor increase individual clutch sizes (Delaitre et al., in prep). Another recent study with blue tits found that HIPVs increased female ovarian follicle size, but that was restricted to fast exploring

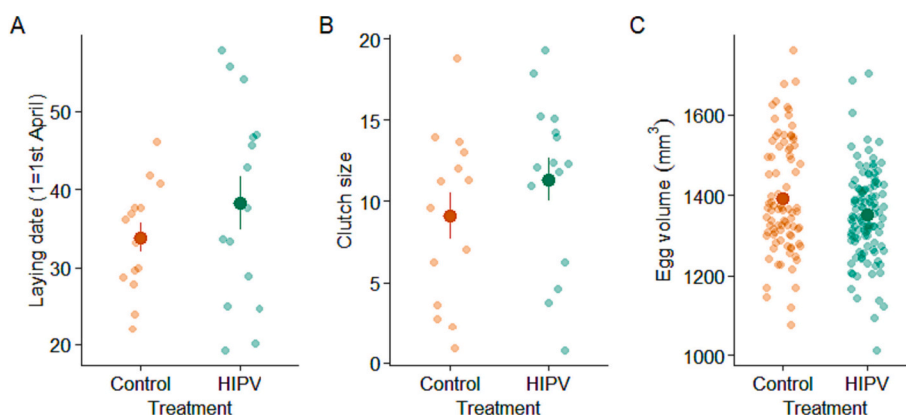


Fig. 2. Effect of HIPVs on reproductive traits in great tits.

Females did not significantly (A) advance their laying date ($n = 29$), (B) lay larger clutches ($n = 29$) or (C) produce larger eggs ($n = 208$) when exposed to HIPVs. Large dots and error bars represent mean \pm SE, smaller dots depict raw data.

