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Title

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

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Abstract

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

Keywords

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

Introduction

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

In Japan, populations of ambrosia beetle *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae) are considered to have reached epidemic proportions in recent years. As vectors, their attacks on apparently healthy-looking trees lead to Japanese oak wilt (Ito and Yamada 1998; Kobayashi and Ueda 2005). Although they attack several species of Fagaceae, beetle reproductive success varies by tree species (Kato et al. 2001; Kobayashi et al. 2004). In brief, forest tree species fall into three types for *P. quercivorus*: suitable Fagaceae, unsuitable Fagaceae, and non-host tree species. In such an environment, we suggest that *P. quercivorus* preferentially selects suitable Fagaceae trees using visual or olfactory cues. Conversely, we postulate that tree species are avoided by *P. quercivorus* when these trees are associated with a reduced level of beetle fitness.

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

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

Materials and methods

Study site and tree species

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

Beetle activity in the infestation process

Numbers of *P. quercivorus* that flew to the trees were determined using sticky paper traps (Kobayashi and Hagita 2000; Ueda and Kobayashi 2001b). Two strips of sticky paper (Kamikiri-hoihoi; Earth Biochemical Co., Ltd., Tokushima, Japan), each 4 × 50 cm, were attached longitudinally to the upper and lower sides of each tree trunk up to 50 cm above the ground. We enumerated male (NFM) and female (NFF) beetles that flew to the bark of each tree (per 400 cm^2, i.e., total area of sticky paper attached to each tree) by weekly counts of beetles caught in traps.

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

Within natural forests, intense *P. quercivorus* flight activity occurs close to the ground (up to 2.5 m above soil level) (Igeta et al. 2004), and beetle attacks are concentrated on basal parts of trees (Hijii et al. 1991). Because it was difficult to count all beetles that flew to a tree and all holes that they bored, we restricted monitoring of NFM, NFF, and NH to the area up to 50 cm above ground.

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

Model selections

To discern differences in beetle activity parameters (BAPs) among tree species, we used generalized additive models (GAM) and generalized additive mixed models (GAMM). The best models for predicting BAPs were selected using R 2.11.1 (R Development Core Team 2010). Generally, BAPs fluctuate with time following a unimodal trajectory (Urano 2000; Ueda and Kobayashi 2001b). Thus, we built the nonlinear effect of time into the models predicting BAPs. Linear effects of tree size were also incorporated because BAPs increase with increasing tree size (Akaishi et al. 2006; Yamasaki and Futai 2008). Moreover, we must consider the effect of beetle aggregation caused by the pheromone. This beetle uses an aggregation pheromone to attract conspecifics (Ueda and Kobayashi 2001a; Tokoro et al. 2007), and the consequent mass attack by the beetle may conceal primary 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, cm^2) 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 cm^2) 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 cm^2) 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

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

Discussion

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

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

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

PBM was analyzed to detect differences among host tree species in beetle activity during phase 2, and the results supported our hypothesis. In addition to temporal fluctuations in beetle activity and the effect of tree size, the effect of tree species was detected; the proportions of male beetles that bored holes out of those that had flown to trees were lower for *Q. serrata* and *C. crenata* than for *Q. crispula* (Fig. 3). The same tendency has been reported for *Q. salicina*, which has lower susceptibility to *P. quercivorus* 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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Table 1. Numbers of trees observed, trees on which male *Platypus quercivorus* were trapped, trees on which beetle holes were observed, trees on which female beetles were trapped, and dead trees.

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

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 cm^2 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).

