1 **Honeybees optimize their foraging behaviour in relation to spatio-temporal**
2 **changes in nectar and pollen availability**

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15 Short title: Spatio-temporal changes in honeybee foraging

16 **Abstract**

17 Intensified agriculture increasingly threatens wild and managed bees by promoting
18 landscape uniformity and reducing floral resource availability whereas urban areas can
19 provide continuous floral resources within green spaces and private gardens. Mass-
20 flowering events of crops and trees, such as lime trees (*Tilia* spp.), can provide ample
21 floral resources but only for short time periods. Using waggle dance decoding, pollen
22 analysis and bee abundance recordings, we investigated the temporal shift in honeybee
23 foraging behaviour in response to lime tree mass-flowering. Honeybees in urban areas
24 extended their foraging range during lime tree flowering. Foraging behaviour of
25 honeybees in rural areas did not change to such an extent and honeybees foraged in
26 sown flower strips. Our results suggest that honeybees optimize their foraging
27 behaviour to exploit highly rewarding resources instead of extending foraging ranges in
28 times of floral resource scarcity.

29

30 *Apis mellifera* / waggle dance / pollen analysis / flower strips / lime trees

31

32 **1. Introduction**

33 Bees are increasingly threatened by a variety of stressors such as parasites, pesticides,
34 habitat loss and food scarcity resulting in declined bee abundance and bee species
35 diversity (Brown and Paxton 2009; Goulson et al. 2015; Cariveau and Winfree 2015).
36 As bees are important pollinators of agricultural crops, threats to bees can put
37 agricultural yields and global food security at risk (Potts et al. 2010; Garibaldi et al.
38 2013). Bee declines are particularly apparent in areas with intensive agriculture which
39 are typically uniformly structured, do not constantly provide flowering plants

40 throughout the entire season and contain large proportions of non-entomophilous crops
 41 (Steffan-Dewenter and Kuhn 2003; Kovács-Hostyánszki et al. 2017). Urban areas, in
 42 contrast, provide temporarily constant flower resources and higher flower diversity (e.g.
 43 in green spaces and private gardens), resulting in higher bee abundance and bee species
 44 diversity (Theodorou et al. 2016; Martins et al. 2017). Temporary floral resource
 45 scarcity in rural areas might especially be costly for agricultural production as
 46 continuous resource availability is crucial to support pollinators, and hence the delivery
 47 of ecosystem services (Schellhorn et al. 2015). Low floral resource availability has been
 48 shown to negatively affect size and health of colonies of the European honeybee (*Apis*
 49 *mellifera* L.), the most important pollinator worldwide, making them more prone to
 50 damages by the parasitic mite *Varroa destructor* Anderson & Trueman (Brodschneider
 51 and Crailsheim 2010; Requier et al. 2017; Wintermantel et al. 2019).

52 Resources are not only variable in space and time, but also differently used by bees
 53 depending on functional traits. Accordingly, bees can be grouped into honeybees,
 54 bumblebees and other wild bees (from here on referred to as wild bees; Rollin et al.
 55 2013). Wild bees comprise mainly solitary species, use locally available flower
 56 resources in semi-natural habitats (SNH) and some species are specialized to feed on
 57 particular plant families, genera or species (Michener 2000; Rollin et al. 2013).

58 Bumblebees form independently-founded annual colonies composed of 70 to 1800
 59 individuals (Cueva del Castillo et al. 2015) and use both locally available resources in
 60 SNH and highly rewarding resources, such as agricultural crops or flower strips
 61 (Westphal et al. 2006a; Rollin et al. 2013). Most bumblebee species forage on a vast
 62 variety of flower species. Their foraging distances can reach up to 3000 m (Westphal et
 63 al. 2006b; Wolf and Moritz 2008) and foraging behaviour is adapted to spatio-temporal

64 availability of floral resources (Westphal et al. 2006a). Honeybees live in colonies of
65 several thousand individuals with queens that reproduce over multiple seasons and
66 hibernate as a colony. They mostly forage for highly rewarding resources and due to
67 their complex social organization foraging sites can be communicated to nestmates
68 (Rollin et al. 2013; Sponsler et al. 2017). Foraging distances of honeybees are often
69 below 1000 m, but in extreme cases foraging distances can reach up to 14 km (Visscher
70 and Seeley 1982; Beekman and Ratnieks 2000; Couvillon et al. 2014; Danner et al.
71 2016; Balfour and Ratnieks 2017; Danner et al. 2017; Bänsch et al. 2020).

