THE LIFE-HISTORY AND BIOLOGY OF THE BARK BEETLE, *IPS LATIDENS* (LECONTE)(COLEOPTERA:SCOLYTIDAE)

by

Daniel R. Miller

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Name: Daniel R. Miller

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Examining Committee

Chairman: Dr. L. D. Druehl

Dr. John H. Borden, Senior Supervisor

Dr. A. T. Beckenbach

Dr. John A. McLean, Associate Professor, Faculty of Forestry, University of British Columbia, Public Examiner

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Author:

(signature)

Daniel R. Miller

(name)

10 Feb 1984

(date)

ABSTRACT

The life-history and biology of Ips latidens (LeConte) were investigated using bark-sandwich and whole-log rearing methods. In contrast to other Ips spp., some females initiated galleries under female-biased sex ratio conditions, 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 1.95 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 the distribution of headcapsule 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 per gallery system; hence, harem size in scolytid species cannot always be inferred from the number of egg tunnels in each gallery, and examinations of galleries in the field to determine productivities of individual females should be verified by laboratory experiments. The mean generation time of I. latidens in the laboratory was 2.07X greater than in 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 one generation, and possibly 2 broods, per year. Pest management practices should be timed for an early flight period in late May-early July, and include slash disposal and winter salvage logging operations.

DEDICATION

To those who study biology, and attempt to dissolve the mythical distinction between pure and applied research.

ACKNOWLEDGEMENTS

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INTRODUCTION

The bark beetle, *Ips latidens* (LeConte)[1] (Coleoptera:Scolytidae), generally attacks the tops and limbs of dead, dying or weakened coniferous trees and/or slash, particularly lodgepole and ponderosa pines, *Pinus contorta* var. *latifolia* Engelm. and *P. ponderosa* Dougl. *ex* Laws., in British Columbia (Bright 1976). Under favorable 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).

In British Columbia I have found *I. latidens* infesting boles of large-diameter pines. Within the area of a *D. ponderosae* infestation, some trees of substantial size may also be infested with *I. latidens* or *I. pini* (Say) (J.H. Borden[2], pers. comm.). If mortality due to *Ips* spp. has been mistakenly attributed to *D. ponderosae*, then damage caused to mature pines by ips should be reassessed to gain a realistic knowledge of their impact on the forest resource. As intensive forest management practices are implemented, operations such as thinning and spacing may result in large numbers of *I. latidens* emerging from slash and attacking the remaining trees in plantations.

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[1] Formerly *Orthotomicus latidens* (LeConte) *sensu* Hopping; *Ips guildi* Blackman; *Tomicus spinifer* Eichhoff; *Ips longidens* Swaine; *Ips latidens* (LeConte) *sensu* Swaine; *Tomicus latidens* LeConte (Bright and Stark 1973; Wood 1982).

[2] Centre for Pest Management, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6.

Relatively little is known about the life history or basic biology of I. latidens. Blackman (1919) examined over 100 engravings made by I. latidens in eastern white pine, P. strobus L. Males 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 in the bark, and sometimes engraved in the sapwood (Chamberlin 1958; Bright and Stark 1973; Bright 1976; Furniss and Carolin 1977; Wood 1982).

Lanier (1966) and Lanier and Oliver (1966) have described a 'sex-ratio' (SR) phenomenon in which females transmit a factor to their offspring resulting in all-female broods. Several authors (Wood et al. 1967; Lanier and Wood 1975; Furniss and Livingston 1979) have observed I. latidens responding to terpene alcohol pheromones being tested for other Ips spp.

Without basic information on the life history and population dynamics of I. latidens, it is very difficult to assess either the direct impact of I. latidens upon forested ecosystems or its interactions with other bark beetles. In the southern United States there was a 27X 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). As I. latidens is sympatric with the aggressive bark beetles, D. ponderosae and I. pini, it is imperative that the biology of I. latidens be known in order to develop successful pest management practices in lodgepole and ponderosa pine forests in British Columbia.

My objectives were to:

1. describe the gallery characteristics of I. latidens in detail,
2. describe the behavior of adult and larval I. latidens within phloem tissue,
3. determine the number of larval instars,

4. estimate the duration of each stage, the generation time, and the interval between flight periods,
5. determine the reproductive potential of *I. latidens*, and
6. examine the implications of *I. latidens* biology on forest pest management.

MATERIALS AND METHODS

COLLECTION OF BEETLES AND HOST MATERIAL

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, B.C. Within 3 days the exposed ends of all bolts were sealed with hot, melted parafin wax. Infested bolts not immediately used for rearing were stored at 4-12 °C and 20-30% R.H. Uninfested bolts were stored outside in a roofed enclosure.

REARING METHODS

Colonies

Colonies to produce large numbers of *I. latidens* and *I. pini* were maintained in separate rearing cages at 25-35 °C and approximately 40% R.H. Colonies were started by allowing 50-150 beetles reared from field-infested bolts to attack 2-4 uninfested bolts; attack usually occurred within a day. Whenever beetles seemed more inclined to fly than attack, the cages were covered with dark plastic. Emergent beetles from mature broods were collected daily from the cage walls and stored on moistened tissue paper in glass jars at 4-8 °C.

Pill-capsule technique

In a method similar to that used by Borden (1967) gelatin pill capsules (No. 00, Parke, Davis and Co., Ltd., Brockville, Ontario) were used to restrict beetle activity to a small area on a bolt. Beetles were placed within 8-mm-diameter holes made through the bark and phloem with a cork borer. Each hole was covered with the long portion (8x20 mm) of a separated capsule, held in place with masking tape. Capsules were removed to allow introduction of additional beetles and replaced with new capsules.

Arena-bolt technique

Since pill capsules were ineffective in restraining *I. latidens*, a petri dish enclosure technique (Hosking 1972; Zanuncio 1981) was used, and modified to permit beetles to bore their own entrance holes through the bark. Holes (1 cm diameter) were made through the tops and bottoms of plastic petri plates (35x10 mm or 60x15 mm) using a hot spike. The separated portions of the plates were affixed with Hyplar^{R} modelling paste (M. Grumbacher, Inc., New York, N.Y.) to partially-debarked bolts with the open side facing the bark surface. Beetles were introduced through the hole of each arena, and the holes were sealed with transparent tape.

