

1 **Title**

2 Discrimination among host tree species by the ambrosia beetle *Platypus*
3 *quercivorus*

4

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29 **Abstract**

30 The ambrosia beetle *Platypus quercivorus* is a vector for the fungus that
31 causes Japanese oak wilt, and susceptibility to infestation by *P. quercivorus*
32 varies by tree species. We postulated that *P. quercivorus* discriminates
33 among host tree species differing in susceptibility to attack. To test this
34 postulate, we counted the number of flying male beetles (NFM), the number
35 of holes bored by male beetles (NH), and the number of flying female
36 beetles (NFF) per unit area of bark surface in three fagaceous tree species:
37 *Quercus crispula* (with high susceptibility to infestation) and *Q. serrata* and
38 *Castanea crenata* (both with low susceptibility). NFM and NH were used to
39 calculate the proportion of male beetles that bored holes out of those that
40 flew to the tree (PBM). We used generalized additive models to predict NFM,
41 NFF, and PBM. The locations of trees, expressed as x and y coordinates,
42 numbers of weeks after the first male beetle's flying (WEEK), diameters of
43 trees 130 cm above ground (DBH), and tree species (SP) were incorporated
44 into the models as candidate explanatory variables. The best-fit models for
45 NFM and NFF included WEEK and DBH and the effect of location; SP was
46 not included in the models. For PBM, the best-fit model included WEEK,
47 DBH, and SP. The results indicate that male *P. quercivorus* prefer *Q.*
48 *crispula* to *Q. serrata* and *C. crenata* and that selection is made before

49 boring holes on trees, but that *P. quercivorus* do not discriminate among host
50 species when they fly to trees.

51

52 **Keywords**

53 *Castanea crenata*, Host selection, Japanese oak wilt, *Quercus crispula*,

54 *Quercus serrata*

55 **Introduction**

56

57 In general, ambrosia and bark beetles use weakened trees as hosts
58 (Wood 1982). Random flight and random landings on trees are thought to
59 reduce beetle fitness in environments with low densities of weakened trees;
60 accordingly, beetles select appropriate hosts through visual or olfactory cues
61 (Byers et al. 2004; Zhang and Schlyter 2004; Pureswaran and Borden 2005;
62 Campbell and Borden 2006). The beetles start to attack healthy trees *en*
63 *masse* when they reach epidemic population sizes (Paine et al. 1997).
64 Subsequently, resource availability for the beetles increases dramatically,
65 especially in forests that are dominated by suitable host tree species. Even
66 during these epidemic phases, beetles need to select hosts carefully in forests
67 with high diversities of tree species, many of which are unsuitable.

68 In Japan, populations of ambrosia beetle *Platypus quercivorus*
69 (Murayama) (Coleoptera: Platypodidae) are considered to have reached
70 epidemic proportions in recent years. As vectors, their attacks on apparently
71 healthy-looking trees lead to Japanese oak wilt (Ito and Yamada 1998;
72 Kobayashi and Ueda 2005). Although they attack several species of
73 Fagaceae, beetle reproductive success varies by tree species (Kato et al.
74 2001; Kobayashi et al. 2004). In brief, forest tree species fall into three types

75 for *P. quercivorus*: suitable Fagaceae, unsuitable Fagaceae, and non-host
76 tree species. In such an environment, we suggest that *P. quercivorus*
77 preferentially selects suitable Fagaceae trees using visual or olfactory cues.
78 Conversely, we postulate that tree species are avoided by *P. quercivorus*
79 when these trees are associated with a reduced level of beetle fitness.

80 Lower *P. quercivorus* preference for particular tree species can be
81 identified by reduced beetle activity in several phases of the infestation
82 process. The infestation process of *P. quercivorus* can be divided into four
83 phases. In phase 1, male beetles fly to a tree; in phase 2, they bore shallow
84 holes in the bark; in phase 3, female beetles fly to the tree; and in phase 4,
85 after mating, male and female beetles construct galleries in the sapwood for
86 reproduction (Soné et al. 1998; Esaki et al. 2004). Previous studies on beetle
87 host selection strongly suggest that *P. quercivorus* avoids unfavorable tree
88 species in the earlier phases of infestation (phases 1–3) (Urano 2000;
89 Yamasaki and Futai 2008). Exclusion of unfavorable trees before landing
90 has been suggested for bark beetles that use conifers as their hosts; they use
91 olfactory cues to distinguish non-host broad-leaved tree species from the
92 correct host tree species (Zhang 2003; Byers et al. 2004; Zhang and Schlyter
93 2004). Moreover, pre-landing exclusion of thinner trees and post-landing
94 exclusion of trees with infection histories (for which there are reduced

95 probabilities of successful beetle reproduction) have been demonstrated in
96 field studies of *P. quercivorus* (Urano 2000; Yamasaki and Futai 2008).

