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1 **Aromatic plants in blue tit *Cyanistes caeruleus* nests: no negative effect on blood-**  
2 **sucking *Protocalliphora* blow fly larvae**

3

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21 Abstract

22 Nesting birds use several behavioural or physiological defence mechanisms against  
23 parasites. On Corsica, female blue tits (*Cyanistes caeruleus*) incorporate fresh fragments  
24 of a limited number of aromatic plants in the nest cup, from the end of nest construction  
25 until fledging. Some of these plants negatively affect bacterial growth and host location  
26 by blood-sucking mosquitoes in laboratory conditions. In natural populations, Corsican  
27 blue tit chicks are exposed to the highest levels of blood-sucking ectoparasitic blow flies  
28 (*Protocalliphora* sp.) reported in Europe. These ectoparasites can have severe negative  
29 effects on chick development and survival probabilities, especially when food constraints  
30 are elevated. Here we investigated in several natural Corsican blue tit populations the  
31 hypothesis that aromatic plants brought to the nest have anti-blow fly effects during the  
32 chick-rearing stage. We predicted that: 1) the amount of aromatic plants should be  
33 negatively related to blow fly infestation intensity across nests, 2) experimental addition  
34 of aromatic plants in nests should reduce blow fly infestation intensity, and 3) nestlings  
35 should be in better physical condition in nests where aromatic plants were experimentally  
36 added. No significant relation was found between the amount of aromatic plants in nests  
37 and blow fly infestation intensity. Experimental addition of aromatic plants did not  
38 reduce blow fly infestation intensity and did not affect the chick phenotypic parameters  
39 we measured. We conclude that aromatic plants in blue tit nests are not used as a defence  
40 against ectoparasitic *Protocalliphora* blow flies in our study population.

41 Keywords

42 blue tit, *Cyanistes caeruleus*, blow fly, *Protocalliphora sp.*, ectoparasite, aromatic plants,

43 nest protection hypothesis, anti-parasite defence

44 Introduction

45 Some bird species bring to their nests green plants which are rich in volatile secondary  
46 compounds (Wimberger 1984, Clark and Mason 1985). The selected plant species often  
47 represent a small, non-random fraction of the available species in the habitat (Gwinner  
48 1997, Gwinner et al. 2000, Lambrechts and Dos Santos 2000). Three, non-mutually  
49 exclusive, main hypotheses on the functional significance of the use of greenery by birds  
50 have been proposed in the literature. First, breeding birds may exploit the anti-parasite  
51 properties of plant secondary compounds to repel, kill or impair the development of nest  
52 ectoparasites, and therefore affect host-parasite interactions (the nest protection  
53 hypothesis, e.g. Wimberger 1984, Clark and Mason 1985). Second, the chemical  
54 compounds of fresh plant fragments may stimulate the host immune system  
55 independently from potential detrimental effects on ectoparasites, and perhaps reduce  
56 endoparasite loads or pathogen infection probabilities (the drug hypothesis, Gwinner et  
57 al. 2000). Finally, the use of green plants by males during nest building may play a role  
58 in mate attraction, for instance when the ability to find particular plants reflects aspects  
59 related to territory and/or individual quality beneficial to chicks (the courtship hypothesis,  
60 Fauth et al. 1991, Gwinner 1997, Brouwer and Komdeur 2004, Polo et al. 2004, Veiga et  
61 al. 2005).

62 Field investigations experimentally demonstrating influences of fresh plant  
63 material on nest ectoparasite loads or offspring characteristics are rare. Clark and Mason  
64 (1988) first demonstrated a positive effect of green plant addition in nests of the  
65 European starling *Sturnus vulgaris*. Experimental addition of green plant fragments from  
66 day 10 before-hatching until day 13 post-hatching reduced the number of hematophagous