Bark-sandwich technique

A variety of bark "sandwich" preparations have been used to observe scolytid behavior *in situ* (Reid 1955; Hopping 1961; Thomas 1961; Beanlands 1966; Balogun 1969; Borden 1969; Schmitz 1972; Gouger *et al*. 1975). The basic design consists of: (1) a viewing surface of glass or plexiglass, against which is pressed (2) a bark section with the phloem tissue inward,

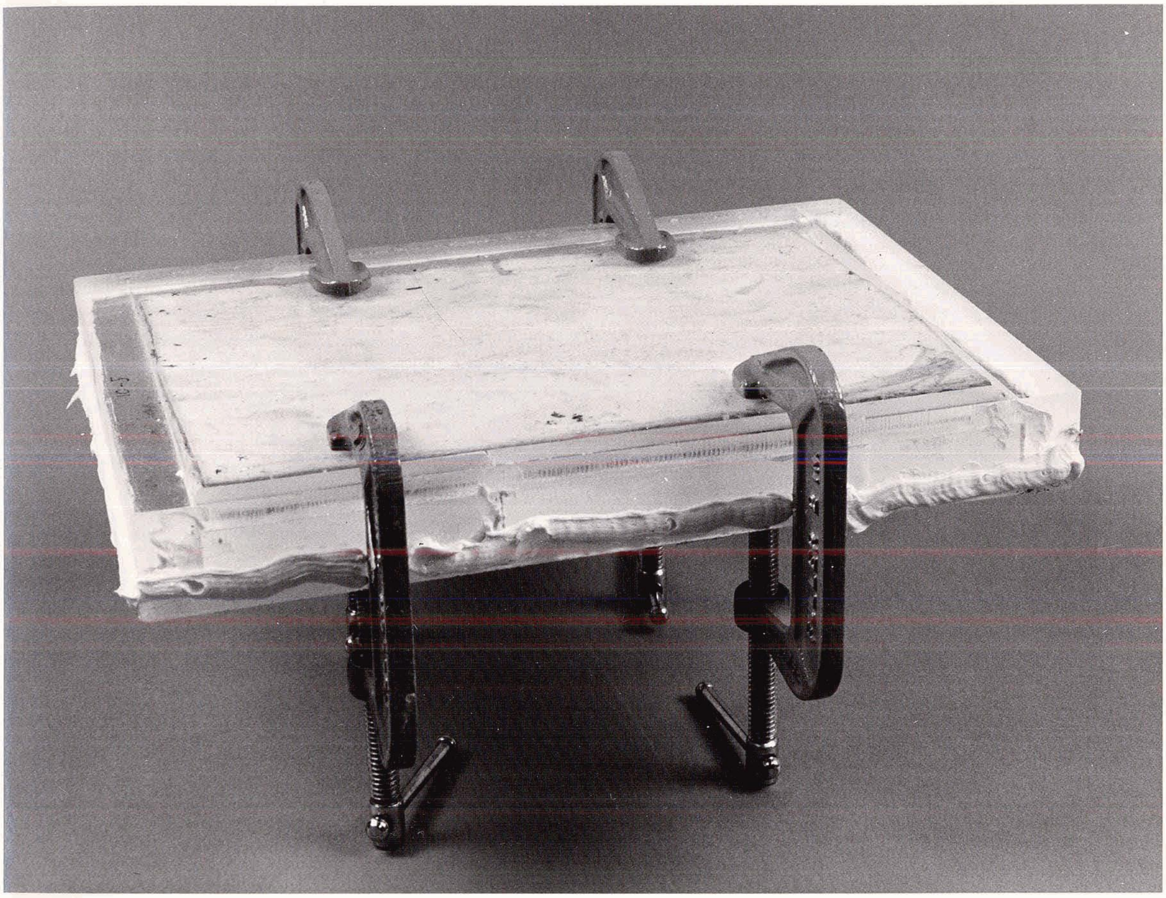
(3) a glass, wood or plexiglass section on the outside of the bark section forming the "sandwich", (4) bolts, clamps or tape to hold the preparation together, and sometimes (5) hot parafin wax or tape to seal the exposed edges of the bark section.

Two major drawbacks of existing sandwich designs are: (1) localisation 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. Therefore, I modified the technique by placing the bark section in a plexiglass box with a styrofoam pad on the outside (Fig. 1). The inward bow of the plexiglass top of the sandwich caused by the sides of the box acting as fulcra, and the spongy nature of the styrofoam, resulted in most of the pressure from 4 clamps being evenly distributed over the entire bark surface. This method resulted in a bark preparation with minimal damage to phloem tissue and maximal contact between the phloem and viewing surfaces, thereby ensuring reliable observations of beetle activities _in situ_.

Sandwiches were made in boxes of 2 sizes; internal dimensions of 13.8x 20.0 cm and 20.0x30.1 cm. Bark sections corresponding to these dimensions were removed with knife and chisel from uninfested and partially-debarked bolts, and placed into each box with the phloem against the bottom. A styrofoam pad and plexiglass top were then added, and the sandwich clamped shut and sealed with acrylic-latex caulk.

Beetles were introduced through 8-mm-diameter holes (in the plexiglass top of each box) that extended through the styrofoam layer to the bark surface. Small sandwiches had either 1 entry hole in the center of the preparation or 3 spaced 5 cm apart in a V-configuration. Large sandwiches

Fig. 1. Plexiglass-styrofoam bark sandwiches.



had 5 entry holes approximately 7 cm apart in a W-configuration.

SEX DIFFERENTIATION

Determination of the sex of adult *I. latidens* using secondary sexual characters described by Lanier and Cameron (1969) proved difficult and unreliable; the *pars stridens* on the frons was rarely detected. Therefore the elytral declivities of 378 adult beetles were examined for sex-specific characters in order to develop some reliability in experiments. The sex of each beetle was then determined by examination of the dissected genitalia, and the specimen mounted for reference. Thereafter, mounted beetles were reviewed before live beetles were examined and separated into 3 categories: males, females and unknowns. Beetles in the unknown category were not used in rearing experiments. In addition to reviewing mounted beetles, I also examined 15 groups of 10-12 live beetles during the first month of experiments in which sex was a controlled factor. The declivity of each beetle was examined for sex-specific characters and the dissected genitalia examined for verification of sex.

REARING EXPERIMENTS

Gallery characteristics and behavior

I attempted to rear broods of *I. latidens* many times: 7 times as mass colonies, 88 times in 50 bark sandwiches, and 254 times on 44 arena bolts with 1-15 arenas per bolt. A total of 342 separate galleries was used to estimate various population parameters, such as fecundity and sex ratios, determine gallery characteristics, and observe the behavior of *I. latidens*. For comparative purposes I reared broods of *I. pini*: 5 times as mass colonies, 7 times in sandwiches and 24 times in 3 arena bolts for a total of 31 separate galleries. Daily collections of emmergent beetles from colonies of both species were used to determine emergence patterns from field- and laboratory-infested logs. Sex ratios amongst 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 localised at 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 per male. The sex of all beetles was verified by examination of dissected genitalia.

Development

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

I examined 17 galleries of I. latidens in bark sandwiches to estimate generation and developmental times for each stage of the life-cycle at 25-35 °C. In 15 sandwiches monogamous pairs were used, while in 3 sandwiches 2 females and 1 male were introduced into each entry hole. Comparisons were made with 6 galleries of I. pini in bark sandwiches at 25-35 °C. Monogamous pairs were used in 5 sandwiches, while the sixth had 2 females with a male. Daily observations were made until all viable larvae had developed to teneral adults or until excessive fungal growth or lack of visibility precluded any observations. Sandwiches were then dismantled and the sex of brood adults determined by examination of dissected genitalia.

Brood survivorship

Brood survivorship was determined from 101 galleries on 8 arena bolts and 63 galleries in 33 sandwiches, for a total of 164. In all rearings monogamous pairs were introduced into each arena or sandwich entry hole. Single, monogamous pairs of *I. latidens* were introduced into each of 22 arena-bolts, and kept in separate rearing cages at 25-35 °C, in order to determine the reproductive success of individual females. The sex of all brood adults were determined by examination of dissected genitalia.

