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1 **Odours of caterpillar-infested trees increase testosterone concentrations in**  
2 **male great tits.**

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28 **Abstract**

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

45

46 **Keywords:** Birds, herbivore-induced plant volatiles, olfaction, reproduction, reproductive  
47 hormones, seasonal timing

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## 63 **Introduction**

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

77           In seasonally reproducing species, photoperiod has been shown to be the primary cue  
78 used by organisms to orchestrate their breeding phenology (Nelson 1985; McAllan and  
79 Dickman 1986; Nelson 1986; Dawson 2008; Rani and Kumar 2014; Nakane and Yoshimura  
80 2019). Changes in photoperiod are, however, the same every year, meaning that photoperiod  
81 alone can not predict yearly variation in the optimal timing of breeding. These species, as well  
82 as non-seasonal organisms (Porton et al. 1987; Hart et al. 2006; Frederick et al. 2012), must  
83 therefore rely on additional cues to decide when exactly to reproduce (Cumming and Bernard  
84 1997; Voigt et al. 2011; Ngalameno et al. 2017). Temperature, for example, has been shown  
85 to exert an influence on the timing of reproduction (Gorman et al. 1981; Crick et al. 1997; Visser  
86 et al. 2009; Schaper et al. 2012; Chambers et al. 2013; Williams et al. 2015; Wegge and  
87 Rolstad 2017). However, several studies failed to show such a causal link with phenology and  
88 its underlying physiological mechanisms (Dawson 2005; Perfito et al. 2005; Visser et al. 2011;  
89 Caro et al. 2013; Verhagen et al. 2020).

90 In the well-studied tree-caterpillar-passerine food chains (Perrins 1970; Visser et al.  
91 1998; Both et al. 2009), nestling growth and nestling survival of several insectivorous bird  
92 species almost exclusively depend on the availability of a few caterpillar species (mainly the  
93 winter moth - *Operophtera brumata*, and the green oak tortrix - *Tortrix viridana*) (Dias and  
94 Blondel 1996; Naef-Daenzer and Keller 1999; Thomas et al. 2001; Gienapp and Visser 2006).  
95 Caterpillars on the other hand entirely depend on the leafing of a few tree species for their  
96 development (Du Merle and Mazet 1983; Buse and Good 1996; van Asch and Visser 2007;  
97 van Asch et al. 2012). Plant phenology has therefore been suggested to be one of the  
98 supplementary cues that birds could use to predict the phenology of their food source, and  
99 thereby their timing of reproduction. Many studies have indeed found correlations between tree  
100 phenology and laying dates in wild populations of insectivorous birds (Nilsson and Källander  
101 2006; Bourgault et al. 2010; Cole et al. 2015; Hinks et al. 2015; Szulkin et al. 2015), but whether  
102 there is a causal relationship between the two, and through which sensory path this relationship  
103 could come about, is not well understood yet (Visser et al. 2002; Schaper et al. 2011; Voigt et  
104 al. 2011).

105 Trees respond to insect grazing by releasing Herbivore Induced Plant Volatiles (HIPVs)  
106 (Dicke and van Loon 2000; Arimura et al. 2005; Dicke and Baldwin 2010) that carnivorous  
107 arthropods and parasitoids use to locate their insect prey (Turlings et al. 1990; Kugimiya et al.  
108 2010; Fontana et al. 2011; Giunti et al. 2016). By attracting predators of insects feeding on the  
109 plants, HIPV release provides indirect protection to the plant (Kessler and Baldwin 2001; Kant  
110 et al. 2009; McCormick et al. 2012). Although birds have been considered anosmic for a long  
111 time, it has been shown that foraging birds can discriminate between caterpillar-infested and  
112 uninfested trees only by smell (Amo et al. 2013; Mrazova et al. 2019; Graham et al. 2021; Sam  
113 et al. 2021), and can recognise and orient to an artificial odour mimicking HIPVs (Mäntylä et  
114 al. 2014; Rubene et al. 2022). In a recent study using artificial HIPVs, the authors found an  
115 innate attraction to those odours in blue tits (*Cyanistes caeruleus*), and birds increased their  
116 reproductive investment by producing more nestlings when artificial HIPVs were added in their  
117 breeding territories (Delaitre et al, in prep.). HIPVs thus represent a promising cue that birds

118 could use to infer the phenology of their prey and modulate their reproductive investment  
119 accordingly. However, whether those volatile compounds influence the reproductive  
120 physiology and behaviour of birds has not been explored yet.

