

1 **Seasonal patterns of resource use within natural populations of burying**
2 **beetles**

3
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15 **Keywords:**

16 seasonality, phenology, reproductive success, age-structure, cuticular hydrocarbons, burying
17 beetles

18

19 **Abstract**

20 For organisms in temperate environments, seasonal variation in resource availability and weather
21 conditions exert fluctuating selection pressures on survival and fitness, resulting in diverse adaptive
22 responses. By manipulating resource availability on a local spatial scale, we studied seasonal
23 patterns of resource use within natural populations of burying beetles (*Nicrophorus vespilloides*) in a
24 Norfolk woodland. Burying beetles are necrophagous insects that breed on vertebrate carcasses.
25 They are active in Europe between April and October, after which they burrow into the soil and
26 overwinter. Using breeding and chemical analyses, we compared the fecundity and physiological
27 state of beetles that differed in their seasonal resource use. We found seasonal patterns in carrion
28 use by wild burying beetles, and correlated differences in their reproductive success and cuticular
29 hydrocarbon profiles. Our results provide novel insights into the seasonal correlates of behaviour,
30 physiology and life history in burying beetles.

31 **Introduction**

32 Seasonality can be a strong and critical source of environmental variability for organisms in
33 temperate environments (Williams et al. 2015). It can impose fluctuating selection pressures on
34 survival and fecundity that give rise to a great diversity of adaptive responses (Varpe 2017, Zhang
35 et al. 2019) leading to temporal variations in fitness (e.g. Ohgushi 1991) that contribute to
36 population dynamics (Morgan et. al 2001, Ragland & Kingsolver 2008, Johnson et al. 2016).
37 However, seasonal cycles are steadily being disrupted by climate change, resulting in climate-
38 induced extinctions, distributional and phenological changes, and species' range shifts in wild
39 populations (Easterling et al. 2000). Theoretical predictions suggest that phenological shifts could
40 be highly variable both among and within populations because the consequences of climatic
41 change could vary across the geographical range of a species and impact individuals differentially
42 (Heard et al. 2012). Furthermore, intraspecific variation in phenological responses to climate
43 change pose a threat to ecosystem functioning because they can desynchronise and disrupt
44 ecological interactions (Heard et al. 2012, Thackeray et al. 2016) and ecosystem functioning
45 (Grimm et al. 2013, Schmitz 2013). Understanding the ecology and evolution of phenological traits
46 in a wide range of species is key to developing a deeper understanding of how climate change
47 affects adaptation, species persistence and biodiversity.

48
49 Here we describe seasonal patterns of reproduction in the burying beetle, *Nicrophorus vespilloides*.
50 Burying beetles (*Nicrophorus* species) are necrophagous insects that live in seasonal environments.
51 They breed in Europe and North America between April and October, with variation in
52 abundance depending on the species (Dekeirsschieter et al. 2011). At the end of their breeding
53 period, burying beetles burrow into the soil and overwinter as adults or in the pre-pupal stage for
54 some species (Pukowski 1933, Peck & Kaulbars 1987, Ratcliffe 1996). Burying beetles breed on
55 small vertebrate carcasses and therefore serve a key ecological function in decomposition and
56 nutrient recycling. Their carrion breeding resource acts both as a mating arena for adult beetles
57 and a food resource for developing larvae but it is ephemeral and unpredictably distributed (Scott
58 1998). Carrion can be scarce, making competition among burying beetles to secure ownership
59 correspondingly intense. Through an elaborate system of bi-parental care (Milne & Milne 1976),
60 burying beetles conceal carrion from rivals and defend it from attack. Together the pair removes
61 any fur or feathers, rolls the flesh into a ball, covers it in antimicrobial fluids and buries it below
62 ground where it becomes an edible nest for the developing larvae.

63 Seasonality in reproductive behaviour varies greatly among *Nicrophorus* species. While *N. vespillo*
64 populations studied by Meierhofer et al. (1999) in Bielefeld, Germany, did not differ in the number
65 of offspring produced throughout the season, the period of parental care was significantly higher
66 in spring, compared to early or late summer. This is likely mediated by lower temperatures in
67 spring, which slow down offspring development and therefore prolong the period during which
68 offspring require parental defence from attack. Furthermore, natural populations of *N. orbicollis* in
69 southern New Hampshire, United States produced heavier broods in the first few weeks of the
70 breeding season compared to later broods (Scott & Traniello 1990). This could be attributed to
71 less intense competition with flies at the beginning of the season or, potentially, to strategically
72 greater levels of investment in first broods. In other work, Wilson & Fudge (1984) sampled two
73 different sites in Michigan, United States using large and small mice carcasses, and found a large
74 amount of unexplained variation in brood size. At one of the sampling sites, *N. orbicollis* beetles
75 had fewer offspring in early summer (June) while *N. defodiens* had more offspring in late summer
76 (August).

77
78 We investigated whether seasonal variation in reproductive behaviour was linked to seasonal
79 variation in resource use within a wild population of *N. vespilloides*. Recent work (Wettlaufer et al.
80 2021) on carrion beetles (Silphidae) in south-eastern Ontario, Canada suggests that competition
81 for carrion may have led to resource partitioning between ecologically similar species through
82 seasonal differences in beetle activity and abundance. Across a broad geographical area, burying
83 beetle species and populations also appear to have differentially adapted to breed on different
84 species of vertebrates, depending on local vertebrate diversity (Wilson & Fudge 1984, Hocking et
85 al. 2007). There is one report of differential resource use involving sympatric species of burying
86 beetles- *N. investigator* and *N. defodiens*- specialising on aquatic versus terrestrial carrion (Hocking et
87 al. 2007). Together these studies suggest that resource use influences niche partitioning among
88 species, though it is unknown whether similar patterns exist within species.

89
90 Resource partitioning within species can become associated with seasonality in reproduction if the
91 different resource types used for breeding are available at different times of the year, as has been
92 shown by the apple maggot fly *Rhagoletis pomonella* (Bush 1969, Mattson 2015). In this species, fly
93 reproduction is critically dependent on host fruits which become the mating arena for adults and
94 then the diet for their developing larvae, thereby serving the same function as carrion does for
95 burying beetles. In the last two centuries, *R. pomonella* has evolved a new race that specialises in
96 breeding on apples rather than the ancestral hawthorn host fruit. It has achieved this host shift

97 through a phenological shift in its reproduction to coincide with the earlier fruiting time of apples
98 (Egan et al. 2015).

99

100 We hypothesized that similar seasonal resource-based partitioning could potentially happen within
101 *N. vespilloides*, since the relative abundance of mammalian and avian carcasses available to the
102 beetles potentially varies across the beetle breeding season. In the UK, there is considerable
103 mortality among fledgling songbirds in late spring and early summer (Newton 1998, Chase et al.
104 2005, Clapham 2016, Capstick 2017) whereas rodent populations show high mortality in mid-late
105 summer (Moffat 1910, Harris 1979, Merritt et al. 2001, Haberl & Krystufek 2003, Clapham 2016).
106 The adaptive partitioning of resources within a population, driven by seasonal variation in resource
107 availability, could lead to differences in reproductive success, if sub-populations become
108 temporally separated and specialise on different carrion types.

109

110 We further hypothesized that any seasonal variations in resource use could be manifested in a
111 beetle's cuticular hydrocarbons, which could then potentially be used as a marker for identifying
112 any resource specialisation that exists between sub-populations (Haberl & Krystufek 2003, Chase
113 et al. 2005). Cuticular hydrocarbons (CHCs) are hydrophobic compounds present on the
114 arthropod cuticle. They have been shown to evolve locally and adaptively to environmental
115 variation in geography, latitude and seasonality experienced by natural populations of *D.*
116 *melanogaster* (Ingleby et al. 2013, Rajpurohit et al. 2017). Furthermore, Steiger et al. (2007) found
117 that beetles maintained on a diet of insects versus vertebrate carrion differed significantly in their
118 cuticular signatures. Cuticular hydrocarbons also have been known to differ based on dietary
119 resources in several insect species and can facilitate differential mating (Liang & Silverman 2000,
120 Buczkowski et al. 2005, Ferveur 2005, Chung & Carroll 2015).

