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論　　文

Reproductive success of the ambrosia beetle *Platypus quercivorus* on *Quercus laurifolia* planted in Japan

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日本に植栽された *Quercus laurifolia* におけるカシノナガキクイムシの繁殖成功度

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Mortality of *Quercus laurifolia* trees that had been planted in Japan occurred in 2006. This was caused by an attack by the ambrosia beetle *Platypus quercivorus*, which causes a disease called Japanese oak wilt and results in mass mortality of Fagaceae trees in Japan. In order to study the infestation of *Q. laurifolia* by *P. quercivorus*, dead trees were cut into bolts, and the density of holes bored by *P. quercivorus* was examined for each bolt. Tube traps were attached to each hole in the bolts of the cut trees, and the number of offspring that emerged from the hole during 2007 (the year following the infestation) was counted. Similar to other Japanese Fagaceae species, the density of holes bored by *P. quercivorus* decreased with increase in the height of *Q. laurifolia*. The sex ratio of the emerged beetle was biased towards males, and the number of offspring per hole ranged from 0 to 41. The effects of the height and the hole density on the number of offspring were analyzed with zero-altered negative binomial models with a hurdle component and a truncated count component. The results of the hurdle component in the model for zero counts showed that the probability that one or more beetles emerged from holes was negatively affected by the height above the ground. According to the results of the count component of the model for positive counts, the number of offspring showed a unimodal distribution, with a peak at around one in the density of holes per 100 cm^2.

Key words: Japanese oak wilt, laurel oak, reproductive success rate, zero-altered negative binomial model

京都に植栽されていたローレルオーク（*Quercus laurifolia*）が，日本各地でブナ科樹木の集団枯死被害（ナラ枯れ）を引き起こしているカシノナガキクイムシ（*Platypus quercivorus*）によって 2006 年に枯死した．枯死したローレルオークは伐採して玉切りし，丸太毎に穿孔密度を調査した後，各穿孔穴に羽化トラップを取り付け，2007 年に脱出してきた次世代のカシノナガキクイムシの頭数を調査した．日本の他のブナ科樹木の場合と同様に，カシノナガキクイムシの穿孔密度は地上高が高くなるに従い低くなっていた．脱出虫の性比は雄に偏っており，1 穿孔穴あたりの脱出頭数は 0 頭から 41 頭だった．地上高と穿孔密度が脱出頭数に及ぼす影響を zero-altered negative binomial model を用いて解析した．その結果，1 頭以上の次世代虫が脱出する確率には地上高が負の影響を及ぼしていた．また，1 頭以上の脱出頭数は穿孔密度に対して一山型の分布を示し，樹幹上の穿孔密度が 100cm^2 あたり 1 個程度の時に最大となっていた．

キーワード：ナラ枯れ，ローレルオーク，繁殖成功度，zero-altered negative binomial model

1. Introduction

Mass mortalities of healthy trees caused by ambrosia beetles, which transport the pathogenic fungus *Raffaelea* sp. from tree to tree, have been reported recently (Hong et al., 2006; Alfaro et al., 2007; Fraedrich et al., 2008). Until recently, these beetles were thought to attack only weakened trees; however, now it appears that they also attack healthy trees and cause damages to forests. It has been suggested that increases in population level have caused these changes in the types of tree attacked by the beetle (Paine et al., 1997), and environmental changes such as global warming are considered to be some of the factors affecting the population changes of these beetles (Kamata et al., 2002). Because of the dramatic changes in environments now in progress, we must pay attention to population trends in the ambrosia beetle, which have the potential to cause severe damage to forests.

In Japan, Japanese oak wilt has been a serious problem in recent years (Ito and Yamada, 1998;

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Kobayashi and Ueda, 2005). This disease is caused by the pathogenic fungus *R. quercivora*, and its insect vector, the ambrosia beetle *Platypus quercivorus* (Ito et al., 1998; Saito et al., 2001; Kubono and Ito, 2002; Kinuura and Kobayashi, 2006). Hole boring activity of *P. quercivorus* and subsequent mortality of trees were reported for 12 species of Fagaceae: *Castanea crenata*, *Castanopsis cuspidata* var. *sieboldii*, *Quercus acuta*, *Q. acutissima*, *Q. crispula*, *Q. glauca*, *Q. myrsinaefolia*, *Q. phillyraeoides*, *Q. salicina*, *Q. serrata*, *Q. variabilis*, and *Pasania edulis* (Kobayashi and Ueda, 2005). Because *P. quercivorus* has the ability to attack a wide variety of apparently healthy Fagaceae trees, we can suppose that the beetle can also attack Fagaceae trees that are not native to Japan. A risk assessment of *P. quercivorus* was carried out in 2005 for natural resources in the US (Davis et al., 2005); however, at that time, no data were available on the susceptibility of *Quercus* species native to the US to this beetle.

