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AUTHOR(S):

Yamasaki, Michimasa; Futai, Kazuyoshi

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Title

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

Names and addresses of the authors

Michimasa Yamasaki^{*1} and Kazuyoshi Futai^{*2}

^{*1}: Laboratory of Forest Biology, Division of Forest and Biomaterials

Science, Graduate School of Agriculture, Kyoto University, Kyoto, Japan

^{*2}: Laboratory of Environmental Mycoscience, Division of Environmental

Science and Technology, Graduate School of Agriculture, Kyoto University,

Kyoto, Japan

Address of the corresponding author (Michimasa Yamasaki)

Laboratory of Forest Biology, Division of Forest and Biomaterials Science,

Graduate School of Agriculture, Kyoto University, Kitashirakawa

Oiwake-cho, Sakyo-ku, Kyoto 606-8502, Japan

Tel: +81-75-753-6479

Fax: +81-75-753-6129

E-mail: risei@kais.kyoto-u.ac.jp

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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

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

When discerning differences in beetle activity among tree species, it is necessary to take into account other variables that affect behavior. Reported effects of host tree size on beetle activity (Akaishi et al. 2006; Yamasaki and Futai 2008) show that it is necessary to compare beetle activity on different tree species within the same size class. However, this is difficult to achieve in a field study. Assuming that there are

1 linear relationships between tree size and beetle activity parameters (BAPs); and

2 normal distributions in BAPs,

analysis of covariance is appropriate for the detection of differences among tree species. Even when the first assumption is satisfied, BAPs may not be normally distributed. In addition, beetle activity fluctuates with time, and the relationship between time and beetle activity is apparently nonlinear (Urano 2000; Ueda and Kobayashi 2001b). Moreover, beetle activity may show dramatically high values at particular locations because of the effect of the beetle's aggregation pheromone (Ueda and Kobayashi 2001a; Tokoro et al. 2007), and this effect must be taken into consideration. Accordingly, we 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 cm^2 , 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

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

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

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

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

Results

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

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

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

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

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

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

With regard to PBM, the best model ($n = 137$) included the effects of WEEK, DBH, and SP. Predicted PBM increased with increasing WEEK, peaked at WEEK = 4, and then remained stable until WEEK = 10 (Fig. 3). The estimated degrees of freedom of smoothing term WEEK was 3.89 ($p = 0.004$). The effects of DBH on PBM were positive (the estimated coefficient was 0.11, $p = 0.005$); PBM increased with increasing DBH (Fig. 3). When 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.

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

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

Third, effects of tree size were detected for NFM and NFF (Fig. 2e, f). Increases in NFM and NFF with increasing DBH corroborate previous 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).

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

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361

362

363 **References**

364

365 Akaishi D, Kamata N, Nakamura K (2006) Initial stage of an infestation of
366 *Platypus quercivorus* (Coleoptera: Platypodidae) in a secondary forest
367 dominated by *Quercus serrata* and *Quercus variabilis* (in Japanese
368 with English summary). J Jpn For Soc 88:274-278

369 Byers JA, Zhang Q-H, Birgersson G (2004) Avoidance of nonhost plants by
370 a bark beetle, *Pityogenes bidentatus*, in a forest of odors.
371 Naturwissenschaften 91:215-219

372 Campbell SA, Borden JH (2006) Integration of visual and olfactory cues of
373 hosts and non-hosts by three bark beetles (Coleoptera: Scolytidae).
374 Ecol Entomol 31:437-449

375 Esaki K, Kato K, Kamata N (2004) Stand-level distribution and movement
376 of *Platypus quercivorus* adults and patterns of incidence of new
377 infestation. Agric For Entomol 6:71-82

378 Hijii N, Kajimura H, Urano T, Kinuura H, Itami H (1991) The mass
379 mortality of oak trees induced by *Platypus quercivorus* (Murayama)
380 and *Platypus calamus* Blandford (Coleoptera: Platypodidae): the
381 density and spatial distribution of attack by the beetles. J Jpn For Soc
382 73:471-476

