

## Relationships between catches in flight and emergence traps of the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Col.: Scolytidae)

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### ABSTRACT

Daily emergence of the mountain pine beetle from lodgepole pine trees was monitored in the field by using caged bolts and by counting emergence holes on standing trees. Flying mountain pine beetles, pine engraver beetles and *Pityogenes plagiatus knechteli* (Swaine) were captured daily in two types of barrier traps. Daily totals of emergence holes and emergence into cages were moderately correlated with daily captures by both types of barrier traps. A simple model of daily emergence was developed based on estimates of brood density, daily proportions of brood adults, and daily proportions of brood adults ready to emerge. Daily catches of pine engravers and *P. plagiatus knechteli* were highly intercorrelated, but correlations with catches of mountain pine beetle were low for both species. The results are discussed in relation to beetle emergence and flight behaviour.

### INTRODUCTION

The onset and timing of the emergence of mountain pine beetles, *Dendroctonus ponderosae* Hopkins or mpb, depend on a number of factors. In combination, the distribution in time of attacks by the parent beetles and accumulation of heat above the temperature threshold for development (Bentz *et al.* 1991, Safranyik 1978, Safranyik and Whitney 1985), are the major determinants of the life-stage distribution of broods. Moisture conditions during adult maturation are also important because new adults need a period of feeding of up to 10 days (more during cool, rainy weather). Mature beetles begin emerging when ambient temperatures reach about 16°C (Reid 1962, Schmid 1972, Billings and Gara 1975) and the emergence rate increases with temperature up to about 30°C (Rasmussen 1974). Above 30°C, both hourly and daily emergence decline. As a consequence of these relationships, once emergence has started, and the age structure and density of broods are known, the diurnal pattern of emergence during the flight period (i.e., relative frequencies of emerged beetles per unit of time during the day) can be predicted based on heat accumulation above the temperature threshold for emergence (Safranyik *et al.* 1989).

Traps or host materials are often used to monitor bark beetle emergence and flight activity, sometimes in combination with population aggregation pheromones. Trapping can provide relative measures of populations or expected damage levels (Brown 1977, Lie and Bakke 1981, Hübertz *et al.* 1991). A variety of trap types have been used for trapping the beetles, both when flying (e.g. barrier and funnel traps, sweep nets) and emerging (e.g. emergence cages, sleeve traps) (Chapman and Kinghorn 1955, Avis 1971, Hines and Heikkinen 1977, Hosking 1979, Lindgren 1983, Schmitz 1984, Safranyik and Linton 1985). Emergence holes may also be counted to monitor daily or seasonal emergence.

A high positive correlation between the number of beetles emerging and numbers flying in a given period is implicit in the use of flight traps for monitoring emergence or population levels. Spatial and temporal variations in emergence behaviour are common results of differences in attack history, tree and site conditions, weather factors, and the distribution and abundance of suitable host materials. The design, density, and deployment (location and timing) of traps are important factors affecting the strength of the association between trap catches and emergence or population levels.

The objectives of this study were to:

- a) describe the relationship between daily captures of flying mpb in passive barrier traps and daily emergence from caged bolts;

- b) develop an empirical model of mpb emergence density based on temperature, pre-emergence density and age structure of broods;
- c) relate the emergence pattern of two common associates of mpb, *Ips pini* (Swaine) (pine engraver beetle or peb), and *Pityogenes plagiatus knechteli* (Swaine) (ppk) to temperature and the emergence pattern of mpb.

The results and discussion concentrate on mpb, as it is the primary pest species. Peb and ppk are normally secondary attackers, usually incapable of successfully attacking a healthy host. They normally infest mpb attacked trees, or trees weakened by some other agent.

## MATERIALS AND METHODS

The study area was located approximately 100 kilometers west of Williams Lake, B.C., near Tsh Lake. The site was generally flat, uniformly forested, 5.86 ha in area, with about 2 ha of 2-3m high esker-like ridges in the southeast portion. Within the stand were three groups of 15-20 mature lodgepole pine *Pinus contorta* var. *latifolia* Dougl. attacked in 1984 and containing brood mpb which would mature and emerge in the summer of 1985. The three groups occupied the corners of a triangle of about 100 m per side. The study area was surrounded on three sides by open meadows 10-40 m wide, and on the fourth side by an immature (<40 yr. old) lodgepole pine stand containing a few veteran Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Within the study area, the tree cover averaged 592.3 stems  $\geq 5$  cm dbh per ha, which consisted of 83% lodgepole pine, 11% engelmann spruce (*Picea engelmannii* Parry) (mainly in depressions), and the balance scattered Douglas-fir and aspen (*Populus tremuloides* Michx.). The average age of the pine in 1985 was 102 years with an average DBH of 25.02cm. All trap installations were completed by the last week of June 1985.