In August 2006, mass mortality of the laurel oak (*Q. laurifolia* Michx.) was observed in Kyoto city, Japan, resulting from an attack by *P. quercivorus*. *Quercus laurifolia* is native to the southeastern part of the US, and the trees in question were planted in Japan in 1955. Because there have been no previous reports on the infestation of *P. quercivorus* in oak trees not native to Japan, we will first describe its infestation pattern. In general, holes bored by *P. quercivorus* concentrate in basal parts of the tree, and their density decreases with height (Hijii et al., 1991; Inoue et al., 2003; Kobayashi and Nozaki, 2003). Therefore, we need to consider whether the distribution of *P. quercivorus* holes shows a similar tendency in *Q. laurifolia*. Assuming that the distribution is similar across the species, what is the reason for the selection of the basal part of the tree? It is necessary to consider whether the reproductive success rate of *P. quercivorus* varies with increase in height, and whether the reproductive success rate of *P. quercivorus* in *Q. laurifolia* is higher or lower than in oak species native to Japan. The suitability of *Q. laurifolia* for the beetle, which can be estimated by the reproductive success of the beetle, is important information required in this risk assessment.

The number of offspring emerging from each entrance hole is a direct measure of the reproductive success of *P. quercivorus*, and a previous study has shown a high percentage with zero offspring (Kobayashi et al.,

2004a). Zero inflation in reproduction could be attributed to multiple sources of zero in the course of the *P. quercivorus* infestation in trees, which are better understood with a brief description of *P. quercivorus* reproductive behavior. First, male *P. quercivorus* beetles fly to a tree and bore shallow holes in it. There, they wait for female beetles and, when they have successfully mated, the male and female beetles construct long galleries in the sapwood for their offspring (Soné et al., 1998a; Esaki et al., 2004). Therefore, reproductive success may be zero in cases where there is no participation by female beetles. Even if male beetles successfully mate with females, reproductive success may also be zero because of competition among conspecifics for spaces to construct galleries. Bad sapwood conditions, for example resistant properties of the attacked trees, may also yield zero offspring even if male and female beetles mate successfully. Therefore, it is important to take into account these possible sources of zero when analyzing the number of emerged offspring per hole.

The objective of this study was to provide basic information about (1) the infestation patterns of *P. quercivorus* in *Q. laurifolia*, and (2) the suitability of *Q. laurifolia* as a host tree for *P. quercivorus*. With respect to the first objective, we counted the number of entrance holes bored by *P. quercivorus* from the base to the top of the trees and described changes in hole density with height. The second objective was achieved by counting the number of offspring that emerged from the entrance holes of *P. quercivorus* in the year following the initial infestation. Our third objective was to clarify (3) the effects of the height and density of the entrance holes on the reproductive success of *P. quercivorus*, and we simultaneously modeled (a) the probability that one or more offspring emerge from holes and (b) the number of offspring per hole, using a zero-altered negative binomial (ZANB) model.

2. Materials and methods

2.1 Site description and material trees

This study was conducted at Kamigamo Experimental Station, Field Science Education and Research Center, Kyoto University, which is located in the suburbs of Kyoto, central Japan (35°04′ N, 135°46′ E). Five laurel oak trees were found dead in August 2006 (Fig. 1) with a

Fig. 1. *Quercus laurifolia* trees killed by the attack of the ambrosia beetle *Platypus quercivorus*.

large amount of frass around the base of the trees, which was produced by the boring activity of *P. quercivorus*. The seeds from which these five trees were grown had been provided by the Morris Arboretum of the University of Pennsylvania in 1955. Initially they were germinated in the nursery, and later, in 1958, transplanted to the position, beside a forest road, where they grew until 2006.

Four of the five dead trees were cut down in September 2006: Tree 2 was cut down on September 4, Trees 1 and 3 were cut down on September 11, and Tree 4 was cut down on September 25. The diameters at breast height (DBH; 130 cm above ground) and heights of the tree were measured for each tree. Hewed trees were cut into bolts of 1 m or 50 cm in length. The perimeters of each bolt were measured, and the bark surface areas of each bolt were calculated assuming that the shape of the subject surface was a trapezoid.