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

134         If HIPVs exert an effect on bird reproduction, we should observe effects of this olfactory  
135 signal on the mechanisms coordinating reproduction, i.e. on their reproductive hormone levels.  
136 Supporting this hypothesis, Graham et al. (2021) recently found that blue tit males with higher  
137 testosterone concentrations spent more time close to a tree infested with caterpillars compared  
138 to an uninfested tree. Gonads, which produce sex steroids, also developed faster in more  
139 exploratory (a personality trait) female blue tits exposed to HIPVs (Caro et al. 2023). Since  
140 HIPV emissions reflect the timing of emergence and the abundance of caterpillars in the  
141 environment (Horiuchi et al. 2003; Girling et al. 2011; McCormick et al. 2012; Miresmailli et al.  
142 2012), by detecting HIPVs in early spring, songbirds could adjust their onset of breeding to  
143 synchronize the feeding period of their chicks with the timing of maximal caterpillar biomass  
144 (Marciniak et al. 2007), and adjust their clutch size to match the predicted food availability in  
145 their breeding territory (Hussel and Quinney 1985; Marciniak et al. 2007).

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

154

## 155 **Methods**

### 156 *Ethical note*

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

159

### 160 *Birds and experimental set-up*

#### 161 *Birds*

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

172

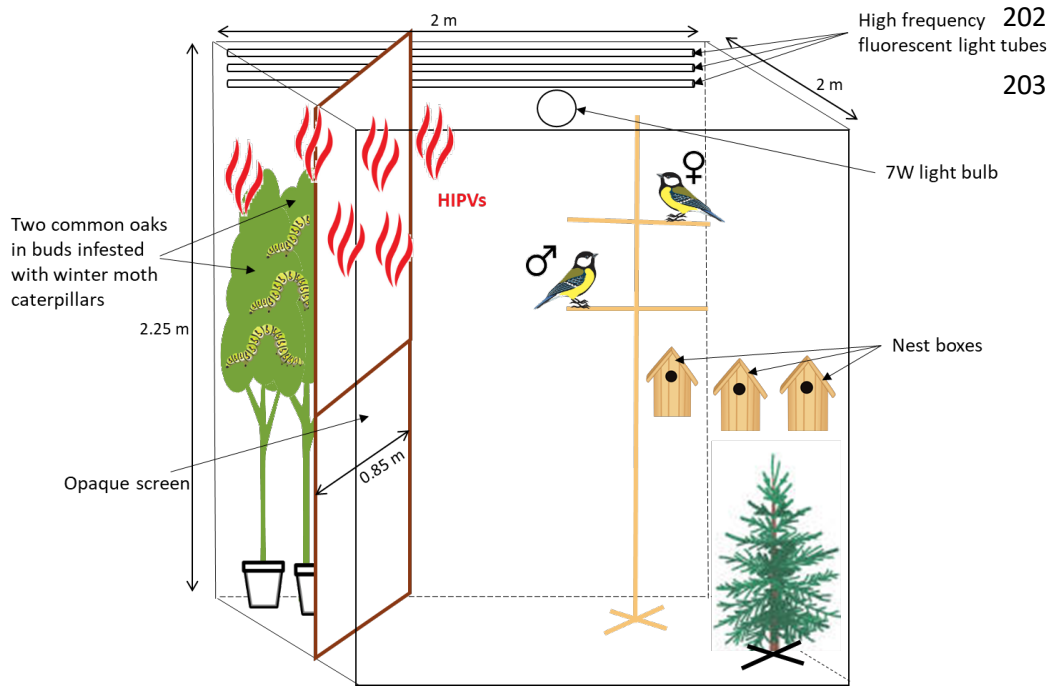
173

174 *Housing in climate-controlled aviaries*

175 To enhance the chances that birds successfully breed in climate-controlled aviaries, a  
176 preference test to pair females with one of their preferred males was conducted. In short,  
177 females could visit six males in a carousel-shaped six-choice chamber for 90 minutes, and  
178 mate choice was inferred from the amount of time females spent close to each male (see  
179 Delaitre et al. 2023, for details). Time spent by the females in the choice zone of the male has  
180 been shown to predict courtship behaviors, pair formation and reproductive success in other  
181 studies (Balzer and Williams 1998; Gonçalves and Oliveira 2003; Witte 2006; Zandberg et al.  
182 2017). In zebra finches for example, the time females spent in front of a male correlates  
183 positively with the number of solicitation displays directed to that male, therefore, linking mate  
184 preference measured by courtship displays with preference measured through the time a  
185 female spends with a male (Witte 2006). Similarly, in the above-mentioned study, we showed  
186 that female great tits paired with a male with which they spent more time, laid earlier (Delaitre  
187 et al. 2023).

