Life history of a secondary bark beetle, *Pseudips mexicanus* (Coleoptera: Curculionidae: Scolytinae), in lodgepole pine in British Columbia

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Abstract—*Pseudips mexicanus* (Hopkins) is a secondary bark beetle native to western North and Central America that attacks most species of pine (*Pinus* L. (Pinaceae)) within its range. A pair of life-history studies examined *P. mexicanus* in other host species, but until now, no work has been conducted on lodgepole pine (*Pinus contorta* Douglas *ex* Louden var. *latifolia* Engelm. *ex* S. Watson). *Pseudips mexicanus* in lodgepole pine was found to be polygynous. Galleries were shorter, offspring smaller, and the eggs laid per niche and the potential progeny fewer than in populations from California and Guatemala. Development from the time of female attack to emergence of adult offspring took less than 50 days at 26.5 °C, and the accumulated heat required to complete the life cycle was determined to be 889.2 degree days above 8.5 °C, indicating that in the northern portion of its range *P. mexicanus* is univoltine. Determination of these life-history traits will facilitate study of interactions between *P. mexicanus* and other bark beetle associates in lodgepole pine.

Résumé—*Pseudips mexicanus* (Hopkins) est un scolyte de l'écorce secondaire, indigène de l'ouest de l'Amérique du Nord et de l'Amérique centrale, qui attaque la plupart des espèces de pins (*Pinus* L. (Pinaceae)) dans son aire de répartition. Deux études ont examiné le cycle biologique de *P. mexicanus* chez d'autres espèces d'hôtes, mais à ce jour, aucun travail n'a été réalisé sur le pin tordu (*Pinus contorta* Douglas *ex* Louden var. *latifolia* Engelm. *ex* S. Watson). *Pseudips mexicanus* est polygyne sur le pin tordu. Les galeries sont plus courtes, les rejetons plus petits, et les oeufs pondus par niche et la progéniture potentielle moins nombreux que dans les populations de Californie et du Guatemala. Le développement depuis l'attaque des femelles jusqu'à l'émergence des rejetons adultes prend moins de 50 jours à 26,5 °C et la chaleur accumulée nécessaire pour compléter le cycle biologique est estimée à 889,2 degrés-jours au-dessus de 8,5 °C, ce qui indique que *P. mexicanus* est univoltin dans la partie nord de son aire de répartition. La détermination de ces traits du cycle biologique facilitera l'étude des interactions entre *P. mexicanus* et les autres scolytes de l'écorce qui lui sont associés sur le pin tordu.

[Traduit par la Rédaction]

Introduction

One of the approximately 50 species of bark beetles (Coleoptera: Curculionidae: Scolytinae) that use lodgepole pine, *Pinus contorta* Douglas *ex* Louden var. *latifolia* Engelm. *ex* S. Watson (Pinaceae), as a host (Bright 1976) in western Canada is *Pseudips mexicanus* (Hopkins). Previously known as *Ips mexicanus* (Hopkins), it in-

fests lodgepole pine throughout the distribution of that tree species, which ranges from Alaska to Guatemala (Bright 1976; Wood 1982). It attacks unthrifty trees (Trimble 1924) and is not considered an economic pest in Canada. However, *P. mexicanus* is often found co-inhabiting the bases of trees with endemic or low populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Safranyik and Carroll 2006),

an eruptive bark beetle species currently in outbreak across British Columbia and parts of Alberta. Although *D. ponderosae* has been studied extensively, especially in the epidemic phase (Amman and Cole 1983; Raffa and Berryman 1983; Safranyik *et al.* 1999; Safranyik and Carroll 2006), little is known about the life history of *P. mexicanus*. Therefore, prior to examining any potential interaction of *P. mexicanus* with such species as endemic *D. ponderosae*, its life history must be understood.

Trimble (1924) examined some aspects of the basic biology of *P. mexicanus* (as *I. mexicanus*) in Monterey pine, *Pinus radiata* D. Don, in California (*e.g.*, sex ratio of attacking beetles, gallery construction, head-capsule sizes for each instar, duration of development for each life stage, and number of eggs laid per egg niche). Schwerdtfeger (1956) studied *P. mexicanus* (as *I. mexicanus*) in Mexican white pine, *Pinus ayacahuite* C.A. Ehrenb., in Guatemala and determined the length of time required for development from egg to adult. Struble (1961) expanded on Trimble's (1924) paper by commenting on predators, parasitoids, and potential measures for controlling *P. mexicanus* in California. Fox *et al.* (1991) examined the potential for *P. mexicanus* to vector the pitch canker fungus (*Fusarium subglutenans* (Wollenw. and Reinking) P.E. Nelson, Toussoun and Marasas) in Monterey pine in California.

The objective of this study was to determine the life-history characteristics of *P. mexicanus* in lodgepole pine in British Columbia. A field survey was conducted to examine attack and ovipositional characteristics; a complementary laboratory study examined development characteristics, voltinism, and number of larval instars. Additionally, this study determined that the biology of *P. mexicanus* in lodgepole pine differs from that of populations inhabiting other pine species in California and Guatemala.

## Materials and methods

Field study

To study the attack and ovipositional characteristics of *P. mexicanus*, infested trees were located in July 2005 by conducting a detailed survey of seven lodgepole pine stands totalling 28 ha. The stands were either pine-dominant or co-dominant and located at Angstad Creek (49°51′N, 120°46′W, mean elevation 1300 m), 28 km south of Merritt, British Columbia. Pine-dominant stands are characterized by a pine component of >50% of tree species present, with individual pine trees extending above the crowns of other species; in pine co-dominant stands the largest pines are of a similar height to surrounding trees species (Avery and Burkhart 2002). Diameter at breast height (DBH, 1.3 m above the ground), phloem thickness, and tree age were collected by randomly placing one variable-radius plot in each stand. A basal area factor 5 prism was used in all stands. For all pine trees, phloem thickness at DBH was recorded as the mean of two measurements, the first taken on the north side and the second on the east side. Phloem was removed using a 1.5 cm diameter cork punch and thickness determined to the nearest 0.1 mm using a microscope equipped with an ocular micrometer.