Two types of passive (unbaited) barrier traps were used. Six pairs of nondirectional traps were hung from uninfested pine trees at 60° intervals surrounding each group of infested trees. These were similar to traps described in Schmitz *et al* (1980), and had four 15X30 cm barriers at right angles to each other above a funnel leading to a single collecting jar. They were suspended from ropes so that the bottoms of the barriers were 2 m above the ground. In addition, four larger (90X150cm) unidirectional traps were hung in the approximate center of each group of infested trees. These large traps were suspended from poles between trees in such a way that one trap in each group faced each cardinal direction, and would thus capture insects flying from that direction. The lower edges of the large barriers were also 2 m above the ground.

One bolt, 35 cm long, was cut from the base of each of six pines infested in 1984. The bolts were then placed in individual window screen emergence cages placed near the stumps from which the bolts were cut in order to observe daily emergence of mpb. The 35 cm bolt length corresponded to the depth of the previous winter's snow; above that virtually all of the mpb were killed during the winter (the mean maximum height at which live larvae were found was 53 cm (Safranyik and Linton 1991)).

A .5 m wide band extending from the duff line to the height of the estimated snow depth during the previous winter on each of four 1984 infested trees in one group was painted with light-colored latex paint to enhance the visibility of newly-made exit holes (Safranyik and Linton 1985). In order to exclude them from the 1985 counts, all existing exit/entrance holes were marked before 1985 emergence began. Three times during the flight period, 15X15 cm bark samples were removed from eighteen 1984 infested trees and the brood examined to determine stage of maturity.

Insects were collected from all traps and new exit holes through the painted bands were counted and marked each morning from July 09 to August 10, and on August 12. The collections were preserved in 70% alcohol and stored until examined and counted. In the lab, the total captures of mpb, peb and ppk were recorded, and their sex determined.

Air temperatures were obtained using Campbell Scientific Instruments Ltd. model 201 thermistor sensors mounted in Stevenson screens. Underbark temperatures were taken using thermocouples inserted under the bark of the caged bolts. Data were recorded on a Campbell Sci-

entific Instruments Ltd. CR-21 data logger having a ten second scan rate, outputting summary statistics every 30 minutes. Degree-days were calculated by counting the number of hours when the air temperature exceeded 16°C and dividing the sum by 24.

The relationship between catches of beetles in flight traps and emergence traps was analysed using regression and correlation analysis. A general model of daily mpb emergence was developed based on attack and emergence behaviour, and the effects of temperature on maturation, emergence and flight activity. Model parameters were estimated from field data.

## RESULTS AND DISCUSSION

### A model of beetle emergence

The following empirical model for daily emergence ( $E_k$ ) is based on estimates of pre-emergence brood density ( $D$ ), daily proportions of the unemerged brood that are mature (tanned) adults ( $P_k$ ), and daily proportions of the mature brood adults ready to emerge ( $Q_k$ ). The following is a brief description of model development. For the 1st, 2nd and 3rd days of emergence, the corresponding numbers of emerged beetles ( $E_{i=1,3}$ ) are given by the series  $DP_1Q_1$ ,  $(D-DP_1Q_1)P_2Q_2$ , and  $(D-DP_1Q_1)(D-DP_1Q_1)P_2Q_2)P_3Q_3$ , respectively. It can be shown that these series can be written in the following equivalent forms to express emergence on any given day  $K$  in terms of  $D$ ,  $P$  and  $Q$ .

