

LIFE HISTORY AND BIOLOGY OF *IPS LATIDENS* (LECONTE)
(COLEOPTERA: SCOLYTIDAE)

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Abstract

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The life history and biology of *Ips latidens* (LeConte) were investigated using bark-sandwich and whole-log rearing methods. In contrast with other *Ips* spp., some females initiated galleries under conditions of female-biased sex ratios, and sometimes 2 or more males were present in a gallery. In general, however, *I. latidens* exhibited typical ipine characteristics. A single male usually admitted 1–3 females into a gallery. Females oviposited at a rate of 2.25 eggs/day and achieved a mean fecundity of 64.4 eggs. The larval stage comprised 80% of the generation time (egg to teneral adult) and analysis of head-capsule widths disclosed 3 larval instars. The mean survivorship within broods was 56.0% after 70 days; the reproductive success of monogamous pairs of beetles was 36.1 teneral adults. Single females constructed 3–4 egg tunnels/gallery system; hence, harem size cannot always be inferred from the number of egg tunnels in each gallery. The mean generation time in the laboratory was 2.07 × greater than for *I. pini*. By comparing laboratory data on *I. latidens* with laboratory and field data on *I. pini*, the generation time of *I. latidens* is estimated at 64–124 days in the field. In south-central British Columbia, *I. latidens* probably has 1 generation, and possibly 2 broods, per year.

Résumé

Le cycle vital de la biologie de *Ips latidens* (LeConte) ont été étudiés par élevage sur écorce en sandwich et sur bûche entière. Contrairement à ce qui se passe chez d'autres *Ips* spp., certaines femelles ont initié des galeries lorsqu'un sexe ratio biaisé en faveur des femelles prévalait, et on a observé la présence occasionnelle de 2 ou plusieurs mâles dans une galerie. Cependant, *I. latidens* présentait généralement les caractéristiques typiques des ipines. Un mâle admettait normalement de 1 à 3 femelles dans une galerie. Les femelles ont pondu à raison de 2,25 oeufs/jour, réalisant une fécondité moyenne de 64,4 oeufs. Le développement larvaire comptait pour 80% du temps de génération (de l'oeuf à l'adulte nouveau) et l'analyse de la largeur de la capsule céphalique a révélé 3 stades larvaires. La survie moyenne des couvées était de 56,0% après 70 jours. Le succès de reproduction des couples monogames a été de 36,1 adultes nouveaux. Les femelles isolées ont construit 3 ou 4 tunnels par système de galeries. La durée moyenne d'une génération au laboratoire était de 2,07 fois plus longue que pour *I. pini*. Une comparaison des données de laboratoire portant sur *I. latidens* avec des données de laboratoire et de terrain sur *I. pini* permet d'estimer la durée d'une génération de *I. latidens* à 64–124 jours sur le terrain. Il est probable qu'au centre-sud de la Colombie-Britannique, *I. latidens* a 1 génération par année et produit 2 couvées.

Introduction

The bark beetle, *Ips latidens* (LeConte) (Coleoptera: Scolytidae), generally attacks the tops and limbs of dead, dying, or weakened coniferous trees or slash, particularly lodgepole and ponderosa pines, *Pinus contorta* var. *latifolia* Engelm, and *P. ponderosa* Dougl. ex Laws., respectively, in British Columbia (Bright 1976). Under certain conditions adults may kill trees; during outbreaks of the mountain pine beetle, *Dendroctonus ponderosae* Hopk., populations of *I. latidens* may increase to such numbers in the crowns and slash of trees killed by *D. ponderosae* that they can successfully attack and kill many small trees (Furniss and Carolin 1977).

Within infestations of *D. ponderosae* in British Columbia, we have found lodgepole pines infested largely by *I. latidens* and *I. pini* (Say). Such tree mortality may be mistakenly attributed to *D. ponderosae*. As intensive forest-management practices are implemented, operations such as thinning and spacing may result in large numbers of *I. latidens* and/or *I. pini* emerging from slash and attacking the standing trees in plantations.

Blackman (1919) examined more than 100 engravings made by *I. latidens* in eastern white pine, *P. strobus* L. Like male *I. pini*, male *I. latidens* are polygamous, each excavating a nuptial chamber in the phloem of a tree from which females in his harem construct egg tunnels, resulting in a characteristic star-shaped gallery, sometimes engraved into the sapwood (Chamberlin 1958; Bright and Stark 1973; Bright 1976; Furniss and Carolin 1977; Wood 1982).