The number of holes bored by *P. quercivorus* was counted for all bolts of the four trees. Usually, trees attacked by *P. quercivorus* are also exploited by *P. calamus*. Holes made by the two *Platypus* species were discriminated by the diameter of the hole entrance. It has been reported that the diameters of the hole entrances bored by *P. calamus* and *P. quercivorus* range from 0.8 to 1.2 mm and 2.1 to 2.9 mm, respectively (Inoue et al., 2003). Therefore, we regarded holes with a diameter of

less than 1.5 mm as being produced by *P. calamus*, and holes with a diameter of more than 1.5 mm as being produced by *P. quercivorus*. The density of holes bored by *P. quercivorus* per 100 cm^2 of bark surface was calculated for each bolt, using the number of holes counted and the calculated surface area.

The density of holes per unit bark surface area was examined to establish whether it affects the reproductive success of *P. quercivorus* in this study. Because the beetles use sapwood to construct galleries, the density of holes per unit sapwood volume may be a more appropriate measure, although we could not calculate this parameter because of a lack of information on the sapwood thickness. However, when *P. quercivorus* select positions for boring holes, they are unable to use the density of holes inside the sapwood as a measure of crowding, as this is not visible, but they can use the bark surface hole density. In this context, the density of holes per unit bark surface area is also a candidate variable that may affect the reproductive success of the beetle.

2.2 Reproductive success

For 18 bolts cut from the base to the top of Tree 3, both cut sections of the bolts were sealed with paraffin to prevent the inside of the bolts from drying out. The sealed bolts were placed in the field (Fig. 2), and the next generation of the *P. quercivorus* beetles that had bored

Fig. 2. Bolts of *Quercus laurifolia* sealed with paraffin. Emergence traps were attached to each hole bored by *Platypus quercivorus*.

holes in the trees in 2006 was captured in 2007, to estimate the reproductive success rate of *P. quercivorus* in laurel oak. Spitz tubes with screw caps (polyethylene, 16 mm in diameter and 100 mm in length) were used as traps to collect beetles. We bored a hole, 5 mm in diameter, on the cap of the tube and fixed it around the *P. quercivorus* entrance holes on the bark surface, attaching it by the eyelet (4.6 mm in diameter of the inside holes, 12 mm in length). The spitz tubes were then screwed on to these caps fixed on the bark surface. We checked the beetles that emerged from their holes and were trapped in the spitz tubes from May to November 2007 in one-week intervals.

The numbers of trapped male and female *P. quercivorus* were counted for each hole, and the bias in the sex ratio was tested by Pearson's chi-squared test and the simulation using R 2.14.0 (R Development Core Team, 2011). The simulation was conducted 1000 times for each offspring number from one to 100, setting the probability of male occurrence to 0.5. The confidence interval (95%) of the sex ratio equaling 0.5 was determined from the result of the simulation.

The following four indices of reproductive success were calculated for *Q. laurifolia*, (a) percentage of holes with one or more offspring emerged, (b) mean number of offspring for all examined holes, (c) mean number of offspring for holes with one or more offspring emerged and (d) maximum number of offspring among all holes examined. Calculated indices were compared with those on *Pasania edulis* (Soné et al., 2000), *Q. serrata*, and *Q. crispula* (Kobayashi and Hagita, 2000; Kobayashi and Nozaki, 2003; Kobayashi et al., 2004a; Kobayashi, 2006) obtained by previous studies. In cases when these indices were shown at the individual tree level in previous studies, mean values were calculated for each tree species for the purpose of comparison.

2.3 Statistical analyses

The relationship between the height and the density of the entrance holes was analyzed using a generalized linear mixed model. The response variable of the model was the number of the entrance holes of each bolt, and the candidate explanatory variable was the original height of each bolt. Because the response variable was count data, we assumed the error structure of the model as a Poisson distribution. The link function was set to logarithmic, which ensures the fitted values are positive, and the model was offset by the natural logarithm of the bark surface area. Individual tree numbers were incorporated into the model as random intercepts because the data taken from the same tree were likely to be more related to each other than to the data taken from different trees. The analysis was conducted using the *lme4* package of R 2.14.0 (R Development Core Team, 2011).

