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Optimal attack density in the larch bark beetle, *Ips cembrae* (Coleoptera: Scolytidae)

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Summary

1. The effects of attack density of the larch bark beetle, *Ips cembrae* (Heer) (=*Ips subelongatus* Motsch.) on the gallery length, egg and offspring adult production and mortality were studied in 0·1 m^2 bark samples from 100 larch trees (*Larix dahurica* Turcz) during the summer of 1989 in a burned area of the Tu Qiang Forest District, Great Xingan Mountains, P.R. China.

2. The results show that there is a positive linear relationship between gallery length and number of egg niches. The number of egg niches and offspring adults produced per gallery declined exponentially with attack density, and the egg to adult mortality increased exponentially as the attack density increased in the absence of host resistance.

3. The exponential relationships are attributed to intraspecific competition between female parent adults for breeding space and between larvae for limited food resources.

4. In addition, there are two optimal attack densities, 13·9 attacks per 0·1 m^2 and 8·7 attacks per 0·1 m^2, at which the number of egg niches (935) and offspring adults (496) are maximal, respectively. An upper threshold of attack density, 31·8 attacks per 0·1 m^2, beyond which the number of offspring adults produced from a bark area become less than the input of parent adults was also found.

Key-words: intra-specific competition, population dynamics, fecundity, fire, host resistance.

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Introduction

The attack density on the host tree is of great importance for bark beetle reproduction and population dynamics. Most tree-killing bark beetles attack by boring into the bark and feeding in the phloem-cambium layer. Pheromones are used by most species, both to locate mates and to find a suitable place to feed and reproduce (Byers 1989a). Another key function of aggregation pheromones appears to be that in each species they induce a mass aggregation of individuals which collectively overcome the tree's oleoresin resistance mechanism. *Ips cembrae* (Heer) (=*subelongatus* Motsch.) also uses an aggregation pheromone during colonization of its host tree (Stoakley *et al.* 1978; Kohnle *et al.* 1988; Yu & Zhang 1988; Fu *et al.* 1988; Qiu *et al.* 1988; Zhang *et al.* 1991). It is evident that a certain lower threshold number or density of beetles is required to kill a particular tree and ensure the survival of participating adults and their offspring (brood). However, after this density is reached during the colonization sequence, further increases in density of attacking beetles result in increasingly detrimental effects on reproduction due to intraspecific competition between the larvae (Beaver 1974; Berryman 1974; Light, Birch & Paine 1983; Anderbrant, Schlyter & Birgersson 1985). The nature of the competition is probably a combination of interference competition (direct effects such as cannibalism) and exploitative competition (indirect effects such as eating the limited food resource). The adverse effects of competition become apparent even at very low densities when beetles colonize wind-thrown trees and burned trees that are less able to inhibit the beetles from feeding (Raffa & Berryman 1983).

There are reports of intraspecific competition and the effects of attack density on offspring production in several bark beetle species in the genera *Ips*, *Dendroctonus*, *Scolytus*, and *Tomicus* (=*Blastophagus*). These reports have shown that offspring number per female decreases at higher attack densities (Miller & Keen 1960; McMullen & Atkins 1961; Ogibin 1973; Beaver 1974; Berryman 1974; Mayyasi *et al.* 1976; Light *et al.* 1983; Anderbrant *et al.* 1985; Sauvard 1989; Anderbrant 1990).

The larch bark beetle, *I. cembrae*, is one of the most destructive pest insects of larch plantations and natural stands (*Larix kaempferi* and *L. polonica* in Europe, *L. dahurica* Turcz in Asia). The beetle not only infests weakened trees, wind-thrown trees and burned trees, but at higher population densities also attacks healthy trees. The life history of the beetle has been investigated as well as the effects of weather, incidence of attacked trees within stands, and vertical distribution of attack density along the trunk of burned trees (Balogun 1979; Yu, Guo & Cheng 1984; Zhang, Liu & Chu 1989; Zhang *et al.* 1990; Yu *et al.* 1991).