Trees infested with *P. mexicanus* (identified by the presence of fine-grained reddish boring dust on the trunk at the base of the tree) were located and assessed for damage (physical injury or infection), and their DBH, phloem thickness, and age were determined. The infested trees were harvested in September 2005 and the bark was peeled between 1.0 and 1.5 m from the base to confirm the presence of *P. mexicanus*. The bottom 1.0 m of the bole of each tree was taken to the Canadian Forest Service laboratory in Victoria, British Columbia. The ends of each log were sealed with paraffin wax to reduce desiccation and the logs were then stored at 4 °C until placement in individual rearing cages in March 2006 to allow resident beetles to complete their life cycle. Cages were constructed using 0.25 mm polyethylene mesh and were located in a greenhouse chamber kept at 20 °C. Emerging beetles were collected daily and stored in 70% ethyl alcohol until their sex was determined and pronotal width measured using a dissecting microscope equipped with an ocular micrometer. Other bark beetle species were also collected and identified (Bright 1976).

After beetle emergence was complete (*i.e.*, no emergence in any cage for >5 consecutive days), the bark was removed from the logs and the *P. mexicanus* galleries were examined in detail. Attack sites were examined for pitch exudation and evidence of necrotic lesions (which would indicate a defensive response by the tree upon attack (Reid *et al.* 1967; Nebeker *et al.* 1993)). The form of each gallery system was classified as either "ovipositional" (at least one gallery arm with egg niches (Fig. 1A)) or "amorphous" (numerous gallery arms with no evidence of egg laying (Fig. 1B)). For ovipositional galleries the

Fig. 1. (A) Amorphous gallery typical of overwintering *Pseudips mexicanus*. Note the absence of egg niches and the apparent randomness in gallery length and direction. (B) Ovipositional gallery of *P. mexicanus*. Note the distinctive shape of the gallery and the presence of egg niches (EN) on the outside of the curve (NC, nuptial chamber).
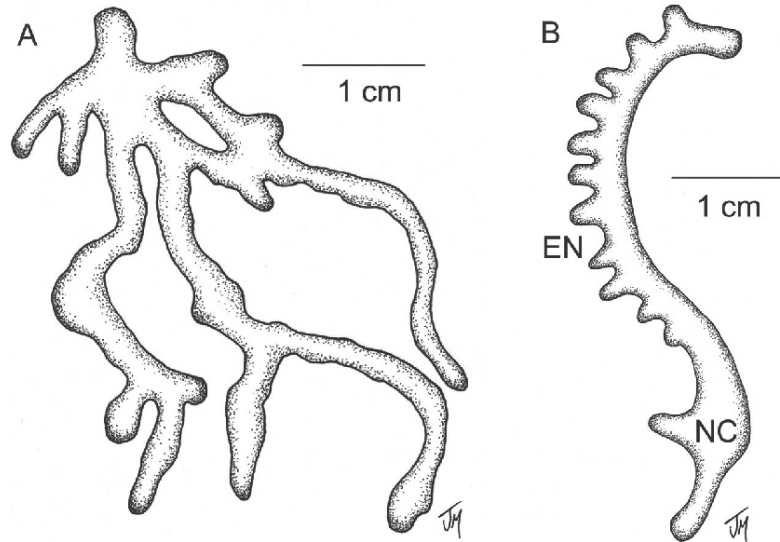
presence of a nuptial chamber, the number of ovipositional-gallery arms extending from the nuptial chamber, ovipositional-gallery length, and density of egg niches were recorded. The number of eggs laid per niche was determined by counting the larval traces originating from each of three egg niches randomly selected from 12 randomly selected galleries. The number of potential progeny was calculated by multiplying the mean number of eggs laid per niche by the mean number of niches per gallery. The sex ratio of attacking adults was not quantified exactly, as not all gallery systems contained adults when the logs were dissected. Following Trimble (1924), the sex ratio of attacking adults was estimated by assuming that one female created each gallery arm. One male was assumed to be present if a nuptial chamber was evident.

Additional qualitative observations of gallery form were made in early May 2005 on 10 trees mass-attacked by *D. ponderosae* in 2004 that were subsequently attacked by *P. mexicanus* in spring 2005. The trees mass-attacked by *D. ponderosae* were identified from the fading yellow crown and pitch tubes on the bole (Safranyik and Carroll 2006). The presence of fresh boring dust was used to locate *P. mexicanus* attacks and the lower 1.0 m of the bole was peeled *in situ* to reveal gallery systems. The presence of amorphous galleries with beetles in

residence was recorded but details of ovipositional galleries were not noted.

Laboratory study

Life-history characteristics of *P. mexicanus* were determined by rearing insects in lodgepole pine logs at different temperatures. The study was conducted in 2004 and repeated in 2005. Parent beetles used in the study were reared out of logs cut from infested trees at Angstad Creek as described above or collected from Lindgren funnel traps (Lindgren 1983) baited using 40 mg racemic ipsenol and ipsdienol bubble-cap lures (Phero Tech, Inc., Delta, British Columbia) with release rates of 0.4 and 0.2 mg/day, respectively, hung at Angstad Creek and Aberdeen Plateau (50°5′N, 119°11′W, elevation approximately 1300 m). Additional beetles were collected from the base of *D. ponderosae*-infested trees at Angstad Creek. Beetles were maintained alive until needed in vials containing moist paper towel and were mated within 8 days of emergence or collection.