$$E_k = D \left[ \sum_{i=0}^{k-1} (1 - P_i Q_i) \right] P_k Q_k \quad (1a)$$

$$E_k = (D - \sum_{i=1}^{k-1} E_i) P_k Q_k \quad (1b)$$

Equation (1b) is more transparent since it is readily seen that  $E_k$  is simply the product of unemerged brood density (the terms inside the brackets) and the values of  $P$  and  $Q$  for day  $K$  following the onset of beetle emergence. An empirical formula was developed for estimating  $P_k$  ( $\hat{p}_k$ ) as a function of time ( $T$ ) in days since the first occurrence of young adults (assumed to be July 1), based on sampling 18 infested trees 3 times during the study period.  $P_k$  was a hump-backed function on  $T$  in the experimental area because some parent beetles that survived the winter extended their galleries and laid more eggs in late May-early June of 1985 which resulted in a highly skewed brood age distribution. Consequently, as the brood resulting from eggs laid in 1984 matured and emerged, the young larvae from eggs laid in the spring of the current year constituted the bulk of the unemerged broods. Hence,  $P_k$  at first increased on  $T$  and later declined. When mpb flight is not protracted and all eggs hatch before the onset of winter the relationship curve between  $P_k$  and  $T$  is sigmoid (Bentz *et al* 1991). Equation (2) was developed by plotting both the mean of  $\hat{p}_k$  and the mean proportion of 1984 broods ( $Z$ ) over the corresponding  $T$ -values for each of the three sampling times. A sigmoid curve (Bentz *et al* 1991) was fitted by eye to the  $P_k$  vs  $T$  relationship (the expression inside the first set of square brackets on the right side of eqn (2)) and the parameters were determined by graphical analysis. The expression inside the second set of square brackets on the right hand side of eqn (2), also fitted by graphical analysis, represents the relationship between  $z$  and  $t$ .

$$\hat{p}_k = [(0.0131)/(0.01 + 0.99 \exp(-0.28t))] [1 - \exp(-5.36 + 0.16t)] \quad (2)$$