67 mites in nests relative to control nests. Adding green material to the nest did not influence  
68 chick mass or feather development, but resulted in higher levels of blood haemoglobin in  
69 nestlings. Clark and Mason's experimental design did not simulate starling natural  
70 behaviour because males usually stop bringing greenery to the nest before the start of  
71 incubation (Gwinner 1997, Brouwer and Komdeur 2004). In another starling study,  
72 Fauth et al. (1991) experimentally removed green nest material after the end of clutch  
73 completion, whereas control nests still contained greenery added by males during  
74 courtship and nest building. The two treatments did not differ in ectoparasite loads,  
75 breeding success, chick condition or post-fledging survival. In a third experiment  
76 comparing herb and grass nests, herbs selected by starlings did not reduce ectoparasite  
77 loads, but affected both chick body mass and blood parameters (hematocrit, lymphocyte  
78 and basophil counts; Gwinner et al. 2000, Gwinner and Berger 2005). Most  
79 investigations in bird species other than starlings also failed to demonstrate a significant  
80 negative influence of fresh plants on nest-dwelling ectoparasites. In the wood stork  
81 *Mycteria americana*, green plant material in nests had no repelling effect on dermestid  
82 beetle larvae *Dermestid nidum* (Rodgers et al. 1988). Dawson (2004) found that  
83 experimentally-added yarrow *Achillea millefolium* in nests of the non greenery-using tree  
84 swallows *Tachycineta bicolor* had no negative effects on blow fly or flea infestation  
85 levels. An exception is Shutler and Campbell's (2007) recent study in tree swallow nests  
86 showing negative effects of yarrow on flea number, although not on blow fly pupae  
87 numbers.

88         On Corsica, hole-nesting female blue tits (*Cyanistes caeruleus*) actively  
89 incorporate fresh fragments of aromatic plants in the nest cup (e.g. *Lavandula stoechas*,

90 *Achillea ligustica*, *Helichrysum italicum*, *Mentha suaveolens*). They daily add fresh  
91 aromatic plant fragments in the nest between the end of nest construction until fledging,  
92 and replenish the nest with fresh fragments of the same plant species quickly after  
93 experimental removal (Lambrechts and Dos Santos 2000, Petit et al. 2002, Mennerat  
94 pers. obs.). The plant species found in blue tit nests represent only a small fraction of the  
95 plants available in the habitat (Petit et al. 2002). A noticeable difference between starling  
96 and blue tit plant-adding behaviours is that blue tits keep adding aromatic plants during  
97 the whole nestling period, which suggests that these plants have a little role in mate  
98 attraction. Some of the selected plants possess antiseptic, fungicidal or insecticidal  
99 properties (Petit et al. 2002, Rossi et al. 2007), and repel blood-sucking mosquitoes in  
100 laboratory conditions (Lafuma et al. 2001). In free-ranging blue tit populations on  
101 Corsica, nests are infested with very high numbers of *Protocalliphora* blood-sucking  
102 blow fly larvae attacking nestlings (Hurtrez-Boussès et al. 1999). Adult female blow flies  
103 visit bird nests and lay eggs in the nest material just after the chicks hatch, and keep  
104 visiting bird nests throughout the whole nestling period (Bennett and Whitworth 1991,  
105 Hurtrez-Boussès et al. 1999). Blow fly larvae grow into three successive, blood-sucking  
106 larval stages, and remain in the nest material until they emerge as adults after their pupal  
107 phase (Bennett and Whitworth 1991, Heeb et al. 2000). In Corsican blue tit populations,  
108 blow fly larvae have pronounced detrimental effects on nestling development, fledgling  
109 mass, hematocrit and post-fledging survival; they also influence aspects related to chick  
110 behaviour and parental care, including investment in nest sanitation (Hurtrez-Boussès et  
111 al. 1997, 1998, 2000, Banbura et al. 2004, Simon et al. 2004, 2005, Charmantier et al.  
112 2004). Other nest ectoparasites, such as fleas, ticks, lice or mites, are rarely observed in

113 these populations (prevalences <3%, Hurtrez-Boussès et al. 1997, A. Mennerat pers.  
114 obs.).

115 Here we investigate whether fresh aromatic plant fragments incorporated in  
116 Corsican blue tit nests have significant negative effects on blow fly infestation, as  
117 predicted by the nest protection hypothesis. We used both an observational approach to  
118 examine the relationship between aromatic plants and blow fly infestation in non-  
119 manipulated nests, and an experimental test of the effects of aromatic plants on blow fly  
120 infestation intensity and nestling body condition.