121

122 We tested these hypotheses by investigating seasonal patterns of resource use within a natural
123 population of *N. vespilloides* in Thetford Forest, Norfolk, UK. We first tested for evidence of
124 seasonality in resource use by investigating whether *N. vespilloides* beetles from early summer (June)
125 were more likely to be trapped on mice or chick carrion compared with those from late summer
126 (August). Next, with laboratory experiments, we tested which carrion type yielded the greater
127 reproductive success and whether this differed between beetles that were trapped in June versus
128 August. Finally, we tested whether beetles that were attracted to different types of carrion during
129 the early, mid, and late field season also differed predictably and seasonally in their cuticular
130 hydrocarbons (CHCs).

131 **Materials and methods**

132 **I. Is there seasonal variation in the trapping frequency of burying beetles on chick and**
133 **mice carrion between June and August?**

134
135 Study area and trapping methods

136 We sampled the burying beetle population at Thetford Forest (52°20'39.5"N 0°32'14.9"W),
137 Norfolk, UK from May to October in 2017 at the trap locations shown in Supplementary figure
138 1, under permit from Forestry Commission England. We used carrion-baited beetle traps
139 (Japanese Beetle Trap Kit from Scotts Co., not treated with any pheromones), suspended in
140 vegetation 1-2m above ground. The bottom half of the trap was filled with Miracle-Gro compost,
141 and a small dead vertebrate was placed on the top as bait. The contents of the trap were collected
142 at intervals and brought back to the lab for processing. The trap was then refilled and rebaited.
143 After processing in the lab, no beetles were released back into the field.

144
145
146 Beetles were sampled using a paired-trap arrangement, in which we placed two beetle traps- one
147 baited with a dead domestic chick and the other baited with a dead mouse- near each other at each
148 trap location and recorded the number of beetles found in each trap. The traps within each
149 experimental pair were placed 1-2 m apart. Pairs of traps were placed 200- 400 m apart from each
150 other. With this design, beetles were given a simultaneous choice between a dead mouse and a
151 dead chick. Each time we rebaited a trap with carrion, we rebaited it with the alternate carrion
152 type. Therefore, if a mouse carcass had been placed in the trap previously, it was replaced by a
153 chick carcass on the next sampling trip to ensure that the trap location itself did not bias beetle
154 catch. The mice and chick carcasses used were matched in weight (30-40 g).

155
156
157 Processing field-caught beetles

158 At the lab, we used carbon-dioxide to immobilise each beetle and brush off any mites stuck to it.
159 We recorded the pronotum width and sex of each *N. vespilloides* beetle we trapped. We compared
160 beetles collected at two different time points during the burying beetle season: the first set was
161 collected in June 2017 after 10 days of trapping between 4 June and 14 June; and the second set
162 was collected in August 2017 after 15 days of trapping between 4 August and 19 August. The 10
163 trapping locations (Supplementary figure 1) were the same across both sampling periods.

164 **II. Does reproductive success vary with carrion substrate and / or season?**

165

166 *Measuring reproductive performance*

167 After collecting beetles from the traps, measuring and identifying them, we put each *N. vespilloides*
168 individual into its own personal small plastic box (12 cm × 8 cm × 2 cm) and fed it 1 g of beef
169 mince. The beetles were stored alone in their boxes for 7-10 days to ensure that any newly eclosed
170 individuals had had sufficient time to become sexually mature before we measured their
171 reproductive performance.

172

173 For breeding, we placed a pair of beetles (one male and one female) in a larger plastic breeding (17
174 cm x 12 cm x 6 cm) box half filled with Miracle-Gro compost and provided with either a chick or
175 mouse carcass. Each member of the pair had been trapped on the same type of carrion and we
176 bred them on the same carrion they were trapped upon. This method was used twice, once for
177 beetles collected in June and once for those collected August, yielding four treatments in all.

178

179 The mass of the carcass provided for reproduction was recorded and kept consistent within each
180 treatment. We then placed the breeding box inside a cupboard so that it was shielded from light
181 to mimic the low light conditions typically experienced by beetles as they breed below ground.
182 Eight days after pairing the beetles (i.e. the point at which the larvae had completed development
183 and were starting to disperse away from the remains of the carcass), we counted and weighed the
184 surviving larvae from each pair.

185

186 We used the following measures to record reproductive success in our experiments:

- 187 - Brood failure: We recorded the total number of broods that failed to produce any larvae:
188 0 denoted broods that failed, 1 denoted those that had at least one surviving larva at 8 days
189 post dispersal.
- 190 - Brood size: The total number of dispersing larvae 8 days post breeding.
- 191 - Average larval mass: Total mass of the brood at dispersal (g) divided by the brood size.
- 192 - Larval density: Brood size divided by the mass of the carrion used for breeding (g).
- 193 - Carcass use efficiency: (total brood mass (g) divided by original carrion mass (g)) x 100%

194

195 In June, 53 pairs of beetles trapped on mice (MM) and 24 pairs of beetles trapped on chicks (CC)
196 successfully produced broods with at least one larva. There were 4 failed broods (3 on mice
197 carcasses and 1 on a chick carcass). In August, 16 pairs of beetles trapped on mice (MM) and 25

198 pairs of beetles trapped on chicks (CC) produced broods with at least one larva. There were 7
199 failed broods (2 on mice carcasses and 5 on chick carcasses). The failed broods were excluded
200 from analyses of reproductive success.

201

202 **III. Do beetles that are attracted to different types of carrion also differ predictably and** 203 **seasonally in their CHCs?**

204 For this experiment, we sampled a total of 63 females; 32 trapped on chicks and 31 trapped on
205 mice. 40 females were collected on 23 May 2017 (“early” season- 20 on chicks and 20 on mice). 6
206 females were collected on 14 June 2017 (“mid” season- 3 on chicks and 3 on mice). 17 females
207 were collected on 4 September 2017 (“late season”- 9 on chicks and 8 on mice). After removing
208 the mites from the body of the beetles, we isolated up to two female beetles from each trap
209 individually in a glass vial for 15-20 min before storing them in a fresh vial at -80 °C. Later, we
210 processed the beetles for CHC extraction by allowing them to thaw at room temperature for 30
211 min. We then soaked them in 4 ml of solvent (99% hexane, HPLC grade) for 20 mins. We
212 transferred the extract obtained to a clean vial and allowed it to evaporate completely in a fume
213 hood under nitrogen gas. At this stage, the sealed vials were shipped to Prof. Patrizia d’Ettorre’s
214 lab at Université Sorbonne Paris Nord for analysis and characterisation.

215

216 *CHC analysis and characterisation*

217 We resuspended the extract in 400 µl of pentane (HPLC grade) and added an internal standard
218 (C18, Octadecane at 16ng/µL) to each extract. The internal standard was used to determine the
219 absolute amount of cuticular compounds present in each sample. We then analysed 2µl of the
220 extracts using GC-MS (Agilent Technologies 7890A gas-chromatograph coupled to a 5975C Mass
221 Spectrometer equipped with a HP5MS GC column (30 m × 0.25 mm × 0.25 µm) and operated at
222 70 eV in the electron impact ionization mode). The carrier gas used was helium at 1 ml/min. The
223 column oven was programmed as follows: an initial hold of 1 min at 70°C, then increased to 200°C
224 at 35°C/min, to 320°C at 4°C/min (held for 20 min).

225

226 We identified cuticular hydrocarbons based on their retention times (compared to standards) and
227 fragmentation patterns. We manually integrated the chromatograms and converted the peak areas
228 of the total hydrocarbon fraction using the MSD ChemStation software by Agilent Technologies,
229 Inc.

230 Data visualisation and statistical analysis

231 *Field and reproductive success data*

232 We carried out all statistical analyses to test our predictions using R (RStudio version 1.3.959) with
233 generalised linear models (GLM) and generalised linear mixed models (GLMM) using the lme4,
234 glmmr and MASS packages. Analysis-of-variance tables for model objects were calculated using
235 the ‘car’ package. Post-hoc comparisons using Tukey’s HSD test were carried out using the
236 package ‘lsmeans’. The asymptotic test for the equality of coefficients of variation (CV) was carried
237 out using the ‘cvequality’ package (Feltz & Miller 1996).