To date there have been no attempts to study intraspecific competition and density-dependent population dynamics of this beetle. The objectives of the present study were (i) to identify the relationship between attack density and offspring production, and (ii) to determine the optimal attack density for reproduction in the absence of host resistance.

Methods

The experiment was conducted during the summer of 1989 in natural larch stands (*L. dahurica*), Tu Qiang Forest District, Great Xingan Mountains, China, that had been burned in a great forest fire in 1987. Extensive areas of burned trees and weakened trees provided abundant food resource and breeding space for bark beetles after this fire. Thus, an outbreak of *Ips cembrae*, a dominant species in this area, was rapidly elicited (Zhang *et al.* 1989). The flight period of this beetle in the region extends from mid-May through June. There is usually a second attacking flight, of much lesser intensity, in August which consists mostly of emerging offspring adults. A week before the first flight period (from 4 to 8 May 1989), 100 larch trees that were not infested by any stem-infesting insects were selected and cut down. These trees were located in several larch stands burned to various degrees in which local bark beetle population densities varied greatly as judged from the large range in subsequent colonization densities. The age (A), height (H) and diameter at breast height (dbh) of these selected trees ranged from: A, 90–150 years; H, 10–20 m; and dbh, 20–35 cm. These laying trees were attacked by *I. cembrae* during the flight period. After the parent adults emerged from these trees (by 13 July), a rectangular bark sample (20×50 cm) at breast height (a suitable reproduction site for *I. cembrae*, Zhang *et al.* 1990) was cut from each tree. In each sample the attack density (attacks per $0{\cdot}1\,m^2$), number of egg galleries per attack (per family), egg gallery length, number of egg niches and pupal chambers per egg gallery were recorded.

Results

Effects of attack density on length of egg gallery and number of galleries per family

The gallery system of a family usually consists of a polygynous male and three females with their egg galleries (tunnels). The average length of egg galleries and number of egg galleries per family system at different attack densities are shown in Table 1. The range of attack densities on the selected trees ranged from 0 to 36 attacks per $0{\cdot}1\,m^2$ and the length of egg galleries varied from 1·8 to 14·5 cm. This variation in attack density allows us to describe the relationship between attack density and offspring production. According to the analysis of the data from the 100 trees, a significant negative relationship between the length of the egg gallery and density was found (Fig. 1). The egg gallery length (Y_l) declines exponentially with attack density (X) and is fitted best by the curve:

$$Y_l = 11{\cdot}97e^{-0{\cdot}046X};\ r^2 = 0{\cdot}91 \qquad \text{eqn 1}$$

There was no significant relationship between the number of egg galleries per family and attack density (Table 1). The gallery system of one male and three females is maintained by behavioural mechanisms

Table 1. Effect of attack density on the egg galleries per family, gallery length, eggs per gallery, and production of offspring adults per gallery ($n = 100$)

Attacks per $0{\cdot}1\,m^2$	n	Egg galleries per family	Gallery length (cm) ± SD	Eggs per gallery ± SD	Offspring adults per gallery ± SD
0–5	11	3·02	12·03 ± 1·19	53·06 ± 10·37	39·95 ± 7·94
5–10	16	2·96	7·38 ± 0·70	30·01 ± 5·37	17·69 ± 4·26
10–15	27	3·0	5·85 ± 0·39	22·11 ± 1·86	10·92 ± 1·75
15–20	17	3·0	5·24 ± 0·26	17·16 ± 2·08	6·42 ± 1·26
20–25	11	3·03	4·66 ± 0·40	13·45 ± 1·12	3·86 ± 0·76
25–30	11	2·95	3·98 ± 0·61	9·94 ± 2·32	2·41 ± 0·60
30–35	4	2·79	2·32 ± 0·26	5·2 ± 0·82	1·15 ± 0·14
>35	3	2·78	1·74 ± 0·11	3·23 ± 0·15	0·74 ± 0·06