RESULTS AND DISCUSSION

SEX DIFFERENTIATION

Consistently high accuracy within male and female categories as determined by examination of dissected genitalia (Table 1), 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. Beetles were categorised 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.

Single, qualitative traits, efficient for Californian populations

Table 1. Accuracy in differentiating the sexes of Ips latidens on the basis of secondary sexual characters of the elytral declivity.

Category	April-May 1983			Sept 1983		
	Observed[1]	Determined(%)[2]		Observed[1]	Determined(%)[2]	
		Male	Female		Male	Female
Males	74	89.2	10.8	51	94.1	5.9
Females	85	9.4	90.6	132	6.8	93.2
Unknowns	17	41.2	58.8	87	43.7	56.3
Total	176	46.3	53.7	270	39.3	60.7

[1] based on secondary sexual characters of elytral declivities.

[2] based on examinations of dissected genitalia.

(Lanier and Cameron 1969; Bright 1976; Wood 1982), are not easily used by persons unfamiliar with I. latidens nor are they adequate for differentiating the sexes of a significant portion of beetle populations in British Columbia; the sex of 23% of adults examined could not be determined on the basis of declivital characteristics. Hence for British Columbian populations of I. latidens, sex should be determined on the basis of multiple declivital characteristics, at least some of which should be quantitative and normalised to body measurements.

GALLERY CHARACTERISTICS AND BEHAVIOR

Gallery initiation and maintenance

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 initiate most galleries, excavating triangular nuptial chambers (mean area=11.9 mm^2; SD=2.61; n=9) from which female-constructed egg tunnels radiate outward. Females may initiate galleries in female-biased sex ratio situations; 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 behind galleries containing ovipositing females to join females in female-initiated galleries.

Seventy-one single females constructed tunnels, possibly in preparation for mates or as a consequence of feeding. In 3 arenas, 3 ovipositing females were found alone in female-initiated egg tunnels. Since mating is necessary before oviposition can occur, even in SR females, (Lanier and

Oliver 1966), either males and/or females travelled 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%.

Males in sandwiches blocked gallery entrances with their declivities, presumably defending their harems. 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 seemed more efficient in preventing entry by females; 48% of females did not enter a male's gallery, and initiated their own. In *I. paraconfusus* Lanier male guarding behavior does limit 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 as used by *Scolytus ratzeburgi* Jans (Mel'nikova 1964) to regulate humidity within galleries were common in *I. pini* galleries, but rare in *I. latidens* galleries. 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

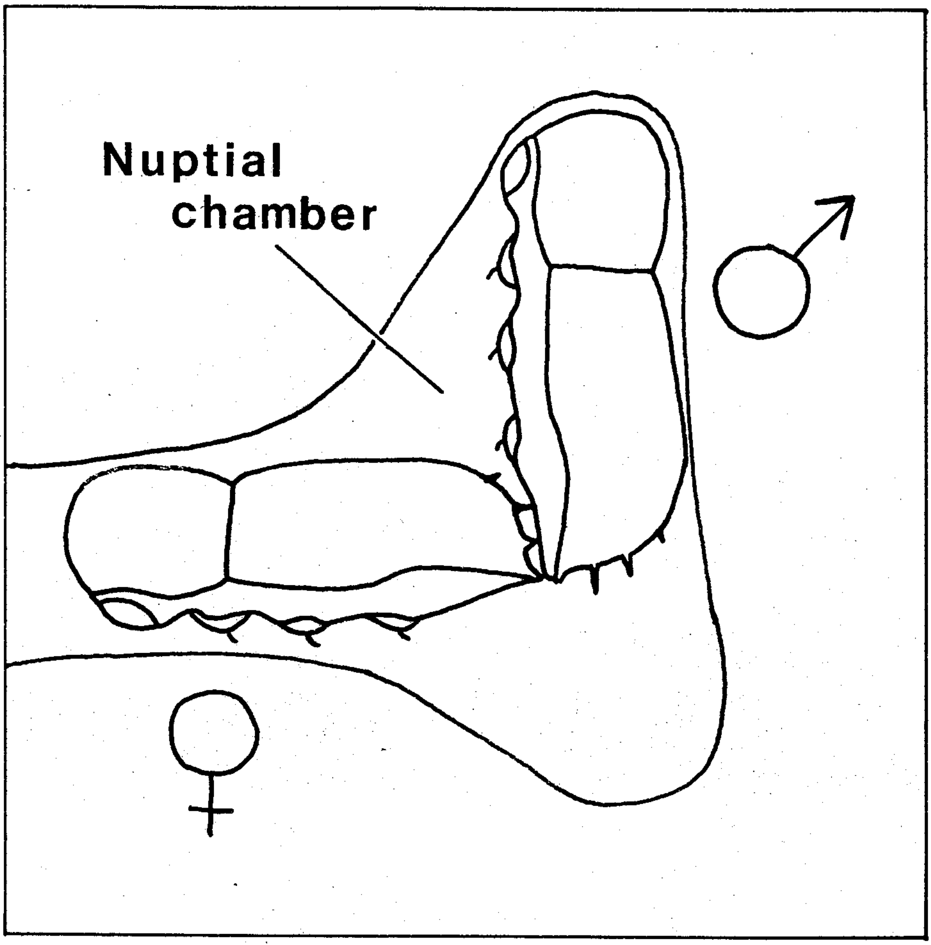
Frequent shoving matches occurred between females and the resident male at the junction of egg tunnels and the nuptial chamber, particularly preceeding mating and oviposition.

As in many other scolytids (Kirkendall 1983), *I. latidens* mated repeatedly; in all 12 matings I observed, females had previously oviposited in their respective egg tunnels, and 4 matings involved the same pair of adults. Mating lasted 20-120 sec; comparable to *I. avulsus* (Gouger *et al*. 1975), *I. pini* (Thomas 1961; Schmitz 1972) and *I. cembrae* Heer (Balogun 1970). The copulatory position of *I. latidens* was similar to *I. avulsus* but differred from *I. pini* and *I. cembrae*, with the body axes perpendicular to each other rather than parallel (Fig. 2).

Oviposition was only observed once in a bark sandwich, and was similar to *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 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 minor 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 1.95 egg niches/day; 0.78X slower than *I. pini* (t test, $p < 0.1$)

Fig. 2. Copulatory position of *I. latidens* in *P. contorta* var. *latifolia* bark sandwiches.