238

239 **I. Is there seasonal variation in the trapping frequency of burying beetles on chick and**
240 **mice carrion between June and August?**

241 We calculated the average number of beetles per day by dividing the total number of *N. vespilloides*
242 beetles found in a trap by the number of days the traps had been left out for. We focussed on the
243 two different timepoints for which we also measured reproductive outcome, namely June and
244 August 2017, using a GLMM that included carrion type and sampling month as fixed effects, and
245 trap ID and sampling date (to account for any differences in sampling effort) as random factors
246 with a Poisson error structure. The total number of *N. vespilloides* beetles found in a trap on the
247 sampling day was used as the response variable.

248

249 **II. Does reproductive success vary with carrion substrate and / or season?**

250 We examined the effect of month trapped, carcass type used for breeding and their interaction on
251 the following measures of reproductive success:

- 252 - brood success versus failure, using a multivariate logistic regression model with a binomial error
- 253 term
- 254 - the number of dispersing larvae, using a GLM with a Poisson error term
- 255 - average larval mass using a linear model
- 256 - larval density using a linear model
- 257 - carcass use efficiency using a linear model

258

259 By chance, beetles trapped in August 2017 were bred on significantly heavier carcasses in the
260 laboratory (30.98 ± 2.1 S.D (g)) than beetles trapped in June 2017 (21.20 ± 1.20 S.D (g)), though
261 within each month, carcass mass was consistent between chick and mice treatments. To assist our
262 interpretation of the data, we carried out supplementary experiments to investigate the relationship
263 between carcass size and reproductive performance in Thetford beetles. We collected data from a

264 second generation of lab breeding beetles, derived from the wild-caught beetles trapped in
265 Thetford Forest. The beetles were bred in two groups. One group bred on 12 October 2017 and
266 another group bred on 26 October 2017. The first group bred on small chick and mice carcasses
267 (8.23 ± 0.70 S.D (g)) and the latter on significantly larger chick and mice carcasses (20.64 ± 1.20 S.D
268 (g)). The chicks used for small carcasses were quail chicks and the chicks used for larger carcass
269 treatment were domestic chicks.

270

271 Using measures of reproductive performance, we examined the effect of carcass size (taken as a
272 categorical variable for “small” and “large” carcasses), and carcass type, and their interactions on
273 brood size and average larval mass as described above.

274

275 When arriving at a minimal model using GLMs and GLMMs to explain our results, we removed
276 non-significant terms and interactions using stepwise elimination. When presenting the results
277 from post-hoc analyses, we list all the terms that were tested, and their statistics at the last point
278 when they were retained in the model.

279

280 **III. Do beetles that are attracted to different types of carrion also differ predictably and** 281 **seasonally in their CHCs?**

282

283 To analyse the chemical profile of both sets of beetles, we selected 17 most regularly occurring
284 GC-MS peaks (Supplementary figure 2, Supplementary table 1). These represented the
285 hydrocarbons we had identified and integrated using the MSD ChemStation software.

286

287 We carried out the clustering analyses and visualisation of the data using *gplots*, *cluster* and *dendextend*
288 packages in R (RStudio version 1.3.959).

289

290 We log-normalised the peak areas within each sample using the following formula (Aitchison
291 1982):

292

$$Z_{ij} = \ln \left[\frac{Y_{ij}}{g(Y_j)} \right]$$

293

294 where Z_{ij} is the transformed area of peak i for beetle j ; Y_{ij} is the area of the peak i for beetle j ; and
295 $g(Y_j)$ is the geometric mean of the areas of all peaks for beetle j .

296 For the clustering analysis, we used the divisive analysis (DIANA) technique. In this approach, all
297 our samples are assumed to be in a single cluster at the beginning of the analysis (Seber 1984).
298 They are then divided into two clusters with the least similarity and this process is repeated
299 iteratively until each observation is placed in one cluster. This top-down hierarchical clustering
300 approach is considered better for identifying large clusters in the data, such as broad-scale
301 differences in resource use and preference (Seber 1984, Theodoridis & Koutroubas 2008).

302

303 Cluster validation of our data indicated one outlier (Sample M13E). We confirmed this visually
304 using a 2-dimensional scatterplot before removing the outlier. We then repeated our clustering
305 analysis using DIANA. Clusters which are demarcated in the principal component analysis (PCA)
306 plot, are based on the integer vector, with group memberships derived using the 'cutree' function
307 of the *dendextend* package.

308 Results

309

310 **I. Is there seasonal variation in the trapping frequency of burying beetles on chick and** 311 **mice carrion between June and August?**

312

313 In June 2017, mean catch per trap per day was 1 ± 0.29 (SEM – standard error of the mean) beetles
314 on chick carcasses and 2.91 ± 0.60 (SEM) beetles on mice. In August 2017, the mean catch per day
315 was 1.01 ± 0.32 (SEM) beetles on chick carcasses and 0.9 ± 0.27 (SEM) beetles on mice. There was
316 a significant interaction between month and trap-bait on the number of beetles caught (Figure 1,
317 Table 1). In June, beetles were more likely to be caught on mice than on chicks (Tukey post-hoc
318 comparison: z ratio= -9.244, $p < 0.0001$), whereas by August they were equally likely to be found
319 on both sorts of carrion (Tukey post-hoc comparison: z ratio=1.006, $p=0.3144$).

320

321 **II. Does reproductive success vary with carrion substrate and / or season?**

322

323 We did not find any significant differences in the chance of brood failure across all our treatments,
324 regardless of the time of collection in the field and the type of carrion they bred upon
325 (Supplementary table 2).

326

327 However, we found that beetles trapped in June produced more surviving larvae than the August-
328 trapped beetles, regardless of the carrion they bred upon (Supplementary figure 3A, Table 2). In
329 addition, we found that June-caught beetles tended to produce even larger broods on mice than
330 any other treatment (Table 2, Tukey post-hoc comparison: z ratio= -3.051, p-value= 0.0023). We
331 also found that the June and August beetles had a different coefficient of variation in their brood
332 size. Beetles bred in August had a greater coefficient of variation in brood size ($CV=0.605$)
333 compared to those bred in June ($CV=0.284$; Test for equality of CV: test statistic= 26.38341, p
334 < 0.0001).

335

336 We found a significant interaction between month of trapping and carrion type used for breeding
337 on average larval mass at dispersal (Supplementary figure 3B, Table 3). When June-trapped beetles
338 were bred on mice, they produced smaller larvae than any other combination of trapping months
339 and carrion type– probably because the larvae developed in a larger brood (Table 3, Tukey post-
340 hoc comparison: t ratio= 2.333, p-value= 0.0214).

341 We used larval density and carcass use efficiency to further compare reproductive performance
342 between June and August-trapped beetles as these two measures take into account the variation in
343 carcass mass (Figure 2).

344

345 Broods bred from June-trapped adults produced larvae at significantly higher density on the
346 carcass compared to broods bred from August-trapped adults (Figure 2A, Table 4). There was no
347 significant effect of carcass type on larval density nor was there a significant interaction between
348 the type of carcass the beetles bred on and month in which the adults were trapped (Figure 2A,
349 Table 4).

350

351 Beetles trapped in June utilised both chick and mice carcasses significantly more efficiently than
352 beetles trapped in August (Figure 2B, Table 5). There was no significant effect of carcass type on
353 how efficiently beetles used the carcasses, nor any significant interaction between carcass type and
354 sampling date. We found that beetles bred in August had a greater coefficient of variation in carcass
355 use efficiency (CV=0.320) compared to those bred in June (CV=0.222; Test for equality of
356 coefficients of variation: test statistic= 43.93225, p-value<0.0001).

357

358 By chance, beetles trapped in August 2017 were bred on significantly heavier carcasses in the
359 laboratory (30.98 ± 2.1 S.D (g)) than beetles trapped in June 2017 (21.20 ± 1.20 S.D (g)), though
360 comparing beetles trapped within each month, carcass mass was consistent between chick and
361 mice treatments. The size range used in this experiment still corresponds with the size of carrion
362 that *N. vespilloides* are able to use in nature (Müller et al. 1990, Otronen 1988), but we carried out
363 further analyses to test whether carcass size alone could account for the results we found, rather
364 than the date of trapping.