Two healthy lodgepole pine trees were felled early in the summer of 2004 and three trees were felled in 2005 at Angstad Creek. Each tree had a DBH of approximately 20 cm. The lower 3 m of the bole was removed and cut into 20 cm long logs. The bark was scored vertically to the sapwood in a 1 cm wide strip on opposite sides of the log to create two separate resource patches.

Hot paraffin wax was applied to all cuts to reduce desiccation. Each side of the scored log was manually infested with *P. mexicanus*, using the gelatine-capsule technique (Lanier and Wood 1968). One male was introduced into an entrance hole prepared in the centre of each side and left overnight (Safranyik and Linton 1983). Beetles that did not initiate attack after 24 h were replaced. Once the male beetle had successfully entered the log, two females (Trimble 1924) were placed in the gelatine capsule. Females that did not enter logs after 24 h were replaced. After successful beetle introduction, logs were placed vertically in individual 20 L plastic buckets each altered in the laboratory to have a 5 cm diameter ventilation hole near the middle of the bucket wall covered with 0.25 mm polyethylene mesh and a 20 mL collecting vial attached just below the bucket lip on the opposite side from the ventilation hole.

Nine rearing buckets were placed in each of three walk-in growth chambers (Conviron PGV36, Controlled Environments Ltd., Winnipeg, Manitaba) in 2004 and five growth chambers in 2005. In 2004 the chambers were set at constant temperatures of 20.0, 23.5, and 28.8 °C and in 2005 at 14.1, 20.5, 23.4, 28.9, and 33.6 °C. Subtle variation in chamber temperature was due to differences between individual chambers. Temperatures were determined by placing a data logger (HOBO H8 Pro Temp, Onset Computer Corporation, Pocasset, Massachusetts) in each chamber for the period of the study, and were maintained at ±1.5 °C with ambient humidity. A 16L:8D regime was used to encourage emerging beetles to enter the collecting vials. Buckets were checked every 5 days until the first beetle appeared in a collection vial, after which time they were checked daily. Beetles found dead in the base of the bucket were counted as emerged. Re-attack by emerging beetles was reduced by placing all bolts on 1 cm tall rubber legs to elevate them above the reach of crawling beetles. Collected beetles were placed in 70% ethyl alcohol.

Development rate

The developmental characteristics of *P. mexicanus* were assessed by recording the development time from introduction of female beetles until emerging adults appeared at different temperatures. The mean development time was estimated by counting the days between beetle introduction and the first day of emergence of more than four beetles per temperature (this accounted for parent beetle emergence). The minimum thresh-old and optimum temperatures for development were determined and the development rate at each temperature was calculated by taking the reciprocal of the mean length of time in days (Campbell *et al.* 1974). The minimum temperature was determined by extrapolating a regression line. The optimum temperature was calculated by finding the maxima of a quadratic curve (see Data analysis below).

Voltinism

Voltinism of *P. mexicanus* was determined by calculating the number of degree days required by *P. mexicanus* to complete its life cycle from the time of infestation to adulthood. This was compared with the total number of available degree days over a period of 1 year at two different locations. Environment Canada weather data from the Merritt STP station (50°6′N, 120°48′W, elevation 588 m) between 1 June 2004 and 31 May 2005 (Environment Canada 2007) were used. A second set of data was collected at Angstad Creek with HOBO temperature data loggers from July 2003 to June 2004. The Merritt site was chosen as the closest permanent weather station with current data. If the calculated number of degree days was less than the total number of available degree days at a particular station, then *P. mexicanus* could be described as univoltine or multivoltine, otherwise *P. mexicanus* could not complete 1 generation per year (semivoltine).

Instars

Pseudips mexicanus larvae were collected from the manually infested logs to determine the head-capsule width for each instar. During both 2004 and 2005, one bucket per growth-chamber temperature was periodically chosen at random and the associated log dissected to assess developmental progress. Larvae were collected from all peeled logs from the 23.5 °C chamber in 2004 for head-capsule measurement. This temperature was chosen to ensure that all larval stages were present at the time of log dissection. At other temperatures, either eggs had not hatched or larvae had progressed to a later life stage at the time of the dissection, resulting in one or more missing instars. Head-capsule widths and the number of larval instars were determined by examining 195 larvae (Prebble 1933).

Data analysis

Field study

Data not meeting assumptions of normality and homogeneity of variance were transformed

by $Y = \log_{10}(X + 1)$. The characteristics (DBH, phloem thickness, and age) of infested host trees were compared with those of healthy trees sampled in the prism plots using an independent samples t test. Gallery characteristics were measured in the naturally infested trees and the values reported as the mean ± SE. An independent-samples t test was used to determine whether size was sexually dimorphic by comparing pronotal widths. Pronotal width was chosen as a metric for size because it is static, whereas body length may vary as a result of changes in internal fluid content after beetle death. A log likelihood ratio test (G test) was performed to assess the divergence of observed sex ratios in wild populations of both attacking adults and emerged offspring from the ratios reported in the literature.

Laboratory study

A regression analysis of development rate as a function of temperature was conducted. The development rates calculated at six temperatures (not including temperatures at which beetle survival was zero) were used to determine the optimum development temperature for *P. mexicanus* by deriving the maximum point of the curvilinear model fit to the data. Simple linear regression was used with rate and temperature to estimate the lower threshold of development through extrapolation of the model to $Y = 0$. Only temperatures through which the development rate increased approximately linearly (excluding temperatures higher than would normally be encountered by the insect in nature) were included in this model (Gilbert and Raworth 1996). Larval head-capsule widths were grouped graphically by examining natural breaks in the data, and the rate of change between instars was compared with previous research. All tests followed Sokal and Rohlf (1995) and were conducted using SPSS (SPSS Inc. 2004) with $\alpha = 0.05$.

