Monogamy in the bark beetle *Ips latidens*: ecological correlates of an unusual mating system

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Abstract. 1. The diversity of mating systems in bark beetles (Coleoptera: Scolytidae) is poorly understood. *Ips latidens* (LeConte) is a small-bodied species of a harem polygynous genus whose mating system in nature had not been established previously. This study examines the breeding biology of *I. latidens* breeding in recently dead ponderosa pine (*Pinus ponderosa*) in California. It was expected that both the heterogeneous habitat quality inherent in dead trees and small body size would favour polygyny.

2. Contrary to expectations, *I. latidens* was found to be monogamous on the basis of excavations of 131 galleries conducted throughout the oviposition period at two wind-felled trees and at four sites composed of freshly-cut logs. Males left the galleries much sooner than females (50% gone by 24 and 36 days, respectively).

3. Individual females made up to four egg gallery arms extending from the male nuptial chamber, with the number of arms and the length of individual arms increasing with the age of the gallery. The relationship between total gallery length and gallery age was consistent among the trees and log sites, and did not depend on the presence of the male.

4. *Ips latidens* bred in a wide range of tree diameters (10–24 cm), and occurred in both pure aggregations and in aggregations with two other bark beetle species, *Dendroctonus brevicomis* and *I. paraconfusus*. The presence of the other species did not appear to influence negatively the density of *I. latidens*.

5. Monogamy in *I. latidens* may be due to lower male mortality during dispersal associated with a greater range of suitable breeding habitat than occurs for other *Ips* species, resulting in an even sex ratio at breeding sites.

Key words. Habitat availability, mating system, residence time, Scolytidae.

Introduction

Bark beetles (Coleoptera: Scolytidae) are remarkable for their diversity of mating systems (Kirkendall, 1983). Most species are apparently monogynous, where each female originates an egg gallery independently within the inner phloem of trees (S. L. Wood, 1982). Among monogynous gallery systems, pair bonds between males and females may be minimal or prolonged; the latter situation is referred to as a monogamous mating system (Kirkendall, 1983). In contrast, some prominent bark beetle taxa exhibit harem polygyny, a mating system rarely observed in invertebrates (Kirkendall, 1983). In harem

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polygyny, males initiate nuptial chambers to which several females are attracted for oviposition in egg galleries, and males remain with their mates and brood for much of the oviposition period, which can last several weeks (Reid & Roitberg, 1994).

Kirkendall (1983) proposed two main hypotheses, not mutually exclusive, to account for harem polygyny in bark beetles. The first proposes that there is a biased adult sex ratio due to disproportionate male mortality during dispersal between breeding sites (Annila, 1971), whereas the second hypothesis is the polygyny threshold model (Searcy & Yasukawa, 1989). Of these two possibilities, Kirkendall (1983) favoured the polygyny threshold hypothesis. He argued that harem polygynous species tend to inhabit recently dead trees that are likely to be variable in quality such that females may choose to mate polygynously in high quality habitat rather than monogamously in poor quality habitat. Those species inhabiting living trees, where habitat quality is assumed to be more

homogeneous, tend to be monogynous (Kirkendall, 1983). In addition, Kirkendall (1983) predicted that polygyny would correlate negatively with body size, because offspring of polygynous species would experience greater competition and therefore reach a smaller size. However, in the years since Kirkendall's (1983) comprehensive review, little progress has been made in testing these or other hypotheses for the intriguing diversity of mating systems in bark beetles (Schlyter & Zhang, 1996).

Harem polygyny is best known in the Tribe Ipini within Scolytidae, in which all species are characterized as having this mating system (S. L. Wood, 1982). However, even within the economically significant genus *Ips*, the mating system of many species has not been observed directly in nature. One such species is *Ips latidens*, one of the smallest members of the genus, with a body length of 2–3 mm that is almost half of most congeners. This species, found across North America, breeds in the dead or dying limbs and bole of pines (*Pinus* spp.), but may occasionally kill smaller trees when populations are large (S. L. Wood, 1982). Its mating system is considered to be harem polygynous based on a gallery pattern that has several gallery arms (Blackman, 1919) and on laboratory observations (Miller & Borden, 1985). On the basis of body size and the presumed heterogeneity of its breeding habitat, Kirkendall's (1983) hypotheses predict that polygyny should be more extreme in *I. latidens* than in other *Ips* species. The goal of the current study was to determine the breeding system of *I. latidens* in nature and to relate this to its breeding habitat.