188 From early February, birds were housed in opposite-sex pairs in 36 climate-controlled  
189 chambers (2 x 2 x 2.25 m) as described in Delaitre et al (2023)(figure 1). Briefly, photoperiod  
190 and temperature were set to mimic natural conditions prevailing outside at the time of the  
191 experiment. Three 58 W high frequency fluorescent tube lights served as the main source of  
192 lighting. Before sunrise and after sunset, a second 7 W incandescent light bulb simulated dawn  
193 and nightfall for five minutes each. From a logistical point of view, it was not possible to adjust  
194 the aviary temperatures to match the outside temperatures on a daily basis. As a result, the  
195 simplest logistical solution was to set the temperatures of the next eight days in aviaries based  
196 on the temperatures of the previous eight days in the wild. Hourly temperatures were  
197 determined from The Royal Netherlands Meteorological Institute (KNMI) database. Perches,  
198 an artificial tree and three nest boxes, allowing females to select their breeding cavity, were  
199 available in each aviary. In order to hide the potted oak trees, a screen (0.85 x 2.25 m, figure  
200 1, figure S1) made of an opaque white fabric was installed in the back-left corner of each  
201 aviary. No visual or acoustic interactions were possible between the pairs.





204 **Figure 1: Housing of birds in climate-controlled aviaries.**

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

214

215 *Oak Trees*

216 160 common oak trees (*Quercus robur*; approx. 2 m high, and 0.5 m of diameter) grown  
 217 in pots were used as sources of odour. From early January, trees were maintained at different  
 218 locations to spread out timing of bud burst over the season. A group was maintained in an  
 219 open area fully exposed to sun ( $n = 60$ ), one was placed in the corner of a building in the shade  
 220 ( $n = 45$ ), and the last group was kept on the east side of a building with partial exposure to sun  
 221 ( $n = 55$ ). Caterpillars being unable to perforate the protective scales of the oak tree buds (Du  
 222 Merle and Mazet 1983), the oaks were considered ready to use in the experiment when the  
 223 buds began to elongate and to lose their scales (stage 4, figure S2). Out of the 160 trees, 108  
 224 were used in the experiment.

225

226 *Caterpillars*

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

232

233 *Bud infestation*

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

254 caterpillars and trees were available for new infestation, we stopped changing trees and let  
255 them progress in the aviaries until the final blood samples were taken (see details below).

256

### 257 Reproduction monitoring

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

271

### 272 Physiological measures

#### 273 Blood samples

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

282

283 *17 $\beta$ -estradiol assay*

284 The assay procedure used for 17 $\beta$ -estradiol assay is described in detail in Delaitre et  
285 al (2023) and validated for blue and great tits (Caro et al. 2019). Concisely, plasma 17 $\beta$ -  
286 estradiol (E<sub>2</sub>) was measured using a commercially available double-antibody <sup>125</sup>I-E<sub>2</sub>  
287 radioimmunoassay (DSL-4800, Ultra-sensitive Estradiol RIA, Beckman Coulter, Brea, CA,  
288 USA) modified to increase the sensitivity of the assay (Charlier et al. 2010; Caro et al. 2019).  
289 Steroids were extracted from 30  $\mu$ L of plasma, dried under nitrogen gas at 40°C, and  
290 reconstituted overnight with PBSg (PBS with 0.1% gelatin) containing 0.7% ethanol (Caro et  
291 al. 2019). Recovery value after extraction was 91.5%. Samples were then assayed in duplicate  
292 and counted on a gamma counter. Seven assays were needed to estimate the concentration  
293 of the 250 samples. The intra- and inter-assay coefficients of variation were 3.73% and 4.10%,  
294 respectively. Assay sensitivity was 0.65 pg/mL. E<sub>2</sub> was only assayed in females and not in  
295 males because we were not able to sample enough plasma to assay both testosterone and  
296 E<sub>2</sub>. E<sub>2</sub> would have been interesting to measure in males as well as it is a key determinant of  
297 male-typical behaviors, although this mostly results from local conversion of androgens by  
298 aromatase within the brain (Soma et al. 2003; Ball and Balthazart 2004).