The effects of the height and the density of the entrance holes on the reproductive success of *P. quercivorus* were examined using a ZANB model. The response variable of the model was the number of *P. quercivorus* offspring per entrance hole, and candidate explanatory variables of the model were: (1) height of the entrance hole above the ground; and (2) the density of holes around it. The height of each entrance hole was represented by the height of the vertical center of the bolt to which each hole belongs. The density of holes around each entrance hole was represented by the density of holes calculated for the bolt to which each hole belongs. Therefore, all entrance holes that belong to the same bolt had the same values for height and density of holes.

The ZANB model is a two-part model used for analyzing count data that contain more zeros than expected, based on the negative binomial distribution (Zuur et al., 2009). In the first step (the hurdle component), the data are considered as zeros versus non-zeros and a binomial model is used to model the probability that a non-zero value is observed. In the second step (the count component), the non-zero data are modeled with a truncated negative binomial model that cannot produce zeros. For each step, a different set of explanatory variables can be used.

We constructed the full model with both the height and the density included as explanatory variables for both the hurdle component and the count component of the model. With respect to the density, we also included the quadratic term for the full model because there was presumed to be a non-linear effect of the density on the reproductive success of *P. quercivorus*. The least significant terms were removed from the model one by one, and the fitness of the reconstructed model was compared with that of the original model by using the likelihood ratio test. Model selection was carried out until further removal of the terms caused a significant

decrease in the likelihood of the model (Zuur et al., 2009). Terms dropped in the model selection process were regarded to have no effects on the response variables.

The analyses described above were conducted using R 2.14.0 (R Development Core Team, 2011). The model application was carried out using the *pscl* package, and the model selection by the likelihood ratio test was performed using the *lmtest* package.

3. Results

Table 1 shows the DBH and height, as well as the density of beetle holes, of the four dead *Q. laurifolia* trees attacked by *P. quercivorus*. The DBH of trees ranged from 42.4 cm to 72.3 cm, and the height of trees ranged from 20.5 m to 25.6 m (Table 1). The densities of beetle holes were relatively high on Trees 2 and 3, which had a small diameter, and were relatively low on Trees 1 and 4, which had a large diameter (Table 1).

Height had a significant negative effect on the number of entrance holes bored by *P. quercivorus* (Table 2), as there was a decrease in the density of holes bored by *P. quercivorus* with increase in height (Fig. 3). In the case of Trees 2 and 3, holes bored by *P. quercivorus* were concentrated on the base of the trees, and their holes were observed up to 18 m above ground (Fig. 3). The densities of holes bored by *P. quercivorus* were 2.06 and 1.90, respectively, at the bases of Trees 2 and 3 (Fig. 3).

Table 1. Profiles of dead *Quercus laurifolia* trees attacked by the ambrosia beetle *Platypus quercivorus*. These dead trees were cut into bolts, and the number of holes bored by *P. quercivorus* and the bark surface area was measured for each bolt. The density of beetle holes was calculated by dividing the total number of beetle holes by the total area of the bark surface.

	Diameter at 130 cm above ground (cm)	Height (m)	Density of beetle holes (100 cm⁻²)
Tree 1	72.3	25.6	0.15
Tree 2	42.4	23.0	0.90
Tree 3	49.7	21.5	0.93
Tree 4	65.6	20.5	0.05

Table 2. Results of a generalized linear mixed model (n = 129) to predict the number of entrance holes bored by *Platypus quercivorus* on four *Quercus laurifolia* trees. Individual trees were incorporated into the model as random intercepts. The estimated coefficient, its standard error, z statistic, and *P* value are shown.

Predictor	Estimate	SE	z value	*P*
Height	-0.0992	0.004094	-24.233	<0.001***

***: *P* < 0.001

In the case of Trees 1 and 4, the density of holes bored by *P. quercivorus* was low, in comparison with that in Trees 2 and 3: the values were 0.61 on Tree 1 and 0.26 on Tree 4, at the bases of each tree (Fig. 3).

The seasonal occurrence of male and female *P. quercivorus* that emerged from *Q. laurifolia* bolts is shown in Fig. 4a. Beetle emergence started in May, showed its peak in mid-June, and most beetles had emerged by mid-August (Fig. 4a). Male and female beetles showed a similar pattern of emergence. Figure 4b shows changes in the cumulative percentage of emerged male and female beetles. A slight delay was observed in the initiation of the emergence of females; the cumulative percentage of emerged males exceeded 50% on June 15, and that of females exceeded 50% a week later (Fig. 4b). The male sex ratio of the beetles emerging from *Q. laurifolia* (72%) was significantly higher than 50% (Pearson's chi-squared test, χ^2 = 58.6318, d.f. = 1, $P < 0.001$). Figure 5 shows the relationship between the number of offspring and the male sex ratio. When the simulation was conducted by setting the probability of male occurrence to 0.5, about one sixth of the data fell outside the 95% CI (Fig. 5).