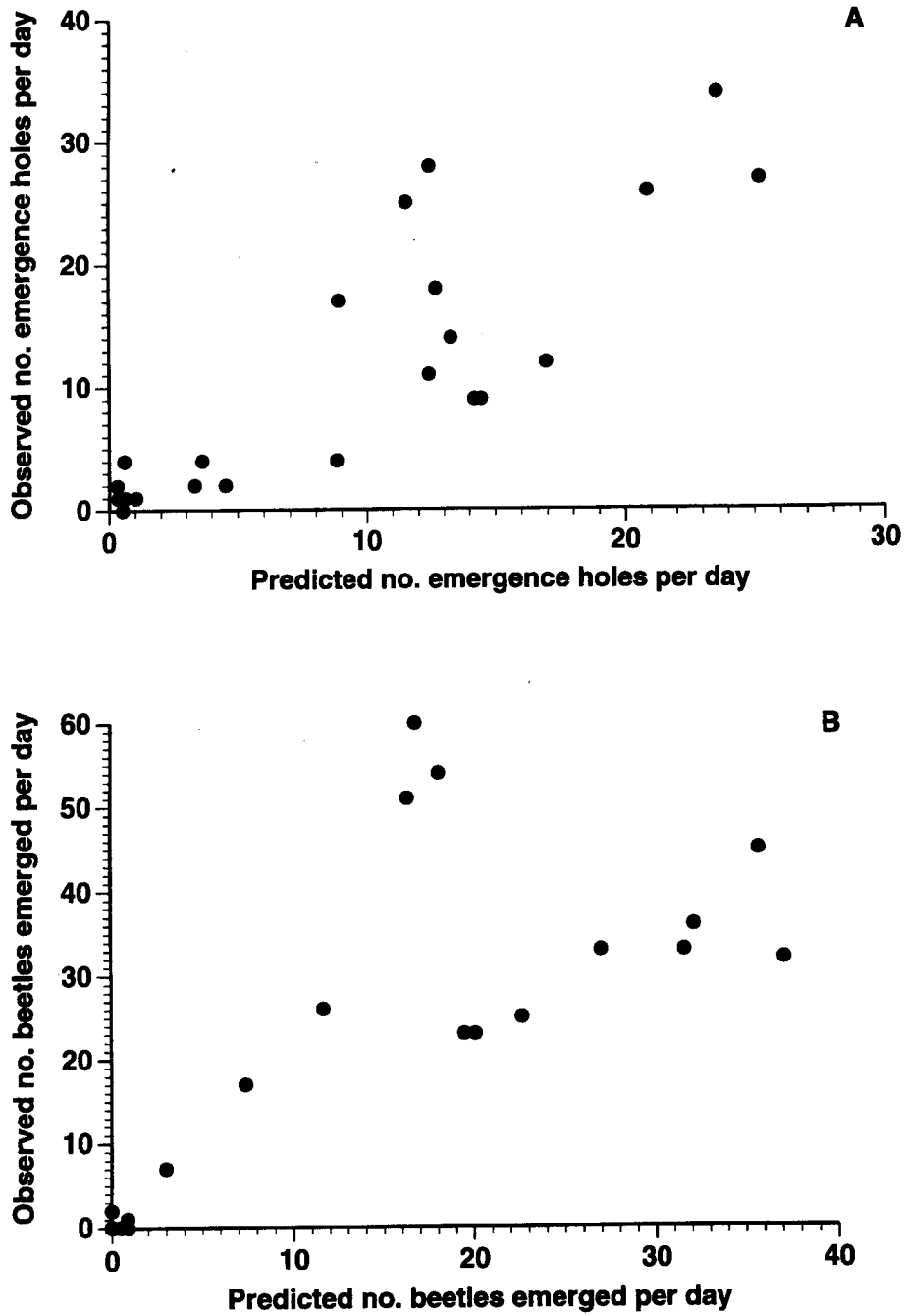
$$t > 33, \hat{p}_k = 0$$

$q_k$  was estimated ( $\hat{q}_k$ ) as a function of daily degree-days ( $h_k$ ) above a threshold of 16°C:

$$\hat{q}_k = (1/6)h_k, \quad h_k \leq 6$$

$$\hat{q}_k = 1, \quad h_k > 6 \quad (3)$$

This formula was used for simplicity, recognizing that most mature adults emerged when daily maximum temperatures were near or above 25°C.



**Figure 1.** Relationship between observed daily accumulation of emergence holes (A) and beetle emergence (B) for the mountain pine beetle and predicted density from eqn. 1. Estimates of  $Q_k$  in eqn. 1 were based on ambient temperature data from Tshu Lake 1985.

The numbers of beetles (720) under the bark of 6 caged trees (lower boles, total bark area 4.05 m<sup>2</sup>) and the number of emergence holes (362) on the painted areas of 4 trees were used as estimates of  $D$  in conjunction with eqns (2) and (3) to model daily emergence and daily accumulations of emergence holes ( $E_k$ ) during 23-days from July 9 to July 31, inclusive. Both ambient and underbark temperatures were used in eqn (3) to model emergence. Estimates of  $E_k$  from eqn. 1 were regressed on corresponding observed  $E_k$ -values (regression was conditioned to have 0 intercept) to assess the performance of the model (Fig. 1). The slopes ( $b$ ) of regressions of observed vs predicted daily counts of emerged beetles were comparable and were not significantly different from unity ( $p > 0.05$ ) when either ambient ( $b = 1.056$ ) or underbark temperatures ( $b = 1.042$ ) were used in calculating  $Q_k$  in eqn 2. The corresponding coefficients of determination ( $r^2$ ) were 0.685 and 0.638. The corresponding statistics for predicting daily accumulations of emergence holes were ( $b = 1.107$  and  $1.132$ ) and ( $r^2 = 0.781$  and  $0.787$ ). The fit of the model to the daily beetle emergence and emergence hole data is satisfactory considering that  $P$  was estimated from observation of beetle maturation only on three occasions and a limited number of samples, and that the formula for  $Q$  (eqn. 3) was derived from conceptual relations between heat accumulation and beetle emergence. However, in addition to these factors, the variation between observed and predicted values in Fig. 1 could have been affected by formulation of the model. In particular, in eqn 1, the fate of those mature beetles that did not emerge in any given day owing to inadequate heat accumulation (as estimated by eqn 3) is not considered explicitly. Therefore, even if  $Q$  was modelled very precisely, eqn 1 would tend to underestimate daily beetle emergence, especially following days for which the value of  $Q$  was less than 1. This problem of model formulation needs further research.