365

366 Testing the relationship between carcass size and reproductive performance in Thetford-derived beetles

367 Second generation beetles (F1 progeny) from Thetford were bred on small carcasses (8.23 ± 0.70
368 S.D (g)) and large carcasses (20.64 ± 1.20 S.D (g)), and within each group carcass mass was
369 consistent between chick and mice treatments.

370

371 We found that both carrion type and carrion size had an effect on brood size, though there was
372 no interaction between them (Supplementary figure 4, Supplementary table 3). Beetles bred on
373 mice carcasses produced significantly larger broods compared to those bred on chicks
374 (Supplementary figure 4, Supplementary table 3). Broods on both larger chick and larger mice

375 carcasses were significantly larger than those on smaller chicks and smaller mice (Supplementary
376 figure 4, Supplementary table 3).

377

378 We found that beetles that bred on larger carcasses also produced significantly larger larvae
379 (Supplementary table 4). However, mice carcasses within each treatment tended to produce smaller
380 larvae and this is likely explained by our finding that beetles produced larger broods on mice. We
381 did not find any significant interaction between the carcass type and carcass size on average larval
382 mass at dispersal.

383

384 Consistent with the results from wild beetles, beetles produced broods of significantly higher larval
385 density on smaller carcasses (Supplementary table 5). However, in contrast to wild populations,
386 there was significant correlation between larval density and carcass type, with beetles bred on mice
387 carrion producing broods with significantly greater larval density.

388

389 Broods utilised mice carrion significantly more efficiently than chick carrion but there was no
390 significant effect of carcass size on how efficiently beetles used the carcasses, nor any significant
391 interaction between carcass type and carcass size on carcass use efficiency (Supplementary table
392 6). Unlike the wild-caught beetles, there were no significant differences between the coefficients
393 of variation across all measures of reproductive success between beetles bred on large and small
394 carcasses (Supplementary table 7).

395

396 **III. Do beetles that are attracted to different types of carrion also differ predictably and**
397 **seasonally in their CHCs?**

398

399 Our data revealed divergence in the CHC profiles of beetles trapped at different time points in the
400 field season, that was greater than the divergence in CHC profiles between beetles trapped on
401 different types of carrion (Figure 3, Supplementary table 8).

402

403 From the four major clusters in our data, the first one was the largest- composed of 46 beetles. All
404 6 of the mid-season beetles were within this cluster, along with 38 early-season beetles and 2 late-
405 season beetles. Only one early season beetle lay outside of the first cluster. The clusters 2, 3 and 4
406 were much smaller clusters and they were mainly composed of late season beetles. The clustering
407 we observed (Figure 3, Supplementary table 8) explained 53.8% of the variation in our CHC data.

408 **Discussion**

409 We studied seasonal patterns of resource use in *N. vespilloides*, by manipulating resource availability
410 on a local spatial scale in a Norfolk woodland using traps baited with mammalian and avian carrion.
411 We compared the wild burying beetles collected in early and late summer and investigated whether
412 the type of carrion resource that *N. vespilloides* beetles were trapped upon was associated with their
413 reproductive success and differences in their cuticular hydrocarbons.

414
415 Beetles trapped in June were more likely to be found in the traps baited with mice whereas those
416 trapped in August were equally likely to be found in mice-baited and chick-baited traps. If this
417 trapping pattern reflects an adaptive preference for breeding on mice in June then beetles trapped
418 in June should have greater reproductive success on mice over chicks. We did not find consistent
419 support for this prediction. Beetles that were trapped in June and bred on mice produced more
420 larvae than beetles in all other treatments (Supplementary figure 3A, Table 2). However, we also
421 observed that beetles trapped in June had greater reproductive success in general and produced
422 larvae at greater densities on both chick and mice carcasses (Supplementary figure 3A, Figure 2A).
423 Furthermore, June-trapped beetles used both chick and mice carcasses significantly more
424 efficiently than beetles caught in August.

425
426 August-trapped beetles were by chance bred on significantly larger carcasses, so it is important to
427 consider the role that carcass size played in the results we observe and whether carcass size is a
428 potential confounding effect. Previous work in other labs has shown that larger carcasses are
429 generally associated with larger broods and heavier larvae (Bartlett & Ashworth 1988, Scott &
430 Traniello 1990, Creighton 2005). We found the same pattern in our lab (Supplementary figure 4).
431 Just as in the previous work, we too found that beetles that bred on larger carcasses produced
432 larger broods, with larger larvae. Therefore, beetles from Thetford Forest behave in a similar way
433 to other burying beetle populations. If their breeding performance was solely affected by carrion
434 size, then August-trapped beetles should have shown higher reproductive success than June-
435 trapped beetles. Yet we found the opposite pattern. Unlike the wild-caught beetles, we did not
436 find any significant differences between the coefficients of variation across all measures of
437 reproductive success in beetles bred on large and small carcasses in the lab (Supplementary table
438 7). We conclude, therefore, that our results are not caused by the August-trapped beetles being
439 bred on larger carrion.

440 In short, we found that June-trapped beetles produced larger broods on mice, comprising smaller
441 larvae. However June-trapped beetles did not more produce more larvae per gram of carrion, or
442 convert carrion more efficiently into larvae, than beetles trapped on chicks or caught in August. A
443 conservative interpretation of these data is that the beetles trapped in June were not specialists in
444 breeding on mice but rather were simply of higher quality than those trapped in August. August-
445 trapped beetles were more variable in their reproductive success, which suggests that the beetles
446 breeding in August were in turn more variable in quality.

447

448 Just as with other insect species, there is likely to be seasonal variation in the age structure of
449 natural *N. vespilloides* populations. In Europe, *N. vespilloides* adults emerge from overwintering in
450 late spring. Presumably only higher quality individuals are able to survive the winter months and
451 they might then breed twice in one year (Pukowski 1933, Scott 1998). Offspring from the first
452 broods produced each year will have sufficient time to reach sexual maturity and produce one
453 brood themselves before the annual breeding season comes to a close. Therefore by August, the
454 breeding population is likely to comprise a combination of older adults and more recently eclosed
455 individuals (Pukowski 1933, Urbański & Baraniak 2015): an instance of ‘generational smearing’
456 (Bjørnstad et al. 2016). This could account for which the greater variation in the reproductive
457 success that we observed in August-trapped beetles. It could also explain why we did not see
458 equivalent carrion-related variation in reproductive success in the experiments that used beetles
459 bred in the lab rather than wild-caught individuals.

460

461 Previous lab experiments on *N. vespilloides* have indicated that even when females switch strategies
462 from reproductive restraint to terminal investment, older females have lower reproductive success
463 due to senescence-related constraints (Cotter et al. 2011). Furthermore, work on natural
464 populations of burying beetles has indicated a decline in brood mass in *N. orbicollis* populations
465 later in the breeding season (Scott & Traniello 1990). An age-structured population could partly
466 explain why the quality of individuals in late summer was apparently lower on average than earlier
467 in the year. Whether this pattern exists in other *N. vespilloides* populations remains to be seen.
468 Different populations could have different age structures in late summer, depending on local life
469 history strategies and on local ecological conditions.

470

471 Our analyses of beetle CHCs provides further evidence against the possibility of individual
472 specialisation on particular carrion substrates and support for the alternative interpretation that
473 there is simply seasonal variation in adult beetle quality. In *Nicrophorus* beetles, these cuticular

474 compounds act as contact pheromones and they are an important means by which beetles
475 recognise conspecifics and distinguish between the sexes (Steiger et al. 2007, Steiger et al. 2008).
476 In addition, beetles raising a brood use 'breeding status' related CHC signatures to distinguish
477 between their nestmate and an intruding conspecific (Müller et al. 2007, Steiger et al. 2007, Steiger
478 et al. 2008).

479

480 We found no association between beetle CHC profiles of beetles and the type of carrion they were
481 trapped upon. It may be that individuals in the field are not sufficiently consistent in their use of
482 carrion for there to be a carcass-use related signature in their CHCs. Alternatively, since diet-related
483 differences in CHCs are due to the incorporation of dietary hydrocarbons into cuticular lipids, it
484 may be that the hydrocarbons derived from birds and mammals are insufficiently different to leave
485 a diet-based signature on the cuticle (Liang & Silverman 2000, Blomquist 2010, Otte et al. 2014).