97 When discerning differences in beetle activity among tree species, it is
98 necessary to take into account other variables that affect behavior. Reported
99 effects of host tree size on beetle activity (Akaishi et al. 2006; Yamasaki and
100 Futai 2008) show that it is necessary to compare beetle activity on different
101 tree species within the same size class. However, this is difficult to achieve
102 in a field study. Assuming that there are
103 1 linear relationships between tree size and beetle activity parameters
104 (BAPs); and
105 2 normal distributions in BAPs,
106 analysis of covariance is appropriate for the detection of differences among
107 tree species. Even when the first assumption is satisfied, BAPs may not be
108 normally distributed. In addition, beetle activity fluctuates with time, and the
109 relationship between time and beetle activity is apparently nonlinear (Urano
110 2000; Ueda and Kobayashi 2001b). Moreover, beetle activity may show
111 dramatically high values at particular locations because of the effect of the
112 beetle's aggregation pheromone (Ueda and Kobayashi 2001a; Tokoro et al.
113 2007), and this effect must be taken into consideration. Accordingly, we
114 used a generalized additive model with nonlinear effects of time and location

115 as alternative methods for investigating differences in beetle activities
116 among tree species.

117 Capture of wild *P. quercivorus* with chemical traps is considered an
118 effective method for protecting fagaceous trees. A kairomone is emitted
119 from trees and may affect host selection by *P. quercivorus*, but its chemical
120 nature is as yet unknown. However, the beetle's aggregation pheromone has
121 been identified (Kashiwagi et al. 2006). Unfortunately, a synthetic
122 pheromone failed to capture the beetle effectively (Kamata et al. 2008).
123 Determining differences in beetle activity among tree species will help to
124 clarify ecological relationships, a necessary first step in establishing an
125 effective trapping method for wild beetles. Thus, we investigated how *P.*
126 *quercivorus* activity varies through phases of the infestation processes on
127 three species of Fagaceae differing in susceptibility: *Q. crispula* (high
128 susceptibility), *Q. serrata* (low susceptibility), and *Castanea crenata* (low
129 susceptibility).

130

131 **Materials and methods**

132

133 Study site and tree species

134

135 The study was conducted at Ashiu Forest Research Station in Kyoto,
136 Japan (35°18'N, 135°43'E), where substantial dieback of *Q. crispula* has
137 been underway since 2002. From July to October 2004, we studied
138 infestation patterns of *P. quercivorus* on tree specimens >10 cm in diameter
139 130 cm above ground (DBH). Twenty-two *Q. crispula*, eight *Q. serrata*, and
140 seven *C. crenata* trees were selected for study within a 25 × 25-m plot
141 established on a south-facing slope of a secondary forest, at an altitude of
142 approximately 500 m. The forest was dominated by *Q. crispula*, *Carpinus*
143 *laxiflora*, and *Acer sieboldianum*. DBH, perimeter at 50 cm above the
144 ground, and perimeter at ground height were measured for each tree at the
145 beginning of the study. Setting the southwestern point of the plot as the
146 origin, we also measured the coordinate position of each tree in
147 two-dimensional space.

148

149 Beetle activity in the infestation process

150

151 Numbers of *P. quercivorus* that flew to the trees were determined using
152 sticky paper traps (Kobayashi and Hagita 2000; Ueda and Kobayashi 2001b).
153 Two strips of sticky paper (Kamikiri-hoihoi; Earth Biochemical Co., Ltd.,
154 Tokushima, Japan), each 4 × 50 cm, were attached longitudinally to the
155 upper and lower sides of each tree trunk up to 50 cm above the ground. We
156 enumerated male (NFM) and female (NFF) beetles that flew to the bark of
157 each tree (per 400 cm², i.e., total area of sticky paper attached to each tree)
158 by weekly counts of beetles caught in traps.