383 Igeta Y, Esaki K, Kato K, Kamata N (2004) Spatial distribution of a flying

384 ambrosia beetle *Platypus quercivorus* (Coleoptera: Platypodidae) at
385 the stand level. Appl Entmol Zool 39:583-589

386 Inoue M, Nishigaki S, Nishi N (2000) Attack by the oak borer, *Platypus*
387 *quercivorus*, to living oak trees (in Japanese with English summary).
388 Appl For Sci 9(1):127-131

389 Ito S, Yamada T (1998) Distribution and spread of the mass mortality of oak
390 trees (in Japanese). J Jpn For Soc 80:229-232

391 Kamata N, Esaki K, Kato K, Igeta Y, Wada N (2002) Potential impact of
392 global warming on deciduous oak dieback caused by ambrosia fungus
393 *Raffaelea* sp. carried by ambrosia beetle *Platypus quercivorus*
394 (Coleoptera: Platypodidae) in Japan. Bull Entomol Res 92:119-126

395 Kamata N, Esaki K, Mori K, Takemoto H, Mitsunaga T, Honda H (2008)
396 Field trap test for bioassay of synthetic
397 (1*S*,4*R*)-4-isopropyl-1-methyl-2-cyclohexen-1-ol as an aggregation
398 pheromone of *Platypus quercivorus* (Coleoptera : Platipodidae). J For
399 Res 13:122-126

400 Kashiwagi T, Nakashima T, Tebayashi S, Kim CS (2006) Determination of
401 the absolute configuration of quercivorol, (1*S*,4*R*)-*p*-menth-2-en-1-ol,
402 an aggregation pheromone of the ambrosia beetle *Platypus*
403 *quercivorus* (Coleoptera: Platypodidae). Biosci Biotech Bioch
404 70:2544-2546

- 405 Kato K, Esaki K, Igeta Y, Kamata N (2001) Comparison of reproductive
406 success of *Platypus quercivorus* among four species of the family
407 Fagaceae (preliminary report) (in Japanese). Chubu For Res 49:81-84
- 408 Kobayashi M, Hagita M (2000) Process of mass mortality of oak trees and
409 capture of *Platypus quercivorus* Murayama (Coleoptera:
410 Platypodidae) (in Japanese with English summary). Appl For Sci
411 9(1):133-140
- 412 Kobayashi M, Nozaki A, Kinuura H (2004) Influence of sap on reproduction
413 of *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae) (in
414 Japanese). Appl For Sci 13:155-159
- 415 Kobayashi M, Shibata S (2001) Infestation of *Platypus quercivorus*
416 (Murayama) (Coleoptera: Platypodidae) at a newly damaged forest by
417 the beetle (I): Investigation in Maizuru, Kyoto Prefecture (in Japanese
418 with English summary). Appl For Sci 10(2):73-78
- 419 Kobayashi M, Ueda A (2001) Infestation of *Platypus quercivorus*
420 (Murayama) (Coleoptera: Platypodidae) at newly damaged forests by
421 the beetle (II): Investigation in Wachi and Keihoku, Kyoto Prefecture
422 (in Japanese with English summary). Appl For Sci 10(2):79-84
- 423 Kobayashi M, Ueda A (2005) Wilt disease of Fagaceae trees caused by
424 *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae) and the
425 associated fungus: Aim is to clarify the damage factor (in Japanese

- 426 with English summary). J Jpn For Soc 87:435-450
- 427 Paine TD, Raffa KF, Harrington TC (1997) Interactions among scolytid bark
428 beetles, their associated fungi, and live host conifers. Annu Rev
429 Entomol 42:179-206
- 430 Pureswaran DS, Borden JH (2005) Primary attraction and kairomonal host
431 discrimination in three species of *Dendroctonus* (Coleoptera:
432 Scolytidae). Agric For Entomol 7:219-230
- 433 R Development Core Team (2010) R: A language and environment for
434 statistical computing. In. R Foundation for Statistical Computing,
435 Vienna, Austria
- 436 Shiomi S, Osaki S (1997) Mass mortality of *Quercus serrata* and *Q.*
437 *mongolica* in Hyogo Prefecture (in Japanese). Appl For Sci 6:197-198
- 438 Soné K, Mori T, Ide M (1998) Life history of the oak borer, *Platypus*
439 *quercivorus* (Murayama) (Coleoptera: Platypodidae). Appl Entmol
440 Zool 33:67-75
- 441 Tokoro M, Kobayashi M, Saito S, Kinuura H, Nakashima T, Shoda-Kagaya
442 E, Kashiwagi T, Tebayashi S, Kim CS, Mori K (2007) Novel
443 aggregation pheromone, (1*S*,4*R*)-*p*-menth-2-en-1-ol, of the ambrosia
444 beetle, *Platypus quercivorus* (Coleoptera: Platypodidae). Bull For For
445 Prod Res Inst 6:49-57
- 446 Ueda A, Kobayashi M (2001a) Aggregation of *Platypus quercivorus*