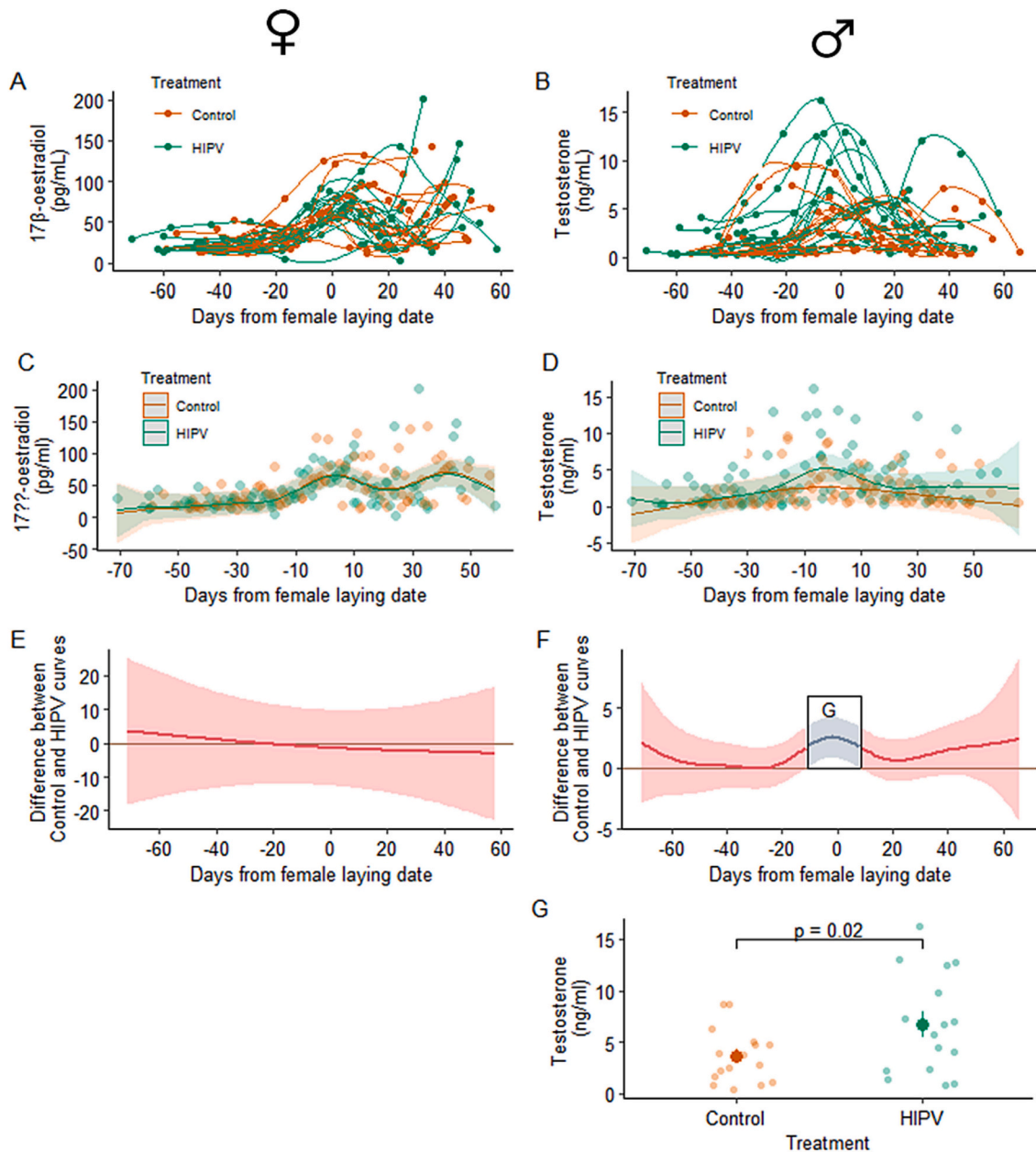


Fig. 3. Hormonal profiles for 17β-estradiol (E_2) in females and testosterone (T) in male great tits.

A–B: E_2 /T profiles of females/males relative to the female egg laying date. Each line depicts one individual.

C–D: E_2 /T profiles of females/males in the HIPV and control groups. Predicted values of the GAM model and 95% confidence interval are depicted.

E–F: The line represents the differences between the mean control and the mean HIPV curves from Figs. C–D for E_2 and T levels, respectively. The area around the line represents the 95% confidence interval for the estimation of this difference. Line and area are red when the confidence interval overlap zero, i.e. that hormone concentration between the control and the HIPV curves are not significantly different, otherwise they are blue. T concentration is significantly different around the laying period, from 11 days before laying to 8 days after.

females, a proxy for personality (Caro et al., 2023). The absence of a clearer effect of HIPVs on female reproduction remains surprising given that HIPVs represent a seemingly good predictor of caterpillar phenology and abundance in spring, when insectivorous birds like great tits start breeding. HIPVs are indeed already emitted when oak tree buds are growing and young caterpillars just hatched from their eggs (Graham et al., 2023), and high concentrations of HIPVs in the environment indicate higher herbivorous insect availability (Horiuchi et al., 2003; Girling et al., 2011; Miresmailli et al., 2012). The present results are also surprising knowing that female tits are able to detect HIPVs and to use them in a foraging context (Amo et al., 2013; Rubene et al., 2019; Graham et al., 2021; Sam et al., 2021; Rubene et al., 2023). We presently

see three potential explanations for the lack of an effect of HIPVs on reproductive timing and investment in our captive great tits.

First, the influence of supplementary cues on reproductive traits is generally subtle and often requires long-term experiments with large sample sizes to be able to detect an effect at the individual level. For example, while several correlative studies conducted in the field have repeatedly shown a link between temperature and seasonal timing of reproduction in birds (Visser et al., 2003; Dunn, 2004; Charmantier et al., 2008), it took almost ten years of experiments in controlled conditions to understand the direct effect of temperatures on timing of reproduction in great tits (Visser et al., 2009; Schaper et al., 2012; Verhagen et al., 2020). In the present study, it is important to stress that

we only conducted this experiment for one breeding season, and with only 30 females analyzed. Advancing laying dates experimentally using supplementary cues has generally proven difficult, very few studies using natural photoperiodic profiles managed to induce laying earlier than what females would normally do (Nilsson and Svensson, 1993; Gienapp and Visser, 2006; Visser et al., 2009; Schaper et al., 2012).