486

487 Nevertheless we found some indication that the CHC profiles of different beetles clustered
488 according to the time of year when they were trapped (Figure 3). Furthermore, we found greater
489 variation in the CHCs of late-season beetles than early-season beetles. Since the cuticular profiles
490 of the beetle vary according to their reproductive state (Steiger et al. 2007, Scott et al. 2008), this
491 is consistent with our inference that there are seasonal differences in individual quality, age and
492 breeding status within wild populations.

493

494 Many other insect species are also multivoltine, producing more than one generation in a year
495 which can result in age-structured populations (Wagner et al. 1984, Tauber et al. 1986, Gurney et
496 al. 1992, Molleman et al. 2006, Carey et al. 2008, Bjørnstad et al. 2016). Variation in age structure
497 has been studied in depth for managing populations of insect pest species (Tauber et al. 1986,
498 Bonsall & Eber 2001, Cook et al. 2008, Rock et al. 2015), but it is not yet known how it contributes
499 to the dynamics of wild *N. vespilloides* populations.

500

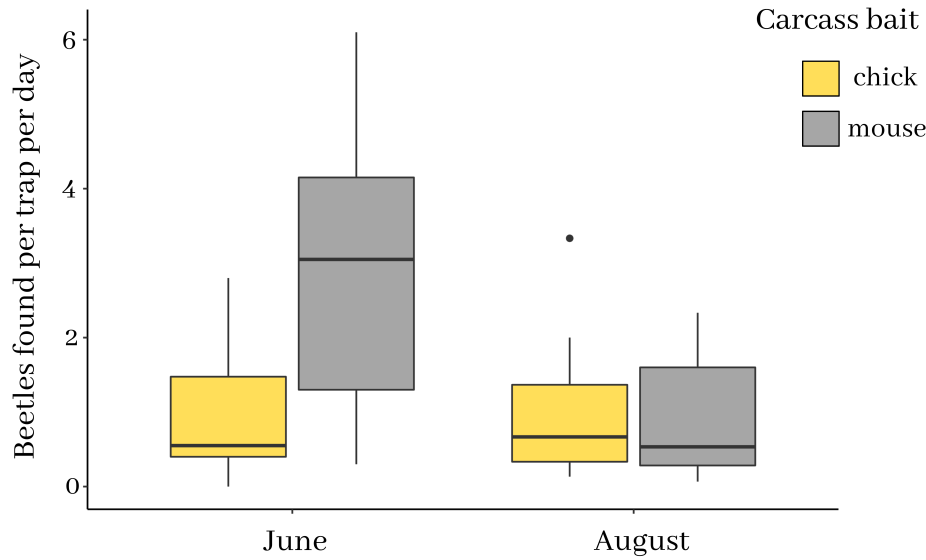
501 Cyclic variation in rates of survival, reproductive success and developmental times in insect
502 populations may be driven by fluctuations in the availability and quality of resources, interspecific
503 competition, and the effects of abiotic environmental factors such as annual variation in
504 temperature (Varley et al. 1973, Plant and Wilson 1986, Haridas et al. 2016). It is crucial to grasp
505 how environmental fluctuations influence the dynamics of insect populations, particularly given
506 that warming and rapid climate change are predicted to drastically affect species distribution and
507 abundance globally (Meehl and Tebaldi 2004, Tylianakis et al. 2008, Paaijmans et al. 2013, Vasseur

508 et al. 2014). In recent years, a growing number of studies have investigated the impacts of unnatural
509 temperature shifts associated with global climate change on natural populations (Deutsch et al.
510 2008, Guo et al 2011, Colinet et al. 2015, Stoks et al. 2017). Yet, several groups of insects go
511 unrepresented in climate change research (Guo et al 2011). Further work is needed to investigate
512 how populations respond to natural variation in their biotic and abiotic environments to better
513 predict long-term species' responses to global change (Perez & Aron 2020). Our work has
514 generated novel insights into how wild populations respond to fluctuating selection pressures
515 arising from seasonality in one such understudied group of animals.

516 **Figures**

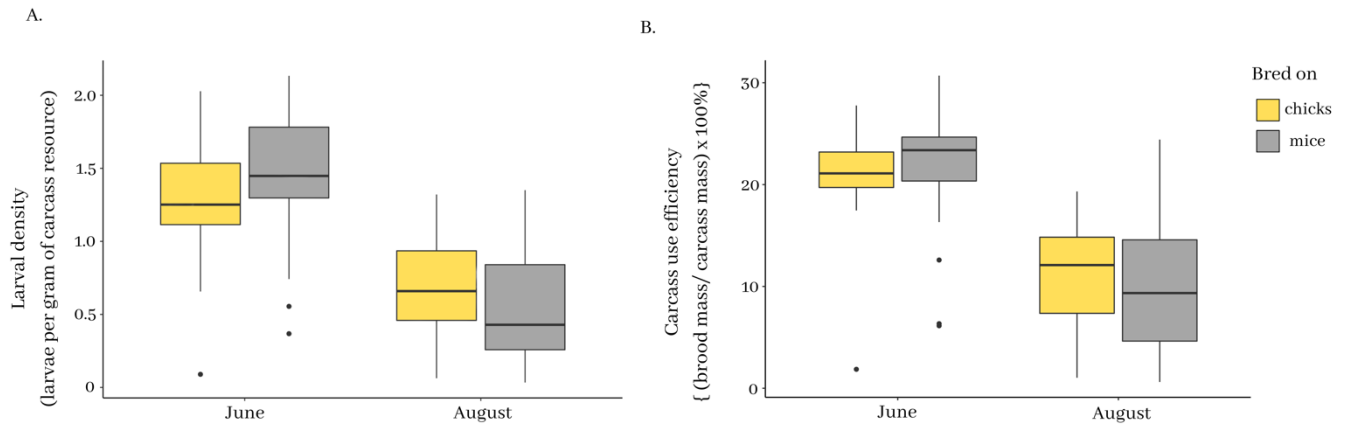
517

518



519

520 **Figure 1: The number of *N. vespilloides* beetles trapped on chick and mouse carrion at two**
521 **timepoints during the 2017 field season.** The number of beetles caught per trap per day in traps
522 that were chick-baited (yellow bars) and mouse-baited (grey bars), from June 2017 (N= 391 beetles
523 over 10 days) and August 2017 (N = 287 beetles over 15 days;). The box bounds represent the
524 inter-quartile range (IQR), the whiskers represent 1.5 * IQR, the central horizontal line is the
525 median, and the single points are outliers in the data.