Methods

This study was conducted at the Blodgett Forest Research Station near Georgetown, California, in April and May 1992. Observations of the breeding biology of *I. latidens* were made at several sites that were colonized naturally by this species but probably differed in habitat quality. The primary study site (Chinfall) was a wind-felled ponderosa pine (*Pinus ponderosa*) that was colonized solely by *I. latidens*. This tree was 6 m long, with a base diameter of 19 cm and a top diameter of 11.5 cm. It was located in an open stand of ponderosa pine, with direct late afternoon sun. The second site (Bacchi) was another wind-felled ponderosa pine located 27 km from the first site in a clearing receiving direct midday sun. The fallen bole was 14 m long, with a base diameter of 24 cm and a top diameter of 11.5 cm. Four other sites comprised cut logs obtained from two healthy trees felled on 22 April 1992 and cut into 1-m lengths. Log diameters ranged from 16 to 30 cm. Five logs were assigned randomly to each of the four sites, with the constraint that at least two logs from each tree were at each site. Logs were laid end-to-end in shaded areas within ponderosa pine stands and colonization by bark beetles was allowed to occur naturally. Two of these sites were 50 m apart and less than 100 m from the Chinfall site, whereas the remaining two sites were 50 m apart and more than 6 km from any other site.

The breeding phenologies of *I. latidens* and other bark beetles were monitored by marking new attacks daily (with a

Table 1. Gallery age and total gallery length for galleries having one, two, or three arms in *Ips latidens*.

No. of arms	n	Gallery age (days)				Total gallery length (mm)			
		Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
1	12	11.7[a*]	3.0	1	30	17.5[a]	1.8	7	27
2	42	18.9[a]	1.3	5	40	59.7[b]	3.3	34	127
3	42	24.0[b]	1.6	6	39	79.7[c]	3.5	35	142

*Values within a column with different superscripts are statistically different (Tukey–Kramer test, $P < 0.05$).

few exceptions) using pins labelled with the date. Attacks by the three species of bark beetles observed in this study (see below) were distinguished by the size of frass particles and the size of the entrance hole, verified by dissecting a sample of galleries. The location of all attacks within a site was mapped according to species.

The breeding behaviour of *I. latidens* was determined by dissecting galleries on several occasions after colonization was complete. To avoid effects of previous dissections on the behaviour of remaining beetles, a single day's dissection was restricted to small areas, and successive series of dissections were separated from each other by at least 20 cm. Each beetle collected during dissections was placed individually in a labelled gel capsule. All collected beetles were sexed at a later date using the sexually dimorphic declivital spines (Lanier & Cameron, 1969), and pronotal widths were measured to the nearest 0.024 mm using a dissecting microscope fitted with an ocular micrometer. Gallery measurements included the number of gallery arms and the total gallery length for all arms. In addition, for some gallery systems, the length of each gallery arm was measured individually, together with the number of eggs in each arm. The most detailed dissections were conducted at the Chinfall site (ninety-nine galleries dissected), where four series of dissections were conducted at approximately weekly intervals (Table 1). At the other sites, dissections were less intensive (Bacchi: twenty-nine galleries, log sites: fifteen galleries), and galleries not containing adults were not measured.