159 At the same time, we counted the number of holes (NH) bored by *P.*
160 *quercivorus* on the surface of a trunk (excluding areas covered by traps) up
161 to a height of 50 cm above the ground. Double counting of holes was
162 prevented by marking previously counted holes with colored push-pins. The
163 surface area over which beetle holes were counted was calculated by
164 assuming the shape of the subject surface was trapezoidal.

165 Within natural forests, intense *P. quercivorus* flight activity occurs
166 close to the ground (up to 2.5 m above soil level) (Igeta et al. 2004), and
167 beetle attacks are concentrated on basal parts of trees (Hijii et al. 1991).
168 Because it was difficult to count all beetles that flew to a tree and all holes

169 that they bored, we restricted monitoring of NFM, NFF, and NH to the area
170 up to 50 cm above ground.

171 On 29 May 2005, we examined subject trees and classified those with
172 no leaf flush as dead.

173

174 Model selections

175

176 To discern differences in beetle activity parameters (BAPs) among tree
177 species, we used generalized additive models (GAM) and generalized
178 additive mixed models (GAMM). The best models for predicting BAPs were
179 selected using R 2.11.1 (R Development Core Team 2010). Generally, BAPs
180 fluctuate with time following a unimodal trajectory (Urano 2000; Ueda and
181 Kobayashi 2001b). Thus, we built the nonlinear effect of time into the
182 models predicting BAPs. Linear effects of tree size were also incorporated
183 because BAPs increase with increasing tree size (Akaishi et al. 2006;
184 Yamasaki and Futai 2008). Moreover, we must consider the effect of beetle
185 aggregation caused by the pheromone. This beetle uses an aggregation
186 pheromone to attract conspecifics (Ueda and Kobayashi 2001a; Tokoro et al.
187 2007), and the consequent mass attack by the beetle may conceal primary
188 differences in BAPs among tree species. For instance, BAPs of trees that

189 received mass attacks may be significantly higher than those of lightly
190 attacked trees irrespective of tree species, and low DBH trees with low
191 beetle infection probabilities may have high BAP values when adjacent high
192 DBH trees receive mass attacks. Thus, we regarded the effects of spatial
193 heterogeneity in mass attack, and built them into the model. Taking the
194 effects of these covariates into consideration, we determined whether the
195 “tree species” factor was included in the best models as an explanatory
196 variable for predicting BAPs.

197 To detect differences among tree species in BAPs in phases 1 and 3,
198 NFM and NFF were fitted by GAMMs with log link function under the
199 assumption that these data follow a negative binomial distribution. The
200 candidate explanatory variables were the number of weeks after the first
201 male beetles flew (WEEK), DBH, 2D smoothing effects of location
202 (coordinates of each tree, 2D), and tree species (SP). We assumed a
203 nonlinear effect for WEEK and 2D and a linear effect for DBH and SP. The
204 models were offset by the natural log of the subject surface area of sticky
205 paper (400 cm²). Individual trees were incorporated into the models as a
206 random intercept. The least significant term was removed from the models,
207 and we refitted the models until all terms were significant.

208 To detect differences in BAPs in phase 2, we analyzed the proportion of
209 male beetles that bored holes out of those that flew to the tree (PBM) using

210 the data with NFM > zero. PBM was calculated from the number of holes
211 newly bored by male beetles per subject bark surface area of each tree
212 (AREA, cm²) and the assumed number of flying male beetles per AREA.
213 The latter was calculated by dividing NFM by the subject surface area of
214 sticky paper (400 cm²) and then multiplying it by AREA. PBM was fitted by
215 a GAM with logit link function under the assumption that these data follow a
216 binomial distribution. To deal with the overdispersion of the model, we
217 corrected the standard errors of coefficients by multiplying them by the
218 dispersion parameter. The candidate explanatory variables were WEEK,
219 DBH, and SP. We assumed a nonlinear effect for WEEK and linear effects
220 for DBH and SP. As in the case of the models for NFM and NFF, the least
221 significant term was removed from the model, and we refitted the model
222 until all terms were significant.