#### Comparison of mpb emergence, trap catches and trap types

Daily emergence of mpb/m<sup>2</sup> of bark from caged trees ( $Y_c$ ), daily catches/m<sup>2</sup> of trap area in large barrier traps ( $Y_e$ ) and smaller barrier (flight) traps ( $Y_f$ ), were all linearly related to daily emergence hole numbers per m<sup>2</sup> ( $X$ ) on the painted trees. The respective equations were as follows:

$$Y_c = 0.1507 + 0.4155X \quad (4)$$

$n = 26, r^2 = 0.693, S_{yx} = 2.540$

$$Y_e = 0.4275 + 0.0148X \quad (5)$$

$n = 22, r^2 = 0.090, S_{yx} = 0.426$

$$Y_f = 0.5031 + 0.0580X \quad (6)$$

$n = 26, r^2 = 0.239, S_{yx} = 0.670$

$$Y_f = 0.0619 + 0.1935 Y_e \quad (7)$$

$n = 25, r^2 = 0.155, S_{yx} = 0.215$

Regression eqns (4), (6) and (7) were statistically significant; the first two at the 99% and the third at the 95% probability level. However, with the exception of eqn (4), only up to about 24% of the total variation in the respective independent variables was explained by the regression equations. The intercepts of regressions (5) and (6) were significantly different from 0 at the 99% and 95% probability levels, respectively.

Excluding variation in daily counts of emergence holes and emerged beetles due to experimental techniques, these two variables are normally highly correlated but have a non-linear relationship (Safranyik and Linton 1985). However, when they were measured on different samples, as was done in our experiment, differences in host characteristics, attack history and microclimate were reflected in different rates of beetle emergence among infested hosts. The reliability of emergence hole counts may be affected by the presence of holes made by other species of subcortical insects. Moreover because of differences in underbark and ambient temperatures, the beetles may cut emergence holes up to several days before they emerge. For these reasons, when measured on small and separate samples, the densities of emerged beetles and emergence holes will normally have only moderate correlation.

Emerged beetles may disperse over large areas and search for suitable hosts to attack. Con-

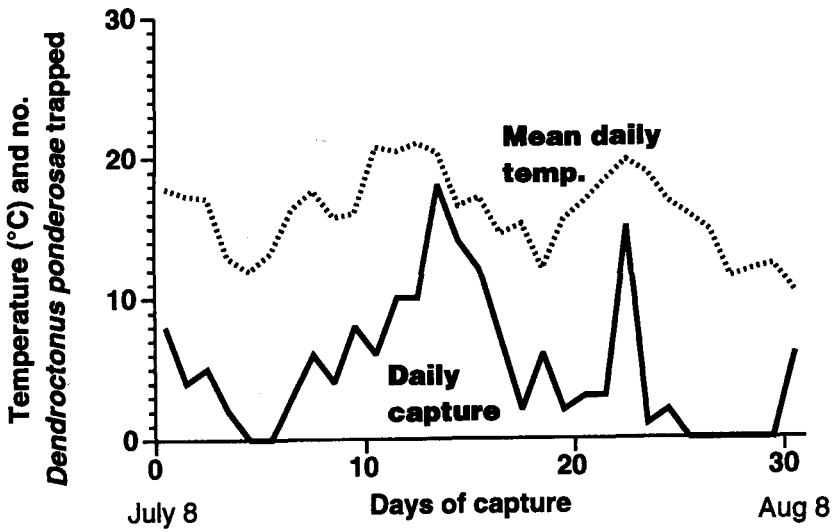


Figure 2. Mean daily temperature and daily capture of mountain pine beetle in passive barrier traps, Tsuh Lake, 1985.