Second, the sole presence of HIPVs might not be sufficient to trigger laying and increase investment in reproduction. Contrary to males that already exhibit robust gonadal response to the change in day length (Farner and Wilson, 1957), female reproduction results from a complex association of several environmental cues (Wingfield and Kenagy, 1991; Ball and Ketterson, 2008; Nakazawa et al., 2023), which could explain why it is difficult to show an effect of each cue tested in isolation of the others. This mainly owes to the supplementary nature of those cues, which only modulate the powerful effect of photoperiod (Wingfield et al., 1992). Temperature, food and water availability, social cues from conspecifics or heterospecifics are all cues that birds are likely to use to decide when to breed and how much to invest in it (Chmura et al., 2019), and females, more than males, might integrate those cues together for their annual reproductive decisions (Caro et al., 2009). For example, social interactions among breeding pairs were by design completely excluded from this study. If this isolation was necessary to precisely control the odorous signals to which each pair of birds was exposed, we cannot exclude that neighboring pairs are eavesdropping each other's in the wild, or that they come to some kinds of mutual agreements. In that context, future studies should consider testing the interactive action of multiple cues, like HIPVs and temperature for example.

Third, for an unknown reason, great tits in climate aviaries started laying particularly early in 2021. It was in fact one of the first times that captive females at the NIOO laid earlier than great tits in the wild (first egg date in our experiment: 7th April; first egg date in the wild: 17th April), which on average lay three weeks earlier than in captivity (Visser et al., 2009). Inducing an even earlier lay date in our experiment was thus probably even more difficult than usual. Our captive birds also lay surprisingly large or small broods compared to the wild. We have observed some clutches with only 1 ($n = 2$), 2 ($n = 1$) or 3 ($n = 1$) eggs and others with 18 ($n = 1$) and 19 ($n = 2$) eggs, whereas the usual average clutch size in great tit varies from 7 to 12 eggs (Perrins and McCleery, 1989). Such a large, unexplained, variance in clutch size renders the detection of a HIPV treatment effect quite challenging.

We found no evidence for an effect of our HIPV treatment on 17β -estradiol (E_2) levels in females. Given that E_2 is tightly correlated with rapid yolk development (Williams et al., 2004), and that we found no effect of HIPVs on laying dates or clutch sizes, finding no link between E_2 and HIPVs might therefore not be surprising. E_2 is also under control of the gonadotropin hormone LH, which in female great tits was found not to be influenced by the visual presentation of leafing branches and caterpillars (Schaper et al., 2011). On the other hand, in a recent study we found an effect of HIPVs on the growth of ovarian follicles, which produce E_2 , but that was restricted to a subset of females that were more exploratory when exposed to a novel environment (a proxy for personality) (van Oers and Naguib, 2013; Caro et al., 2023).

In conclusion, our results do not provide evidence that odours released by developing tree buds in response to caterpillar infestation trigger laying or increase reproductive investment in female great tits, even though they have been shown to attract females as well as males in a foraging context (Amo et al., 2013; Rubene et al., 2019; Graham et al., 2021), and to modulate female gonadal responses in some cases (Caro et al., 2023). The picture in males is clearer, with a higher plasma testosterone in the presence of HIPVs (Graham et al., 2021). The fact that males are generally less picky than females in terms of environmental signals eliciting a reproductive activation suggests that HIPVs might well be a player in the reproduction of insectivorous birds, but that it is challenging to detect and requires longer, or more complex experimental designs. Future studies should now focus on how detection of HIPVs could affect reproductive decisions, offspring condition and

reproductive success in the wild, and on how females weigh the different environmental signals shaping their reproductive decisions.

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CRedit authorship contribution statement

Ségolène Delaitre: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Marcel E. Visser:** Conceptualization, Project administration, Writing – review & editing, Methodology, Resources. **Kees van Oers:** Conceptualization, Methodology, Project administration, Writing – review & editing, Resources. **Samuel P. Caro:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

The datasets needed to reproduce the analyses will be available on DRYAD.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2024.105491>.

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