223

224 **Results**

225

226 The DBHs of the 37 observed fagaceous trees ranged from 10.4 to 22.2
227 cm for *Q. crispula*, 11.9 to 32.2 cm for *Q. serrata*, and 16.2 to 25.0 cm for *C.*
228 *crenata*. Male beetles were trapped on 31 of these observed trees (Table 1).
229 We found holes bored by beetles and we trapped female beetles on 22 of

230 these 31 trees (Table 1). By the end of the study period, five *Q. crispula* trees
231 and one *C. crenata* tree had died (Table 1). Calculating tree mortality as the
232 proportion of dead to infected trees, mortalities of *Q. crispula*, *Q. serrata*,
233 and *C. crenata* were 38.5% (5/13), 0% (0/3), and 16.7% (1/6), respectively.

234 The host visitation period of *P. quercivorus* for each tree species is
235 shown in Fig. 1. The first visitation of *P. quercivorus* was observed from
236 July to October on *Q. crispula* and from July to August on *Q. serrata* (Fig. 1).
237 In the case of *C. crenata*, the first beetle visitation was observed in July on
238 all trees (Fig. 1). Beetle visitation lasted 1–10 weeks on *Q. crispula*, 1–11
239 weeks on *Q. serrata*, and 1–12 weeks on *C. crenata* (Fig. 1). Among the six
240 dead trees, two *Q. crispula* and one *C. crenata* were visited by *P.*
241 *quercivorus* from July, and the remaining three *Q. crispula* were visited by *P.*
242 *quercivorus* from August (Fig. 1).

243 The total numbers of NFM and NFF per unit area (100 cm²) over the
244 research period are shown in Fig. 2a, b. Generally, the numbers of flying
245 beetles were high on the six dead trees and the trees surrounding them (Fig.
246 2a, b).

247 The best models for predicting NFM and NFF (n = 427 for each model)
248 included the effects of 2D, WEEK, and DBH. The 2D smoothing effects on
249 NFM and NFF are shown in Fig. 2c, d, respectively. Zonations of high

250 values were observed in predicted values of NFM and NFF (Fig. 2c, d), and
251 these areas correspond to the locations of six dead trees (Fig. 2a, b). The
252 estimated degrees of freedom of smoothing term 2D was 21.76 ($p < 0.001$)
253 for NFM and 19.93 ($p < 0.001$) for NFF. Figure 2e, f shows the effects of
254 WEEK and DBH on NFM and NFF, respectively. Predicted NFM and NFF
255 increased with increasing WEEK, peaked at WEEK values of 2 or 3, and
256 then decreased with further increases in WEEK (Fig. 2e, f). The estimated
257 degrees of freedom of smoothing term WEEK was 4.02 ($p < 0.001$) for NFM
258 and 5.78 ($p < 0.001$) for NFF. As shown in previous studies (Kobayashi and
259 Hagita 2000), the peak of NFF was observed a little later than the peak of
260 NFM. We assumed linear effects of DBH on NFM and NFF, and the fitted
261 models demonstrated significant positive effects of DBH on these variables
262 (Fig. 2e, f; the estimated coefficients were 0.31 for NFM and 0.31 for NFF, p
263 < 0.001 for each estimate).

264 With regard to PBM, the best model ($n = 137$) included the effects of
265 WEEK, DBH, and SP. Predicted PBM increased with increasing WEEK,
266 peaked at WEEK = 4, and then remained stable until WEEK = 10 (Fig. 3).
267 The estimated degrees of freedom of smoothing term WEEK was 3.89 ($p =$
268 0.004). The effects of DBH on PBM were positive (the estimated coefficient
269 was 0.11, $p = 0.005$); PBM increased with increasing DBH (Fig. 3). When
270 the coefficient for *Q. crispula* was set to zero, the coefficients estimated for

271 *Q. serrata* (-1.38, $p = 0.002$) and *C. crenata* (-1.60, $p < 0.001$) were both
272 significantly lower than zero, showing significantly lower PBM on *Q.*
273 *serrata* and *C. crenata* than that on *Q. crispula* (Fig. 3).