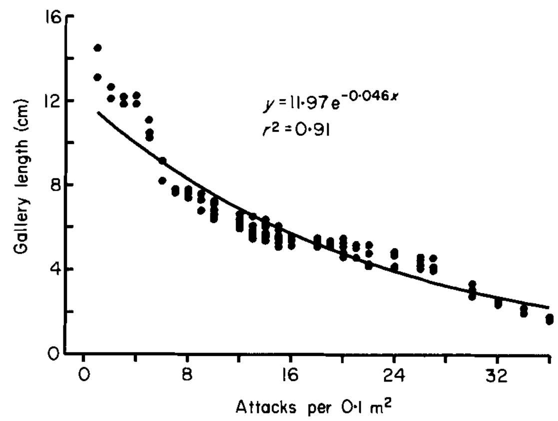

Fig. 1. Effect of attack density on the gallery length in *Ips cembrae* ($n = 100$).

involving pheromonal communication (Zhang *et al.* 1991).

Relationship between the number of eggs and egg gallery length

The relationship between the number of eggs (Y_e) and egg gallery length (X) from the data (Fig. 2) is:

$$Y_e = 5{\cdot}22X - 9{\cdot}3;\ r^2 = 0{\cdot}96 \qquad \text{eqn 2}$$

This equation is appropriate only when $X > 3$. This equation shows that the number of eggs increases linearly with egg gallery length. A similar relationship between the two variables ($Y = 3{\cdot}26X - 1{\cdot}8$) was found for *I. cembrae* in a larch plantation (Yu *et al.* 1984).

Effect of attack density on the fecundity of parent adults

The differences between fecundities of bark beetles are expected to depend on the nutritional conditions as influenced in part by intraspecific competition. The attack density of the population does influence adult fecundity due to competition for the phloem-cambium layer (Table 1). The number of egg niches per gallery (Y_e) declines exponentially with attack density and is fitted best by the curve:

$$Y_e = 60{\cdot}98e^{-0{\cdot}072X},\ r^2 = 0{\cdot}95 \text{ (Fig. 3)} \qquad \text{eqn 3}$$

From this it can be inferred that each female is capable of producing an average of 61 viable eggs under conditions of no competition. This agrees closely with the result of Yu *et al.* (1984) who found the average number of eggs per female was about 59·1 under very low attack density conditions.

In studies of population dynamics, an important concern is to determine population quantity produced (output) from a certain bark area (e.g. 0·1 m²) based on attack density (input). Hence, it is necessary to find the relationship between the number of eggs in a certain bark area and the attack density. As indicated by previous studies (Yu *et al.* 1984; Zhang *et al.* 1991) and Table 1, the gallery system uniformly consists of three egg galleries. Now let Y_n represent the number of eggs in 0·1 m² bark area, then:

$$Y_n = 3Y_eX = 182{\cdot}94Xe^{-0{\cdot}072X}$$
$$\text{(Fig. 4, upper curve)} \qquad \text{eqn 4}$$

In order to find the maximum value of Y_n, where an optimal density exists, the derivative of the curve is taken:

$$Y'_n = 182{\cdot}94[e^{-0{\cdot}072X}(-0{\cdot}072X) + e^{-0{\cdot}072X}] =$$
$$182{\cdot}94e^{-0{\cdot}072X}(1 - 0{\cdot}072X) \qquad \text{eqn 5}$$

Then when $Y'_n = 0$ there are only two possible solutions:

$e^{-0{\cdot}072X} = 0$, $X = \infty$(no solution); $1 - 0{\cdot}072X = 0$, $X = 13{\cdot}9$