72 If floral resources are locally scarce honeybees uphold the required food quality and
73 quantity by increasing their foraging range (Steffan-Dewenter and Kuhn 2003; Danner
74 et al. 2016; Danner et al. 2017; Bänsch et al. 2020). After mass-flowering events of
75 agricultural crops (such as oil seed rape or sunflowers) honeybees in rural landscapes
76 switch to flower resources in SNH or to agricultural weeds (Rollin et al. 2013; Requier
77 et al. 2015; Sponsler et al. 2017). Pollen resource use by honeybees can be inferred
78 from pollen load analysis and nectar resource use from honey stomach analysis of
79 returning foragers (Garbuzov et al. 2015; Danner et al. 2016; Balfour and Ratnieks
80 2017; Marzinzig et al. 2018; Bänsch et al. 2020).

81 Honeybees communicate the distance and direction to a rewarding foraging site to their
82 nestmates with a waggle dance which is performed by returning foragers (von Frisch
83 1967; Couvillon 2012). Waggle dance decoding can be used to detect foraging habitats
84 of honeybees, however identifying exact foraging locations is impossible (Schürch et al.
85 2013; Balfour et al. 2015; Balfour and Ratnieks 2017; Bänsch et al. 2020).

86 Here we investigate the spatio-temporal changes of honeybee foraging behaviour in
87 rural and urban landscapes in response to lime tree (*Tilia* spp. L.) mass-flowering. We

88 inferred honeybee foraging habitats from waggle dance decoding and analysed resource
89 use by pollen analysis. Additionally, we determined abundances of honeybees,
90 bumblebees and wild bees in foraging habitats. We addressed the following hypotheses:
91 (1) According to their foraging strategies honeybees, bumblebees and wild bees exploit
92 different foraging habitats. (2) Mass-flowering trees and sown flower strips are the most
93 important foraging resources for honeybees in urban and rural areas, respectively. (3)
94 Honeybees tend to exploit highly rewarding resources and adapt their foraging distances
95 to spatial and temporal variation in relation to the availability of floral resources in
96 different foraging habitats.

97

98 **2. Material and Methods**

99 *Experimental design*

100 We positioned two honeybee observation hives each in an urban landscape (41% urban
101 area within 1 km radius) of Göttingen (Lower Saxony, Germany) and in a rural
102 landscape (94% arable field within 1 km radius) south of the city. Each observation hive
103 had two frames positioned above each other and consisted of approximately 2000
104 worker bees and one queen bee (Supplement Fig. 1). In the field we mapped the most
105 dominant land use types and potential bee foraging habitats within a radius of 1 km
106 around the locations of the hives using QGIS 3.12.3 and classified them as arable field,
107 sown flower strip (mostly *Phacelia tanacetifolia* Benth.), SNH (including forests,
108 extensively used grasslands and botanical gardens) and urban area (including built-up
109 areas, roads, green spaces and private gardens). Additionally, we mapped aggregations
110 of more than two lime trees.

111

112 *Waggle dance decoding*

113 During June and July 2018, we recorded honeybee waggle dances of returning foragers
 114 over a period of four weeks resulting in four record days per hive of which two were
 115 during and two after lime tree flowering. Records were taken at random times of the day
 116 under similar weather conditions with temperatures above 15°C, no rain and little wind.
 117 Video recordings of the bee activity in the hives lasted for 30 minutes and were
 118 conducted using a camcorder (Sony HDR CX240E). We decoded all waggle dances of
 119 nectar and pollen foragers with four or more circuits following the protocol from
 120 Couvillon et al. (2012). If dances consisted of more than four circuits, we decoded four
 121 consecutive circuits in the middle of the dance leaving out the first and last circuit. The
 122 angle of the dance was measured in relation to a vertical line to the ground. The
 123 direction of the dance can be decoded by adding the angle of the dance to the vertical
 124 line to the azimuth of the sun at the time of the dance. From the four decoded circuits,
 125 we calculated the mean duration and the mean direction of the waggles. All dances
 126 which aimed at foraging sites closer than 100 m were considered to be local dances and
 127 the distance to the foraging site was set to 100 m as waggle dance decoding can be
 128 erroneous for such dances (Schürch et al. 2013).