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

Fig. 1

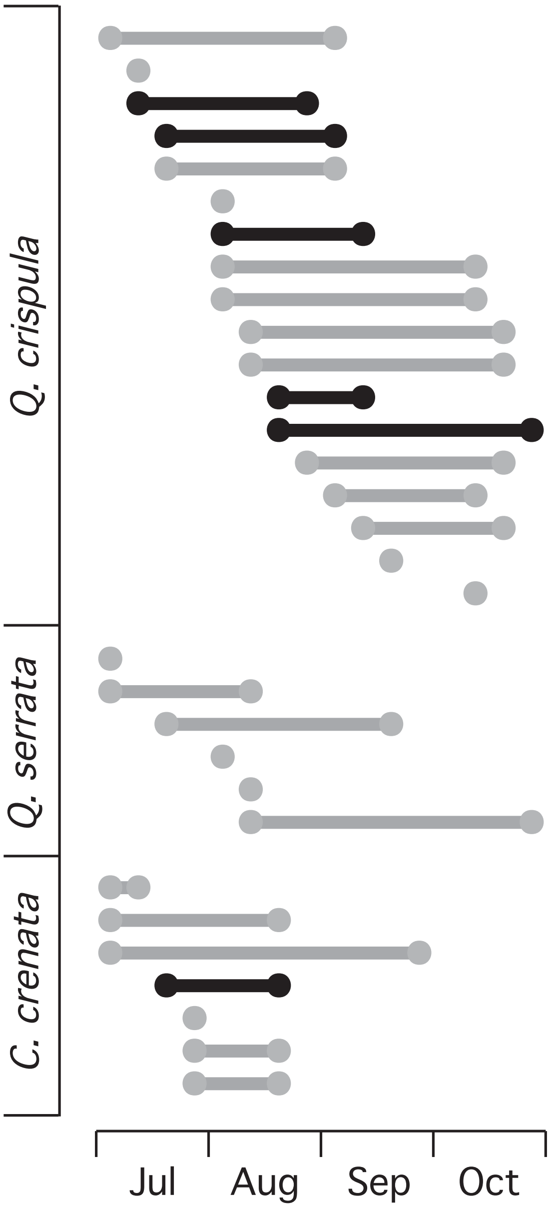


Fig. 2

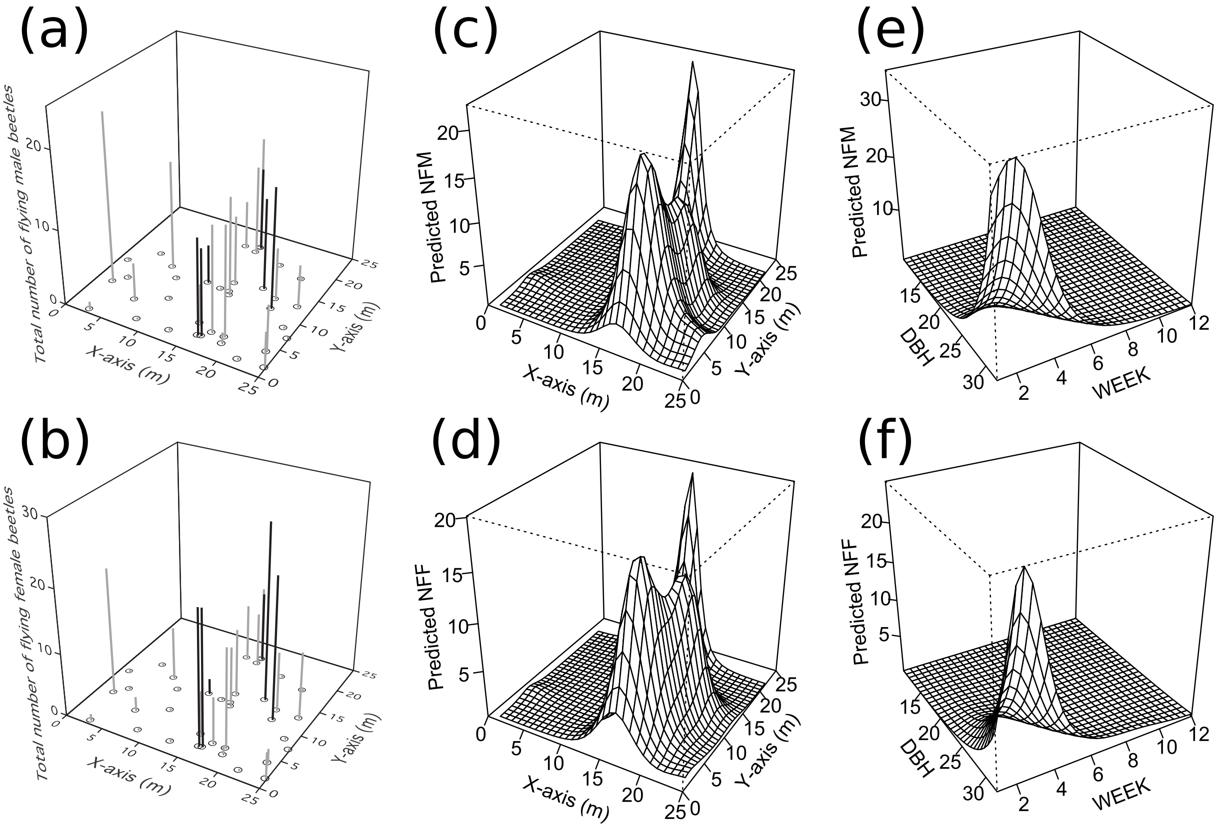
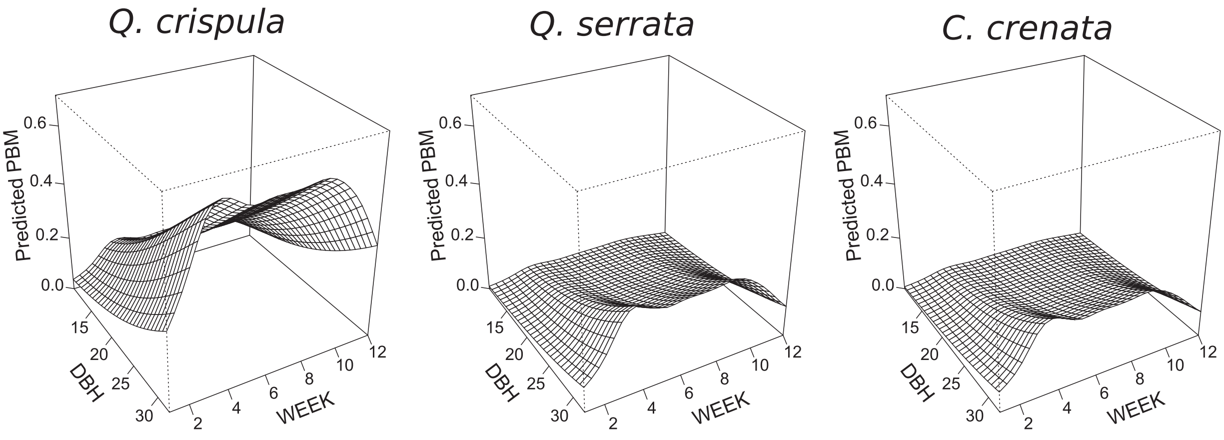

(a)
Total number of flying male beetles
0
10
20
X-axis (m)
0
5
10
15
20
25
Y-axis (m)
0
5
10
15
20
25
(b)
Total number of flying female beetles
0
10
20
30
X-axis (m)
0
5
10
15
20
25
Y-axis (m)
0
5
10
15
20
25
(c)
Predicted NFM
5
10
15
20
X-axis (m)
0
5
10
15
20
25
Y-axis (m)
0
5
10
15
20
25
(d)
Predicted NFF
5
10
15
20
X-axis (m)
0
5
10
15
20
25
Y-axis (m)
0
5
10
15
20
25
(e)
Predicted NFM
10
20
30
DBH
15
20
25
30
WEEK
2
4
6
8
10
12
(f)
Predicted NFF
5
10
15
20
DBH
15
20
25
30
WEEK
2
4
6
8
10
12

Fig. 3



Q. crispula

Q. serrata

C. crenata