In sum, 596 *P. quercivorus* beetles emerged from 64 out of 346 entrance holes to which the emergence traps were attached. Two other species, *Xyleborus atratus* (62
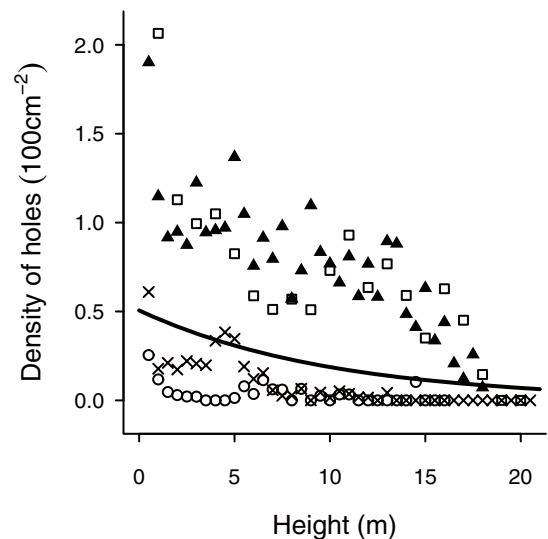

Fig. 3. Density of holes bored by *Platypus quercivorus* per 100 cm² of bark surface of *Quercus laurifolia* in relation to the height above the ground. Data from 4 individual trees, Trees 1, 2, 3, and 4 are shown as crosses, open squares, solid triangles, and open circles, respectively. The solid line shows values predicted by a generalized linear mixed model, which includes individual trees as random intercepts. See Table 1 for profiles of each tree.
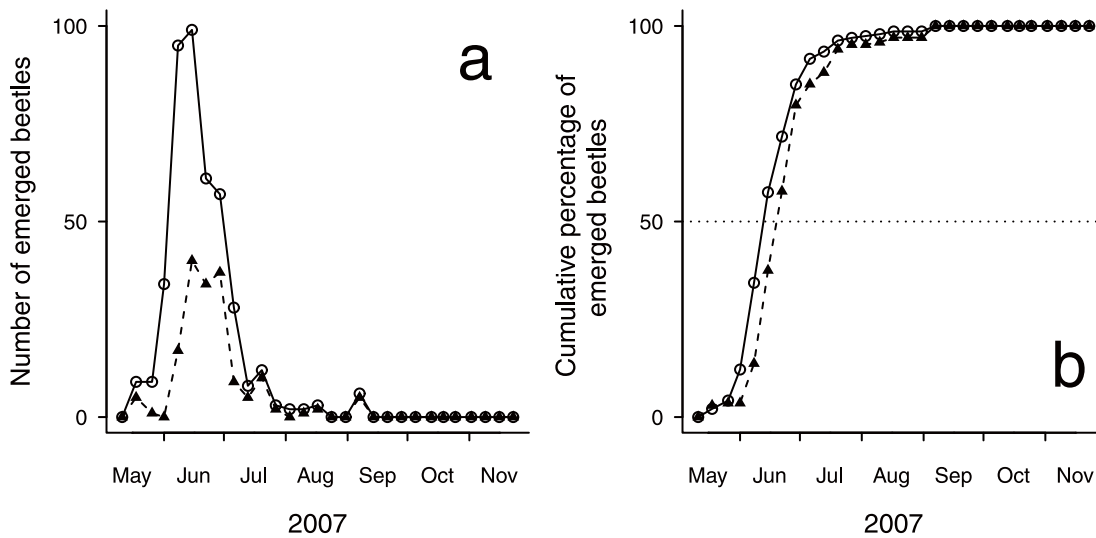
Fig. 4. (a) Seasonal occurrence of male (open circles connected by solid line) and female (solid triangles connected by dashed line) *Platypus quercivorus* beetles that emerged from *Quercus laurifolia* bolts. (b) Changes in the cumulative percentage of emerged male (open circles connected by solid line) and female (solid triangles connected by dashed line) *P. quercivorus* beetles. Data from 64 holes were pooled.
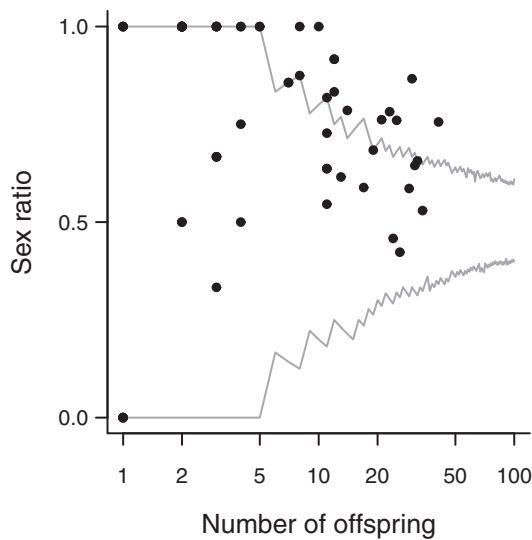