121

## 122 Material and Methods

### 123 a) Study sites and field protocols

124 The study was carried out in 2005 and 2006 in three Corsican blue tit populations  
125 accepting nestboxes for breeding ("Muro-deciduous", 42°33' N, 08°55' E, broad-leaved  
126 deciduous oakwood, *Quercus humilis*; "Muro-evergreen", 42°36' N, 08°58' E, evergreen  
127 oakwood, *Q. ilex*; "Pirio", 42°31' N, 08°46' E, evergreen oakwood, *Q. ilex*; see Blondel  
128 1985 and Lambrechts et al. 1997, 2004 for a detailed description of the sites). All  
129 nestboxes were monitored throughout the breeding season to determine the onset of egg  
130 laying (March 1<sup>st</sup> = day 1), clutch size, hatching date, the number of hatchlings, and the  
131 number of chicks fledged (for a description of the field protocols, see e.g. Blondel 1985;  
132 Lambrechts et al. 1997). Nestlings were weighed at day 9-11 post-hatching when chick  
133 demands are considered to be the highest, and measured and weighted again when chicks  
134 had reached their asymptotic mass at day 14-15 post-hatching. Body mass was measured  
135 to the nearest 0.1g with a Pesola spring balance and tarsus length to the nearest 0.1mm

136 with a digital calliper. Chick body mass and tarsus length are often associated with the  
137 probability to be recruited in the local breeding population (Blondel et al. 1998, Heeb et  
138 al. 1999). Together with body mass, hematocrit determines chick aerobic capacity,  
139 which is related to post-fledging survival in Corsican blue tit populations (Thomas et al.  
140 2007). We therefore used hematocrit as a measure of physiological condition in nestlings  
141 from Pirio. For each chick, around 20  $\mu$ L of blood was collected from the brachial vein  
142 into a heparinised microcapillary tube, and centrifugated for 3 minutes at 13000 rpm.  
143 The hematocrit value was defined as the percentage volume of erythrocytes in the total  
144 blood sample.

145

#### 146 b) Blow fly quantification procedures

147 To avoid loss of blow fly larvae during nest removal, we placed each monitored nest in a  
148 tissue bag, following the method applied by Hurtrez-Boussès (1996). A bag was inserted  
149 under the nest 2 to 4 days before hatching. When chicks were 2-3 days old, the edge of  
150 the bag was pulled up to reach the same level as the top of the nest cup. At day 14-16  
151 post-hatching, after measuring the chicks, nests were collected, enclosed in hermetic  
152 plastic bags and replaced by the same amount of fresh moss. In the laboratory, blow fly  
153 larvae and pupae were sorted out of the nest material and counted. Blow fly larvae  
154 develop into three successive larval stages before pupating. First-stage larvae are  
155 particularly difficult to detect. Therefore, our estimate of blow fly infestation intensity  
156 only included the total number of second-stage larvae, third-stage larvae and pupae,  
157 following the protocols applied by Hurtrez-Boussès (1996) and Heeb et al. (2000).

158

159 c) Quantification of aromatic plants in non-manipulated nests

160 A hundred nests were sampled to examine the relationship between the total amount of  
161 aromatic plants and blow fly infestation intensity at day 14-15 post-hatching (Muro-  
162 deciduous: 2005, 35 nests and 2006: 25 nests; Muro-evergreen: 2005, 25 nests and 2006,  
163 15 nests). To avoid damages to plant fragments caused by e.g. mites or micro-organisms  
164 before sampling of aromatic plant fragments, all nests were microwave-disinfected after  
165 blow fly quantification. During sampling, aromatic plant fragments were separated from  
166 the rest of the nest material, stored in paper bags and allowed to dry at ambient  
167 temperature for several weeks. Dried samples were weighed with a precision balance  
168 (Acculab Pocket Pro C/50) to the nearest 0.002g to obtain the total dry mass of aromatic  
169 plants per nest.