Thus, when $X = 13{\cdot}9$ (13·3–14·6, 95% CI), Y_n is maximal at 935 (891–974, 95% CI). In Fig. 4 (upper curve) it can be seen that Y_n rapidly increases with attack density when less than 13·9 attacks per 0·1 m², but further increases in density of attacking beetles results in gradual decreases in Y_n. This maximum can be considered as an optimum attack

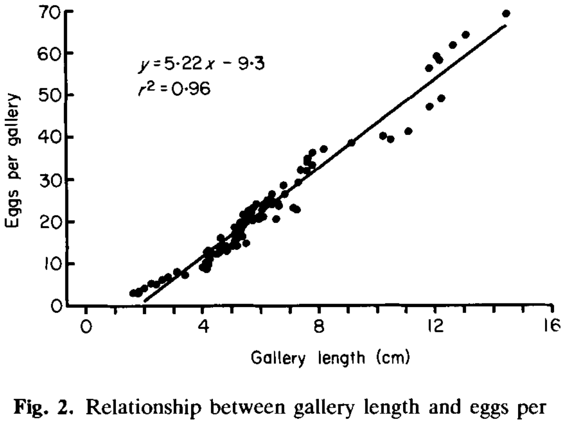

Fig. 2. Relationship between gallery length and eggs per gallery in *Ips cembrae* ($n = 100$).

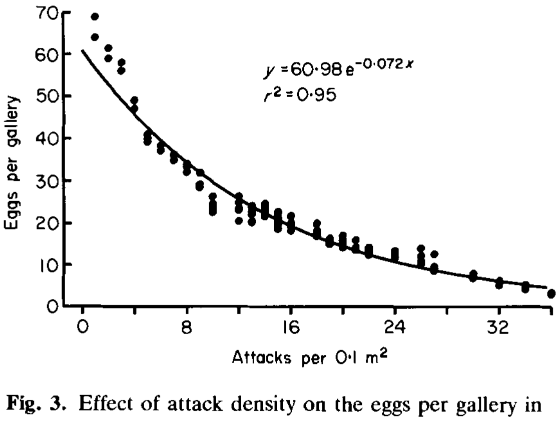

Fig. 3. Effect of attack density on the eggs per gallery in *Ips cembrae* ($n = 100$).

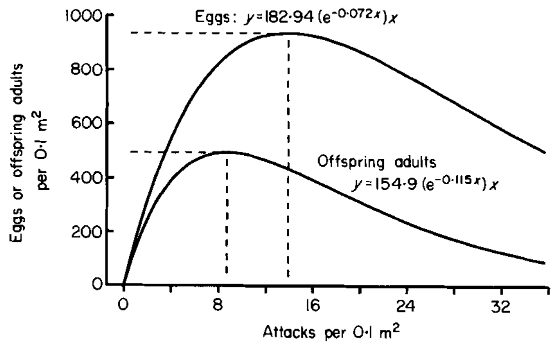

Fig. 4. Optimal attack density of *Ips cembrae* for maximal egg or offspring adult production per $0{\cdot}1\,m^2$ bark area ($n = 100$). Dashed lines indicate the relationship between the maximums and the attack density.

density for the maximum production of eggs in *I. cembrae*.

Effect of attack density on production of offspring adults

Since the relationship between emergence holes and offspring adults in *I. cembrae* at different attack densities has not been established, the density of emergence holes cannot be used as a valid estimate of the offspring adults. Instead, the number of pupal chambers is used (Table 1). An exponential equation:

$$Y_p = 51{\cdot}64e^{-0{\cdot}115X},\ r^2 = 0{\cdot}99 \qquad \text{eqn 6}$$

best describes the relationship between the two variables, where Y_p represents the number of pupal chambers per egg gallery and X is the attack density (Fig. 5). Thus, the production of offspring adults declines exponentially with attack density.