Unlike *I. pini*, relatively little else is known about *I. latidens*. Without basic information on the life history and population dynamics of *I. latidens*, it is difficult to assess either the direct impact of *I. latidens* on forests or its interactions with other bark beetles. Pest-management practices directed against one species may serve only to predispose trees to attack by other scolytids and fail to prevent tree mortality. In the southern United States, there was a 27-fold increase in attack density of *I. avulsus* (Eichhoff) on loblolly pines, *P. taeda* L., treated with inhibitors against the southern pine beetle, *D. frontalis* Zimmerman; all but one of the treatment trees died (Watterson *et al.* 1982). Because *I. latidens* is sympatric with the aggressive bark beetles, *D. ponderosae* and *I. pini*, which may be manipulated with semiochemicals, it is imperative that the biology of *I. latidens* be known in order to develop rational, pest-management practices in British Columbian pine forests.

Materials and Methods

Rearing methods. Uninfested bolts of lodgepole and ponderosa pines, and lodgepole pine bolts infested with either *I. latidens* or *I. pini*, were collected in 1982–1983 from various locations between Manning Park and Princeton, BC. Within 3 days the exposed ends of all bolts were sealed with hot, melted paraffin wax. Laboratory colonies of *I. latidens* and *I. pini* were maintained in separate rearing cages at 25–35°C and approximately 40% RH. Emergent beetles from colonies were collected daily from the cage walls and stored on moistened tissue paper in glass jars at 4–8°C.

To obtain separate galleries, the activities of monogamous pairs of beetles were restricted by either the gelatin-pill-capsule technique (Borden 1967), arena-bolt (Hosking 1972; Zanuncio 1981), or bark-sandwich preparations (Reid 1955; Hopping 1961; Thomas 1961; Beanlands 1966; Balogun 1969; Borden 1969; Schmitz 1972; Gouger *et al.* 1975).

In the arena-bolt technique, the separated portions of plastic petri plates (35 × 10 or 60 × 15 mm) were affixed with modeling paste to bolts with the open side facing the bark surface. Beetles were introduced through a 1-cm-diameter hole in the center of each arena, and the holes sealed with transparent tape.

We modified the bark-sandwich method for use with *I. latidens* to correct 2 major drawbacks of existing designs: (1) localization of pressure along the periphery of the sandwich rather than the central portion, thereby allowing small beetles to leave the phloem tissue without boring through the bark; and (2) rupturing of compressed phloem tissue directly beneath clamps or adjacent to bolts holding sandwiches together. Bark sections were placed in a plexiglass box (internal dimensions of 13.8 × 20.0 and 20.0 × 30.1 cm) with a styrofoam pad between the bark and a plexiglass cover. The inward bow of the plexiglass cover of the sandwich caused by the sides of the box acting as fulcras, and the spongy nature of the styrofoam, resulted in most of the pressure from 4 clamps being evenly distributed over the entire bark surface. Beetles were introduced through 8-mm-diameter holes that extended through the plexiglass cover and the styrofoam layer to the bark surface.

Rearing experiments. A total of 342 separate galleries was used to estimate various population parameters, determine gallery characteristics, and observe the behavior of *I. latidens*. For comparative purposes we reared 31 broods of *I. pini*. Daily collections of emergent beetles from colonies of both species were used to determine emergence patterns from field- and laboratory-infested logs. Sex ratios of emergent beetles were obtained by examination of dissected genitalia.

Harem size was estimated by the number of females allowed into each nuptial chamber. Individual males were restricted to 29 sites on 2 ponderosa pine bolts by the pill-capsule technique, and restrained within 23 arenas on 2 arena bolts of lodgepole pine. Each male received 1 female/day or every second day after evidence of boring was visible, for a total of 4–8 females/male. The sex of all beetles was verified by examination of dissected genitalia.

The number of larval instars of *I. latidens* was determined by examining 749 larvae excised from 79 broods, reared in 10 lodgepole pine bolts, at intervals ranging from 15 to 104 days after infestation. The greatest width of each head capsule, perpendicular to the body axis and along the median plane, was measured with an ocular micrometer.

Estimates of the generation time and developmental times for each stage of the life cycle of both *I. latidens* and *I. pini* were derived from bark-sandwich rearings. The sexes of brood adults were determined by examination of dissected genitalia.

Brood survivorship was determined from 101 galleries on 8 arena bolts and 63 galleries in 33 sandwiches. Single, monogamous pairs of *I. latidens* were introduced into each of 22 arena-bolts, and kept in separate rearing cages at 25–35°C, to determine the reproductive success of individual females. The sex of all brood adults was determined by examination of dissected genitalia.

Linear regression analyses were performed on the oviposition and egg-niche construction data using the Minitab¹ statistical package. Plots of residuals and experimental-lack-of-fit tests did not suggest curvilinearity for any of the regressions. Coefficients of determination (r^2) were corrected for degrees of freedom.

Results and Discussion

Sex differentiation. Determination of the sex of adult *I. latidens* using secondary sexual characters (Hopping 1963; Lanier and Cameron 1969; Wood 1982) proved difficult and unreliable. Therefore the elytral declivities of 378 adult beetles were examined for sex-specific characters and the sex verified by examination of their dissected genitalia. Consistently high accuracy within male and female categories (91.2% in a sample of 125 males and 92.2% in a sample of 217 females) permitted reliable use of individual *I. latidens* of known sex in rearing experiments.