129

130 *Foraging habitats in urban and rural areas*

131 On each observation date, we decoded the first observed dance per hive in the field. We
 132 estimated the distance and direction to the foraging location and chose a flower-rich
 133 habitat which presumably was the foraging site of the dancing honeybee. Within those
 134 habitats we conducted 5 min standardized transect walks during which we counted
 135 honeybees, bumblebees and wild bees and classified the habitats as sown flower strip,

136 SNH (transects in hedgerows and field margins) or urban area (transects in green spaces
137 and gardens). After decoding all waggle dances, we descriptively analysed the spatial
138 distribution of foraging habitats within the area around the hives in which we had
139 mapped land use.

140

141 *Pollen analysis*

142 During lime tree flowering we sampled three honeybees with pollen loads and three
143 honeybees without pollen loads from each hive assuming them to be pollen and nectar
144 foragers, respectively. Overall, we obtained pollen loads from the legs of twelve pollen-
145 collecting honeybees and pollen from the honey stomachs of twelve nectar-collecting
146 honeybees. We identified the amount of lime tree and *P. tanacetifolia* pollen within
147 approximately 200 pollen grains per sampled honeybee. If less than 200 pollen grains
148 were present in the sample, we identified lime tree and *P. tanacetifolia* amount among
149 all pollen grains. *P. tanacetifolia* was the main flowering plant in flower strips and does
150 not grow naturally in the study area. As the number of pollen grains counted differed
151 between samples of foraging honeybees, we first calculated the proportion of lime tree
152 and *P. tanacetifolia* pollen grains within samples from individual honeybees.
153 Subsequently, we calculated the mean proportion of lime tree and *P. tanacetifolia*
154 pollen from pollen loads and from honey stomachs each from the urban and the rural
155 landscape.

156

157 *Data analysis*

158 We compared abundances of the three functional bee groups (bumblebee, honeybee,
159 wild bee) in different transect habitats (flower strip, SNH, urban area) using generalized

160 linear mixed models (GLMM) with a gaussian distribution and square-root-transformed
161 response variable to satisfy model assumptions using the function *glmmTMB* from the R
162 package ‘glmmTMB’ (Brooks et al. 2017). Landscape (urban, rural) and a transect
163 identifier were included as nested random term.

164 We analysed foraging distances in the different landscapes (urban, rural) during and
165 after lime tree flowering with linear mixed-effects models (LME) with the function *lme*
166 from the R package ‘nlme’ (Pinheiro et al. 2018). As we conducted repeated
167 observations on the same hives, a hive and record identifier were included as nested
168 random term.

169 For both models, we performed Tukey’s pairwise post-hoc test with a significance level
170 of 0.05 using the function *emmeans* from the R package ‘emmeans’ (Lenth 2018). All
171 statistics were performed in R 3.5.0 (R Core Team 2018).

172

173 **3. Results**

174 *Bee abundance in foraging habitats*

175 In total, we conducted transects in seven flower strips (FS), in five SNH and in four
176 urban areas (UA) and recorded 837 bumblebees (B), 654 honeybees (H) and 53 wild
177 bees (W). Bumblebee and honeybee abundances in flower strips were significantly
178 higher than wild bee abundance in any habitat type and higher than bumblebee and
179 honeybee abundances in SNH and urban areas (mean abundance $\pm$ SE; FS: B $101.1 \pm$
180 19.0 , H 77.7 ± 11.3 , W 2.3 ± 1.2 ; SNH: B 15.6 ± 4.9 , H 9.2 ± 4.0 , W 5.0 ± 2.2 ; UA: B
181 12.8 ± 4.3 , H 16.0 ± 5.8 , W 3.0 ± 1.8 ; GLMM results in Table I; pairwise comparisons
182 in Supplement Table I; Fig. 1).

183

184 *Waggle dance decoding*

185 In total, we decoded 165 waggle dances with a mean foraging distance of 387.5 m ($\pm$
186 27.0 SE). We retrieved 92 dances from the hives in the rural landscape with a mean
187 foraging distance of 325.4 m ($\pm$ 32.4 SE) and 73 dances from the hives in the urban
188 landscape with a mean foraging distance of 465.8 m ($\pm$ 43.8 SE). In the urban landscape
189 foraging distances during lime tree flowering were significantly higher than foraging
190 distances after lime tree flowering (mean foraging distance [m] $\pm$ SE: during 601.2 $\pm$
191 57.6; after 260.4 $\pm$ 46.7). In the rural landscape foraging distances did not differ
192 significantly during and after lime tree flowering (mean foraging distance [m] $\pm$ SE:
193 during 269.3 $\pm$ 32.6; after 364.8 $\pm$ 49.9; LME results in Table II; pairwise comparisons
194 in Supplement Table II; Fig. 2).