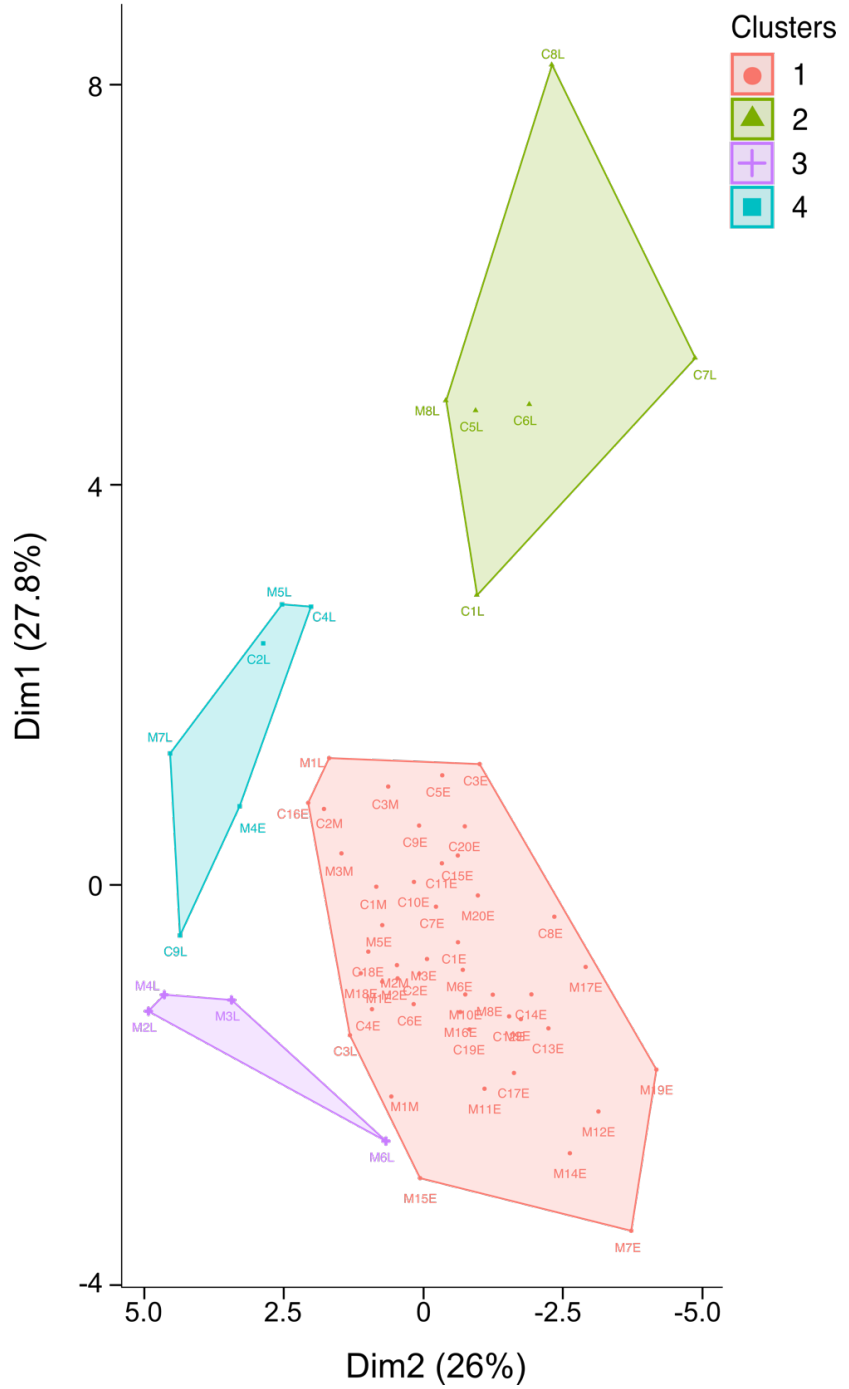
526

527 **Figure 2: Reproductive success of *N. vespilloides* trapped on chick and mouse carrion in**
 528 **June and August 2017 and measured in two different ways: A. larval density and B. carcass**
 529 **use efficiency. Adults were trapped in June and August 2017 at traps baited with either chick**
 530 **carcasses or mice carcasses. Adults were bred on the same carrion substrate they were trapped**
 531 **upon: either dead chicks (yellow bars) or dead mice (grey bars). The box bounds represent the**
 532 **inter-quartile range (IQR), the whiskers represent 1.5 * IQR, the central horizontal line is the**
 533 **median, and the single points are outliers in the data.**

Figure 3:

CHC profiles of *N. vespilloides* beetles trapped on chick and mouse carrion at three timepoints during the 2017 field season. Scatter plot depicting field beetles clustered by their CHC profile along two principal component axes. The y-axis is the first principal component, and the x-axis is the second principal component. Together the two axes explain 53.8% of the variation in the data.

In the sample name, the first letter indicates the carrion type the individual was trapped on (C- chick, M- mouse). The following number is the sample ID, and the last letter indicates the trapping season (E- early, M- mid, L- late).



535 **Tables**

536 Table 1: Model summary showing results of GLMM to test for the effects of carrion type, sampling
 537 month and their interactions on the number of *N. vespilloides* beetles trapped using avian versus
 538 mammalian carcasses in June and August 2017

539

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
Intercept	2.6213	0.1729	15.163	< 2e-16 ***
Carcass-Mouse	-0.1186	0.1179	-1.006	0.31436
Month-June	-0.4187	0.1284	-3.262	0.00111 **
Carcass-Mouse x Month-June	1.0681	0.1155	9.244	< 2e-16 ***

540

541

542 Table 2: Brood size at larval dispersal of *N. vespilloides* beetles trapped in June and August 2017 and
 543 bred on chick carcasses and mice carcasses. Model summary showing results of the GLM to test
 544 for the effects of month trapped, carcass type used for breeding and their interaction on brood
 545 size at dispersal

546

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
Intercept	3.00964	0.04441	67.767	< 2e-16 ***
Carcass bred on-Mouse	-0.16545	0.07489	-2.209	0.027159 *
Month trapped on-June	0.28001	0.05937	4.716	2.4e-06 ***
Carcass bred on-Mouse x Month trapped on-June	0.30736	0.08816	3.486	0.000489 ***

547

548 Table 3: Average larval mass (calculated as total brood mass / number of larvae at dispersal) of
 549 broods from *N. vespilloides* beetles trapped in June and August 2017 and bred on chick carcasses
 550 and mice carcasses. Model summary showing results of the LM to test for the effects of month
 551 trapped, carcass type used for breeding and their interaction on average larval mass at dispersal

552

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>Pr(> t)</i>
Intercept	0.174569	0.006359	27.452	<2e-16 ***
Carcass bred on-Mouse	0.009393	0.010180	0.923	0.3581

Month trapped on-June	-0.002187	0.009086	-0.241	0.8103
Carcass bred on-Mouse x Month trapped on-June	-0.027644	0.012838	-2.153	0.0334 *

553

554 Table 4: Larval density (calculated as total brood size at dispersal / mass of carrion breeding
555 resource at start of breeding) of broods from *N. vespilloides* beetles trapped on chick and mouse
556 carrion in June and August 2017. Model summary showing results of the LM to test for the effects
557 of month trapped, carcass type used for breeding and their interaction on larval density

558

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>Pr(> t)</i>
Intercept	0.61267	0.06057	10.12	<2e-16 ***
Carcass bred on-Mouse	0.08731	0.07555	1.156	0.25
Month trapped on-June	0.80361	0.07498	10.72	<2e-16 ***
Carcass bred on-Mouse x Month trapped on-June	0.29675	0.15457	1.920	0.0574 .

559

560 Table 5: Carcass use efficiency (calculated as (total brood mass at dispersal / mass of carrion
561 breeding resource at start of breeding) x 100%) of broods from *N. vespilloides* beetles trapped on
562 chick and mouse carrion in June and August 2017. Model summary showing results of the LM to
563 test for the effects of month trapped, carcass type used for breeding and their interaction on
564 carcass use efficiency