Nuptial chamber
♂
♀

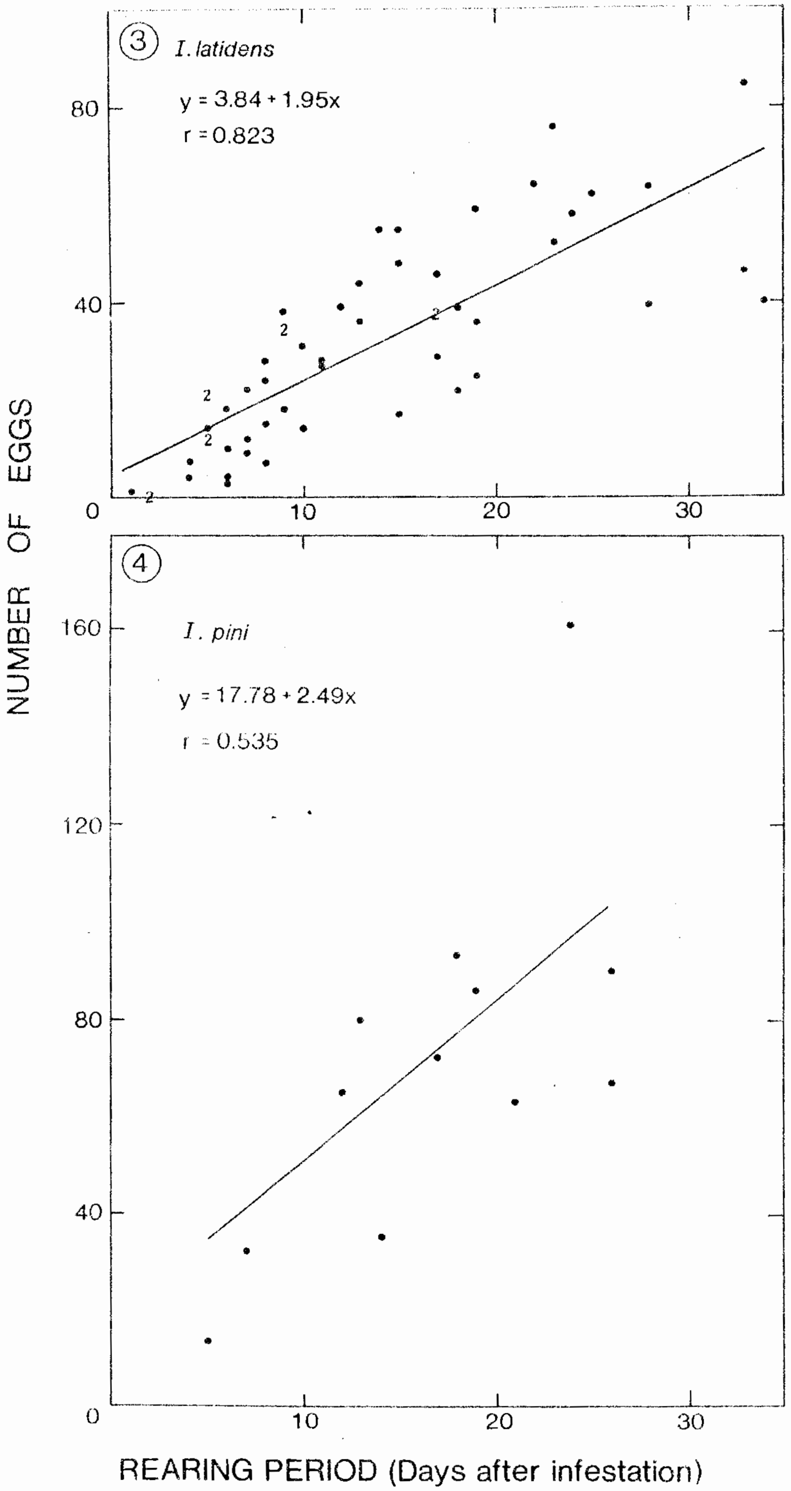
(Figs. 3-4). The distribution of niches ranged from even along both sides of an egg tunnel to all on one side.

In lodgepole pine, the smaller eggs of *I. latidens* were laid singly in niches, spaced closer together than egg niches in *I. pini* egg tunnels; 0.95 and 0.54 egg niches/mm of egg tunnel, respectively (t test, $p < 0.01$)(Figs. 5-6). In jackpine, *P. banksiana* Lamb., and eastern white pine, *I. pini* constructed 0.29-0.32 and 0.50 egg niches/mm of egg tunnel, respectively (Thomas 1961). Niches made by *I. latidens* were spaced farther apart in ponderosa pine (0.51 egg niches/mm of egg tunnel)(Fig. 7) than in lodgepole pine (t test, $p < 0.01$). Kirkendall (1983) suggests that niche spacing by female scolytids is a function of phloem quality; in *Pityophthorus lautus* Eichhoff, niche spacing was strongly correlated with nitrogen content and total available carbohydrates in phloem of the smooth sumac, *Rhus glabra* L.

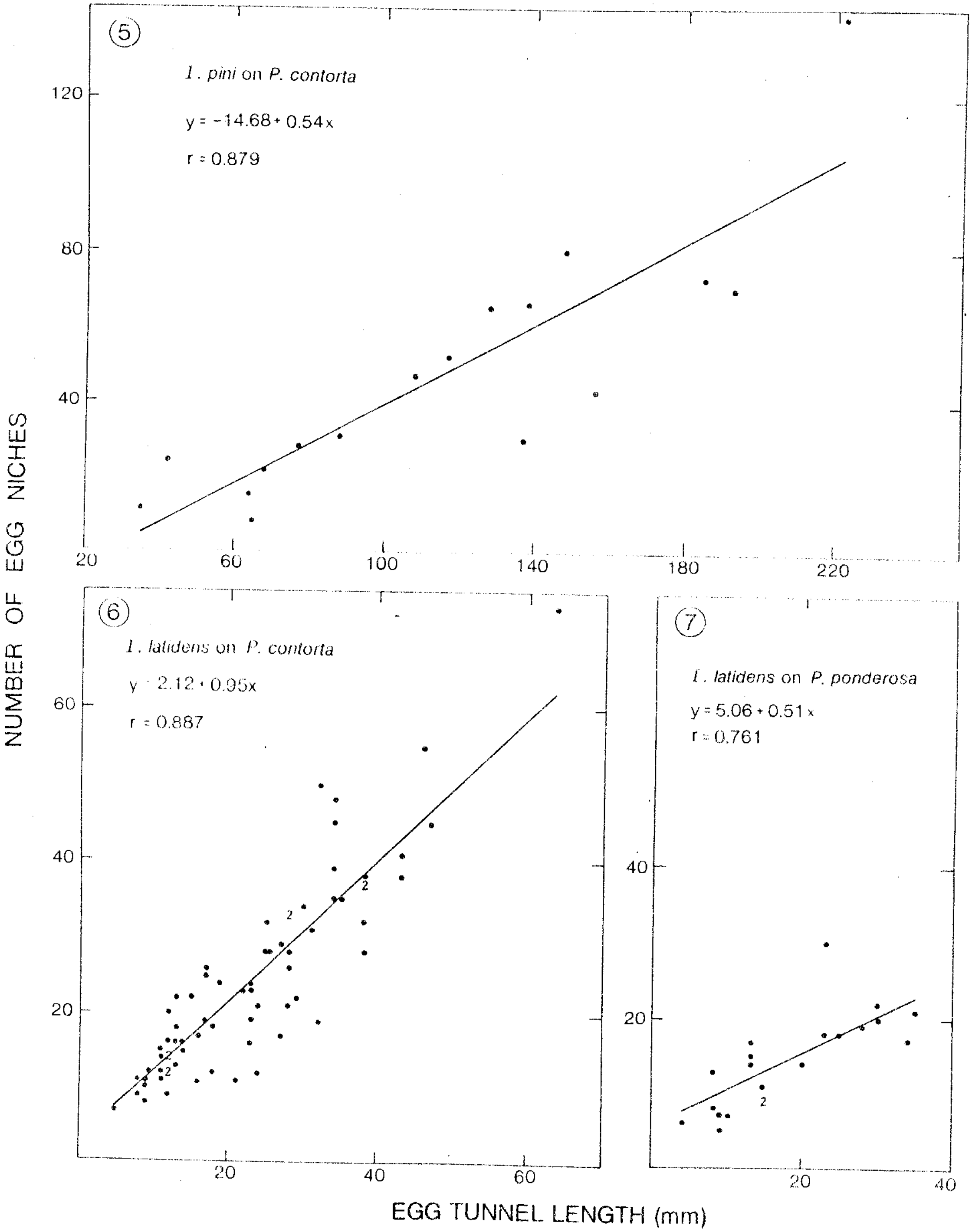
Intraspecific competition is the most important mortality factor in broods of *I. pini* (Schenk and Benjamin 1969) and scolytids in general (Cole 1973, 1975; Ogibin 1973, 1974; Birch 1978; Berryman 1982). Female scolytids such as *I. latidens* may be able to assess resource quality of phloem and space their eggs along egg tunnels in order to minimise intrabrood mortality. Cannibalism amongst larval *I. latidens*, consistent with observations on other scolytids (Schenk and Benjamin 1969; Berryman and Pienaar 1973; Berryman 1974), did occur and suggests that intrabrood competition may occur amongst larvae.