Males tended to have larger declivital spines than females, particularly the third one. In males the third spine was usually long and cylindrical, sometimes tapered, rarely triangular, and parallel to or divergent from the body axis; in females the third spine ranged from triangular to long and tapered, rarely cylindrical, and parallel to or convergent with the body axis.

Single, qualitative traits, efficient for Californian populations (Lanier and Cameron 1969), are not easily used by persons unfamiliar with *I. latidens* nor were they adequate for differentiating the sexes in British Columbia populations; the sex of 23% of 446 adults could not be determined on the basis of declivital characteristics. Beetles were classified as unknowns if declivital spines were intermediate in size and if the third spine was parallel to the body axis, but not triangular or cylindrical. Hence for *I. latidens* in British Columbia, sex should be determined on the basis of multiple declivital characteristics. Normalization

¹Minitab Project, Statistics Department, Pennsylvania State University, University Park, PA.

of some characters to a body measurement such as elytral length or pronotal width (Wood 1982) would probably facilitate sex determinations, particularly for inexperienced persons.

Gallery characteristics and behavior of beetles. Gallery initiation. As in *Polygraphus rufipennis* Kirby (Rudinsky *et al.* 1978) and *I. grandicollis* (Eichhoff) (All and Anderson 1972), *I. latidens* galleries may be initiated by either sex. Males initiated most galleries, excavating triangular nuptial chambers (mean area = 11.9 mm²; SE = 0.87; n = 9) from which female-constructed egg tunnels radiate outward. Females may initiate galleries under conditions of female-biased sex ratios: of 178 females introduced into 27 single-male arenas on lodgepole and ponderosa pine, 12 initiated galleries, were joined by the resident male, and oviposited. The males did not construct nuptial chambers in female-initiated galleries, and left galleries containing ovipositing females to join females in female-initiated galleries.

Seventy-one single females constructed tunnels. In 3 arenas, 3 ovipositing females were found alone in female-initiated egg tunnels. Since mating is necessary before oviposition can occur, even for females that produce all-female broods (Lanier and Oliver 1966), either males and/or females traveled freely between galleries, or females mated prior to introduction into arenas. Pre-emergence mating does occur in *I. grandicollis* (All and Anderson 1972; Witanachchi 1980), the proportion of mated females increasing with time spent as adults under the bark to as high as 89%.

In sandwiches males blocked gallery entrances with their declivities. Males in bolts appeared inefficient in preventing entry by other males into galleries; in 7 of 15 multiple-male arenas, up to 3 males were found in the same gallery. Males with females already in their galleries seemed more efficient in preventing entry by additional females; 48% of females did not enter such galleries, and initiated their own. Male guarding behavior in *I. paraconfusus* Lanier limits the number of females accepted into a gallery to 3 (Borden 1967).

Frass (boring dust and fecal pellets) produced by females in constructing egg tunnels was scooped behind them, pushed with their elytral declivities to the nuptial chamber, and removed to the outside by the resident male. If the male was absent, frass accumulated in the nuptial chamber, preventing passage by females between egg tunnels and the bark surface.

Ventilation holes to regulate humidity within galleries (Mel'nikova 1964) were common in galleries of *I. pini*, but rare in those of *I. latidens*. Possibly *I. latidens* breeds in material that rarely has an excess level of moisture. In the laboratory, adults seemed to prefer the drier sections of phloem in the outer bark and at the ends of bolts.

Mating and oviposition. Frequent shoving matches occurred between females and the resident male at the junction of egg tunnels and the nuptial chamber, particularly preceding mating and oviposition.

As in many other scolytids (Kirkendall 1983), *I. latidens* mated repeatedly; in all 12 matings observed, females had previously oviposited in their respective egg tunnels, and 4 matings involved the same pair of adults. Mating lasted 20–120 s, comparable to *I. avulsus* (Gouger *et al.* 1975), *I. pini* (Thomas 1961; Schmitz 1972), and *I. cembrae* Heer (Balogun 1970). *In copulo*, *I. latidens* assumed a position similar to that of *I. avulsus* but different from *I. pini* and *I. cembrae*, with the body axes perpendicular to each other rather than parallel.