Let Y_a represent the number of offspring adults in a bark area of $0{\cdot}1\,m^2$, then:

$$Y_a = 3Y_pX = 154{\cdot}9(e^{-0{\cdot}115X})X \qquad \text{eqn 7}$$

In order to find the maximum value of Y_a, where an optimal density exists, the derivative of the curve is taken:

$$Y'_a = 154{\cdot}9e^{-0{\cdot}115X}(1 - 0{\cdot}115X) \qquad \text{eqn 8}$$

Then when $Y'_a = 0$ there are only two possible solutions:

$e^{-0{\cdot}115X} = 0$, $X = \infty$(no solution); $1 - 0{\cdot}115X = 0$, $X = 8{\cdot}7$ attacks per $0{\cdot}1\,m^2$.

This means that Y_a has a maximum when X is 8·7 (8·5–8·9, 95% CI) attacks per $0{\cdot}1\,m^2$, i.e. $Y_a = 496$ (482–506, 95% CI; Fig. 4, lower curve). In Fig. 4 the number of offspring adults per bark area sharply increases as attack density increases in the lower density range but after the optimal density of 8·7 attacks per $0{\cdot}1\,m^2$ is reached, the offspring production gradually decreases with further increases in attack density.

Effects of attack density on egg to adult mortality

The percentage mortality from egg to offspring adult at different attack densities can be computed by dividing the offspring adult equation (7) by the egg equation (4), and subtracting the ratio from 100. Let Y_m represent the percentage mortality, then:

$$Y_m = 100 - Y_a/Y_n = 100 - 84{\cdot}7e^{-0{\cdot}043X}$$
(Fig. 6) eqn 9

The equation shows that the mortality from egg to adult exponentially increases with attack density.

As indicated above, the fecundity of parent females and survival percentage of the offspring decreases with density. However, it is important in the population dynamic analysis to know at what attack density the output of offspring adults in a certain bark area is equal to or less than the input of parent adults. Let R represent the ratio of offspring adults to parent adults in a bark area of $0{\cdot}1\,m^2$, then:

$$R = Y_a/4X = 38{\cdot}73e^{-0{\cdot}115X} \qquad \text{eqn 10}$$

Let $R = 1$, then $X = 31{\cdot}8$ attacks per $0{\cdot}1\,m^2$ (30·6–32.8, 95% CI). This indicates that the output of offspring adults is equal to the input of parent adults when the attack density reaches 32 per $0{\cdot}1\,m^2$ (upper

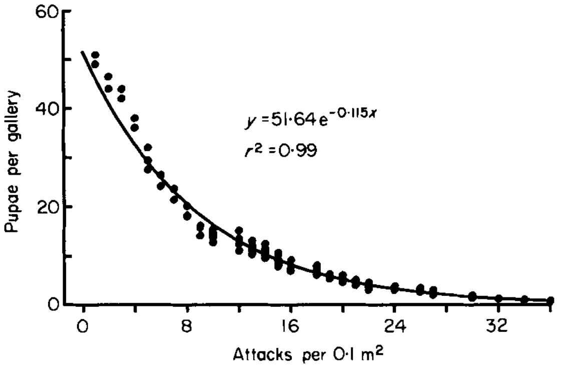

Fig. 5. Effect of attack density on pupae per gallery in *Ips cembrae* ($n = 100$).

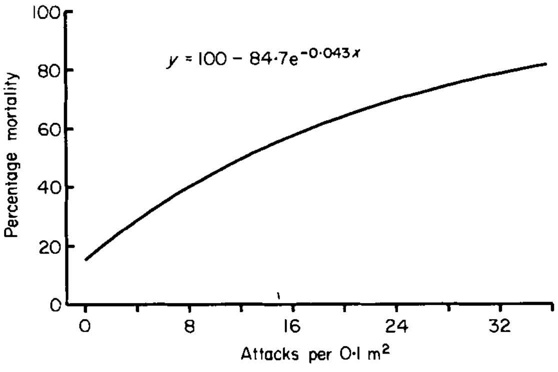

Fig. 6. Effect of attack density on the egg to adult mortality in *Ips cembrae*.

threshold density). At higher parental densities the output of offspring is less than the input of parents.