274

275 **Discussion**

276

277 We monitored the infestation patterns of *P. quercivorus* on 22 *Q.*
278 *crispula*, eight *Q. serrata*, and seven *C. crenata* trees in a secondary forest.
279 The mortality rate of selected *Q. crispula* individuals (38.5%, Table 1) was
280 higher than that of *C. crenata* (16.7%, Table 1) and *Q. serrata* (0%; Table 1).
281 This rank order of susceptibility has been reported previously (Shiomi and
282 Osaki 1997; Inoue et al. 2000; Kobayashi and Hagita 2000; Kobayashi and
283 Shibata 2001; Kobayashi and Ueda 2001; Kamata et al. 2002). Where tree
284 species of different degrees of susceptibility coexist, inappropriate host
285 selection by *P. quercivorus* may result in poor reproduction and, hence,
286 reduced fitness. Thus, we postulated that *P. quercivorus* has a reduced
287 preference for fagaceous trees with low susceptibility. We tested *P.*
288 *quercivorus* preferences by measuring BAPs on different host tree species.
289 The results of model selections predicting these measures of activity partly
290 supported our postulate.

291 First, we examined spatial heterogeneity in NFM and NFF. A previous
292 study conducted in a natural mixed forest dominated by *Cryptomeria*
293 *japonica* suggested that *P. quercivorus* first flies to clusters of *Q. crispula*,
294 not to individual trees (Yamasaki and Sakimoto 2009). This implies that
295 investigations of beetle activity should take into account the effects of
296 neighboring trees. For example, in a phase of mass attack by *P. quercivorus*,
297 trees adjacent to target trees may be severely affected irrespective of their
298 suitability as hosts for the beetle. Moreover, mass attack itself may conceal
299 primary differences in the beetle's preference among tree species. Thus, we
300 used GAMMs in which geographical locations of trees were fitted using
301 splines as trend surfaces, and the patterns of spatial heterogeneity in NFM
302 and NFF (Fig. 2a, b) were well reproduced by the predicted surfaces of the
303 models (Fig. 2c, d).

304 Second, the measured values of NFM and NFF were assumed to
305 fluctuate with time. The values predicted by GAMMs indicated changes in
306 NFM and NFF with time (Fig. 2e, f), and the unimodal patterns of changes
307 were in accord with previous studies (Urano 2000; Ueda and Kobayashi
308 2001b).

309 Third, effects of tree size were detected for NFM and NFF (Fig. 2e, f).
310 Increases in NFM and NFF with increasing DBH corroborate previous
311 studies (Akaishi et al. 2006; Yamasaki and Futai 2008).

312 When applying the model to NFM and NFF, we ignored the effect of
313 the initiation time of visitation by *P. quercivorus*. Because the numbers of
314 flying beetles in a forest fluctuate with time, differences in the initiation time
315 of beetle visitation among tree species may cause differences in the numbers
316 of flying beetles. In this study, however, there were no clear differences in
317 the initiation time of beetle visitation among the three tree species (Fig. 1).

318 Consequently, the best models for predicting NFM and NFF included
319 the effects of location, time, and tree size. Further inclusion of the effect of
320 tree species did not improve the fitness of the model, which suggested that
321 beetles' flying activity did not differ among host tree species. Thus, the
322 hypothesis that *P. quercivorus* discriminates among host tree species in
323 phases 1 and 3 when flying to trees was rejected.

324 PBM was analyzed to detect differences among host tree species in
325 beetle activity during phase 2, and the results supported our hypothesis. In
326 addition to temporal fluctuations in beetle activity and the effect of tree size,
327 the effect of tree species was detected; the proportions of male beetles that
328 bored holes out of those that had flown to trees were lower for *Q. serrata* and
329 *C. crenata* than for *Q. crispula* (Fig. 3). The same tendency has been
330 reported for *Q. salicina*, which has lower susceptibility to *P. quercivorus*
331 infestation (Yamasaki et al. 2007).