Fig. 5. Relationship between the number of offspring of *Platypus quercivorus* that emerged from *Quercus laurifolia* bolts and the male sex ratio. Grey lines show the 95% confidence interval of the male sex ratio obtained by the simulation. The simulation was conducted 1000 times for each offspring number from 1 to 100, setting the probability of male occurrence to 0.5.

beetles from two holes) and *X. lewisi* (one beetle from one hole) were also observed to emerge. Several parameters of the reproductive success of *P. quercivorus* in *Q. laurifolia* were compared with those in another three Fagaceae species reported in previous studies (Table 3). The percentage of holes with successful reproduction was 18.5% in *Q. laurifolia*, and this value was higher than in *Q. serrata* and *Q. crispula* (Table 3). The average number of offspring per hole was 1.72 in *Q. laurifolia*, which was higher than that in *Q. serrata* and lower than that in *Q. crispula* (Table 3). The average number of offspring per hole from which one or more beetles emerged was 9.31 in *Q. laurifolia*, which was lower than in *Q. serrata* and *Q. crispula* (Table 3). In 64 holes that showed successful reproduction, the number of offspring per hole ranged from one to 41. The maximum number of offspring in *Q. laurifolia* was lower than the values reported for *Pasania edulis* and *Q. crispula* (Table 3).

Table 3. Reproductive success of *Platypus quercivorus* in four species of Fagaceae: (a) percentage of holes with one or more offspring emerged; (b) mean number of offspring for all examined holes; (c) mean number of offspring for holes with one or more offspring emerged; and (d) maximum number of offspring among all holes examined. Data for *Quercus laurifolia* were obtained in this study.

	(a) Percentage of successful holes	(b) Average offspring	(c) Average offspring per successful hole	(d) Maximum number of offspring	
Pasania edulis	-	-	-	89	(Soné et al., 2000)
Quercus serrata	0.8%	0.69	17.25	-	(Kobayashi et al., 2004a)
Q. crispula	-	19.50	-	-	(Kobayashi and Hagita, 2000)
	-	12.11	-	-	(Kobayashi and Nozaki, 2003)
	10.7%	7.02	47.05	337	(Kobayashi et al., 2004a)
	-	-	-	558	(Kobayashi, 2006)
Q. laurifolia	18.5%	1.72	9.31	41	

Only the height above the ground was included as an explanatory variable in the hurdle component of the best model to predict the probability of one or more beetles emerging from the hole (Table 4). Height had a negative effect on the probability, and the predicted probability decreased with increase in height (Fig. 6a). The density of holes and the quadratic term of the density were not included in the hurdle component (Table 4), suggesting that the probability of one or more beetles emerging from the hole was not affected by the density of holes around it.

With respect to the count component of the ZANB model, the best model to predict the number of offspring included the density and the quadratic term of the density, and the height was not included in the count component (Table 4). In cases where one or more beetles emerged from the hole, the number of offspring was low at both ends of the density range studied, and showed its peak and a large variance at the middle of the density range studied (Fig. 6b). The predicted curve of the ZANB model showed its peak at around one in the density of holes per 100 cm^2 (Fig. 6b).

4. Discussion

Although the percentage of holes with one or more offspring emerged was higher in *Q. laurifolia* compared with those in *Q. serrata* and *Q. crispula*, the mean number of offspring for all examined holes was lower in *Q. laurifolia* compared with that in *Q. crispula* (Table 3). In addition, the mean number of offspring per hole from which one or more offspring emerged in *Q. laurifolia* was lower than that in *Q. serrata* and *Q. crispula* (Table 3). The maximum number of offspring was 41 in *Q. laurifolia*, and this value is less than half the number

reported in *Pasania edulis* and less than 10% of the number reported in *Q. crispula* (Table 3). These results suggest that the suitability of *Q. laurifolia* as a host for *P. quercivorus* is lower than that of the other three Fagaceae species native to Japan.