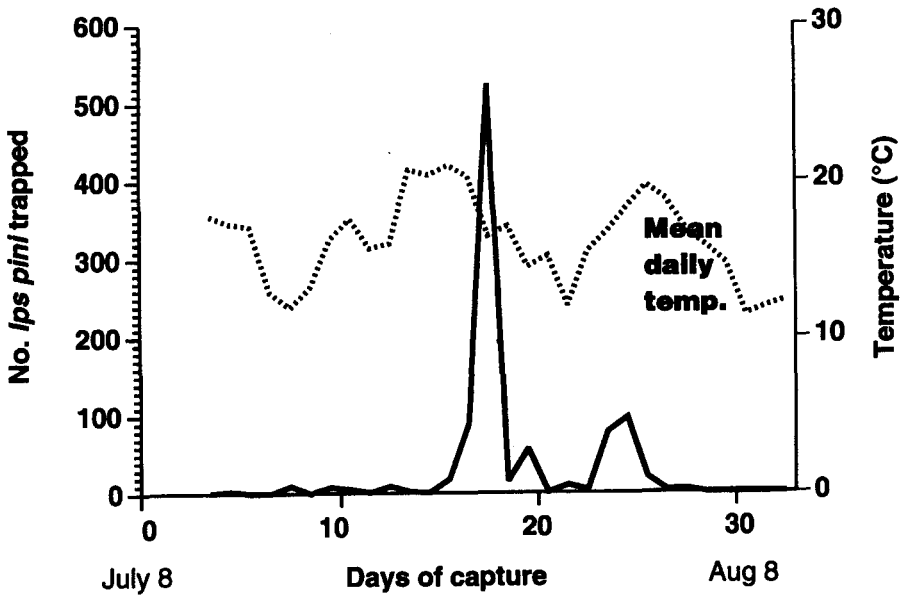


Figure 3. Mean daily temperature and daily capture of pine engraver beetles in passive barrier traps, Tsuh Lake, 1985.

sequently, it is likely that most passive barrier traps sample the beetle population of a large area. Therefore, unless emergence or emergence holes were monitored over the same general area and sampling intensity was high, passive trap catches may be poorly correlated with these variables.

Although the experiments spanned 22-26 days of observation, the samples for beetle emergence and emergence holes were based on only 6 bolts and 4 trees, 36 small barrier traps (eqn 6) and 12 large barrier traps (eqn 5). These small sample sizes notwithstanding, the correlations between daily emergence holes and trap catches were unexpectedly low (eqns 5 and 6). Further studies are needed to determine whether catches in passive barrier traps should be used for monitoring beetle emergence. Likewise, the low correlation between catches in the two types of barrier traps (eqn 7) indicate that results from experiments using different trap designs may not be directly comparable.

#### Emergence and flight of mpb, peb and ppk.

During the study, 194 mpb, 681 peb and 1171 ppk were trapped. Daily capture of mpb (Fig. 2), peb (Fig. 3) and ppk (Fig. 4) during a 37-day period varied with average temperatures (Fig. 2). The greatest catches of all three species occurred following a period when average daily temperature was greater than 20°C for at least 3 consecutive days (Fig. 2). Daily maximum temperatures during the same period ranged from 31.8 to 34.3°C. Catches of mpb were broadly distributed throughout the observation period whereas catches of the other two species peaked sharply on July 15, a day later than peak mpb catch, and then declined (Figs. 2-4). Daily catches of ppk and peb were highly correlated ( $r=0.89$ ,  $N=25$ ). On the other hand, the correlation between daily catches of ppk and mpb was not significant ( $r=0.31$ ,  $N=25$ ) and that between peb and mpb was barely significant at  $p<0.05$  ( $r=.40$ ,  $N=25$ ). The asynchrony of catches of mpb and the other two species is probably a consequence of differences among the species in emergence and flight in relation to temperature. For mpb, daily degree-day accumulation above a threshold temperature of 16°C was not significantly correlated ( $p>0.05$ ) with daily trap catches ( $r=0.30$ ,  $n=25$ ), daily emergence from caged bolts ( $r=0.10$ ,  $n=25$ ) or with daily accumulation of