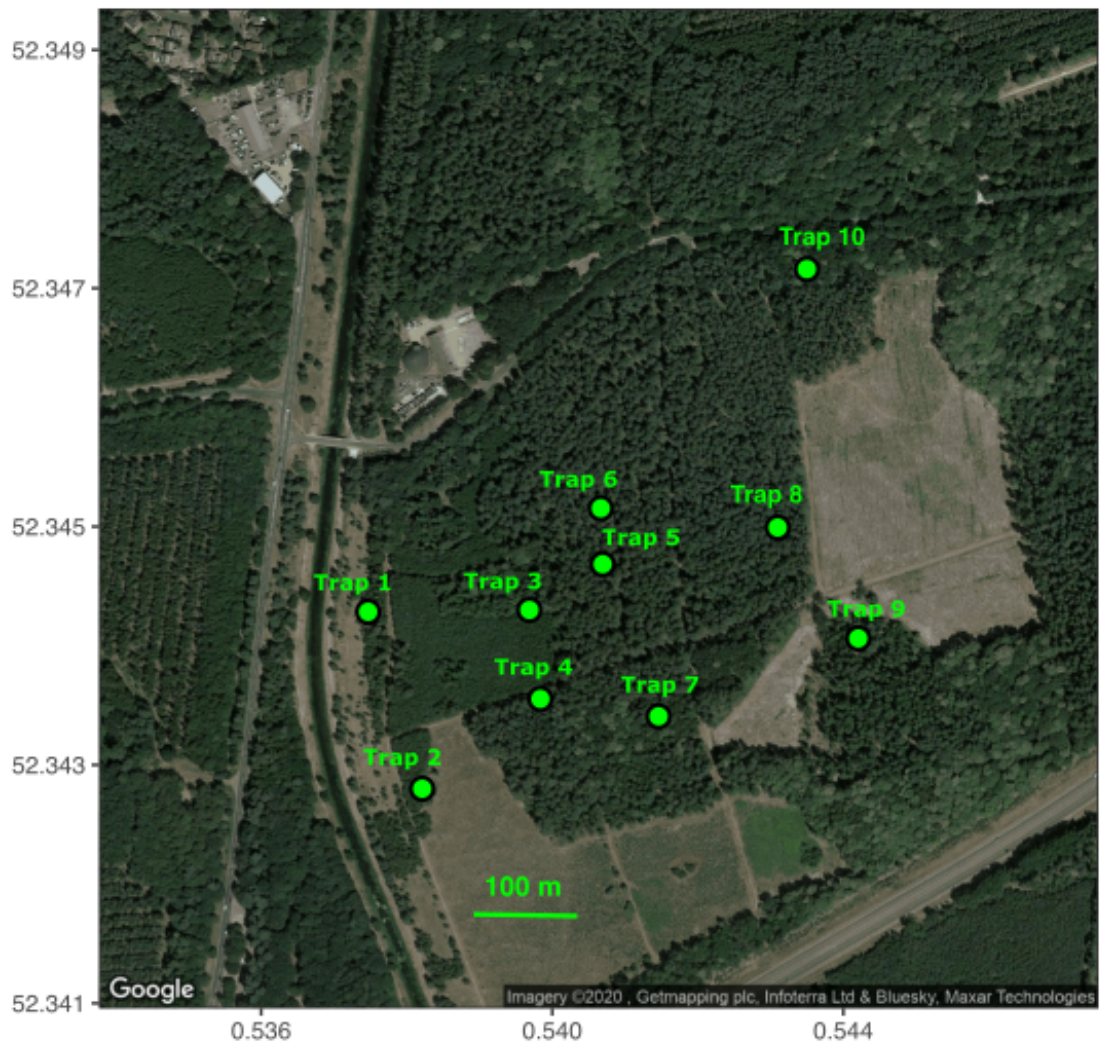
565

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>Pr(> t)</i>
Intercept	10.718	0.830	12.91	<2e-16 ***
Carcass bred on-Mouse	0.4102	1.0406	0.394	0.694
Month trapped on-June	11.104	1.028	10.81	<2e-16 ***
Carcass bred on-Mouse x Month trapped on-June	2.659	2.149	1.237	0.218

566

567 **Supplementary figures**

568



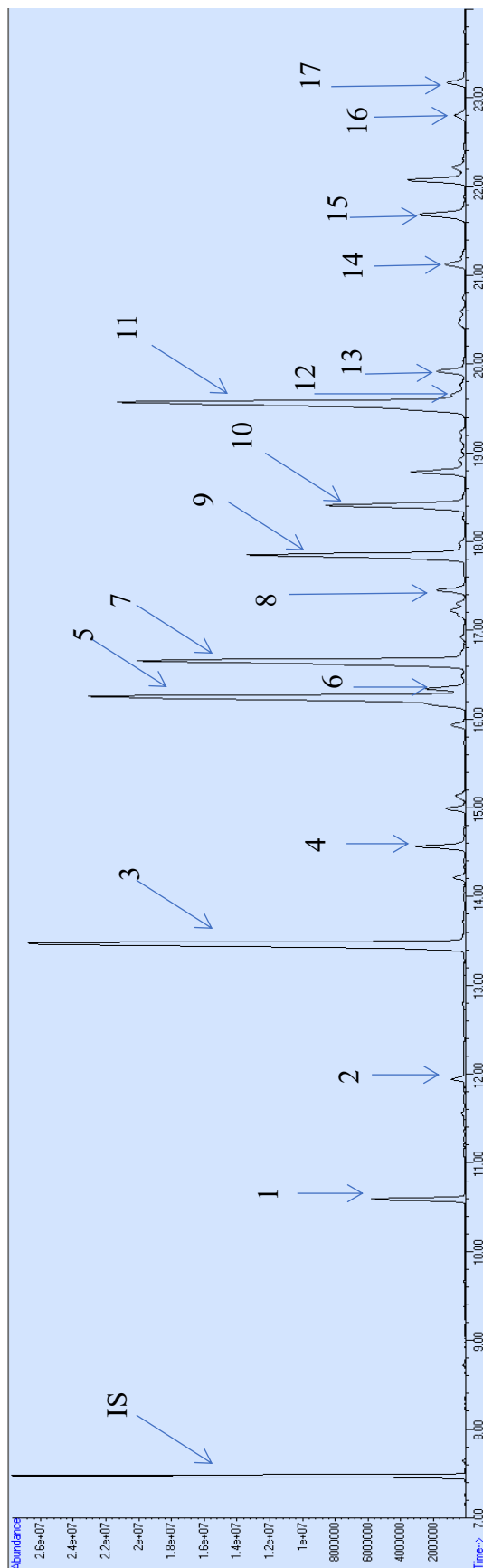
569

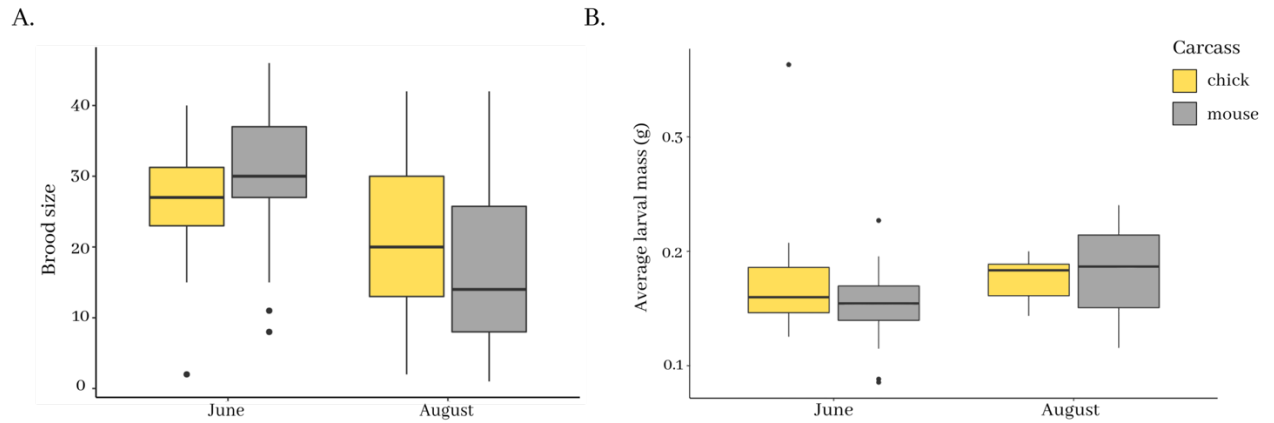
570

571 Supplementary figure 1: Beetle trapping locations in Thetford Forest. The coordinates of each
572 location are represented using the longitude value on the horizontal axis and latitude value on the
573 vertical axis.

574

575 Supplementary figure 2: Gas-chromatogram of the CHC profile of *N. vespilloides*, showing
576 the 17 most regularly occurring peaks in our samples. The x-axis represents retention time,
577 and the y-axis represents signal intensity. Identification of the peaks is provided in Supplementary
578 Table 1





579

580

581 Supplementary figure 3: Fitness correlates of breeding *N. vespilloides* trapped on chick and

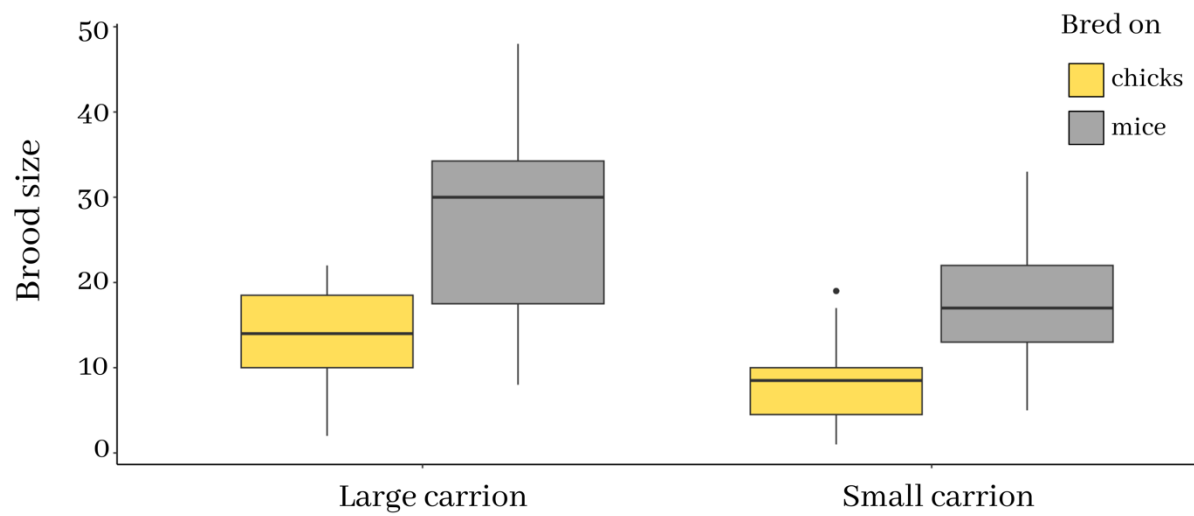
582 **mouse carrion in June and August 2017: A. brood size and B. average larval mass at dispersal**