Linearity of regression lines (Chi^2 test, $p < 0.01$)(Figs. 5-7) suggests that niche spacing is constant regardless of egg tunnel length for both *I. latidens* and *I. pini* for a given quality of phloem resource. Linear relationships between the numbers of eggs and egg tunnel lengths are known for *I. cembrae* (Balogun 1970) and *I. pini* (Thomas 1961). A constant spacing

Figs. 3-4. Rate of niche construction and oviposition by ips in _P. contorta_ var. _latifolia_ at 25-35 °C. Fig. 3, _I. latidens_. Fig. 4, _I. pini_.


③ I. latidens
y = 3.84 + 1.95x
r = 0.823
④ I. pini
y = 17.78 + 2.49x
r = 0.535
NUMBER OF EGGS
0
40
80
120
160
10
20
30
REARING PERIOD (Days after infestation)

Figs. 5-7. Spacing of niches in egg tunnels by female ips at 25-35 °C. Fig. 5, *I. pini* in *P. contorta* var. *latifolia*. Fig. 6, *I. latidens* in *P. contorta* var. *latifolia*. Fig. 7, *I. latidens* in *P. ponderosa*.


⑤
I. pini on P. contorta
y = −14.68 + 0.54x
r = 0.879
120
80
40
20
60
100
140
180
220
⑥
I. latidens on P. contorta
y = 2.12 + 0.95x
r = 0.887
60
40
20
20
40
60
⑦
I. latidens on P. ponderosa
y = 5.06 + 0.51x
r = 0.761
40
20
20
40
2
NUMBER OF EGG NICHES
EGG TUNNEL LENGTH (mm)

of egg niches, rather than a variable ovipositing strategy along an egg tunnel (i.e. spacing niches in the middle of an egg tunnel farther apart), may be an optimisation strategy where loss due to intrabrood competition is offset by the risk of dying before a full complement of eggs is laid.

Fecundity of I. latidens was 64.4 eggs/female (SD=16.26; n=17), not significantly different from that of I. pini (66.6 eggs/female; SD=31.39; n=9)(t test, $p > 0.5$), and comparable to other ips, 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 I. latidens galleries increased over time, with mature galleries having 3-4 egg tunnels (Table 2). Newly-laid eggs were usually found in only one egg tunnel of a gallery, the other, older tunnels having only larvae. Females generally constructed only one egg tunnel at a time, although a few alternated between tunnels. Egg tunnels had a mean length of 29.8 mm (SD=9.77; n=45) and contained an average of 27.4 egg niches each (SD=11.45; n=59).

Since female I. latidens, Pityophthorus lautus (Kirkendall 1983), and I. paraconfusus (Barr 1969) may construct more than one egg tunnel per gallery, harem size in scolytid species cannot always be inferred from the number of egg tunnels in each gallery. Cook et al. (1983) made the same observation for I. avulsus, but suggest that multiple egg tunnels per gallery 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

Table 2. Mean number of egg tunnels constructed within 65 separate monogamous *Ips latidens* galleries in *Pinus contorta* var. *latifolia*.

Days after infestation	Number of galleries	Egg tunnels		
		Total	Mean/female[1]	SD
0-5	12	13	1.08	0.669
6-20	34	61	1.79	0.808
21-35	13	33	2.54	0.878
35	6	20	3.33	0.516

[1] significant differences amongst means, Kruskal-Wallis test, $p < 0.01$

experiments.

Bark beetle attacks are uniformly distributed over bark surfaces (Shepherd 1965; Berryman 1968; Hedden and Gara 1976; Nillsen 1978). Each gallery has a limited phloem resource to utilise for brood production. Hence the construction of multiple short egg tunnels by I. latidens, rather than single long tunnels, per gallery may maximise phloem use while minimising intergallery competition amongst larvae.

I. 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 (SD=1.56; n=39; range= 1-7) in lodgepole pine arena bolts, significantly greater than the mean of 1.8 females/male (SD=0.73; n=21) found in ponderosa pine pill-capsule rearings (t test, $p < 0.01$).

In moderately polygynous scolytid species, 2-4 egg tunnels per 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 among I. latidens females in polygynous galleries for egg tunnel sites; as harem size increases, competition for oviposition sites amongst females should increase.

Therefore, in order to maximise reproductive success, females in polygynous situations would be expected to re-emerge and attempt to establish additional broods, a strategy typical of many scolytids (Borden 1982). Ips latidens in monogamous bark sandwich galleries did not re-emerge while 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 in a gallery ovipositing arise due to phloem quality and size of harems (Kirkendall 1983). In *I. latidens* galleries, the number of eggs/gallery, and egg tunnel length, decreases with an increase in egg tunnels/gallery (Blackman 1919).

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

There may be a selective advantage for males to limit the size of harems as in *I. paraconfusus* (Borden 1967). Even 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 may only be able to sustain a finite number of progeny. Survivorship within *I. paraconfusus* broods in galleries containing 3-4 females each was lower at an attack density of 2 males/dm^2 than 1 male/dm^2 (Light *et al*. 1983).

Some scolytids deposit fewer eggs per gallery in response to increased attack density (Berryman 1982). At high densities spacing between galleries may approach a lower threshold, 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/egg tunnel and re-emerged earlier at a density of 4 parent females/dm^2 than at 2 parent females/dm^2 (Light _et al_. 1983).

Therefore, it seems likely, and testable, that females of polygynous scolytid species like _I. latidens_ may be able to assess attack density and harem size, and adopt appropriate reproductive strategies.