- 447 (Murayama) (Coleoptera: Platypodidae) on oak logs bored by males
448 of the species. J For Res 6:173-179
- 449 Ueda A, Kobayashi M (2001b) Seasonal change of number of *Platypus*
450 *quercivorus* (Murayama) and *P. calamus* Blandford (Coleoptera:
451 Platypodidae) landing on living trees (in Japanese with English
452 summary). J Jpn For Soc 83:77-83
- 453 Urano T (2000) Relationships between mass mortality of two oak species
454 (*Quercus mongolica* Turcz. var. *grosseserrata* Rehd. et Wils. and *Q.*
455 *serrata* Thunb.) and infestation by and reproduction of *Platypus*
456 *quercivorus* (Murayama) (Coleoptera: Platypodidae). J For Res
457 5:187-193
- 458 Wood DL (1982) The role of pheromones, kairomones, and allomones in the
459 host selection and colonization behavior of bark beetles. Annu Rev
460 Entomol 27:411-446
- 461 Yamasaki M, Futai K (2008) Host selection by *Platypus quercivorus*
462 (Murayama) (Coleoptera: Platypodidae) before and after flying to
463 trees. Appl Entmol Zool 43:249-257
- 464 Yamasaki M, Iwatake A, Futai K (2007) A low *Platypus quercivorus* hole
465 density does not necessarily indicate a small flying population. J For
466 Res 12:384-387
- 467 Yamasaki M, Sakimoto M (2009) Predicting oak tree mortality caused by the

468 ambrosia beetle *Platypus quercivorus* in a cool-temperate forest. J
469 Appl Entmol 133:673-681
470 Zhang Q-H (2003) Interruption of aggregation pheromone in *Ips*
471 *typographus* (L.) (Col. Scolytidae) by non-host bark volatiles. Agric
472 For Entomol 5:145-153
473 Zhang Q-H, Schlyter F (2004) Olfactory recognition and behavioural
474 avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark
475 beetles. Agric For Entomol 6:1-19
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*.

Figure legends

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

Fig. 2. Numbers of flying male (**a**) and female (**b**) beetles per 100 cm² of bark surface (NFM and NFF) for 37 subject trees over the research period. The location of each tree is plotted in two-dimensional space. Black and grey bars show data for dead and surviving trees, respectively. NFM (**c**) and NFF (**d**) at each location predicted by generalized additive mixed models. Predictions were made by assuming that the number of weeks after the first male beetle's flying (WEEK) was 2 and the diameter of trees at breast height (DBH) was 20 cm. NFM (**e**) and NFF (**f**) predicted for the combination of various values of WEEK and DBH by generalized additive mixed models. Predictions were made by assuming that the tree was located at the center of the 25 × 25-m study plot (coordinates of the location x = 12.5 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

Figure 1 is a horizontal dot plot showing the distribution of flowering dates for three Quercus species: *Q. crenata*, *Q. serrata*, and *Q. crispula*. The x-axis represents months from July to October. Each species has multiple horizontal lines with dots at the ends, representing individual flowering events. *Q. crenata* shows flowering from mid-July to mid-August. *Q. serrata* shows flowering from early July to late September. *Q. crispula* shows flowering from mid-July to late October. Some lines are thick black, while others are thin grey.

Fig. 2

Fig. 3