The four trees of *Q. laurifolia* in this study were killed by a *P. quercivorus* attack, irrespective of their attack density (Table 1, Fig. 3). Attack densities in Trees 2 and 3 (0.90 and 0.93 per 100 cm^2, Table 1) showed similar values to those reported for *Q. crispula* (1.33 per 100 cm^2, Kobayashi and Nozaki, 2003) and *Q. serrata* (0.9-1.3 per 100 cm^2, Hijii et al., 1991). On the other hand, attack densities in Trees 1 and 4 were relatively low (0.61 and 0.26 per 100 cm^2 at the basal part, Fig. 3). In the case of *Q. crispula* and *Q. serrata*, trees with higher densities of holes (2.08 and 2.67 per 100 cm^2 at the basal part) survived the attack (Kobayashi and Ueda, 2001). The fact that *Q. laurifolia* trees died, irrespective of the beetle attack density, suggests a high susceptibility of this tree species for the pathogenic fungus *R. quercivora*, vectored by *P. quercivorus*. Therefore, *Q. laurifolia* must be recognized as a susceptible species to Japanese oak wilt.

Beetle emergence from *Q. laurifolia* showed a similar pattern to that observed in other *Quercus* species (Kobayashi and Hagita, 2000; Urano, 2000); beetle emergence lasted for two to three months (Fig. 4a). A slight delay was observed in female emergence compared with male emergence (Fig. 4b), and a similar pattern was also reported in *Q. crispula* (Kobayashi and Hagita, 2000) and *Pasania edulis* (Soné et al., 1998a). A considerable difference was observed between the sex ratio of the beetles that emerged from *Q. laurifolia* and that of beetles that emerged from other Fagaceae species. A slight bias toward males has been reported for *P. quercivorus*; the male sex ratio of this beetle was 51% on

Table 4. Results of a zero-altered negative binomial model (n = 346) to predict the probability that one or more offspring emerge from the hole bored by *Platypus quercivorus* on *Quercus laurifolia* (hurdle model) and to predict the number of offspring in cases where one or more offspring emerged from the hole (count model). Estimated coefficients, their standard errors, z statistics, and *P* values are shown for variables included in the best-fit model. Log likelihood of the full model, which includes all variables as explanatory variables, is -346.6 on 9 degrees of freedom, and that of the best model is -347.5 on 6 degrees of freedom.

	Predictor	Estimate	SE	z value	*P*
Hurdle model	Height	-0.2926	0.0651	-4.493	<0.001＊＊＊
	Density	-	-	-	-
	Density^2	-	-	-	-
Count model	Height	-	-	-	-
	Density	28.4931	9.9182	2.873	0.00407＊＊
	Density^2	-14.3271	4.7755	-3.000	0.00270＊＊

＊＊：$P < 0.01$, ＊＊＊：$P < 0.001$

Pasania edulis (Soné et al., 1998a) and 55% on *Q. crispula* (Kobayashi and Nozaki, 2003). The male sex ratio of the beetles emerging from *Q. laurifolia* was 72% (Fig. 4a), and both the statistical test and the simulation (Fig. 5) showed significant bias in the sex ratio. The male *P. quercivorus* beetle is a pioneer in finding a host tree, and the female beetle flies to the tree afterwards; therefore, early emergence of males (Fig. 4b) and late emergence of females (Soné et al., 1998a) are adaptive for this beetle. Considering the low reproductive success of this beetle on *Q. laurifolia* (Table 3), the observed significant male bias (Fig. 5) may be characteristic of the early season, and higher reproductive success may result in a more even sex ratio with female biased emergence in the late season.

As shown in other species of *Quercus* in Japan (Hijii et al., 1991; Inoue et al., 2003; Kobayashi and Nozaki, 2003), the number of entrance holes bored by *P. quercivorus* decreases with increase in height (Fig. 3). Irrespective of the tree species attacked, the height above the ground appears to be an important factor for *P. quercivorus*. The hurdle component of the best model to predict the probability that one or more beetles emerge from the hole indicates the importance of the height for *P. quercivorus*: the probability decreases with increase in height (Fig. 6a). It has been suggested that *P. quercivorus* favors the basal part of the tree for boring holes because

of the large volume of sapwood in this section, which can be used to construct galleries (Hijii et al., 1991). The high water content in the basal part of the attacked and dead trees (Kuroda and Yamada, 1996), which ensures the high growth rate of the beetles' symbiotic fungi (Kobayashi et al., 2004b), is another possible factor determining why *P. quercivorus* favors the basal part of the tree.