Results

Mating patterns

Of 131 galleries that contained at least one *I. latidens*, none contained more than two individuals. Overall, 57.3% of the 131 galleries had two beetles, and this proportion was consistent among the Chinfall site, Bacchi site, and all log sites combined ($\chi^2 = 0.21$, d.f. = 2, $P = $ NS). Pairs of beetles mainly comprised one male and one female (91.3% of sixty-nine galleries where both individuals were sexed), whereas five galleries (7.2%) were identified as having two females, and one gallery (1.4%) was identified as having two males. These data indicate that *I. latidens* has a monogamous mating system.
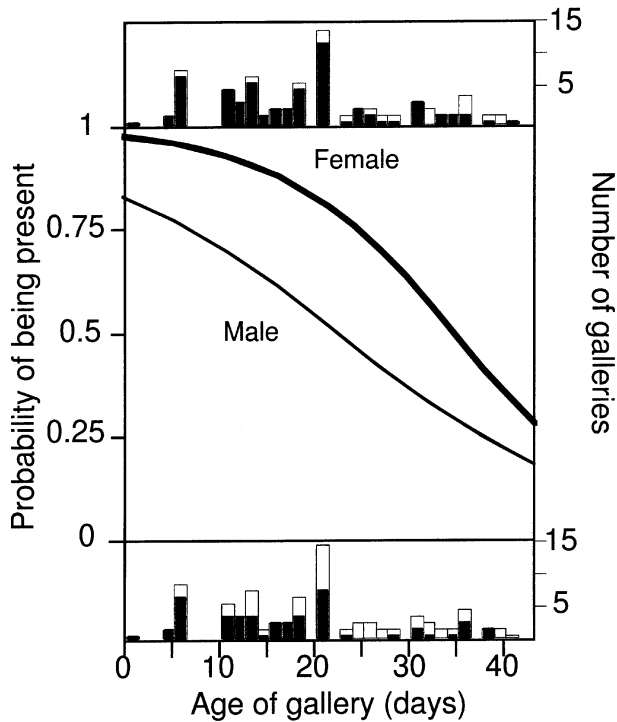
Fig. 1. Probability of a male or female *Ips latidens* being present in a gallery as a function of gallery age, as calculated by logistic regression {females: $P = 1/[1 + \exp(-3.60 + 0.107x)]$, $n = 93$, $P < 0.001$; males: $P = 1/[1 + \exp(-1.63 + 0.069x)]$, $n = 93$, $P < 0.05$}. Data are shown as frequency distributions of galleries for females (top) and males (bottom) that indicate proportion of galleries with individuals present (shaded) and absent (open).

Most of the beetles that were alone in a gallery were female (83.9% of fifty-six galleries), suggesting that males leave the galleries before females leave. This notion was confirmed by a logistic regression of male or female presence as a function of gallery age for the Chinfall site (Fig. 1). Both gallery age and sex were significant predictors of a beetle being present (gallery age: $\chi^2 = 19.48$, d.f. = 1, $P < 0.001$; sex: $\chi^2 = 13.89$, d.f. = 1, $P = 0.001$; no interaction: $P = $ NS). This model predicts that 50% of males had left after 24 days, and 50% of females had left after 36 days. Although males left earlier than females on average, there was considerable variation in the residence time of both sexes (Fig. 1). For example, one male had left by 5 days, whereas another was still present after 38 days. Similarly, the minimum gallery age observed without a female was 6 days, but one female was still present in a gallery that was 40 days old. The presence of one sex did not appear to depend on the presence of the other sex (contingency = 3.39, d.f. = 1, $P = $ NS).

There was a slight sexual dimorphism in body size in *I. latidens*, with the mean female pronotal width equal to 97% of male pronotal width (mean female width: 1.12 ± 0.008 mm, $n = 97$; male width: 1.15 ± 0.007 mm, $n = 63$; $t = 3.30$, $P = 0.001$). There was no evidence of assortative mating by body size ($r = -0.05$, $n = 48$ pairs, $P = $ NS).

Gallery development

Most galleries had more than one arm, with the number of arms increasing with gallery age and total gallery length (Table 1). Three arms were common in older galleries, and one gallery was observed with four arms. The mean length of the longest arm in galleries with more than one arm was 35.2 mm (back-transformed after ln-transformation; 95% CI 31.6–36.0 mm), with no difference between galleries with two or three arms ($t = -0.221$, d.f. = 84, $P = $ NS). However, the length of the longest arm increased with gallery age, when restricting analysis to galleries that had more than one arm (ln-transformed length vs. gallery age: $y = 3.30 + 0.12x$, $R^2 = 0.164$, $n = 82$ galleries, $F = 15.70$, $P = 0.001$). Thus, female *I. latidens* made multiple gallery arms, and seemed to continue extending individual arms after starting new arms.

To determine whether gallery development was influenced by the presence of males or by particular locations, total gallery length was modelled as a function of gallery age, location (Chinfall or Bacchi), and the presence of males. Only active galleries, with females still present, were considered ($n = 82$). Total gallery length varied only as a function of age ($F = 51.14$, $P < 0.001$). This relationship was the same for both sites ($F = 2.43$, $P = $ NS), and there was no detectable effect of having a male present at the time of dissection ($F = 0.40$, $P = $ NS). No interactions between these factors were significant ($P = $ NS). The simple relationship between total gallery length and gallery age was: length (mm) = 27.50 + 1.76 days; $R^2 = 0.41$, $n = 89$, $P < 0.0001$. Egg density was 7.83 ± 0.46 eggs cm^{-1} ($n = 16$ galleries from the Chinfall site); egg density did not vary with gallery age ($F = 1.86$, $P = $ NS).