Results and discussion

Field study

As is typical of the Ipini (Scolytinae), *P. mexicanus* focus their attack on suppressed, weakened, or recently killed trees (Wood 1982). Observations of the 17 harvested trees from which logs were brought to the laboratory in 2005 revealed that although ages did not differ ($t_{59} = -1.66$, $P = 0.10$) (Table 1) in attacked *versus* unattacked trees, DBH was smaller ($t_{59} = 3.70$,

$P < 0.001$) and phloem was thinner ($t_{59} = 4.03$, $P < 0.001$) in trees infested with *P. mexicanus* than in the healthy trees in the prism plots. All trees attacked by *P. mexicanus* had sustained physical injury in the past (broken tops, bole scars) or were infected by lodgepole pine dwarf mistletoe, *Arceuthobium americanum* Nutt. *ex* Engelm. (Viscaceae). Inspection of the pine logs revealed no evidence of host defence in the form of resinous pitch tubes or necrotic lesions under the bark associated with *P. mexicanus* attack sites, confirming that the selected hosts had weakened defences at the time of attack. Trees that are capable of resistance should react to the presence of *P. mexicanus* by exuding resin because of physical trauma to resin canals within the bark tissue, and producing lesions in the phloem and xylem tissues, an induced response to the inoculation of *P. mexicanus* fungal associates as seen in other bark beetle systems (Berryman 1972; Shrimpton 1973; Paine *et al.* 1997).

Dissection of the logs taken to the laboratory, as well as field observations, revealed that *P. mexicanus* prefer the lower bole of suppressed lodgepole pine trees; no attack was noted above 1.0 m. No attacks were found on the upper bole or in branches, and any slash inspected within 10 m of attacked trees was occupied by the pine engraver, *Ips pini* (Say). Thus, the attack behaviour of *P. mexicanus* on lodgepole pine in British Columbia differs from behaviour exhibited by Californian populations of this beetle species (Wood 1982), which were found thriving in *P. radiata* slash (Trimble 1924) as well as in the boles, branches, and cones of trees infected with pitch canker fungus (Fox *et al.* 1990). Schwerdtfeger (1956) also found *P. mexicanus* in the bole, branches, and slash of Mexican white pine. The variation in attack behaviour may be the result of different trophic interactions (such as competition and symbiotic relationships) or climatic factors within the different ecosystems. For example, the propensity of *P. mexicanus* to attack low on the bole in lodgepole pine may be an overwintering adaptation of northern populations. Snow often covers the lower trunk, insulating it and possibly reducing the risk of cold-induced mortality.

Pseudips mexicanus was found cohabiting with a number of other bark beetle species such as endemic *D. ponderosae*, *Orthotomicus latidens* (LeConte), *Hylurgops porosus* (LeConte), and *H. rugipennis* (Mannerheim). Except for *O. latidens* and endemic *D. ponderosae*, these species attacked at very low densities (<2 at-

Table 1. Characteristics of lodgepole pine trees (*Pinus contorta* var. *latifolia*) assessed using a variable-radius plot in seven stands at Angstad Creek, British Columbia, and of individual trees attacked by *Pseudips mexicanus*.

	Trees infested with *P. mexicanus* (*n* = 17)	Stand (*n* = 42)
DBH (cm)	15.7±0.9*a*	21.3±1.0*b*
Phloem thickness (mm)	1.0±0.1*a*	1.4±0.1*b*
Age (years)	118.1±1.9*a*	111.5±2.3*a*

Note: Values are given as the mean ± SE. Means within a row followed by the same letter are not significantly different (independent-samples *t* test, $\alpha = 0.05$).

tacks per tree, on average) and were present in only a few trees. The attack density of *P. mexicanus* (Table 2) was lower than that of endemic *D. ponderosae*, which was present on approximately 37% of the trees at a mean density of 55 attacks/m^2. *Orthotomicus latidens* was present on approximately 50% of the trees at densities slightly greater than *P. mexicanus*. *Orthotomicus latidens* was normally found higher on the bole than *P. mexicanus* and appeared to prefer phloem tissue in more advanced stages of deterioration (Miller and Borden 1985), whereas the species of *Hylurgops* LeConte were found at or below the root collar (lower on the bole than *P. mexicanus*). Trees with endemic *D. ponderosae* lacked *O. latidens*, although *O. latidens* attacks may have been present higher on the bole. *Dendroctonus ponderosae* tended to attack slightly above (but never overlapping) *P. mexicanus* gallery systems. It was not possible to determine which of the secondary species arrived first at these trees, but it appeared that all attacked in spring of the same year, whereas endemic *D. ponderosae* attacks followed *P. mexicanus* infestation later in the summer. The separation between species suggests the use of resource-partitioning strategies where niche demarcation is likely determined by the timing of attack and olfactory means as seen in other insect–host systems (Paine *et al.* 1981; Amezaga and Rodriguez 1998).

Observation of gallery-system forms during the spring field surveys revealed four amorphous *P. mexicanus* galleries in three trees mass-attacked by *D. ponderosae* (Fig. 1A). This form had previously also been noted in weakened hosts not attacked by *D. ponderosae*. Each of these four galleries contained more than three beetles, and there was no evidence of oviposition at the time of observation. *Pseudips mexicanus* has been found to fly in low numbers throughout the summer, peaking in late May and early June and again in early to mid-August (A.L.C., unpublished

data). Similar late-summer flights occur in a number of secondary species (Ayres *et al.* 2001). The purpose of this late flight by *P. mexicanus* is unclear, but it may be used to establish a second gallery or locate suitable overwintering sites. Some bark beetle species (*e.g.*, *D. ponderosae*) overwinter under the bark, whereas others (*e.g.*, *I. pini*) emerge and drop into the duff at the base of their natal tree (Thomas 1961; Safranyik *et al.* 1996). The detection of amorphous galleries containing multiple *P. mexicanus* in the spring and the lack of *P. mexicanus* in the duff (Safranyik *et al.* 1999) strongly suggest that they overwinter under the bark. Dispersal in search of new hosts is very costly (Amman 1984), and overwintering in a host with resource still available would be advantageous, as re-attack rather than spring dispersal could occur, thus reducing mortality risk.