Oviposition was observed only once in a bark sandwich, and was similar to that of *I. pini* (Schmitz 1972) and *I. avulsus* (Gouger *et al.* 1975). The female excavated a niche in the wall of an egg tunnel, pushing most of the boring dust into the nuptial chamber. Once the niche was complete, she backed into the nuptial chamber, turned 180°, re-entered backwards, and then attempted to oviposit in the niche. Following 3 oviposition attempts she laid a single egg, quickly withdrew from the egg tunnel, re-entered head-first, and

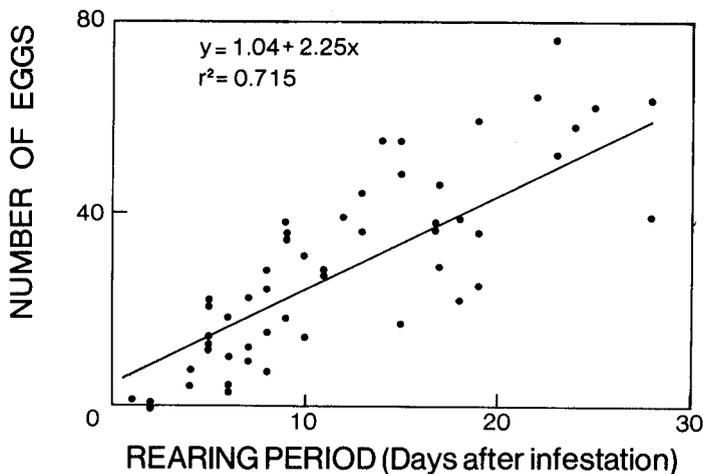


FIG. 1. Rate of oviposition by *Ips latidens* in bark sandwiches of *Pinus contorta* var. *latifolia*.

packed the egg into the niche with some of the boring dust remaining after niche construction. Between attempts the female withdrew into the nuptial chamber, re-entered head-first, and "inspected" the niche, making some alterations. Pushing occurred between the female and the resident male every time the female tried to enter the nuptial chamber to turn around.

Niches were excavated in both walls of an egg tunnel, and sometimes in the top and bottom if the phloem was thick enough as in ponderosa pine, at a rate of 2.25 egg niches/day ($r^2=0.715$; $t=11.57$; $P<0.001$; $df=52$) (Fig. 1). The distribution of niches ranged from even along both sides of an egg tunnel to all on one side.

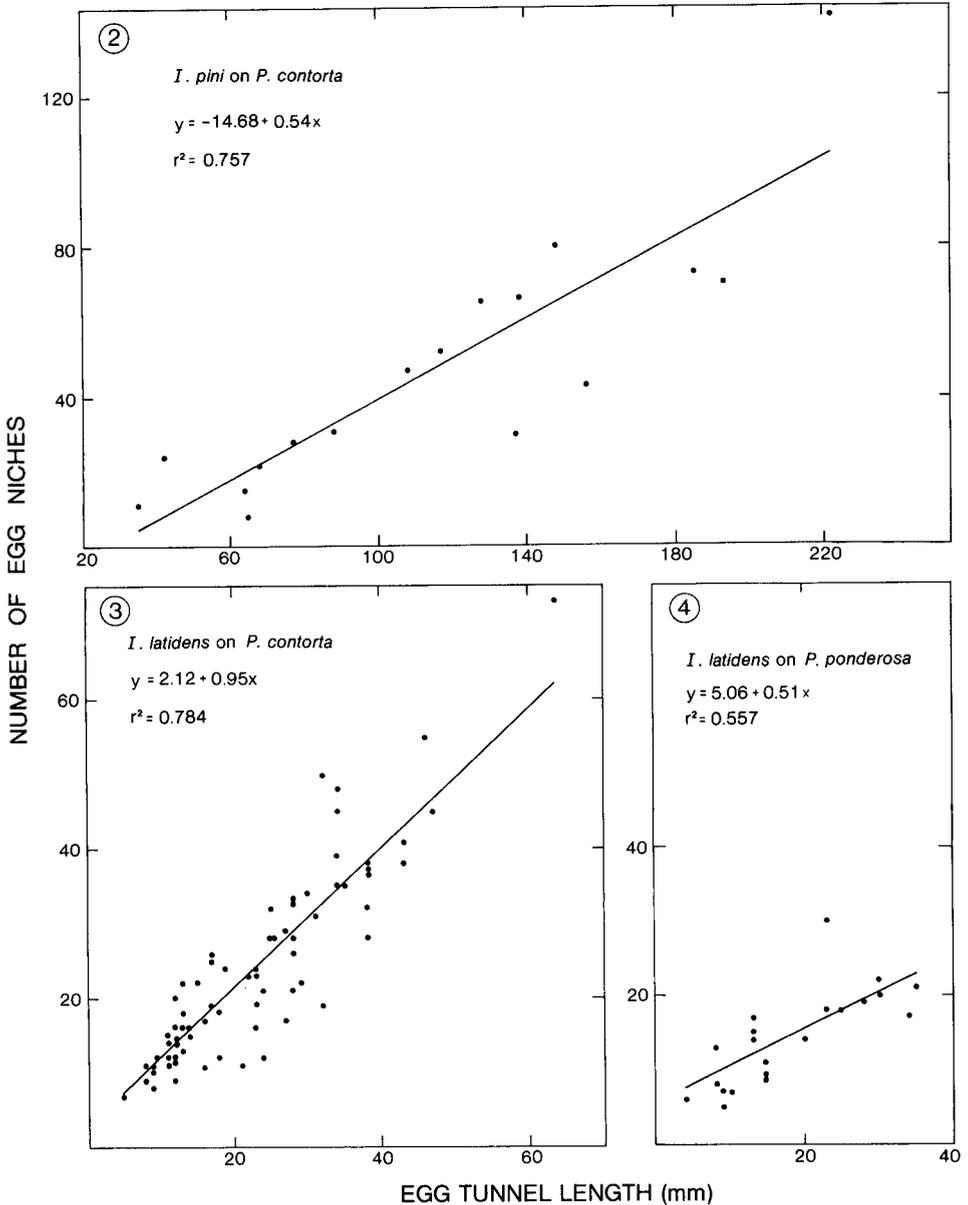
In lodgepole pine, female *I. latidens* laid eggs singly in niches spaced at 0.95 egg niches/mm of egg tunnel ($r^2=0.784$; $t=16.08$; $P<0.001$; $df=70$) (Fig. 3). Female *I. pini* spaced their niches at 0.54 egg niches/mm of egg tunnel ($r^2=0.757$; $t=7.13$; $P<0.001$; $df=15$) (Fig. 2), significantly farther apart than those of *I. latidens* (t -test, $P<0.01$). Niches made by *I. latidens* were spaced farther apart in ponderosa pine (0.51 egg niches/mm of egg tunnel) ($r^2=0.557$; $t=5.11$; $P<0.001$; $df=19$) (Fig. 4) than in lodgepole pine (t -test, $P<0.01$).