170 Aromatic plant fragments were easily identified using morphological  
171 characteristics that clearly differed from moss and twigs. A herbarium of local plants  
172 identified by a botanical specialist was also used as reference.

173

174 d) Experimental protocol

175 In Pirio 2005, two experimental groups of 21 nests were monitored. In nests randomly  
176 assigned to a "treated" group, we added 1g of fresh leaves of two locally abundant  
177 aromatic plants often found in nests (0.5g of *Lavandula stoechas* and 0.5g of  
178 *Helichrysum italicum*), first 3 days before hatching, then daily from day 2-3 post-  
179 hatching until day 14-15 post-hatching. Before adding fresh aromatic plants, we  
180 carefully removed all detectable aromatic plant fragments added by female blue tits or by  
181 the experimenter during previous days. Therefore the quantity of fresh plant fragments in

182 nests remained constant through time and across nests. Nests assigned to the "control"  
183 group received the same treatment as treated nests, but fresh moss (1g) was added instead  
184 of aromatic plants. After drying, 1g of the aromatic plants used in this experiment  
185 weighed approximately 0.3g, which is within the natural range of fresh aromatic plant  
186 fragments daily added in nests by Corsican blue tits (0.03 - 0.31g dry mass per nest per  
187 day, A. Mennerat unpub. data.). Nests were collected at day 14-15 post-hatching, when  
188 chicks were measured and blow fly infestation intensity was quantified as described  
189 before. The two groups did not differ in egg laying date (mean  $\pm$  SD, treated nests:  
190 65.95 $\pm$ 2.31, control nests: 65.19 $\pm$ 2.58; t-test, d.f.=40, t=-1.01, P=0.32) and clutch size  
191 (mean  $\pm$  SD, treated nests: 7.19 $\pm$ 0.81, control nests: 7.43 $\pm$ 1.60; t-test, d.f.=40, t=0.61 ,  
192 P=0.55 ), so we assume we controlled for aspects related to the quality of the parents or  
193 the territory.

194

195 e) Statistical analyses

196 Blow fly infestation intensity was square-root transformed prior to analyses. The  
197 relation between blow fly infestation intensity and amount of aromatic plants in non-  
198 manipulated nests was investigated using a generalised linear model (type 3 'GLM'  
199 procedure, SAS 9.1, SAS Institute Inc.). We included year and habitat type (deciduous vs  
200 evergreen) as fixed factors and brood size as covariate in the model because they may  
201 influence blow fly infestation intensity (Hurtrez-Boussès et al. 1999). We also tested for  
202 the interaction between year and amount of aromatic plants because the relation between  
203 aromatic plants and blow fly infestation may vary according to yearly environmental  
204 fluctuations. A mixed-effects model was also performed with year as a random factor,

205 habitat type (deciduous vs evergreen) as a fixed factor and brood size as a covariate  
206 ('MIXED' procedure, SAS 9.1, SAS Institute Inc.). Since the results of both MIXED and  
207 GLM procedure were approximately the same, we will only present the results from the  
208 GLM analysis, which allows testing for the interaction between year and aromatic plants.

209 To investigate whether adding aromatic plants had an effect on blow fly  
210 infestation and nestling survival, blow fly infestation intensity and brood size at days 14-  
211 15 post-hatching in the two experimental groups were compared with t-tests. As nestling  
212 mass at days 9-11 post-hatching and nestling wing length at days 14-15 post-hatching  
213 were positively correlated with chick age (d.f.=1,  $t=19.6$ ,  $P<10^{-4}$  and d.f.=1,  $t=20.89$ ,  
214  $P<10^{-4}$  respectively), we considered residuals of the regression of both variables against  
215 chick age as corrected variables. We used the first axis of a Principal Component  
216 Analysis (PCA) from the correlation matrix of the three measurements of nestling mass,  
217 tarsus length and wing length (corrected for age) as an estimate of nestling body  
218 condition at day 14-15 post-hatching. The first axis ('PC1') accounted for 53% of the  
219 total variance. We investigated the effects of treatment, brood size and blow fly  
220 infestation intensity on nestling corrected mass at days 9-11, nestling size (PC1) and  
221 nestling hematocrit with mixed-effects models considering chick as statistical unit and  
222 nest as random factor ('MIXED' procedure, SAS 9.1, SAS Institute Inc.). The interaction  
223 between treatment and blow fly infestation intensity was also included because effects of  
224 treatment may be more pronounced under high infestation intensities.