299

300 *Testosterone assay*

301 Plasma testosterone was measured using a commercially available double-antibody  
302 <sup>125</sup>I-testosterone radioimmunoassay (IM1087, RIA Testosterone, Beckman Coulter, Brea, CA,  
303 USA). Steroids were extracted from 50  $\mu$ L of plasma using diethyl ether (DEE). First, 3 mL of  
304 DEE were added to the plasma. The tubes were dipped in a methanol and dry ice bath for 15  
305 seconds and organic phase was poured in another tube. This step was repeated a second  
306 time with the aqueous phase and with 2mL of DEE. The organic phase was then dried under  
307 nitrogen gas at 40°C. Finally, dried samples were resuspended in 120  $\mu$ L of extraction assay  
308 buffer and shaken overnight at 4°C. Recovery value after extraction was estimated at 91%.  
309 Concentrations were adjusted for samples that did not have 50  $\mu$ L of plasma available ( $n = 32$

310 out of 237). Resuspended samples were then assayed in duplicate and tubes were counted  
311 on a gamma counter (Automatic Gamma Counter, Perkin Elmer, Waltham, MA, USA).  
312 Concentrations of testosterone were obtained using a linear regression with the log-  
313 transformed concentrations of the standards provided in the assay kit. The 237 plasma  
314 samples were run across six assays, and the intra- and inter-assay coefficients of variation, as  
315 estimated by assaying one high and one low concentration testosterone standard in duplicate,  
316 were 2.80% and 7.48%, respectively. Assay sensitivity was 0.075 ng/mL. It was defined as the  
317 highest point on the standard curve whose standard deviation did not overlap that of the blank  
318 standard (Wingfield and Farner 1975). No sample was found to be below the detection limit.  
319 We validated the assay following the methods of Caro et al. (2019). Briefly, pooled plasma  
320 samples were spiked with exogenous testosterone and serially diluted. Percentages of tracer  
321 bound ( $B/B_0$ ) from the serial dilutions were parallel to the standard curve (figure S3). As for  $E_2$   
322 in males, we could not assay plasma testosterone in females due to the limited quantity of  
323 plasma available. This could have been interesting given that female testosterone has  
324 sometimes been shown to enhance female aggression (Rosvall 2013; Zysling et al. 2006; but  
325 see Elekonich and Wing 2000; De Ridder et al. 2002), impair or delay onset of breeding  
326 (Clotfelter et al. 2004; Lahaye et al. 2015), reduce clutch size (Rutkowska et al. 2005; López-  
327 Rull and Gil 2009), or influence maternal yolk and by extension chick phenotypes (Schwabl  
328 1993).

329

### 330 Statistical Analyses

331 Analyses were performed in R version 1.3.1093 (R CoreTeam 2019). The lme4  
332 package (Bates et al. 2015) was used for linear mixed-effects and generalized linear mixed-  
333 effect models. Generalized additive models were conducted using the mgcv package (Wood  
334 2017). P-values of mixed-model analyses were obtained with the lmerTest package  
335 (Kuznetsova et al. 2017). Effect sizes were calculated using  $\eta^2$  (Lenhard and Lenhard 2016,  
336 [https://www.psychometrica.de/effect\\_size.html](https://www.psychometrica.de/effect_size.html)). Plots were created with the ggplot2 package  
337 (Wickham 2016).

338 *Reproduction*

339 We compared reproductive parameters between HIPV and control pairs by performing  
340 (i) a linear model on lay date, (ii) a generalized linear model with negative binomial distribution  
341 on clutch size; and (iii) a linear mixed-effect model on egg volume. For clutch size, we also  
342 tried a Poisson distribution, which is regularly used for analysing clutch sizes (e.g. Marini et al.  
343 2017; Thornton et al. 2017; Eyck et al. 2020; Martay et al. 2023). Analysing clutch size with a  
344 Poisson distribution returned a p-value that was close to significance, with larger clutches  
345 under HIPVs ( $z = 1.89$ ,  $p = 0.057$ ,  $\eta^2 = 0.12$ ; details of this statistical model not shown). In the  
346 linear mixed effect model for egg volume, female identification was added as a random  
347 intercept to account for the fact that each female laid several eggs. All models included  
348 treatment as explanatory variable.