583 of broods bred from adults trapped in June and August 2017 on chick carcasses (yellow bars) and

584 mice carcasses (grey bars). The box bounds represent the inter-quartile range (IQR), the whiskers

585 represent 1.5 * IQR, the central horizontal line is the median, and the single points are outliers in

586 the data.



587

588 Supplementary figure 4: Relationship between carrion mass ('small' and 'large') and number
 589 **of larvae at dispersal produced by second-generation Thetford *N. vespilloides* bred on chick**
 590 **and mouse carcasses.** The box bounds represent the inter-quartile range (IQR), the whiskers
 591 represent 1.5 * IQR, the central horizontal line is the median, and the single points are outliers in
 592 the data.

593 **Supplementary tables**

594 Supplementary table 1: Identification of the 17 most regularly occurring peaks in the cuticular
 595 hydrocarbon profile of *N. vespilloides*. Diagnostic ions are provided.

596

	Retention time (min)	Compound	Diagnostic EI ions (m/z)
Internal standard	7.47	C18 (IS) (Octadecane)	254
1	10.59	C21 (Heneicosane)	296
2	11.95	C22 (Docosane)	310
3	13.46	C23 (Tricosane)	324
4	14.57	3MeC23 (3-methyltricosane)	57, 309, 281, 323
5	16.25	C25:1 (Pentacosene)	350
6	16.34	C25:1 (Pentacosene)	350
7	16.66	C25 (Pentacosane)	352
8	17.45	5MeC25 (5-methylpentacosane)	85, 309, 281, 351
9	17.85	3MeC25 (3-methylpentacosane)	57, 337, 309, 351
10	18.42	3,9diMeC25 (3,9dimethylpentacosane)	57, 155, 252, 351, 365
11	19.57	C27:1 (Heptacosene)	378
12	19.66	C27:1 (Heptacosene)	378
13	19.92	C27 (Heptacosane)	380
14	21.13	3MeC27 (3-methylheptacosane)	57, 365, 337, 379
15	21.69	3,9 diMeC27 (3,9-dimethylheptacosane)	57, 155, 281, 379, 393
16	22.81	C29:1 (Nonacosene)	406
17	23.17	C29 (Nonacosane)	408

597

598 Supplementary table 2: Brood success, measured at larval dispersal of *N. vespilloides* trapped in
 599 June and August 2017 and bred on chick carcasses and mice carcasses. Model summary showing
 600 results of the GLM to test for the effects of month trapped, carcass type used for breeding and
 601 their interaction on brood success

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
Intercept	2.1001	0.4325	4.855	1.2e-06 ***
Carcass bred on-Mouse	0.5246	0.6337	0.828	0.408
Month trapped on-June	1.1345	0.6886	1.648	0.099426 .
Carcass bred on-Mouse x Month trapped on-June	-0.7764	1.4818	-0.524	0.60032

602

603 Supplementary table 3: Brood size at dispersal produced by second-generation Thetford *N.*
 604 *vespilloides*, bred on chick and mouse carcasses. Model summary of the GLM to test the effects of
 605 carcass size, carcass type, and their interactions on brood size at dispersal of second-generation
 606 beetles from Thetford beetles in October 2017

607

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
Intercept	2.60122	0.05531	47.031	<2e-16 ***
Carcass Size-Small	-0.44858	0.05078	-8.834	<2e-16 ***
Carcass Type-Mouse	0.71077	0.05688	12.497	<2e-16 ***
Carcass Size-Small x Carcass Type-Mouse	0.04920	0.11381	0.432	0.665

608

609 Supplementary table 4: Average larval mass at dispersal of broods produced by second-generation
 610 Thetford *N. vespilloides*, bred on chick and mouse carcasses. Model summary of the LM to test the
 611 effects of carcass size, carcass type, and their interactions on average larval mass at dispersal

612

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
Intercept	0.187831	0.006342	29.618	< 2e-16 ***
Carcass Size-Small	-0.060102	0.006548	-9.178	1.34e-14 ***
Carcass Type-Mouse	-0.013004	0.006384	-2.037	0.0445 *
Carcass Size-Small x Carcass Type-Mouse	-2.051e-02	1.311e-02	-1.564	0.121

613

614 Supplementary table 5: Larval density at dispersal of broods produced by second-generation
 615 Thetford *N. vespilloides*, bred on chick and mouse carcasses. Model summary showing results of
 616 the LM to test the effects of carcass size, carcass type, and their interactions on larval density

617

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
Intercept	0.5205	0.1249	4.169	6.97e-05 ***
Carcass Size-Small	0.5967	0.1289	4.628	1.22e-05 ***
Carcass Type-Mouse	0.9196	0.1257	7.317	9.70e-11 ***
Carcass Size-Small x Carcass Type-Mouse	0.3994	0.2582	1.547	0.12549

618 Supplementary table 6: Carcass use efficiency at dispersal of broods produced by second-
 619 generation Thetford *N. vespilloides*, bred on chick and mouse carcasses. Model summary showing
 620 results of the LM to test the effects of carcass size, carcass type, and their interactions on carcass
 621 use efficiency

622

<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
Intercept	12.2815	0.9761	12.582	< 2e-16 ***
Carcass Size-Small	0.1202	1.3408	0.090	0.929
Carcass Type-Mouse	10.4399	1.2999	8.031	3.1e-12 ***
Carcass Size-Small x Carcass Type-Mouse	-0.5812	2.7203	-0.214	0.831

623

624 Supplementary table 7: Results of the asymptotic test for the equality of coefficients of variation
 625 on different measures of reproductive success from broods produced by second-generation
 626 Thetford *N. vespilloides* beetles, bred on small and large carcasses

627

<i>Measure:</i>	<i>test statistic</i>	<i>p-value</i>
brood size	0.006646513	0.9350235
average larval mass	0.006805273	0.9342538
larval density	0.1486614	0.6998179
carcass-use efficiency	0.4578437	0.4986334

628

629 Supplementary table 8: Activity season of field-caught beetles within clusters differentiated by
 630 CHC profile

631

Total beetles in cluster	Number trapped during early season	Number trapped mid-season	Number trapped during late season
Cluster 1 (46)	38	6	2
Cluster 2	0	0	6

(6)			
Cluster 3 (4)	0	0	4
Cluster 4 (6)	1	0	5

632

633 **Data availability**

634

635 Data have been made available to reviewers and will be made openly available on the Open Science

636 Framework at the time of publication.

637

638 **Funding**

639

640 Funding support for this project came from St. John's College, Cambridge; the Department of

641 Zoology, University of Cambridge; the Cambridge Philosophical Society; the Leche Trust and a

642 Santander International Mobility Award.

643

644 **Author contributions**

645

646 Swastika Issar: Funding acquisition; Conceptualisation; Methodology; Formal analysis;

647 Investigation; Validation; Visualisation; Writing - review & editing; Writing - original draft. Chloé

648 Leroy: Methodology; Investigation; Validation; Visualisation; Writing - review & editing. Patrizia

649 d'Ettorre: Methodology; Investigation; Validation; Visualisation; Writing - review & editing;

650 Resources. Rebecca M. Kilner: Conceptualisation; Methodology; Supervision; Writing - review &

651 editing; Project administration; Resources. All authors gave final approval for publication.

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