All 81 *P. mexicanus* gallery systems observed on the 17 naturally infested trees (7.0 ± 1.3 attacks/log (mean ± SE)) brought to the laboratory were ovipositional (Fig. 1B). Most of these galleries (97.5%) had associated nuptial chambers, indicating that most of the time a male initiated attack (Miller and Borden 1985). Galleries lacking nuptial chambers may have been started by a female that either mated with a sibling prior to emergence (Lissemore 1997) or mated in an earlier but unsuitable gallery that she later abandoned (Wood 1982). *Pseudips mexicanus* undergo a period of pre-emergence feeding as callow adults (often in groups), which provides opportunities for sib-mating (McNee *et al.* 2000). Although such behaviour does occur (Domingue and Teale 2007), it is not common in the Ipini (Lissemore 1997). Examination of the proportion of virgin females emerging from such mass feeding galleries is required to determine the propensity for sib-mating.

In systems where only one gallery was associated with the nuptial chamber, the ovipositional gallery was either straight or curved. Egg niches

Table 2. Characteristics of attack and ovipositional galleries for *Pseudips mexicanus* populations reared from naturally attacked lodgepole pine trees (*Pinus contorta* var. *latifolia*) at Angstad Creek.

	Mean ± SE	Range	*n*
Attack density (attacks/m^2)	17.0±3.6	1.9–46.8	17
No. of galleries/attack	1.5±0.06	1.0–3.0	81
Gallery length (cm)	5.4±0.2	1.1–17.0	125
No. of egg niches/gallery	7.2±0.4	1.0–23.0	125
No. of egg niches/cm of gallery	1.4±0.07	0.2–5.6	125
No. of eggs/niche	3.5±0.2	1.0–4.0	36
Potential no. of progeny	25.2±0.1		

in straight galleries were on either side, occasionally alternating, while niches in curved galleries were almost exclusively on the outside of the curve (Fig. 1B). In systems where two galleries were present, the galleries curved away from each other, often in an "S" formation with the nuptial chamber at the centre and egg niches on the outside of the curve as reported by both Trimble (1924) and Schwerdtfeger (1956). The shape of the gallery system when two ovipositional galleries are present is likely an adaptation to reduce competition between offspring and improve access to host material (Trimble 1924), because food is often a limiting factor for larvae (De Jong and Sabelis 1988). The S shape permits larvae to fan out from the ovipositional gallery without contacting larvae from the other gallery. Although the S shape likely reduces intraspecific interactions, it does not eliminate them. During log dissections, apparent cannibalism was observed in two cases where a larger larva altered the direction of its gallery. In both instances, these larvae turned into neighbouring galleries and chewed into the inhabitants prior to moving on.

The mean number of individual ovipositional galleries associated with each nuptial chamber (Table 2) was slightly less than that reported by Trimble (1924) and Schwerdtfeger (1956), who found two galleries to be the most common number. The mean number that we found was significantly less than two ($G_1 = 9.47$, $P < 0.05$) and suggests an attack sex ratio of approximately 1.5 females per male, assuming that one female was present to create each gallery. Although females of some species have been observed to create multiple galleries per nuptial chamber (*e.g.*, *O. latidens*; Miller and Borden 1985; Reid 1999), we could not verify this phenomenon from our observations because parent

beetles were not always present when logs were peeled.

Pseudips mexicanus was categorized as polygynous by Trimble (1924) and Schwerdtfeger (1956) but as monogynous by Bright and Stark (1973). Monogynous scolytine species in which the male initiates gallery construction are rare, although polygyny is very common within the Ipini (Wood 1982; Kirkendall 1983). We found that >50% of the gallery systems examined on trees naturally attacked by *P. mexicanus* had at least two radial arms, suggesting that this species is facultatively polygynous. This finding corresponds to Kirkendall's (1983) definition of polygyny (more than one female joining a male in a gallery system). Additionally, males of polygynous species tend to be the larger sex (Kirkendall 1983) and we observed that pronotal widths of male *P. mexicanus* were, on average, 9.4% greater than those of females. Male offspring of *P. mexicanus* in lodgepole pine were significantly larger than female offspring ($t_{361} = -10.48$, $P < 0.001$), with pronotal widths of 1.7 ± 0.1 and 1.6 ± 0.1 mm (mean ± SE), respectively. Pronotal widths ranged from 1.4 to 2.0 mm in males and from 1.4 to 1.9 mm in females.

In our study, *P. mexicanus* galleries in lodgepole pine were shorter (Table 2) than in other tree species, as reported by Trimble (1924) and Schwerdtfeger (1956) (mean lengths 6.5 cm and 9.0 cm, respectively). The mean number of egg niches per gallery in this study (Table 2) was less than half that reported by Schwerdtfeger (1956) who found 16–20. Also, egg-niche density (number of egg niches per centimetre of gallery) was less (Table 2) than reported by either Trimble (1924) or Schwerdtfeger (1956) (2.0 and 3.5 niches/cm, respectively). The mean number of eggs per egg niche was again less than the mean number, 4.0, found in previous

studies (Trimble 1924; Schwerdtfeger 1956). The difference between our study and others in the number of eggs laid per egg niche may be a result of counting larval traces instead of eggs. We may have introduced error and artificially lowered the mean number of eggs per niche by not accounting for possible intermittent egg mortality prior to hatch.