349 *Hormone level analyses*

350 We tested whether the HIPV treatment played a role on plasma steroid levels in both  
351 sexes. Because we measured a different hormone in each sex, we ran separate models for  
352 males and females. None of the females were removed from the dataset but two males were:  
353 one male with only three blood samplings and one male for which all samples were below  
354 detection limit of the assay kit. We used generalized additive models (GAMs) because we did  
355 not want to impose any prior assumption on the shape of the relationship between hormone  
356 levels and time. We tested whether there was variation in  $E_2$  and T concentrations over the  
357 course of the breeding season, whether steroids levels were impacted by the time spent  
358 between the catching and the bleeding of the birds, and whether  $E_2$  and T levels differed  
359 between HIPV and control birds over the course of the breeding season. For this we fitted  
360 GAMs with date (continuous variable, centred on first egg date, and ranging from -71 to 66) in  
361 a spline function, time between catching and bleeding (continuous variable, in seconds,  
362 ranging from 143 to 564 seconds for females, and from 270 to 890 seconds for males), time  
363 of day (continuous variable, in minutes; birds were usually sampled between 8:30 am and  
364 2pm), treatment (HIPVs vs Control) and the interaction between time (days from laying date)  
365 and treatment in a spline function as explanatory variables. The bird identification was added

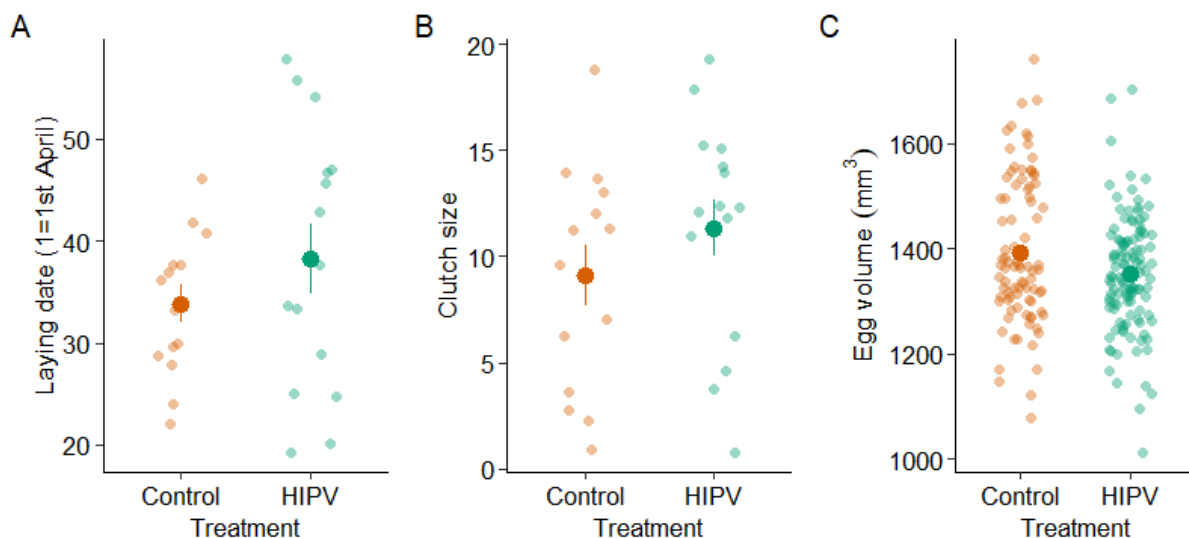
366 as a random intercept to take into account repeated hormone measures for each bird taken  
367 during the course of the breeding season. To identify if at some point, the hormone levels fitted  
368 by the GAM models were significantly different in the HIPV compared to the control groups,  
369 we used the “get\_smooths\_difference” function from the “tidymv” package (Coretta 2022). This  
370 function calculates the difference between the mean control and the mean HIPV curves for  
371 each day and the corresponding 95% confidence interval. When the confidence interval does  
372 not overlap zero, the hormone concentration between the control and the HIPV curves are  
373 considered significantly different.

374

## 375 Results

376 All the 30 pairs included in the analyses built a nest and only one female (from the  
377 control group) did not lay. We found no significant difference in laying date ( $F_{1,27} = 1.26$ ,  $p =$   
378  $0.27$ ,  $\eta^2 = 0.04$ , figure 2A) or clutch size ( $z = 1.055$ ,  $p = 0.29$ ,  $\eta^2 = 0.04$ , figure 2B) between  
379 HIPV and control birds. Out of the 208 eggs measured, we did not find evidence for a significant  
380 effect of the odour treatment on egg volume ( $F_{1,26.67} = 1.13$ ,  $p = 0.29$ ,  $\eta^2 = 0.004$ , figure 2C).  
381 Analyses of the other data relating to egg size (length, breadth, weight) also showed no effect  
382 of the treatment (data not shown).