195

196 *Spatio-temporal variation in honeybee foraging habitats*

197 Returning foragers mostly danced for foraging sites within a 1 km radius around the
198 hives (urban: 7 of 73 dances, rural 5 of 92 dances outside of 1 km radius). In both the
199 urban and the rural landscape foraging sites tended to be west of the hives during lime
200 tree flowering. After lime tree flowering foraging sites were more evenly distributed in
201 both landscapes. (Fig. 3).

202

203 *Pollen composition of pollen and nectar foragers*

204 Overall, we counted 4136 pollen grains from 24 returning foragers during lime tree
205 flowering (mean 199.6 pollen per pollen forager $\pm$ 0.4 SE; mean 145.1 pollen per nectar
206 forager $\pm$ 22.5 SE). In the urban landscape 45.2% of the pollen of nectar-collecting
207 honeybees came from lime trees and no pollen came from *P. tanacetifolia*. Pollen loads

208 of pollen-collecting honeybees in the urban landscape were composed of 8.8% lime tree
209 and 12.3% *P. tanacetifolia* pollen. In the rural landscape pollen of nectar-collecting
210 honeybees was composed of 21.1% lime tree and 12.8% *P. tanacetifolia* pollen. Of the
211 pollen of pollen-collecting honeybees in the rural landscape 10.8% came from lime
212 trees and 53.0% came from *P. tanacetifolia* (Fig. 4).

213

214 **4. Discussion**

215 Based on the combined analysis of bee abundance recordings, waggle dance decoding
216 and analyses of pollen collected by nectar and pollen foragers, we demonstrate that
217 foraging behaviour of honeybees depends on the spatio-temporal availability of highly
218 rewarding resources. Our results furthermore indicate the relevance of lime trees as a
219 nectar source in urban areas and *P. tanacetifolia* as a pollen source in rural areas.

220 Extended honeybee foraging ranges during lime tree flowering and large proportions of
221 lime tree pollen in honey stomachs from nectar foragers in urban areas suggest that
222 honeybees specifically adapt their foraging behaviour to exploit lime tree floral
223 resources during this mass-flowering event. During lime tree flowering honeybees
224 mainly foraged in the urban area west of the hives with aggregations of lime trees.
225 Fewer foraging flights might have been directed at the lime trees east of the hives
226 because those trees were smaller and might have provided less nectar than larger lime
227 trees in the east of the hives (Kreider and Nehrkorn, pers. obs.). In rural areas, in
228 contrast, foraging behaviour of honeybees was not affected by lime tree flowering to
229 such an extent as in urban areas. Instead many foraging flights were directed at sown
230 flower strips south-east of the hives which is mirrored in large proportions of pollen
231 obtained from *P. tanacetifolia* by pollen foragers.

232 In contrast to previous studies (Steffan-Dewenter and Kuhn 2003; Danner et al. 2016;
233 Danner et al. 2017; Bänisch et al. 2020) we found that honeybees did not extend their
234 foraging range in response to floral resource scarcity but extended their foraging range
235 to exploit a highly rewarding resource. This optimization of foraging behaviour in
236 response to the availability of highly rewarding resources implies a trade-off between
237 the distance travelled to a foraging site and the reward that is expected from the
238 resource. This trade-off can be influenced by social organisation and communication of
239 foraging sites if such decreases the energetic costs of foraging, i.e. the time spent
240 searching for food (Cresswell et al. 2000; Lihoreau et al. 2011).

241 Plantation of lime trees in urban areas could effectively contribute to providing constant
242 food supply for honeybees during summer. The extensive use of flower strips by
243 honeybees and bumblebees in the rural landscape highlights that flower strips are an
244 important flower substitute in otherwise flower poor agroecosystems. Especially,
245 generalist bumblebees, such as *Bombus terrestris* L., can benefit from highly rewarding
246 flower strips within their foraging range (Westphal et al. 2006a). However, our
247 abundance counts of wild bees also indicate that wild bees barely benefit from flower
248 strips as many wild bee species rely on particular plant species which typically do not
249 occur in sown flower strips (Rollin et al. 2013). Consequently, different actions than
250 only sowing flower strips need to be taken to conserve wild bees and protect the
251 ecosystem services they provide than for the conservation of honeybees and
252 bumblebees. These conservation actions include the preservation of SNH in rural areas
253 and of flower-diverse garden habitats in urban areas which typically contain relatively
254 high wild bee abundance and species diversity (Rollin et al. 2013; Martins et al. 2017),
255 as well as the restoration of flower diversity in agroecosystems (Winfree 2010).