DEVELOPMENT

Number of larval instars

Dyar's rule (Dyar 1890) has been successfully used to determine the number of larval instars in scolytid species (Thomas 1961; Wilkinson 1963; Hosking and Knight 1976). The distribution of the frequencies of headcapsule widths of 749 _I. latidens_ larvae clearly shows 3 instars in the larval stage (Fig. 8), typical of all species in the tribe Ipini (Wood 1982). Headcapsule width means for successive instars were significantly different, and exhibited a regular, geometric progression (Table 3), as predicted by Dyar's rule (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.

Fig. 8. Frequency distribution of headcapsule widths of 749 larval *Ips latidens*.

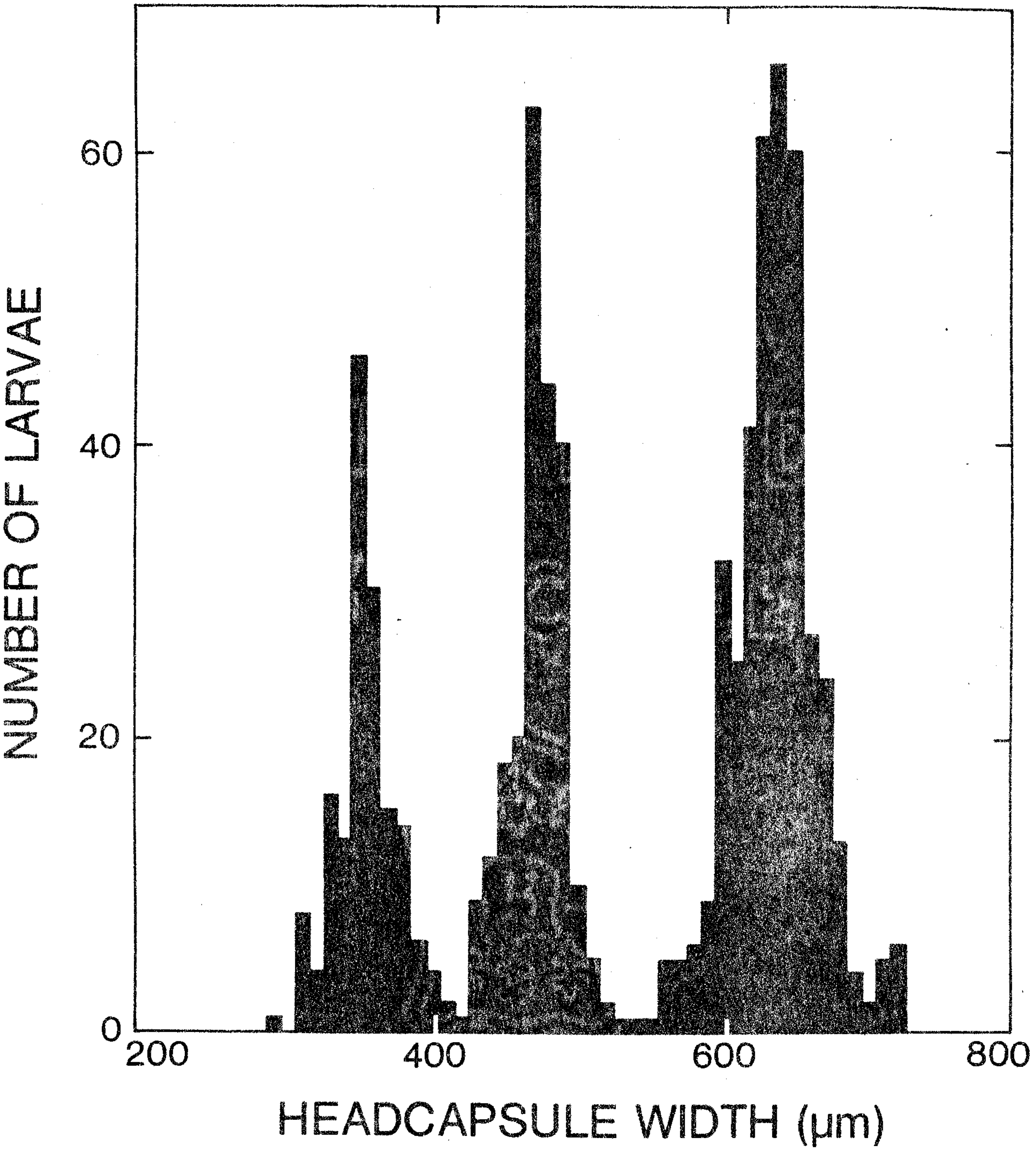

NUMBER OF LARVAE
0
20
40
60
200
400
600
800
HEADCAPSULE WIDTH (μm)

Table 3. Mean headcapsule widths of larval instars of *Ips latidens* (n=749).

Instar	Sample size	Headcapsule width (um)				Dyar's constant[2]
		$\bar{X}$[1]	SD	Minimum	Maximum	
1	156	354	22.0	294	412	------
2	205	472	19.8	423	540	1.33
3	388	636	29.0	552	725	1.35

[1] means significantly different, Kruskal-Wallis test, $p < 0.001$.

[2] ratio of the mean headcapsule widths of one instar to the previous instar.

Development of each stage was significantly longer for I. latidens than for I. pini (t test, $p < 0.01$)(Fig. 9). The generation time (egg to teneral adult) in I. latidens was 2.07X 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 to field data on I. pini at Black Sturgeon Lake, Ontario (Thomas 1961), and in Fredericton, New Brunswick (Prebble 1933), I 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; comparable to many scolytids (Wood 1982). The generation time for I. latidens should range from 64.2 to 99.4 days. Using field data for I. pini near Rocky Mountain House, Alberta (Reid 1955), the generation time may last 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 56.0% (Fig. 10). In an independent experiment, the mean reproductive success of 17 monogamous pairs in lodgepole pine logs was 36.5 teneral adults/pair (SD=18.85); assuming a mean fecundity of 64.4 eggs/female, brood survivorship was 56.7%.

Fig. 9. Duration of developmental periods of *I. latidens* and *I. pini* in *P. contorta* var. *latifolia* bark sandwiches at 25-35 °C (sample sizes given below each bar).