383



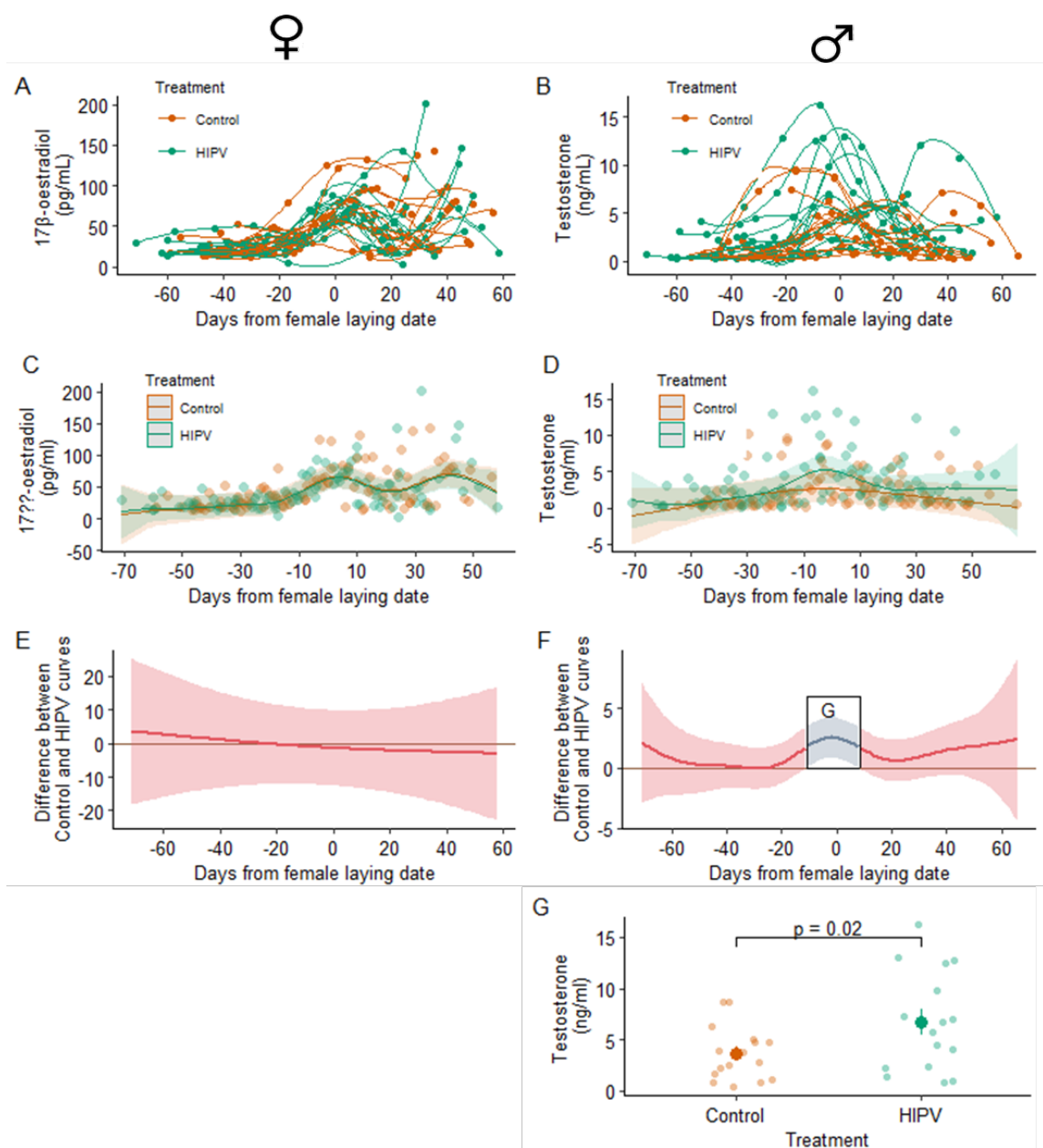
384 **Figure 2: Effect of HIPVs on reproductive traits in great tits.**

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

388  
389 Individual variation in  $17\beta$ -estradiol and testosterone over time are depicted at figures  
390 3A and 3B, respectively. Both hormones varied significantly over time ( $E_2$ :  $F = 6.20$ ,  $p < 0.001$ ,  
391  $\eta^2 = 0.03$ , figure 3A, T:  $F = 2.87$ ,  $p = 0.05$ ,  $\eta^2 = 0.02$ , figure 3B) and were more elevated around  
392 laying. Time between catching and bleeding did not influence  $E_2$  levels of females ( $F = 0.66$ ,  $p$   
393 = 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  
394 decreasing when the time interval increased. The time at which the blood samples were taken  
395 influenced  $E_2$  levels of females ( $F = 13.64$ ,  $p < 0.001$ ,  $\eta^2 = 0.06$ ), and T levels of males ( $F =$   
396 8.89,  $p < 0.01$ ,  $\eta^2 = 0.05$ ), with  $E_2$  levels decreasing, and T levels increasing, when the blood  
397 samples were taken later in the day.