The potential number of progeny produced per female is based on the mean number of eggs laid per niche and the mean number of niches per gallery, resulting in approximately 25 eggs laid per female. Trimble (1924) and Schwerdtfeger (1956) reported egg production to be between 64 and 90 per female. The large disparity may be the result of (*i*) higher temperatures and (*ii*) larger beetles in southern populations. Amman (1972) found that *D. ponderosae* that created ovipositional galleries at higher temperatures produced more eggs. Pines in the south likely experience higher temperatures as suggested by the higher egg-niche density found in Mexican white pine (Schwerdtfeger 1956) than in our study. Beetle size significantly affects egg-laying capacity, with larger beetles able to lay more eggs (McGhehey 1971). Beetles from populations in Mexican white pine were larger (Schwerdtfeger 1956) than the ones we found in lodgepole pine, contributing to the greater reproductive potential. Wood (1982) reported that *P. mexicanus* tend to be 2.5 times longer than wide. Using this ratio and length measurements, the beetles observed by Schwerdtfeger (1956) ranged in length from 1.6 to 2.2 mm (with no sex distinction), with a minimum length 10.6% greater than the minimum we found for females and a maximum length 10.7% greater than that of males in lodgepole pine. The size difference in females could account for the greater egg production by southern beetles. Additionally, differences in host chemistry may result in dissimilar defensive capacities and nutritional values (Kirkendall 1983), leading to variation in number of eggs laid.

Many of the beetle galleries had stained phloem and some staining of the underlying wood, indicating the presence of potentially phytopathogenic fungi associated with *P. mexicanus* as suggested by Struble (1961). Numerous bark beetles are associated with fungi (reviewed in Six 2003). It was noted that pupal chambers of *P. mexicanus* contained white fungal spores and it is probable that teneral adult *P. mexicanus* consumed the spores, because they were not observed in chambers with teneral beetles present.

Other bark beetle species are known to consume fungal spores (Whitney 1971). *Pseudips mexicanus* is apparently associated with a number of fungi, including *Leptographium terebrantis* S.J. Barras and T.J. Perry (K.P. Bleiker, S. Massoumi-Alamoutim, G.D. Smith, A.L. Carroll, and C. Breuil, unpublished data), which is highly pathogenic to pine trees (Eckhardt *et al.* 2004). In addition to providing potential nutritional benefits, the fungi may also play a role in overwhelming tree defences or conditioning the phloem for brood development (Paine *et al.* 1997).

The sex of emerging *P. mexicanus* was determined. The common sex ratio of 1:1 found in species of *Ips* De Geer (Miller and Borden 1985) was used for comparative purposes because this genus is closely related to *Pseudips* Cognato (Cognato 2000). The resulting sex ratio for emerging offspring, 1.6 females per male, was significantly greater than the expected ratio ($G_1 = 13.36$, $P < 0.001$, $n = 296$). Cole (1973) suggested that beetles breeding at low densities should produce offspring with a sex ratio close to 1:1. As crowding increases, the smaller sex is reduced in number. Crowding is likely not occurring with *P. mexicanus* because attack densities are quite low. But if crowding is a limiting factor, the sex ratio should be biased toward males, the larger sex (Safranyik 1976). Though cold is normally a factor in differential survival, because the logs used in this study were collected in autumn prior to frost, the beetles did not experience temperatures below 0 °C. It is possible that the parent beetles are preferentially selecting female offspring when laying eggs; however, this behaviour is common only in species that inbreed (Borsa and Kjellberg 1996; West *et al.* 2005), and we have suggested that sib-mating does not commonly occur in *P. mexicanus*. The difference between observed and expected sex ratios may be the result of using species of a different genus as the standard for comparison.

Laboratory study

Development rate

During the 2005 portion of the experiment, all parent beetles in the 28.9 and 33.6 °C chambers died prior to oviposition. In 2004, however, beetles in the 28.8 °C chamber successfully produced offspring. Temperature and humidity traces indicated that the chambers were functioning normally. Because the dead adults were covered with an unidentified white fungus, mor-

Fig. 2. Rates of development (reciprocal of the mean length of time in days) of *Pseudips mexicanus* from the time of infestation to the emergence of fully mature adults *versus* temperature from data collected in 2004 (□) and 2005 (●). A quadratic curve was applied to determine the optimum temperature for development (arrow). Error bars represent 1 standard error of the mean.


$r^2_{adj.} = 0.939$

$F_{2,5} = 39.415$, $P = 0.007$

$Y = 0.0045X - (8.4867 \times 10^{-5})X^2 - 0.0394$
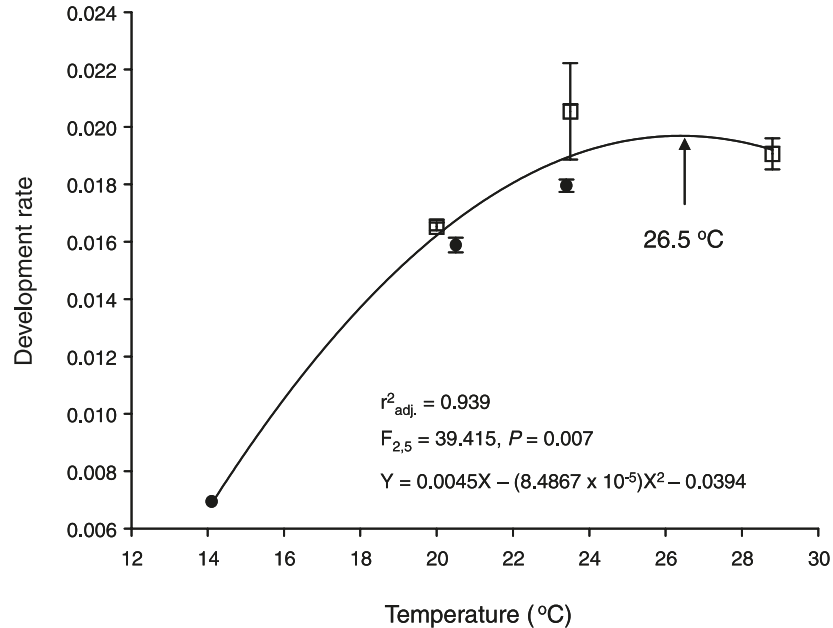
tality of the parent beetles in the 28.9 °C chamber in 2005 may have been due to an entomopathogenic fungus previously introduced into the chambers and not eliminated during cleaning. The data from the 28.9 °C chamber were not used in the models, but the data from the 33.6 °C chamber were assumed to be accurate.