Fecundity of *I. latidens* was 64.4 eggs/female (SE = 3.94; $n=17$), not significantly different from that of *I. pini* (66.6 eggs/female; SE = 10.46; $n=9$) (t -test, $P=0.81$), and comparable to *I. amitinus* (Eichhoff) (Zumr and Soldan 1981), *I. calligraphus* (Germar) (Wood and Stark 1968), *I. avulsus* (Gouger *et al.* 1975), and *I. cembrae* (Balogun 1970).

Harem size and egg tunnels. The number of egg tunnels constructed within monogamous galleries of *I. latidens* increased over time, with completed galleries having 3–4 egg tunnels/female (Table 1). Newly laid eggs were usually found in only 1 egg tunnel of a gallery, the older tunnels having only larvae. Females generally constructed only 1 egg tunnel at a time, although a few alternated between tunnels. Egg tunnels had a mean length of 29.8 mm (SE = 1.46; $n=45$) and contained an average of 27.4 egg niches each (SE = 1.49; $n=59$).

Since female *Pityophthorus lautus* (Kirkendall 1983), *I. paraconfusus* (Barr 1969), *I. concinnus* (Mannerheim), and *I. mexicanus* (Hopkins) (G.N. Lanier², pers. comm.) may also construct more than 1 egg tunnel/gallery, harem size in scolytid species cannot always be inferred from the number of egg tunnels in each gallery. Cook *et al.* (1983)

²State University College of Environmental Science and Forestry, Syracuse, NY.



FIGS. 2-4. Spacing of egg niches in egg tunnels by female ips at 25-35°C. Fig. 2. *Ips pini* in *Pinus contorta* var. *latifolia*. Fig. 3. *Ips latidens* in *Pinus contorta* var. *latifolia*. Fig. 4. *Ips latidens* in *Pinus ponderosa*.

made the same observation for *I. avulsus*, but suggested that multiple egg tunnels are a consequence of multiple monogamous pairs of beetles using the same nuptial chamber rather than single females constructing multiple egg tunnels. Hence examination of scolytid galleries in the field to determine productivities of individual females should be verified by laboratory experiments.

Bark-beetle attacks seem to be uniformly distributed over bark surfaces (Shepherd 1965; Berryman 1968; Hedden and Gara 1976; Nilsen 1978; Byers 1984). Each gallery

Table 1. Mean number of egg tunnels constructed by monogamous, female *Ips latidens* within 65 separate galleries in *Pinus contorta* var. *latifolia*

Days after infestation	Number of galleries	Egg tunnels		
		Total	Mean/female*	SE
0-5	12	13	1.08	0.193
6-20	34	61	1.79	0.139
21-35	13	33	2.54	0.244
>35	6	20	3.33	0.211

*Significant differences among means, Kruskal-Wallis test, $P < 0.01$.

has a limited phloem resource for brood production. Hence the construction of multiple short egg tunnels by *I. latidens*, rather than single long tunnels, per gallery may maximize phloem use while minimizing intergallery competition among larvae.