Discussion

The results of the analyses demonstrate that gallery length, egg niches per gallery, offspring adults per female, and mortality from egg to adult in *I. cembrae* are directly influenced by attack density in the absence of host resistance. Intraspecific competition mainly includes exploitative competition of larvae for food resources, possible cannibalism, and the interference among parent adults for breeding space. In *I. cembrae* and other bark beetles, intraspecific competition causes a decrease in adult fecundity and an increase in offspring mortality (Raffa & Berryman 1983; Anderbrant *et al.* 1985; Jactel & Lieutier 1987; Anderbrant 1990). The length of the egg gallery of *I. cembrae* declines exponentially with attack density (Fig. 1), this phenomenon may be attributed to competition between parent adults for limited breeding space such that females have insufficient room for gallery extension. *I. cembrae* is among the larger in size (4·9–6·0 mm long) of *Ips* species so it would be expected that relatively less progeny could be supported by the phloem than for smaller sized bark beetles.

In *I. sexdentatus* (5·5–8·2 mm long), the largest European species, egg gallery length and numbers of eggs also declined exponentially with increase in attack density (Jactel & Lieutier 1987). It has also been observed in the European spruce bark beetle, *I. typographus* (4·2–5·5 mm), that females turn their galleries in order to avoid contact with other galleries of females or of a competing bark beetle, *Pityogenes chalcographus* (Byers 1989b). The turning away from other galleries would tend to obstruct egg laying and gallery elongation.

The exponential decline in fecundity of females as attack density increases (Fig. 3) reflects the positive linear relationship between number of eggs and the length of the egg gallery (Fig. 2). An optimal attack density (13·9 attacks per 0·1 m^2) at which the number of eggs laid in this bark area is maximized (935) was obtained from the derivative of the exponential regression analysis (Fig. 4). The optimal density is dependent on the condition of the host tree, which in this case could offer no resistance as the trees were felled after being scorched by fire.

The number of offspring adults produced per female decreased with breeding density, especially in the lower density range. The relationship can be described by a declining exponential curve (Fig. 5). The decline with increasing attack density is due partly to decreasing oviposition caused by a shorter gallery (Figs 1–3) and partly to increased mortality (Fig. 6). The number of offspring adults is maximized (496) when breeding density reaches 8·7 attacks per 0·1 m^2. This can be considered an optimal attack density for individuals in a population on the bark area since this is the maximum of offspring output. Experiments with *I. typographus* at five densities on Norway spruce bolts in the laboratory showed an optimal of offspring production at an attack density of about 30 per 0·1 m^2 (Anderbrant *et al.* 1985). The differences in optimal density estimates for the two species can be due to size (*I. typographus* is smaller), in addition to obvious biological and experimental conditions.

The number of offspring of *I. cembrae* emerging from the bark will be less than the input of parent adults when the attack density is greater than 32 attacks per 0·1 m^2. If all beetles breed at densities greater than this upper threshold then the population declines. It is not necessarily maladaptive that certain beetles choose to breed at these above-threshold densities since some offspring are still produced. The risks for some individuals of not finding other more suitable breeding areas may be sufficiently great (e.g. low fat reserves) that it is in their interests to continue breeding in the high density areas. However, other stronger individuals should choose to leave these areas in order to avoid severe competition.

Individual bark beetles have mechanisms that they use in several stages for reducing competition in colonized bark areas. The first stage is that males of *Ips* (*I. paraconfusus* and *I. typographus*) are more diffuse in their orientation to higher release rates of pheromone compared to the direct-path attraction of females (Byers 1983; Schlyter, Byers & Löfqvist 1987; Schlyter, Löfqvist & Byers 1987). This 'indirect' attraction of males to pheromone has also been observed in another polygynous bark beetle, *P. chalcographus* (Byers *et al.* 1988). Thus, many bark beetle species probably can ascertain the colonization density before landing simply by the magnitude of the pheromone concentration. This mechanism can in principle also operate after landing. In fact, walking males of *I. paraconfusus* were inhibited in their orientation to pheromone by high release rates of their pheromone components, while females were not (Byers 1983).