The development rates of insects tend to follow similar patterns — a nearly linear increase followed by a peak and then a rapid decrease (Wagner *et al.* 1984; Logan and Powell 2001). The apparent decrease in the rate of development of *P. mexicanus* at 28.8 °C (Fig. 2) indicates that this species does not tolerate temperatures of this magnitude well during at least one of its life stages. Beetles in the 33.6 °C chamber may have died as a result of heat stress or desiccation of the study logs, and it is assumed that this represents the rapid drop-off to zero development that would be expected. A quadratic curve was fit to the temperatures at which beetles survived in both 2004 and 2005. The peak of the curve is the optimum temperature at which the development rate is highest (Trudgill *et al.* 2005). In our study, this point was approximately 26.5 °C at a rate of 0.020·d^{-1}

(Fig. 2). Taking the inverse of this rate, the optimum time required for *P. mexicanus* to develop from infestation to adulthood was 49.4 days at a constant temperature of 26.5 °C. Trimble (1924) reported that development was completed in 9 weeks but did not give the temperature at which this occurred, and Schwerdtfeger (1956) found that *P. mexicanus* in Mexican white pine took 12–14 weeks at 17 °C to complete their life cycle. The shorter time period required for *P. mexicanus* to reach maturity in our study may represent an adaptation to a colder environment. Faster development in northern climates has been shown for other species with shorter development periods dictated by cooler summers (Bentz *et al.* 2001).

The development rate for *P. mexicanus* within the range of temperatures normally encountered in the environment is shown in Figure 3. The minimum temperature for development, *i.e.*, the lowest point at which metabolic activity contributes to growth and development (Trudgill *et al.* 2005), was estimated to be 8.5 °C. Assessment of beetles reared at 23.5 °C by periodic peeling of logs showed that teneral adults were present after 45 days but no emergence occurred until midway through day 48. Based on this, it ap-

Fig. 3. Minimum temperatures for development of *Pseudips mexicanus* (arrow) extrapolated from the regression of development rate from the time of infestation to emergence of fully mature adults on temperature from data collected in 2004 (□) and 2005 (●). Error bars represent 1 standard error of the mean.
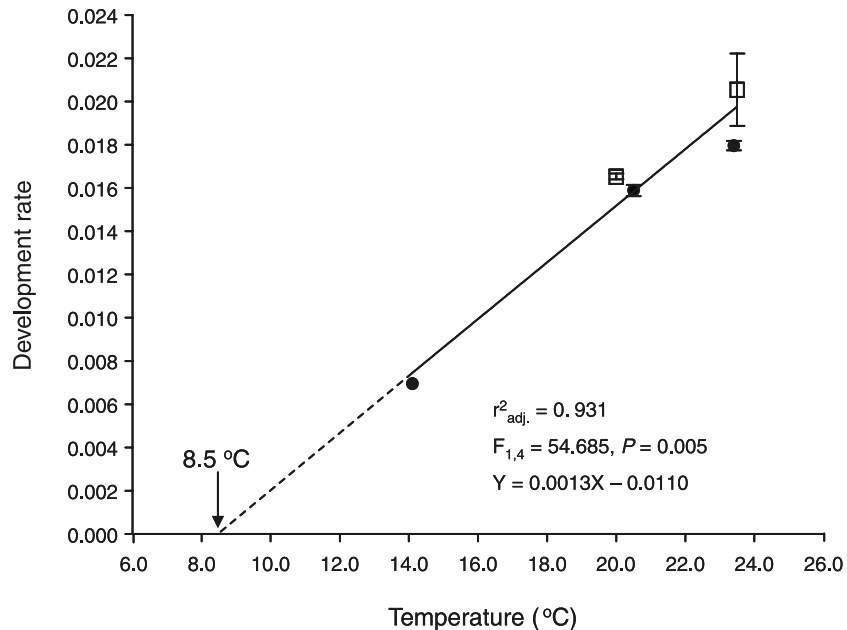
*pears that *P. mexicanus* can complete maturation feeding, common in bark beetles (Wood 1982), in less than 4 days and be prepared to emerge.

Voltinism

The number of degree days required for complete development from the time of infestation by adult *P. mexicanus* to emergence of adults from the brood at 26.5 °C was calculated to be 889.2 degree days above 8.5 °C. At the Merritt STP weather station, 1662 degree days were available between 1 June 2004 and 31 May 2005. At higher elevation within the Angstad Creek watershed a minimum of 982 degree days were available between July 2003 and June 2004 for *P. mexicanus* development. The number of degree days required for 1 generation of *P. mexicanus* corresponds closely with the number of degree days available at Angstad Creek, indicating that populations there are univoltine. In the arid valley near Merritt, *P. mexicanus* may complete up to 1.5 generations per year, but not 2.