Ips latidens is polygynous (Blackman 1919). Results of some rearings to determine harem size were inconclusive due to multiple males in some galleries, female-initiated galleries, lack of male fidelity, damage during debarking procedures, and loss of females from pill capsules and arenas; 40 and 10% of females were lost in pill-capsule and arena-bolt rearings, respectively. The mean number of females within galleries associated with single males was 2.5 females/male (SE = 0.25; $n = 39$; range = 1-7) in lodgepole pine arena bolts, significantly greater than the mean of 1.8 females/male (SE = 0.16; $n = 21$) found in ponderosa pine pill-capsule rearings (t -test, $P < 0.01$).

In moderately polygynous scolytid species, 2-4 egg tunnels/gallery are typically observed (Kirkendall 1983). Assuming that there is an optimal number of egg tunnels that should be constructed in each gallery, then competition should exist for egg tunnel sites among female *I. latidens* in polygynous galleries; as harem size increases, competition for oviposition sites among females should increase.

Therefore, to maximize reproductive success, females in polygynous situations would be expected to re-emerge and attempt to establish additional broods, a strategy typical of many scolytids (Berryman 1982; Stark 1982). Monogamous *I. latidens* in bark sandwiches did not re-emerge whereas females in log colonies did.

As harem size increases, male bias in the operational sex ratio (Emlen 1976; Emlen and Oring 1977) should also increase, assuming that not all remaining males die or emigrate. Selection should favor a strategy whereby a female leaves a gallery when the probability of finding another mate and establishing a new brood is high enough to offset the risk of predation, or death, and the loss of further progeny in the abandoned gallery. A female should leave a gallery either if the harem is too large or when she has laid a complement of eggs suitable for a given harem size. In moderately polygynous species, *Phloeosinus bicolor* Brull., *Ph. thuyae* Perris, *Polygraphus rufipennis*, and *Scolytus piceae* (Swaine), the number of eggs per egg tunnel decreases with an increase in harem size. In *Pityophthorus lautus*, differences in the time spent ovipositing in a gallery arise due to phloem quality and size of harems (Kirkendall 1983). In *I. latidens* galleries, the number of eggs per gallery and the egg tunnel length decrease with an increase in egg tunnels per gallery (Blackman 1919).

Changes in the frequencies of copulation, frass removal, or pushing matches could serve as indicators of harem size or male fitness in galleries of *I. latidens*. Alternatively, females may complete egg tunnels and re-emerge if they are unable to start new egg tunnels.

Intraspecific competition is a major mortality factor within broods of scolytids (Cole 1973, 1975; Ogibin 1973, 1974; Birch 1978; Berryman 1982). There may be a selective advantage for males to limit the size of harems as in *I. paraconfusus* (Borden 1967). Even

Table 2. Mean head-capsule widths of instars of *Ips latidens* ($n = 749$)

Instar	Sample size	Head-capsule width (μm)				Dyar's constant†
		Mean*	SE	Minimum	Maximum	
1	156	354	1.76	294	412	—
2	205	472	1.38	423	540	1.33
3	388	636	1.47	552	725	1.35

*Means are significantly different, Kruskal-Wallis test, $P < 0.001$.

†Ratio of the mean head-capsule widths of one instar to the previous instar.

though the number of eggs per gallery (and per male) increases with harem size in polygynous scolytids (Kirkendall 1983), the reproductive success of a male may decrease if too many eggs are laid; phloem is limited and a given gallery will only sustain a finite number of progeny. Survivorship within broods of *I. paraconfusus* was lower at a density of 6–8 females/dm² than 3–4 females/dm² (Light *et al.* 1983). Cannibalism among larval *I. latidens*, consistent with observations of other scolytids (Schenk and Benjamin 1969; Berryman and Pienaar 1973; Berryman 1974), did occur and suggests that intrabrood competition may occur among larvae of *I. latidens*.

Some scolytids deposit fewer eggs per gallery in response to increased attack density (Berryman 1982). As density increases, galleries may become more closely packed, resulting in less breeding material per gallery. Re-emergence in response to high attack density may occur if harem size is correlated with attack density or if phloem quality at intergallery boundaries deteriorates, assuming females can assess harem size and phloem quality. Female *I. paraconfusus* laid fewer eggs per egg tunnel and re-emerged earlier at a density of 4 parent females/dm² than at 2 parent females/dm² (Light *et al.* 1983).

Therefore, it seems likely, and testable, that females of polygynous scolytid species such as *I. latidens* may be able to assess attack density and harem size, and adopt appropriate reproductive tactics.

Development. Number of larval instars. The distribution of the frequencies of head-capsule widths of 749 larval *I. latidens* shows 3 instars in the larval stage (Table 2), typical of all species in the tribe Ipini (Wood 1982). Means of head-capsule widths for successive instars were significantly different, and exhibited a regular, geometric progression, as predicted by Dyar's rule (Dyar 1890; Taylor 1931; Gaines and Campbell 1935).