256 Nevertheless, flowering trees, such as *Tilia* spp., *Acer* spp. L., *Robinia pseudoacacia* L.
 257 or *Aesculus hippocastanum* L. can play important roles for the provisioning of nectar
 258 and pollen to honeybees, bumblebees and some wild bee species in both rural and urban
 259 areas (Kämper et al. 2016).
 260 During summer mass-flowering trees, such as lime trees, and sown flower strips are the
 261 most important foraging habitats of honeybees in urban and rural areas, respectively.
 262 Honeybees can adapt their foraging behaviour to spatial and temporal variation of floral
 263 resources in different foraging habitats and tend to optimize the exploitation of highly
 264 rewarding resources. In addition, our study shows that honeybees, bumblebees and wild
 265 bees exploit different foraging habitats within their foraging ranges which need to be
 266 restored and managed to conserve diverse wild bee communities and to provide
 267 sufficient floral resources to all managed honeybees, bumblebees and wild bees.

268

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274

275 **Author contributions**

276 CW designed the study. JJK and AN conducted the field recordings, decoded the
 277 waggle dances and determined bee abundances. CK conducted the pollen analysis. JJK
 278 and AN analysed the data with assistance from SB and CW. All authors contributed to
 279 the writing of the manuscript.

280

281 **Competing interests**

282 The authors declare no competing interests.

283

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424

425 **Figure captions**

426 **Table I** Generalized linear mixed model (GLMM) results of square-root-transformed
427 abundance of functional bee groups (bumblebee, honeybee, wild bee) in different
428 transect habitats (flower strip, SNH, urban area). GLMM was fitted with a gaussian
429 distribution. Pairwise comparisons in Supplement Table I.

430

431 **Table II** Linear mixed-effects model (LME) results of foraging distance in the rural and
432 urban landscape during and after lime tree flowering. Pairwise comparisons in
433 Supplement Table II.

434

435 **Fig. 1** Abundance of bumblebees, honeybees and wild bees in flower strips, semi-
436 natural habitats (SNH) and urban areas. Letters over boxplots show differences between
437 groups from Tukey's pairwise post-hoc test ($\alpha = 0.05$). GLMM results in Table I.
438 Pairwise comparisons in Supplement Table I.

439

440 **Fig. 2** Foraging distance of honeybees in rural and urban landscapes during and after
441 lime tree flowering. Letters over boxplots show differences between groups from
442 Tukey's pairwise post-hoc test ($\alpha = 0.05$). LME results in Table II. Pairwise
443 comparisons in Supplement Table II.

444

445 **Fig. 3** Spatial distribution of honeybee foraging habitats. Map shows the location of the
446 hives in Göttingen, Germany. Spherical plots show land use in a 1 km radius around the
447 honeybee hives in the urban and rural landscape, as well as foraging habitats during
448 (open circles) and after (crosses) lime tree flowering. Numbers in the center of the
449 spherical plots show the dances for local foraging sites before / after lime tree
450 flowering.

451

Fig. 4 Proportion of *P. tanacetifolia* and lime tree pollen in honey stomachs of nectar-collecting honeybees and pollen from legs of pollen-collecting honeybees in the rural and urban landscape during lime tree flowering.

Figures and tables

Table I:

	Bee abundance			
	Estimate	SE	z	p
Intercept	9.70	0.59	16.32	<0.001
Honeybee	-1.02	0.84	-1.22	0.223
Wild bee	-8.72	0.84	-10.38	<0.001
SNH	-5.97	0.92	-6.48	<0.001
Urban area	-6.35	0.99	-6.44	<0.001
Honeybee:SNH	0.04	1.30	0.03	0.976
Wild bee:SNH	6.89	1.30	5.29	<0.001
Honeybee:Urban area	1.48	1.39	1.07	0.287
Wild bee:Urban area	6.60	1.39	4.73	<0.001

Table 2:

	Foraging distance [m]			
	Estimate	SE	t	p
Intercept	304.81	59.32	5.14	<0.001
Urban	119.19	86.79	1.37	0.303
Rural:After	69.85	70.26	0.99	0.344
Urban:After	-338.81	103.97	-3.26	0.009

Figure 1:

462

463 Figure 2:

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Figure 3:

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Figure 4:

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