332 We have shown that in the early stages of infestation, *P. quercivorus*
333 has a lower preference for unsuitable host tree species. Male *P. quercivorus*
334 prefer *Q. crispula* to *Q. serrata* and *C. crenata*, and selection is made before
335 boring holes in trees. Discrimination of unsuitable trees within the same
336 species has been demonstrated previously; *P. quercivorus* distinguishes
337 suitable *Q. crispula* trees from unsuitable *Q. crispula* at early stages of
338 infestation (Yamasaki and Futai 2008). Differences in beetle activity both
339 among and within tree species suggest that selective forces have acted on *P.*
340 *quercivorus* during its long co-evolution with the host species, and these
341 forces have led to beetle avoidance of unfavorable host trees. Some
342 proximate factor, for example, a volatile emission from trees, must have
343 been used by *P. quercivorus* to discriminate suitable from unsuitable host
344 tree species. Identification of this factor awaits further studies, which will
345 contribute to the protection of forests dominated by fagaceous trees, the
346 hosts of *P. quercivorus*.

347

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349

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476

477

478

479 **Table 1.** Numbers of trees observed, trees on which male *Platypus*
 480 *quercivorus* were trapped, trees on which beetle holes were observed, trees
 481 on which female beetles were trapped, and dead trees.

482

	Observed trees	With male beetles	With beetle holes	With female beetles	Dead
<i>Q. crispula</i>	22	18	13	13	5
<i>Q. serrata</i>	8	6	3	3	0
<i>C. crenata</i>	7	7	6	6	1

483

484 Data are for *Quercus crispula*, *Q. serrata*, and *Castanea crenata*.

485 **Figure legends**

486

487 **Fig. 1.** Host visitation period of *Platypus quercivorus* for 18 *Quercus*
488 *crispula*, 6 *Q. serrata*, and 7 *Castanea crenata* individuals. Circles
489 connected by a solid line show the first and last days of beetle visitation.
490 Gray circles and lines show data for surviving trees. Black circles and lines
491 show data for dead trees.

492

493 **Fig. 2.** Numbers of flying male (**a**) and female (**b**) beetles per 100 cm² of
494 bark surface (NFM and NFF) for 37 subject trees over the research period.
495 The location of each tree is plotted in two-dimensional space. Black and grey
496 bars show data for dead and surviving trees, respectively.

497 NFM (**c**) and NFF (**d**) at each location predicted by generalized additive
498 mixed models. Predictions were made by assuming that the number of weeks
499 after the first male beetle's flying (WEEK) was 2 and the diameter of trees at
500 breast height (DBH) was 20 cm. NFM (**e**) and NFF (**f**) predicted for the
501 combination of various values of WEEK and DBH by generalized additive
502 mixed models. Predictions were made by assuming that the tree was located
503 at the center of the 25 × 25-m study plot (coordinates of the location $x = 12.5$
504 m and $y = 12.5 m$).

505

506 **Fig. 3.** The proportion of male beetles that bored holes out of those that flew
507 to the tree (PBM), predicted by a generalized additive model. Values are
508 predicted for combinations of various values of the number of weeks after
509 the first male beetle's flying (WEEK) and diameter of trees at breast height
510 (DBH). Predicted values are shown separately for the three studied tree
511 species: *Quercus crispula* (left), *Q. serrata* (center), and *Castanea crenata*
512 (right).