398 The “get\_smooths\_difference” function, from which the curves in figures 3E and 3F  
399 originate, calculated the daily difference between the control and the HIPV curves of figures  
400 3C and 3D, and the 95% confidence interval. The confidence interval of these curves overlaps  
401 zero over the entire breeding period for  $E_2$ , meaning that  $E_2$  concentrations in females were  
402 not significantly different between the control and HIPV groups over the course of the breeding  
403 season (figure 3E, Table S1A). In males, T concentrations were significantly different between  
404 control and HIPV birds around the laying period, from 11 days before laying until eight days  
405 after (figure 3F, Table S1B). An additional linear model including treatment and time between  
406 catching and bleeding, run on the period 11 days before laying to eight days after, confirmed  
407 that testosterone levels were higher in the HIPV group than in the control group for this time  
408 period ( $F_{1,32} = 6.56$ ,  $p = 0.02$ ,  $\eta^2 = 0.17$ , figure 3G).





409 **Figure 3: Hormonal profiles for 17 $\beta$ -estradiol (E<sub>2</sub>) in females and testosterone (T) in male**  
 410 **great tits.**

412 A-B: E<sub>2</sub>/T profiles of females/males relative to the female egg laying date. Each line depicts  
 413 one individual.

414 C-D: E<sub>2</sub>/T profiles of females/males in the HIPV and control groups. Predicted values of the  
 415 GAM model and 95% confidence interval are depicted.

416 E-F: The line represents the differences between the mean control and the mean HIPV curves  
 417 from figures C-D for E<sub>2</sub> and T levels, respectively. The area around the line represents the 95%  
 418 confidence interval for the estimation of this difference. Line and area are red when the  
 419 confidence interval overlap zero, i.e. that hormone concentration between the control and the  
 420 HIPV curves are not significantly different, otherwise they are blue. T concentrations is  
 421 significantly different around the laying period, from 11 days before laying to 8 days after.

422  
 423

424 **Discussion**

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

431

432 One main finding of our study is that males exposed to HIPVs had higher testosterone  
433 (T) levels during the laying period than control males. Graham and colleagues (Graham et al.  
434 2021) found a similar relationship between HIPVs detection and T levels in male blue tits. After  
435 having trained birds to associate the presence of HIPVs with that of food, they found a positive  
436 correlation between the time spent close to the HIPV-emitting trees and male T levels (Graham  
437 et al. 2021). Males could use HIPVs as an environmental signal indicating higher food  
438 abundance (Horiuchi et al. 2003; Girling et al. 2011; McCormick et al. 2012; Miresmailli et al.  
439 2012) and upregulate their T levels accordingly, as it has been observed with other stimuli like  
440 the presence of a nest box in starlings (*Sturnus vulgaris*(Gwinner et al. 2002) or food availability  
441 in zebra finches (*Taeniopygia guttata*(Lynn et al. 2015). Since T concentrations in males are  
442 associated with courtship and mating behaviour (Silverin 1980; Ketterson et al. 1992; Enstrom  
443 et al. 1997; Hill 1999), males could have upregulated their hormonal status in response to  
444 HIPVs to stimulate their female to invest in reproduction.

445 Males reacted to HIPVs, but we did not find that females adjust their timing of laying,  
446 clutch size or egg size when exposed to the odorous treatment. This goes against our initial  
447 prediction of a higher investment of females following detection of HIPVs, but is in line with a  
448 recent study in which adding artificial HIPVs around nest boxes in the wild did not advance  
449 laying, nor increase individual clutch sizes (Delaitre et al., in prep). Another recent study with  
450 blue tits found that HIPVs increased female ovarian follicle size, but that was restricted to fast  
451 exploring females, a proxy for personality (Caro et al. 2023). The absence of a clearer effect

452 of HIPVs on female reproduction remains surprising given that HIPVs represent a seemingly  
453 good predictor of caterpillar phenology and abundance in spring, when insectivorous birds like  
454 great tits start breeding. HIPVs are indeed already emitted when oak tree buds are growing  
455 and young caterpillars just hatched from their eggs (Graham et al. 2023), and high  
456 concentrations of HIPVs in the environment indicate higher herbivorous insect availability  
457 (Horiuchi et al. 2003; Girling et al. 2011; Miresmailli et al. 2012). The present results are also  
458 surprising knowing that female tits are able to detect HIPVs and to use them in a foraging  
459 context (Amo et al. 2013; Rubene et al. 2019; Graham et al. 2021; Sam et al. 2021; Rubene  
460 et al. 2023). We presently see three potential explanations for the lack of an effect of HIPVs  
461 on reproductive timing and investment in our captive great tits.