The number of offspring increased with increase in the hole density, showed its peak at around one in the hole density (per 100 cm^2), and then decreased (Fig. 6b). Therefore, it would appear that the reproductive success of *P. quercivorus* is dependent on both the benefit and the cost of aggregation. Destruction of the defense mechanisms of trees may be a benefit of aggregation; *P. quercivorus* attacks Fagaceae trees en masse (Ueda and Kobayashi, 2001) to overcome the trees' defense mechanisms. Assuming that these effects also apply on a smaller scale, a piece of sapwood for example, the local aggregation of holes (Soné et al., 1998b; Soné et al., 2000) is also important for this beetle. One cost of aggregation must be the competition among conspecifics. Galleries of *P. quercivorus* are constructed in the sapwood of trees extending from the entrance holes (Kobayashi et al., 2001). Because the sapwood is limited in space, local aggregation of entrance holes on the bark surface will cause a high probability of competition for spaces to
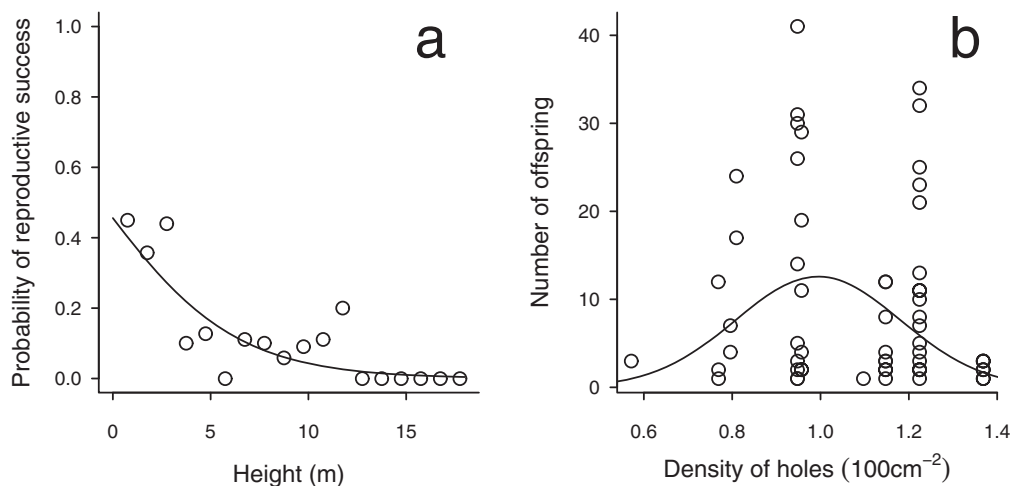

Fig. 6. (a) Relationship between the probability that one or more offspring of *Platypus quercivorus* emerge from holes and the height above the ground. The probability was calculated by dividing the number of holes with successful reproduction by the total number of holes for 18 *Quercus laurifolia* bolts cut from different heights. The line shows the result of the zero-inflation model, which assumes a binomial distribution of the data (0 for zero offspring and 1 for one or more offspring) with logit link function. (b) Relationship between the number of *P. quercivorus* offspring per hole and the density of holes per 100 cm^2 of bark surface. Data for holes with one or more beetles emerged are shown. The line shows the result of the count model, which assumes negative binomial distribution of the data (number of offspring) with logarithmic link function.

construct galleries. It has been reported that the reproductive success rate of grouped galleries of *P. quercivorus* is lower than that of solitary galleries in *Pasania edulis* (Soné et al., 1998b).

In this study, data on offspring number was obtained from 346 beetle holes, and the probability of successful reproduction was predicted using these data. Of these 346 holes, only 64 holes were recorded as having one or more emerged beetles, and the count component of the ZANB model used this small amount of data to predict the positive offspring count. A non-linear effect of hole density was detected by the model; however, the amount of data for the lower and higher density levels was relatively small (Fig. 6b). To ensure the non-linear effect of the density on the reproductive success of the beetle, large datasets with various densities are necessary.

Acknowledgments

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