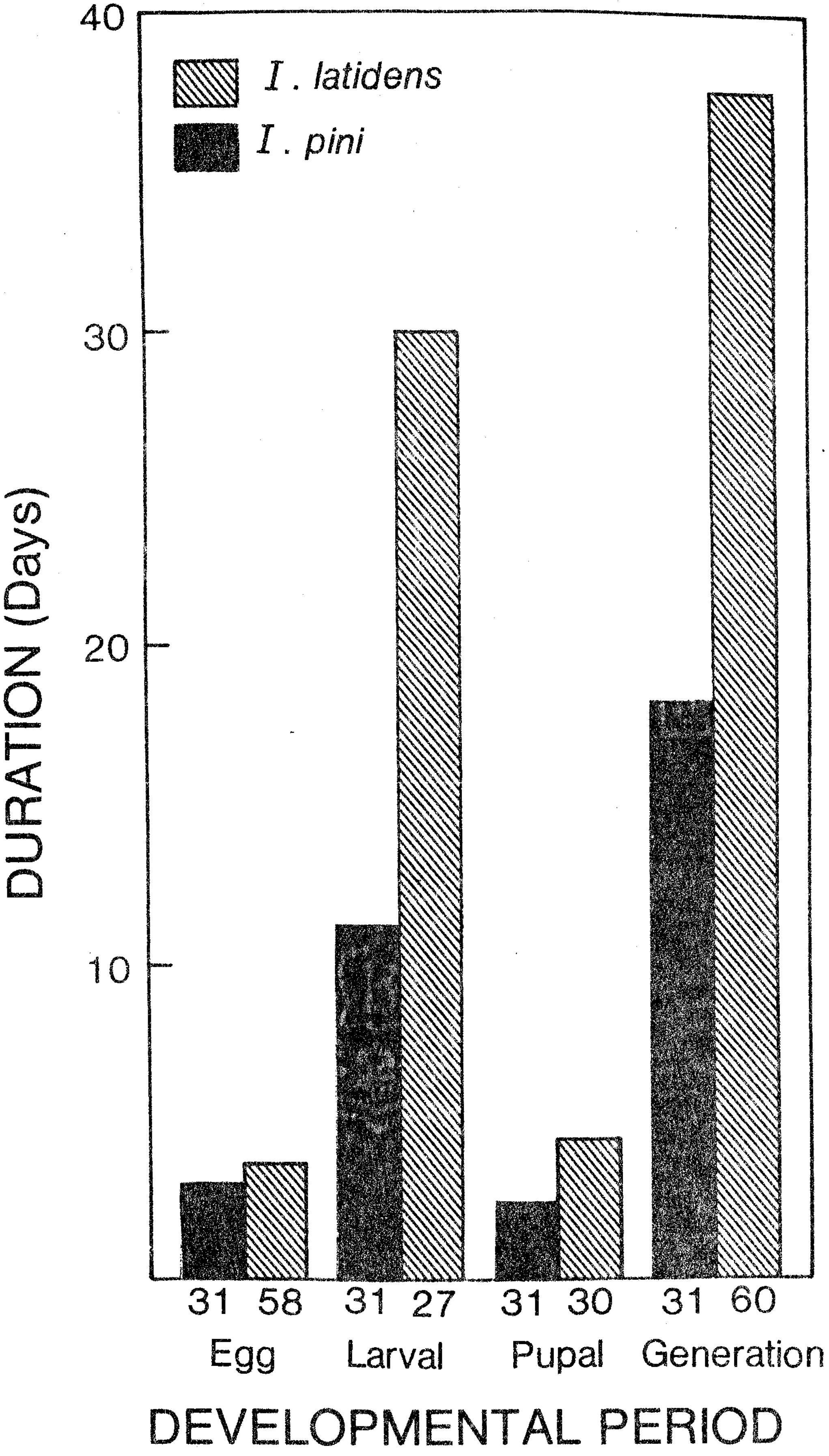
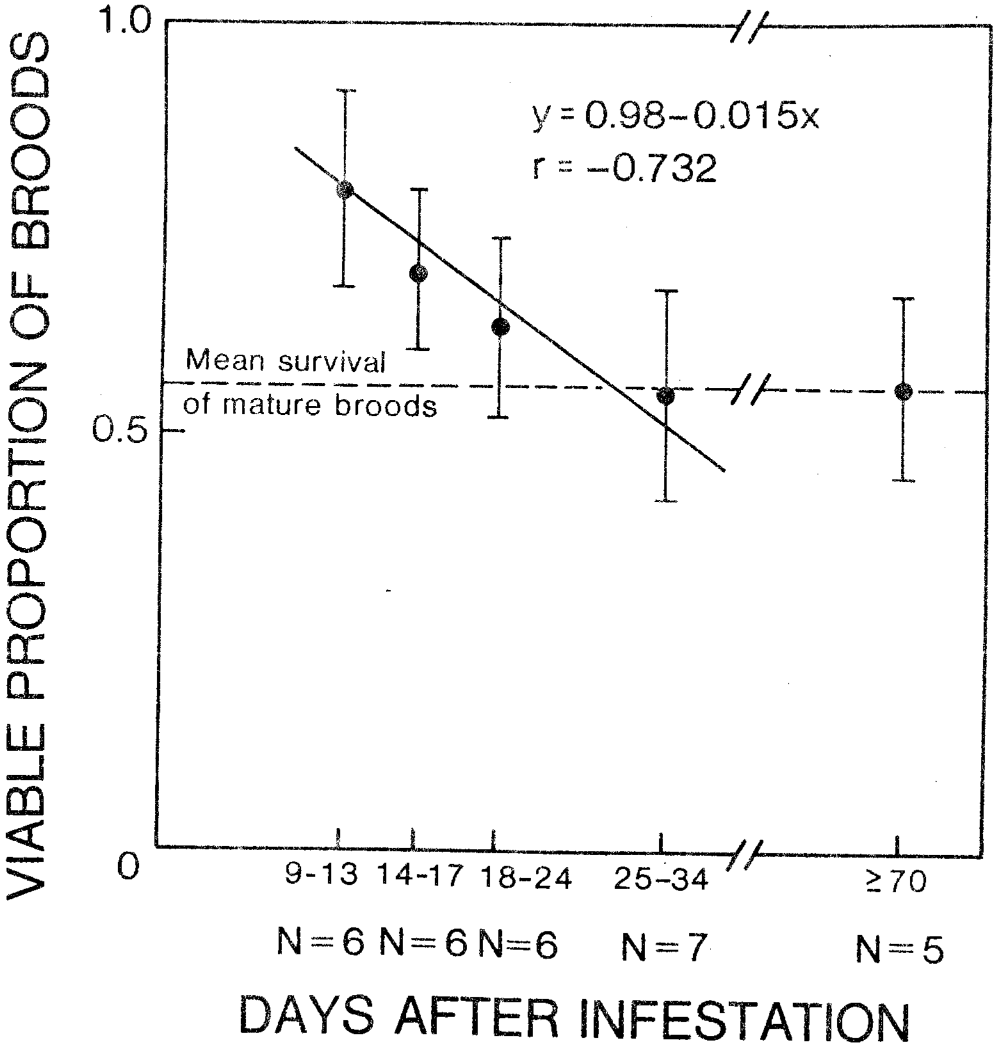

I. latidens
I. pini
DURATION (Days)
40
30
20
10
31
58
31
27
31
30
31
60
Egg
Larval
Pupal
Generation
DEVELOPMENTAL PERIOD

Fig. 10. Survivorship within broods of *I. latidens* in *P. contorta* var. *latifolia* at 25-35 °C.


1.0
0.5
0
VIABLE PROPORTION OF BROODS
y = 0.98−0.015x
r = −0.732
Mean survival
of mature broods
9-13
14-17
18-24
25-34
≥70
N=6
N=6
N=6
N=7
N=5
DAYS AFTER INFESTATION

EMERGENCE PATTERNS

Sex ratio

In ips the typical sex ratio amongst emerging adults is close to 1:1, while the sex ratio amongst attacking beetles or successful beetles is generally female-biased at greater 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* (Annila 1971). In *I. latidens* the sex ratio amongst 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 and Oliver 1966).