225

226 Results

227 Blow fly infestation intensity was not significantly related to the total dry mass of

228 aromatic plant fragments found in non-manipulated nests (d.f.=1, F=1.90, P=0.41,  
229 Figure1). In addition, it was not significantly related to the interaction between year and  
230 the total dry mass of aromatic plant fragments (d.f.=1, F=0.99, P=0.32), nor to habitat  
231 type (d.f.=1, F=0.16, P=0.69). However, nests with larger broods contained more blow  
232 fly larvae (d.f.=1, F=13.85, P<0.001) and blow fly infestation intensity tended to be  
233 higher in 2006 than in 2005 (mean  $\pm$  SD, 2005: 35.9 $\pm$ 26.34; 2006: 44.39 $\pm$ 27.84; d.f.=1,  
234 F=3.55, P=0.06, Table 1).

235 Experimentally adding aromatic plants in nests did not affect blow fly infestation  
236 intensity: treated and control groups did not significantly differ in blow fly infestation  
237 intensity (mean  $\pm$  SD number of blow fly larvae, treated nests: 64.00 $\pm$ 36.29, control  
238 nests: 55.67 $\pm$ 31.11; t-test on square-root transformed numbers: d.f.=40, t=-0.64, P=0.53;  
239 Figure2). Adding aromatic plants did not either affect nestling survival: brood size did  
240 not differ between treated and control nests (mean  $\pm$  SD, treated nests: 6.51 $\pm$ 1.20, control  
241 nests: 6.24 $\pm$ 1.23; t-test: d.f.=40, t=-0.74, P=0.46).

242 Adding aromatic plants in nests did not affect nestling mass at days 9-11 post-  
243 hatching (corrected for chick age), nestling body condition or nestling hematocrit at days  
244 14-15 post-hatching. None of the three response variables was significantly related to  
245 experimental treatment, nor to its interaction with blow fly infestation intensity (Table2).

246 Nestlings at days 9-11 post-hatching were heavier in smaller broods (d.f.=1,  
247 F=6.99, P<0.01), whereas nestling hematocrit was lower in nests with more blow fly  
248 larvae (d.f.=1, F=10.24, P<0.01) and higher in larger broods (d.f.=1, F=10.24, P<0.01,  
249 see Table2).

250

251 Discussion

252 We initially hypothesized that aromatic plant fragments in blue tits nests could  
253 alter nestling detection capacities in adult blow flies, repel adults or larvae, or contain  
254 compounds toxic for adults and/or larvae (e.g. Lambrechts and Dos Santos 2000, Lafuma  
255 et al. 2001). Because blow flies were exposed to aromatic plants at the time when they  
256 lay eggs in blue tit nests, we predicted lower numbers of blow fly larvae in our aromatic-  
257 treated nests, which was not the case. In addition, our two-year study involving one  
258 hundred sampled nests did not reveal any significant correlation between the total dry  
259 mass of aromatic plant fragments and blow fly infestation intensities across blue tit nests  
260 in two oak habitat types. We therefore conclude that the aromatic plant fragments  
261 sampled and used in our experiment have no anti-blow fly effects and therefore could not  
262 protect chicks against blow fly attack. This is also supported by our analyses that chick  
263 traits influenced by blow fly attack (e.g. nestling hematocrit, see Introduction), were not  
264 related to the amount of aromatic plant fragments added in the nest.