Duration of life stages. One brood of *I. pini* and 4 broods of *I. latidens* in bark sandwiches were used to determine the duration of life stages and generation time. Development of each stage was significantly longer for *I. latidens* than for *I. pini* (t -test, $P < 0.01$) (Fig. 5). The generation time (egg to teneral adult) in *I. latidens* was 2.07-fold greater than in *I. pini* (t -test, $P < 0.01$), due mainly to a prolonged larval stage. Neither quiescence nor diapause was observed during the larval stage at 25–35°C. There were no significant differences in the duration of each stage between broods of *I. latidens* (Kruskal-Wallis test, $P > 0.38$).

The mean generation time for *I. pini* reared in bark sandwiches was 42–70% shorter than in the field (Prebble 1933; Reid 1955; Thomas 1961; Schenk and Benjamin 1969). By comparing laboratory data on *I. pini* and *I. latidens* with field data on *I. pini* at Black Sturgeon Lake, Ont. (Thomas 1961), and in Fredericton, NB (Prebble 1933), we estimate that in south-central British Columbia, the egg, larval, and pupal stages of *I. latidens* should last 9.8–12.3, 37.4–67.9, and 13.7–17.6 days, respectively; and the generation time should range from 64.2 to 99.4 days. Using field data for *I. pini* near Rocky Mountain House, Alta. (Reid 1955), the generation time may be up to 124 days.

Brood survivorship. Mortality within broods of *I. latidens* occurred primarily from egg to second-instar larvae, with survivorship within mature broods averaging 55.0%

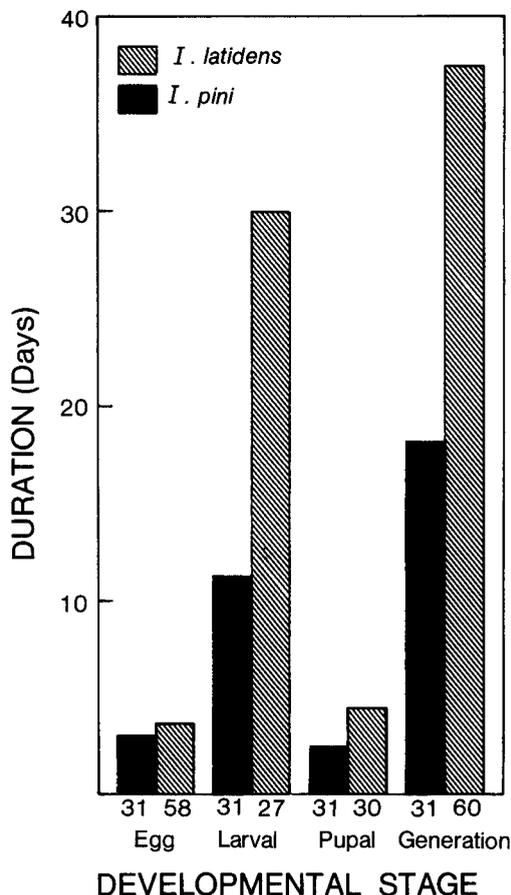


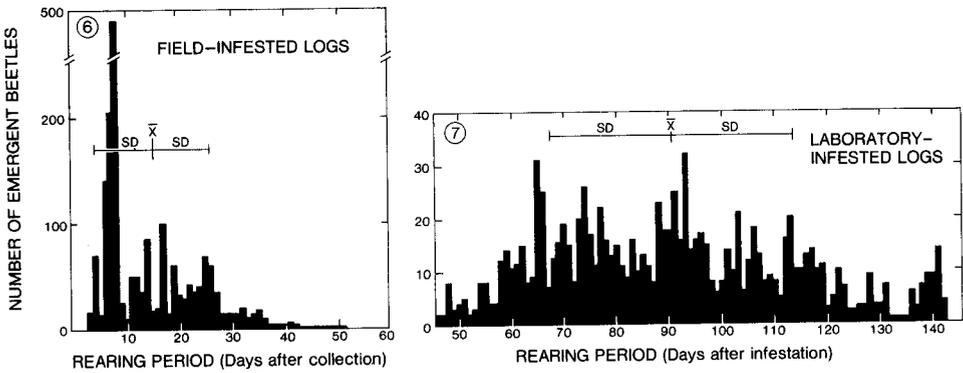
FIG. 5. Duration of developmental periods of *Ips latidens* and *Ips pini* in bark sandwiches of *Pinus contorta* var. *latifolia* at 25–35°C (sample sizes given below each bar).

(SE = 3.46%; $n = 12$). In an independent experiment, the mean reproductive success of 17 monogamous pairs in lodgepole pine logs was 36.5 teneral adults/pair (SE = 4.57); assuming a mean fecundity of 64.4 eggs/female, brood survivorship was 56.7%.