Annual flight periods

Pest management practices against bark beetles are timed around flight periods when adults attack new hosts. The estimated generation time of 64-124 days for *I. latidens* may not be a reliable estimate of the period between flights of attacking adults and their subsequent offspring. In laboratory colonies, first emergence of *I. latidens* progeny occurred 60-65 days after infestation; approximately 1.6X 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 feed for weeks and sometimes even months before 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 chalcographus* L., spermateliosis and vitellogenesis occurs primarily during the maturation feeding period prior to emergence, even though gonads are completely developed prior to feeding (Zumr and Soldan 1981). The flight muscle volume of I. paraconfusus increases 10X during maturation feeding (Borden and Slater 1969). Lipid reserves of D. pseudotsugae Hopkins adults build up to 20% of total dry body weight before they are optimally-ready for dispersal flight (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, B.C., which suggested a single major flight period between late May and early June, and a minor peak in late July, probably representing re-emerged adults (J.L. Madden[2], D.R. Miller 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 two small and related ipine species, Pityogenes knechteli Swaine and Orthotomicus vicinus (LeConte), occupying similar niches in Albertan lodgepole pine forests (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. 11). Emergence from

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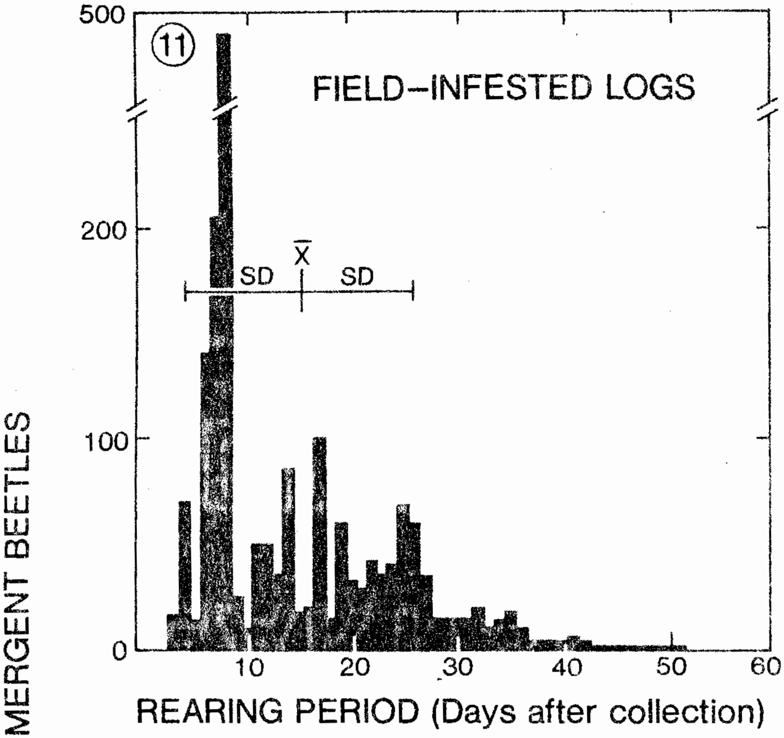
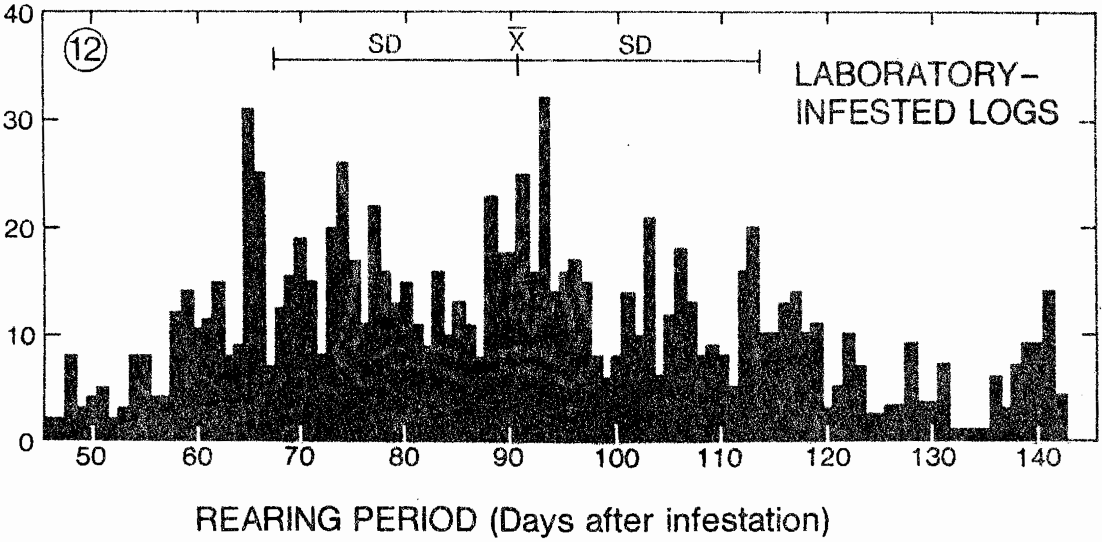
[2] Faculty of Agricultural Science, University of Tasmania, Hobart, Tasmania Australia.

Figs. 11-12. Emergence patterns of *I. latidens* from *P. contorta* var. *latifolia* at 25-35 °C. Fig. 11, Field-infested logs. Fig. 12, Laboratory-infested bolts.


⑪
FIELD–INFESTED LOGS
NUMBER OF EMERGENT BEETLES
500
200
100
0
SD
X̄
SD
10
20
30
40
50
60
REARING PERIOD (Days after collection)


⑫
LABORATORY–
INFESTED LOGS
40
30
20
10
0
SD
X̄
SD
50
60
70
80
90
100
110
120
130
140
REARING PERIOD (Days after infestation)

laboratory-infested lodgepole pine logs was protracted significantly more than from field-infested logs (F test, $p < 0.01$); 90% of the beetles emerged over a 75-day period (Fig. 12).

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 ^{o}C, yet brood development continues even at 5 ^{o}C (Annila 1969).

Like other scolytids (Atkins 1966b), _I. latidens_ exploits ephemeral and patchy habitats, such as the winter's accumulation of wind-downed and diseased trees. Selection should favor individuals emerging and establishing broods as soon as environmental conditions are favorable. Late emergents should be selected against since they would not be as successful in finding adequate phloem or mates.

IMPLICATIONS TO FOREST PEST MANAGEMENT

Ips latidens is not recognised 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. _I. latidens_ could become a pest in intensively-managed forests of the future. In Georgia, damage to young plantation trees from prescribed burns and thinning operations increases the probability of infestations by _Ips_ spp. (Wilkinson and Fotz 1982).

Several management implications should be kept in mind. Monitoring of

I. latidens populations, particularly within unchecked _D. ponderosae_ infestations, can only be done by the laborious and tedious method of examining bark samples. _I. latidens_ does not cause conspicuous pitch tubes as does _D. ponderosae_, nor does it produce copious amounts of frass like _D. ponderosae_ or _I. pini_. Although chemical attractants are known for _I. latidens_ (Wood _et al_. 1976), they have not been verified as pheromones nor tested as monitoring tools.

The possibility exists that effective control of either _D. ponderosae_ or _I. pini_ populations could result in compensatory population growth of and damage by _I. latidens_. Routine sanitation practices such as efficient 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 probably before _I. pini_. Sanitation efforts directed in June and July against _D. ponderosae_ would be ineffective against overwintering populations of _I. latidens_.

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