265 Although we are confident that the aromatic plants sampled do not protect blue tit  
266 chicks against blow fly attack, significant correlations between the aromatic plants and  
267 offspring characteristics or breeding success may have been masked by unidentified  
268 confounding variables, the particular environmental conditions during the study, or the  
269 offspring traits investigated. For instance, inconsistent with former investigations in the  
270 same study population, we did not find a significant relationship between blow fly  
271 infestation intensity and chick size or mass, perhaps because our study was carried out  
272 under highly favourable environmental conditions (own observations, see also Thomas et  
273 al. 2007). Gwinner et al. (2000) found that the positive effect of green nesting material

274 on nestling body mass was greater in highly mite-infested nests. Gwinner and Berger  
275 (2005) also found that the positive effect of herbs on nestling body mass was particularly  
276 revealed under unfavourable conditions (high mite load, low ambient temperature,  
277 prolonged rainfall). Also, aromatic plants may have positive effects on post-fledging  
278 survival that we were not able to estimate with our measures of nestling condition, e.g.  
279 via repellent effects on blood-sucking flying insects that can be vectors of avian  
280 endoparasites (Lafuma et al. 2001), or anti-bacterial effects reducing the risk of pathogen  
281 infection of nestlings (Rossi et al. 2007). More work on potential ectoparasites other than  
282 *Protocalliphora* blow flies is therefore required to better understand ectoparasite-  
283 aromatic plant interactions in blue tit nests, their underlying mechanisms and their  
284 potential consequences on chick survival in wild populations.

285

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293

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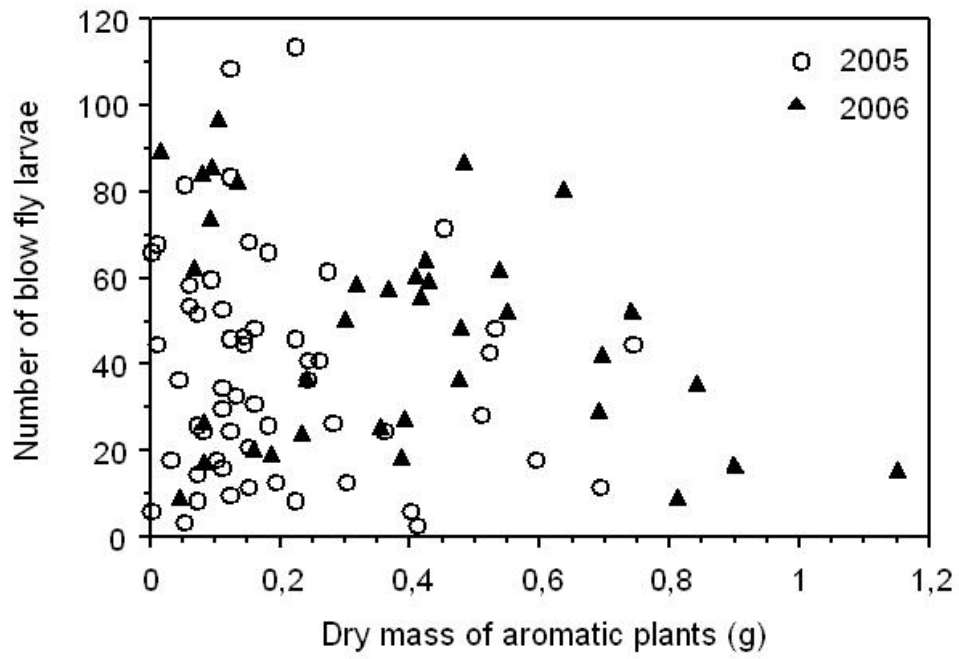
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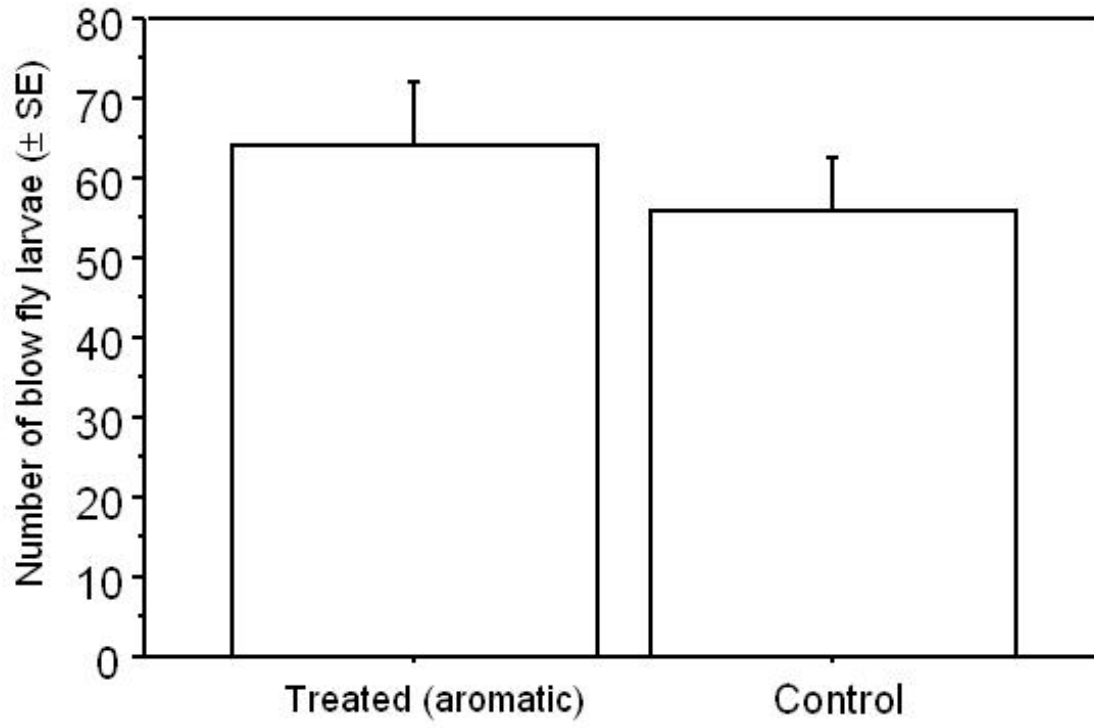
414 Figure 1. Number of blow fly larvae plotted against dry mass of aromatic plants in nests  
415 (N=100 nests).