Breeding habitat

Colonization of the Chinfall, Bacchi, and log sites by *I. latidens* was synchronous, each being attacked first on 26 or 27 April, with the final attacks occurring on 15 May. Colonization densities varied both within and between sites, and this variation can help elucidate the range of habitat used by *I. latidens*.

The Chinfall site was colonized solely by *I. latidens*. A total of 206 galleries was established with a final overall density of 0.90 galleries per 100 cm^2. This density is relatively low, given that gallery arms were only a few centimetres long. Indeed, dissected galleries rarely intersected with other galleries. There was no consistent effect of bole diameter on the density of galleries when the data were grouped for 1-m segments ($R^2 = 0.203$, $n = 6$ sections, $P = $ NS; midpoint diameter range 13–19 cm), although density was markedly lower in the basal metre section (0.60 galleries/100 cm^2) than in the rest of the tree (1.03–1.27 galleries/100 cm^2). The distribution of attacks tended to be spaced regularly at all stages of the colonization phenology, and was significantly regular by the end of colonization [Clark and Evans nearest neighbour distance statistic with edge correction (Sinclair, 1985): observed/expected distance (R) varied from 1.07 to 1.14; final distribution $R = 1.12$, $z = 3.15$, $P < 0.01$].
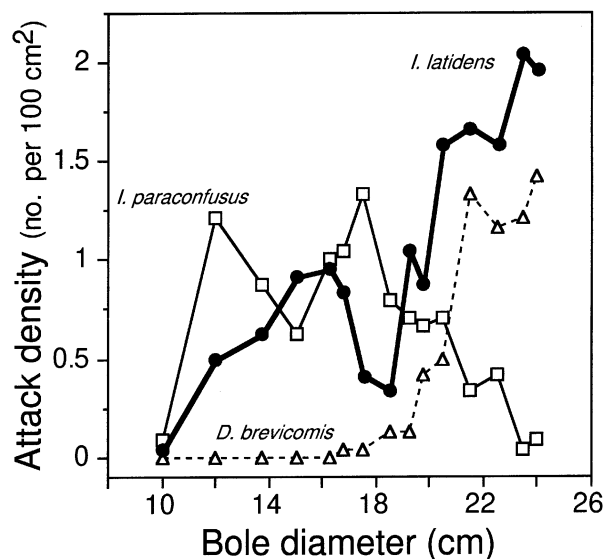
Fig. 2. Density of attacks at the Bacchi site for *Ips latidens, I. paraconfusus* and *Dendroctonus brevicomis* as a function of bole diameter. Each point represents a 1-m section of the bole, beginning at the top of the bole (low end of *x*-axis) and continuing to the base.

The Bacchi windfall site was colonized by *Dendroctonus brevicomis* and *I. paraconfusus* in addition to *I. latidens*. *Ips latidens* had the earliest mean arrival date (4 May), followed by *D. brevicomis* (6 May), and *I. paraconfusus* (7 May) (ANOVA $F = 73.15$, $n = 1174$, $P < 0.0001$; Tukey–Kramer LSD $P < 0.05$ for all pair-wise comparisons). *Ips latidens* colonized the entire mapped length of the bole (14 m), ranging from a bole diameter of 25 cm at the base to 10 cm at the top. To determine the effect of bole diameter, colonization densities were calculated for each metre section for a 24 cm wide strip on the top of the bole. These data indicate that *I. latidens* densities were greater in the larger diameter sections (Fig. 2; linear regression: $R^2 = 0.663$, $n = 14$ sections, $P = 0.001$). A similar pattern was observed for *D. brevicomis* (Fig. 2; second degree polynomial: $R^2 = 0.904$, $P < 0.001$), and densities of *D. brevicomis* and *I. latidens* were correlated positively ($r = 0.884$, $n = 14$, $P < 0.001$). In contrast, *I. paraconfusus* was more common in the smaller diameter sections (Fig. 2; linear regression: $R^2 = 0.648$, $n = 14$, $P = 0.001$), with densities that were correlated negatively with *I. latidens* ($r = -0.870$, $n = 14$, $P < 0.001$). Together these data indicate that *I. latidens* is not restricted to particular tree diameters and co-occurs with other species.