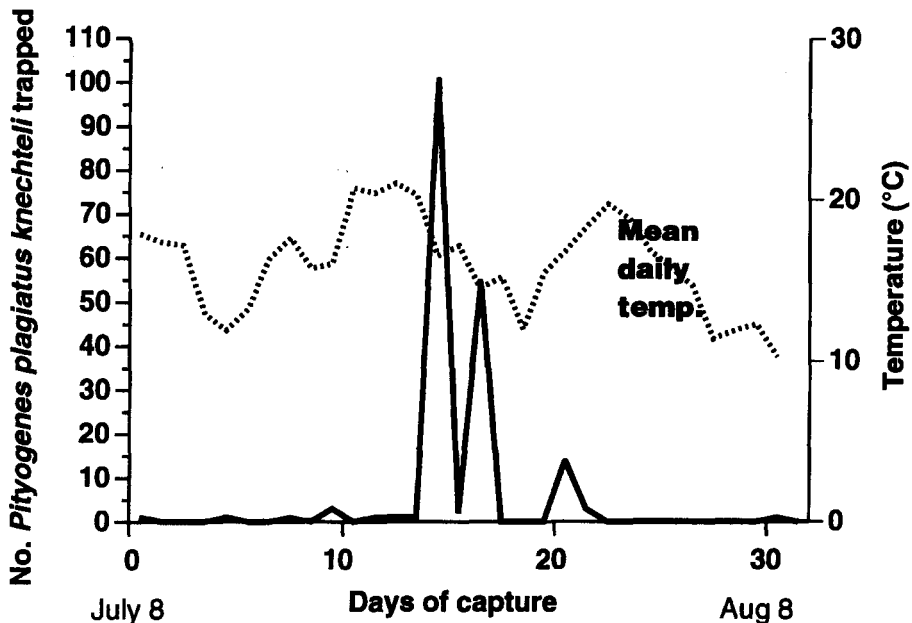


Figure 4. Mean daily temperature and daily capture of *Pityogenes plagiatus knechteli* in passive barrier traps, Tshuh Lake, 1985.

emergence holes on sample trees ( $r=0.35$ ,  $n=25$ ). There is no information on the other species regarding temperature thresholds and heat unit requirements for emergence and flight activity.

In British Columbia, particularly in the Cariboo region, peb produces 1 or 2 generations per year, depending on spring and summer temperatures. The first flight, made by overwintering adults emerging from the duff normally occurs during May and early June, and the second flight, made by reemerging parents plus their brood normally occurs during July-August (Reid 1955). Therefore, the beetles trapped in our experiments were mostly reemerged and first generation beetles. Ppk overwinters both in adult and immature stages (Reid 1955). It appears that during the experimental period, most of the dispersing mature adult pine engravers and ppk originated from broods of parents that overwintered in the adult stage. The mpb trapped were part of the main flight of brood adults that developed in a 1-year life cycle.

The overall female ratio ( $\pm$  one standard deviation) was 0.68 ( $\pm 0.051$ ) for mpb, 0.76 ( $\pm 0.041$ ) for peb and 0.91 ( $\pm 0.069$ ) for ppk. These ratios did not change significantly during the study period. There was no significant difference ( $p > 0.05$ ) between the female ratios for mpb and peb from those reported from field populations (0.67 for mpb (Reid 1962, Safranyik and Whitney 1985; 0.75 for *Ips pini* (Schmitz 1972)). There is no sex ratio information available for ppk. Ppk is, however, polygamous and 3 to 10 females may be associated with one male in gallery systems (Chamberlin 1958). Reid (1955) reported 4-6 egg galleries associated with one nuptial chamber in lodgepole pine slash in Alberta.

Our results indicate that daily rates of mpb emergence can be reliably modelled based on estimates of pre-emergence density, age structure, and daily heat accumulation above the flight threshold temperature. Sample-based estimates of mpb emergence hole densities are highly correlated with corresponding estimates of beetle emergence, indicating that the estimate are a reliable index. However, sample-based daily estimates of both these variables were poorly correlated with daily catches in passive barrier traps. Therefore, daily emergence patterns of mpb cannot be reliably inferred from daily captures in passive barrier traps. Daily flights of mpb, peb and ppk are all closely related to daily mean temperature; daily flights of the latter two species are highly correlated.

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## Effects of female mating status and age on fecundity, longevity and sex ratio in *Trichogramma minutum* (Hymenoptera: Trichogrammatidae)

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### ABSTRACT

Effects of female mating status and age of *Trichogramma minutum* Riley on its fecundity, longevity and offspring sex ratio were determined in the laboratory, using eggs of the variegated cutworm as hosts. Although the mating status of female *T. minutum* did not affect their total fecundity significantly ( $P > 0.05$ ), mated and unmated females showed different allocations of progeny. Mated females deposited significantly more eggs ( $P < 0.05$ ) than those unmated on the first day of exposure to hosts. On subsequent days, however, unmated females parasitized significantly more hosts ( $P < 0.05$ ) than those mated. Mated females laid 82.4% of their total fecundity on the first day of oviposition, whereas unmated females laid 58.3%. The number of eggs parasitized by both groups of females decreased significantly ( $P < 0.05$ ) with parasitoid age. Unmated females lived longer ( $P < 0.05$ ) than their mated counterparts. No significant differences ( $P > 0.05$ ) in clutch size (the number of parasitoid offspring produced per parasitized host) and emergence rate were found between the offspring of mated and unmated female parasitoids. The sex ratio of the offspring of mated females changed significantly ( $P < 0.05$ ) with maternal age: younger females produced a higher proportion of daughters than did older parasitoids. Unmated females produced male offspring only.