Univoltine and multivoltine life cycles may benefit *P. mexicanus* in both northern and southern populations, as they allow for more rapid population growth compared with semivoltine populations. Additionally, the shorter development time may reduce the potential effect of mortality agents (*e.g.*, cold and predation), which can manifest themselves more during a longer development period (Hansen and Bentz 2003). The rapidity with which *P. mexicanus* can progress from infestation to adulthood at high temperatures suggests that it is well adapted to produce more than 1 generation in regions that have longer summers. For example, 3 generations are common in California (Struble 1961). Although degree days are often estimated for pest insect species in order to establish timing of control measures to coincide with susceptible life stages, *P. mexicanus* has not been the subject of any such practice. However, it is important to know how many generations *P. mexicanus* is capable of producing per year so that interactions with other species can be evaluated.

Instars

We found four larval instars for *P. mexicanus* (Fig. 4) and we report head-capsule widths in Table 3. Head-capsule widths for *P. mexicanus* larvae were reported by Trimble (1924) but it appears that an error occurred either in his measurements or during the printing of his findings because he reported the same head-capsule width for both 3rd and 4th instars (Table 3). Another indication of error in Trimble's (1924) data was found by comparing the rate of change from one

Fig. 4. Histogram of head-capsule widths of *Pseudips mexicanus* larvae from lodgepole pine (*Pinus contorta* var. *latifolia*) logs incubated at 23.5 °C, indicating four distinct instars (*n* = 195).
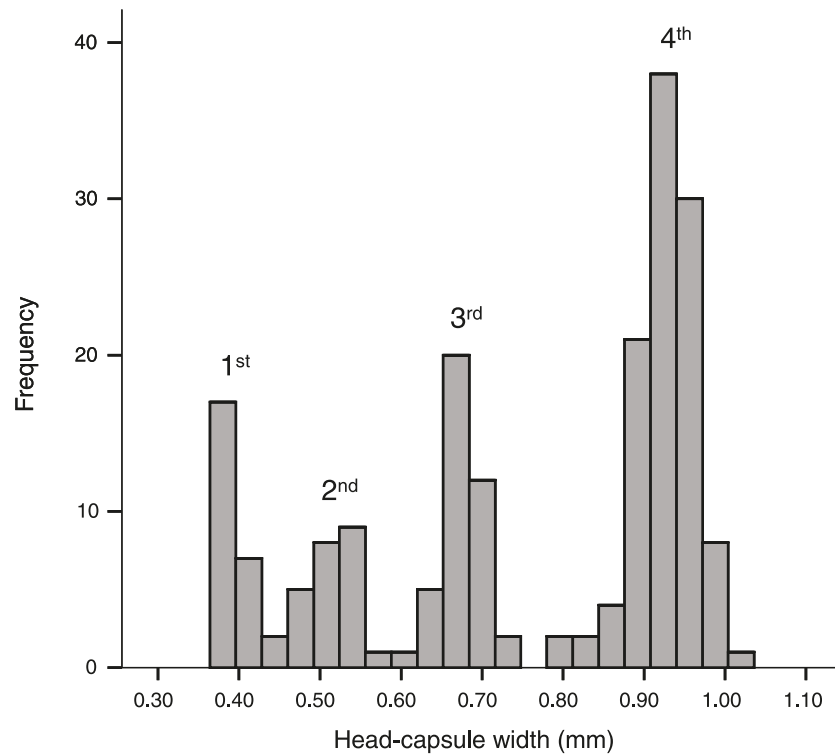

Table 3. Comparison of head-capsule widths (mm), range, and rate of change between instars of *Pseudips mexicanus* from manually infested lodgepole pine (*Pinus contorta* var. *latifolia*) logs in this study with those reported by Trimble (1924).

	Trimble 1924*		This study		
Instar	Head-capsule width	Rate of change	Head-capsule width (mean ± SE)	Rate of change	Range of head-capsule widths
1	0.4		0.38±0.003		0.37–0.40
2	0.9	0.44	0.50±0.006	0.75	0.43–0.57
3	1.2	0.75	0.68±0.005	0.75	0.60–0.78
4	1.2	1	0.93±0.004	0.73	0.83–1.04

*Standard error or standard deviation was not reported.

instar to the next between our data and those of Trimble (1924). Our data, as expected, revealed a linear progression; Trimble's data were nonlinear (Table 3) and did not follow the regular geometric progression described by Dyar (1890). Prebble (1933) and Reid (1962) showed that Dyar's rule was applicable to the bark beetles *Dendroctonus simplex* LeConte and *D. ponderosae*, respectively. The rate of change reported in these two studies was approximately 0.75, similar to our findings for *P. mexicanus* (Table 3).

Summary

Pseudips mexicanus in lodgepole pine forests differs from southern populations in a number of ways. Northern beetles are univoltine, unlike populations in California, which can have as many as 3 generations per year (Struble 1961). Attack behaviour differs as well; northern populations overwinter in the lower portion of the bole, and this is perhaps an adaptation to gain protection from lethally low temperatures. Southern beetles tend to make use of the whole

tree plus downed material. Similarities are apparent across populations in terms of polygyny, ovipositional characteristics (*e.g.*, number of eggs per egg niche), and development rate. In Canada, *P. mexicanus* is a common forest insect that is not an economic threat. Populations of this species do not increase to levels at which live, healthy trees are attacked, unlike *I. pini*, which can cause mortality when conditions are optimal (Thomas 1961). In Monterey pine in California, however, *P. mexicanus* has been a concern because of its ability to disseminate pitch canker fungus (Fox *et al.* 1991). Moribund trees are typical hosts in Canada, and *P. mexicanus* is likely beneficial, through the removal of low-quality material with the aid of other bark beetle species, thereby helping to maintain stand health. Determining attack dynamics, development rate, and voltinism will facilitate studies of interactions between *P. mexicanus* and other species such as endemic *D. ponderosae*.

Acknowledgements

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