416 (Figure 1)



417 Figure 2. Number of blow fly larvae ( $\pm$ SE) in control vs aromatic-treated nests. (t-test:  
418 d.f.=40,  $t=-0.64$ ,  $P=0.53$ , see Results).

419 (Figure 2)



420 Table 1. Relation between (square-root transformed) blow fly infestation intensity and  
421 total dry mass of aromatic plants, brood size, habitat type, year and the interaction  
422 between year and total dry mass of aromatic plants, as tested by a type 3 GLM (see  
423 Methods).

424 (Table 1)

Blow fly infestation intensity			
	d.f.	F	P
Aromatic plants	1	1.90	0.41
Brood size	1	13.85	<0.001
Habitat type	1	0.16	0.69
Year	1	3.55	0.06
Year*Aromatic plants	1	0.99	0.32

425

426 Table 2. Effects of experimental treatment (aromatic vs control nests), blow fly  
427 infestation intensity, brood size and the treatment\*infestation intensity interaction on  
428 nestling mass at days 9-11 post-hatching ('Mass1', corrected for age), nestling body  
429 condition ('PC1') and nestling hematocrit, as tested by mixed-effects models with nest as  
430 random factor (see Methods).

431 (Table 2)

	<b>Mass1</b>			<b>PC1</b>			<b>Hematocrit</b>		
	<b>d.f.</b>	<b>F</b>	<b>P</b>	<b>d.f.</b>	<b>F</b>	<b>P</b>	<b>d.f.</b>	<b>F</b>	<b>P</b>
<i>Nest</i>	36	2.86	<10 <sup>-4</sup>	34	5.13	<10 <sup>-4</sup>	32	4.08	<10 <sup>-4</sup>
<i>Treatment</i>	1	0.01	0.92	1	1.27	0.26	1	2.27	0.13
<i>Blow fly infestation intensity</i>	1	0.37	0.55	1	0.05	0.82	1	10.24	<0.01
<i>Brood size</i>	1	6.99	<0.01	1	0.72	0.40	1	10.24	<0.01
<i>Treatment*Blow fly infestation intensity</i>	1	0.38	0.54	1	1.57	0.21	1	1.04	0.31

432