The second stage for avoidance of high attack densities may occur after landing, resulting in a spacing apart of attacks. This phenomenon has been found in several bark beetle species (cf. Byers 1984). Using a computer program, a minimum allowed distance (*MAD*) of spacing between attacks has been calculated for *I. typographus* to be 2·5 cm. The *MAD* is a behavioural inhibition distance that is characteristic of each species (Byers 1984). The mechanisms for spacing and *MAD* are not known, but several hypotheses have been suggested such as acoustic (in species which stridulate), pheromonal (as above), or visual/chemotactic inspection (Byers 1984). Bark structure may also influence the attack distribution in some species (Safranyik & Vithayasai 1971); and in *I. cembrae* this appears to be the case since adults prefer the deep furrows in the bark for attack sites (personal observations). This behavioural mechanism would tend to uniformly distribute or space the attacks, as long as spacing occurred within the crevice, and also allow a more rapid penetration into the tree.

In Fig. 4, the differences between the egg and adult curves can be attributed to mortality caused by larval competition and natural enemies. Because the mortality caused by natural enemies varied only between 20 and 25% at all attack densities (Q.H. Zhang, unpublished), the differential effects of natural enemies at different attack densities should have been negligible. Since the percentage mortality from egg to adult exponentially increased with attack density, it can be concluded that both fewer eggs per female and higher larval mortality contribute to the dramatic density effect on offspring production. In *I. typographus*, larval gallery length is linearly related to pupal dry weight, indicating that movement of larvae is primarily to acquire food and that under crowded conditions mortality is higher (DeJong & Grijpma 1986).

The final stage for avoiding competition is re-emergence at higher attack densities. The European *I. typographus* and *I. sexdentatus* as well as the American southern pine beetle, *Dendroctonus frontalis*, exhibit earlier re-emergence from the bark when at higher attack densities (Mayyasi *et al.* 1976; Wagner *et al.* 1981a, b; Jactel & Lieutier 1987; Anderbrant 1988, 1989). However, it has not been shown whether the adult re-emergence phenomenon as reported in other bark beetles could be one of the breeding strategies in *I. cembrae* in China.

It must be pointed out that the conclusions in the present study were obtained only in the absence of host resistance. When beetles attack living trees at relatively low densities, the eggs and larvae face a risk of being killed by the exudation of resin, and thus one could expect the survival to increase with density up to a point determined by the vigour and resin flow of the tree, as indicated by Berryman (1974), Raffa & Berryman (1983) and Mills (1986). It is also possible that females lay fewer eggs if the resin content of the phloem/xylem substrate is high, which may further decrease reproductive output at very low densities as discussed by Anderbrant (1990). To date, the effects of density on offspring production in *I. cembrae* in standing, healthy trees remain unknown.

Outbreaks of bark beetles are thought to occur primarily due to an imbalance between host tree resistance and population density of attacking parent bark beetles (Berryman & Stenseth 1989). Host tree resistance to bark beetles is lowered by fire and/or drought conditions (Raffa & Berryman 1983; Geiszler, Gara & Littke 1984; Miller, Whitney & Berryman 1986; Bakke 1989). The optimum method and results presented here can be applied to predict the potential for an outbreak of *I. cembrae* in host stands of low resistance (drought or fire). Attack densities on the bark can be sampled extensively since they are relatively easy to count, compared to counting egg, larval, and pupal densities. These attack density estimates then could be used with the density-dependent relationships found here to aid in predicting the population density of the attacking beetles in the next generation, and thus the potential for an outbreak.

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