462         First, the influence of supplementary cues on reproductive traits is generally subtle and  
463 often requires long-term experiments with large sample sizes to be able to detect an effect at  
464 the individual level. For example, while several correlative studies conducted in the field have  
465 repeatedly shown a link between temperature and seasonal timing of reproduction in birds  
466 (Visser et al. 2003; Dunn 2004; Charmantier et al. 2008), it took almost ten years of  
467 experiments in controlled conditions to understand the direct effect of temperatures on timing  
468 of reproduction in great tits (Visser et al. 2009; Schaper et al. 2012; Verhagen et al. 2020). In  
469 the present study, it is important to stress that we only conducted this experiment for one  
470 breeding season, and with only 30 females analyzed. Advancing laying dates experimentally  
471 using supplementary cues has generally proven difficult, very few studies using natural  
472 photoperiodic profiles managed to induce laying earlier than what females would normally do  
473 (Nilsson and Svensson 1993; Gienapp and Visser 2006; Visser et al. 2009; Schaper et al.  
474 2012).

475         Second, the sole presence of HIPVs might not be sufficient to trigger laying and  
476 increase investment in reproduction. Contrary to males that already exhibit robust gonadal  
477 response to the change in day length (Farner and Wilson 1957), female reproduction results  
478 from a complex association of several environmental cues (Wingfield and Kenagy 1991; Ball  
479 and Ketterson 2008; Nakazawa et al. 2023), which could explain why it is difficult to show an

480 effect of each cue tested in isolation of the others. This mainly owes to the supplementary  
481 nature of those cues, which only modulate the powerful effect of photoperiod (Wingfield et al.  
482 1992). Temperature, food and water availability, social cues from conspecifics or  
483 heterospecifics are all cues that birds are likely to use to decide when to breed and how much  
484 to invest in it (Chmura et al. 2019), and females, more than males, might integrate those cues  
485 together for their annual reproductive decisions (Caro et al. 2009). For example, social  
486 interactions among breeding pairs were by design completely excluded from this study. If this  
487 isolation was necessary to precisely control the odorous signals to which each pair of birds  
488 was exposed, we cannot exclude that neighboring pairs are eavesdropping each other's in the  
489 wild, or that they come to some kinds of mutual agreements. In that context, future studies  
490 should consider testing the interactive action of multiple cues, like HIPVs and temperature for  
491 example.

492 Third, for an unknown reason, great tits in climate aviaries started laying particularly  
493 early in 2021. It was in fact one of the first times that captive females at the NIOO laid earlier  
494 than great tits in the wild (first egg date in our experiment : 7<sup>th</sup> April; first egg date in the wild:  
495 17<sup>th</sup> April), which on average lay three weeks earlier than in captivity (Visser et al. 2009).  
496 Inducing an even earlier lay date in our experiment was thus probably even more difficult than  
497 usual. Our captive birds also lay surprisingly large or small broods compared to the wild. We  
498 have observed some clutches with only 1 ( $n = 2$ ), 2 ( $n = 1$ ) or 3 ( $n = 1$ ) eggs and others with  
499 18 ( $n = 1$ ) and 19 ( $n = 2$ ) eggs, whereas the usual average clutch size in great tit varies from 7  
500 to 12 eggs (Perrins and McCleery 1989). Such a large, unexplained, variance in clutch size  
501 renders the detection of a HIPV treatment effect quite challenging.

502 We found no evidence for an effect of our HIPV treatment on  $17\beta$ -estradiol ( $E_2$ ) levels  
503 in females. Given that  $E_2$  is tightly correlated with rapid yolk development (Williams et al. 2004),  
504 and that we found no effect of HIPVs on laying dates or clutch sizes, finding no link between  
505  $E_2$  and HIPVs might therefore not be surprising.  $E_2$  is also under control of the gonadotropin  
506 hormone LH, which in female great tits was found not to be influenced by the visual  
507 presentation of leafing branches and caterpillars (Schaper et al. 2011). On the other hand, in

508 a recent study we found an effect of HIPVs on the growth of ovarian follicles, which produce  
509 E<sub>2</sub>, but that was restricted to a subset of females that were more exploratory when exposed to  
510 a novel environment (a proxy for personality)(van Oers and Naguib 2013; Caro et al. 2023).

511

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

525

#### 526 **Declaration of interests**

527 The authors have no competing interests to declare.

528

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