513

Fig. 1

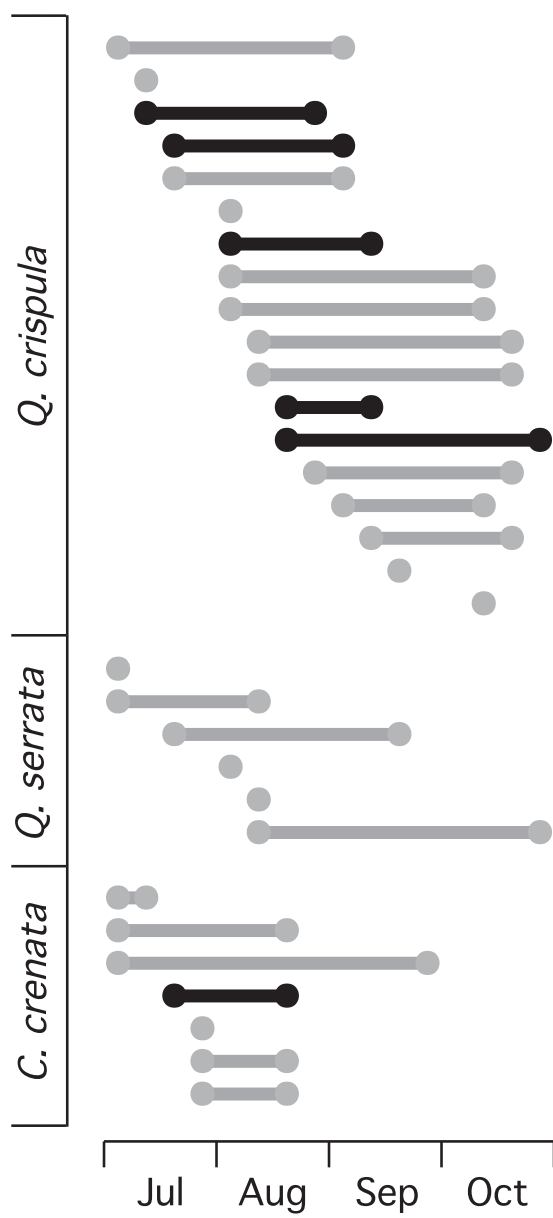


Fig. 2

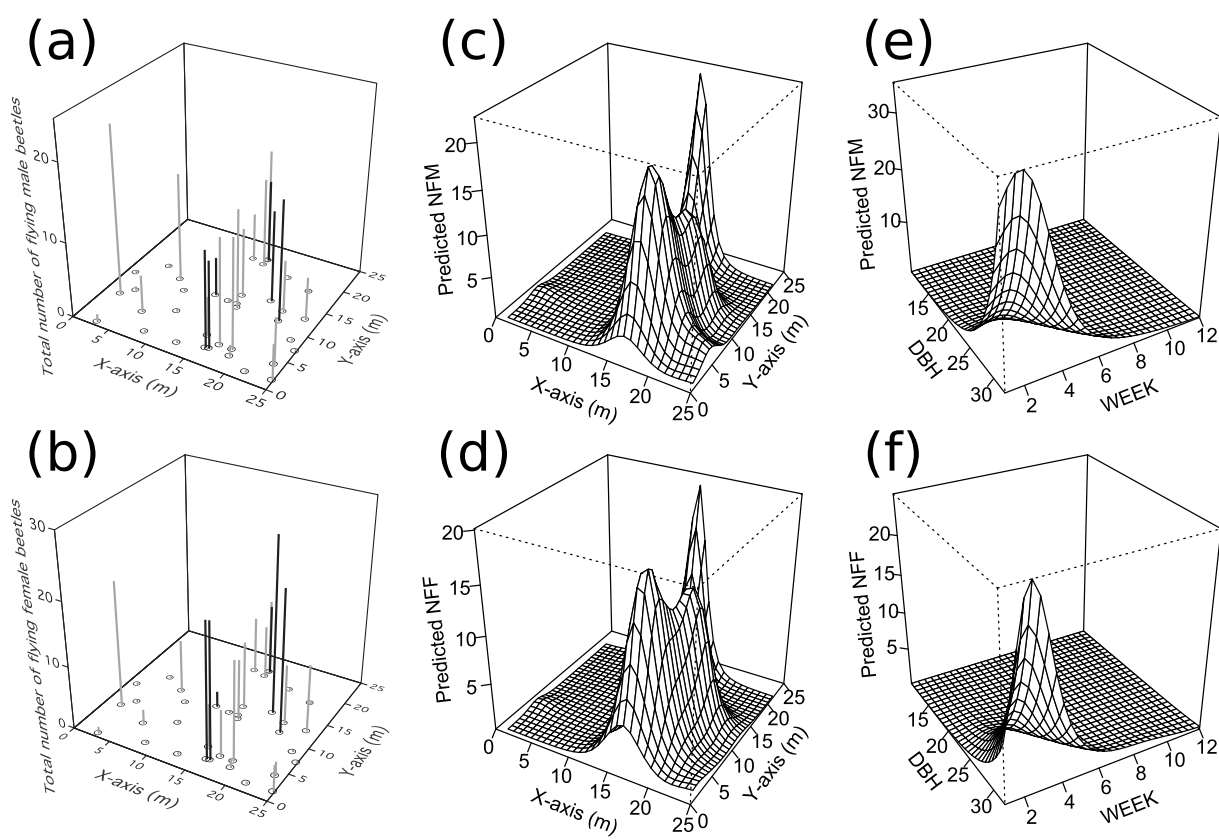


Fig. 3