Emergence patterns. Sex ratio. In ips the typical sex ratio among emerging adults is close to 1:1, whereas the sex ratio among attacking beetles or successful beetles is generally female biased at more than 2 females/male. This phenomenon occurs in *I. paraconfusus* (Struble and Hall 1955; Cameron and Borden 1967), *I. pini* (Schenk and Benjamin 1969; Schmitz 1972), *I. calligraphus* (Cook *et al.* 1983), and *I. typographus* (Annala 1971). In *I. latidens* the sex ratio among tenerals within broods and emerging from logs was not significantly different from 1:1 (t -test, $P > 0.5$). There was no evidence of the “sex ratio” condition of all-female broods (Lanier 1966; Lanier and Oliver 1966).

Annual flight periods. Pest-management practices against bark beetles are timed around flight periods when adults attack new hosts. In laboratory colonies, first emergence of *I. latidens* progeny occurred 60–65 days after infestation, approximately 1.6× longer than the generation time in bark sandwiches.

Maturing teneral *I. latidens* spent considerable time feeding under the bark of lodgepole pine; in eastern white pine, tenerals fed for weeks and sometimes even months before



FIGS. 6-7. Emergence patterns of *Ips latidens* from *Pinus contorta* var. *latifolia*. Fig. 6. Field-infested logs. Fig. 7. Laboratory-infested bolts.

emerging (Blackman 1919). In Wisconsin, *I. pini* took 5-9 days to develop full coloration and sexual maturity, and an additional 5-11 days to feed before emerging from logs (Schenk and Benjamin 1969). In *I. typographus* L., *I. amitinus*, and *Pityogenes chacographus* L., spermateliosis and vitellogenesis occur primarily during the maturation feeding prior to emergence (Zumr and Soldan 1981). The flight muscle volume of *I. paraconfusus* increases 10× during maturation feeding (Borden and Slater 1968). Lipid reserves of *D. pseudotsugae* Hopkins adults build up to 20% of total dry body weight before they emerge from the bark and disperse (Atkins 1966a).

The interval between flights of *I. latidens* adults and their subsequent broods may be so lengthened by maturation feeding, in preparation for dispersal flight and brood production, that only one generation can occur per year in south-central British Columbia. This hypothesis is supported by research in 1983 near Manning Park, BC, that suggested a single major flight period between late May and early July, and a minor peak in late July, probably representing re-emerged adults (D.R. Miller³, J.L. Madden, and J.H. Borden, unpublished results).

Therefore, *I. latidens* in south-central British Columbia probably has a single generation per year with a partial second brood in late summer, as does *I. latidens* in white pine in New York (Blackman 1919) and 2 small and related pine species, *Pityogenes knechteli* Swaine and *Orthotomicus vicinus* (LeConte), occupying similar niches in lodgepole pine forests in Alberta (Reid 1955).

Emergence synchrony. Ninety-one percent of overwintering *I. latidens* in field-infested bolts of lodgepole pine emerged in a 25-day period (Fig. 6). Emergence from laboratory-infested lodgepole pine logs was protracted significantly more than from field-infested logs (*F*-test of homogeneity of variances, $P < 0.01$); 90% of the beetles emerged over a 75-day period (Fig. 7).

Synchrony of emergence by overwintering *I. latidens* may be a consequence of differential mortality of life stages, leaving only mature adults by spring. Alternatively, development may continue at low temperatures such that most of the broods are flight-ready adults by spring. In support of the latter hypothesis, mass flight by *I. typographus* occurs only when ambient air temperature exceeds 20°C, yet brood development continues even at 5°C (Annala 1969).

As in other scolytids (Atkins 1966b), *I. latidens* exploits ephemeral and patchy habitats, such as the winter's accumulation of wind-downed and diseased trees. Selection

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should favor individuals emerging and establishing broods as soon as environmental conditions are favorable. Late emergents should be selected against because they would not be as successful in finding adequate phloem or mates.

Implications to forest pest management. *Ips latidens* is not recognized as a significant forest pest. It does not aggressively attack living trees and its population growth is limited by only 1 generation per year. However, it is ubiquitous, breeds in several conifer species, especially in slash, and has a reproductive potential comparable to other ips. The possibility exists that effective suppression of populations of either *D. ponderosae* or *I. pini* could result in compensatory population growth of and damage by *I. latidens*. Routine sanitation practices such as slash disposal, and sanitation/salvage logging in *D. ponderosae* and *I. pini* infestations, should reduce the probability of attack and infestation by *I. latidens*. However timing is critical; *I. latidens* emerges early in the spring before *D. ponderosae*, and possibly before *I. pini* as well. Sanitation efforts directed against *D. ponderosae* in June and July would be ineffective against overwintering populations of *I. latidens*.

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