The log sites were colonized by both *I. latidens* and *D. brevicomis*. At these sites the two species arrived essentially simultaneously at a given log. For twelve of fifteen logs that had both species, *D. brevicomis* was the first species to arrive (binomial test, $P > 0.05$) but the mean difference in first arrival date for the two species was not significantly different from zero (mean difference 2.1 days, $t = 1.37$, $n = 15$, $P = $ NS). Densities of *I. latidens* on individual logs ranged from 0 to 1.06 attacks per 100 cm^2 (median 0.075 attacks), whereas *D. brevicomis* colonized in densities ranging from 0.02 to 2.08

attacks per 100 cm^2 (median 0.95 attacks). Differences in *I. latidens* densities on these logs were due to tree quality and site effects, whereas log diameter or density of *D. brevicomis* had no detectable effect (ANOVA: tree: $F = 7.08$, $P < 0.05$; site: $F = 3.91$, $P < 0.05$; diameter: $F = 0.10$, $P = $ NS; *D. brevicomis* density: $F = 4.03$, $P = $ NS; no significant interactions; whole model $R^2 = 0.714$, $n = 18$ logs, $P < 0.05$).

Discussion

The mating system of *I. latidens* was monogamous, contrary to previous assertions (S. L. Wood, 1982; Miller & Borden, 1985). In the only previous observations of active breeding in this species, Miller & Borden (1985) observed polygyny in laboratory populations, but only by restricting successive females over the nuptial chambers of individual males. The idea that this species is harem polygynous was also due to the gallery pattern that has multiple arms. However, in some bark beetle species, including *I. latidens*, individual females construct multiple arms (S. L. Wood, 1982; Miller & Borden, 1985). The number of arms per gallery observed in this study (one to four, depending on age) is similar to that reported for monogamous pairs in the laboratory (Miller & Borden, 1985) and to galleries observed in nature in eastern North America (Blackman, 1919), indicating that monogamy may be the typical mating system for this species. Moreover, the mating system of *I. latidens* in the present study was consistent among sites that differed substantially in size and origin of trees, suggesting that variation in habitat quality is not sufficient to explain the occurrence of polygyny in bark beetles (Kirkendall, 1983).

Monogamy in *I. latidens* is surprising, as the breeding biology of this species is otherwise very similar to closely related species that are known to be polygynous. Notable similarities include a breeding habitat of freshly dead or very weakened trees, male initiation of breeding sites, male production of pheromones (Miller *et al.*, 1991), and prolonged male residence in the galleries. The sexual dimorphism in body size (female/male size equal to 97%) is virtually identical to polygynous *Ips* species (Haack *et al.*, 1987; Anderbrant, 1988; Teale *et al.*, 1994). Moreover, although monogyny is common in the Scolytidae (S. L. Wood, 1982), it is uncommon in species in which males initiate the breeding site (Kirkendall, 1983). Thus, there is little in the general biology that would indicate that the mating system of *I. latidens* is atypical for the genus. Certainly the idea that smaller body size would be correlated with greater polygyny (Kirkendall, 1983) is not supported.

An alternative hypothesis for harem polygyny in bark beetles is simply that the adult sex ratio is biased towards females at breeding sites (Kirkendall, 1983), as occurs in most *Ips* species (Reid & Roitberg, 1994; Schlyter & Zhang, 1996). This female bias is apparently due to disproportionate mortality of males, the initiating sex, during dispersal to breeding sites (Annila, 1971; Cook *et al.*, 1983; Kirkendall, 1983). Thus, monogamy in *I. latidens* may occur because breeding habitat is more abundant for this species than for other species of *Ips*, reducing

male mortality and resulting in the equal breeding sex ratios observed in this study. High habitat availability is suggested by the low breeding densities relative to gallery size and the broad range of tree sizes used by *I. latidens*. *Ips latidens* was also able to discover habitat independently (Miller *et al*., 1986; Miller & Borden, 1990) and to coexist with both *D. brevicomis* and *I. paraconfusus*. The negative relationship between *I. latidens* and *I. paraconfusus* densities at the Bacchi site may be spurious because *I. paraconfusus* generally arrived later than *I. latidens*. Both of these *Ips* species use ipsenol as a pheromone (D. L. Wood, 1982; Miller *et al*., 1991), so *I. latidens* can take advantage of habitat discovered by *I. paraconfusus* (D. L. Wood, 1982). In contrast, the other bark beetle species within the ponderosa pine guild (*I. paraconfusus, I. pini, D. brevicomis, D. ponderosae* Hopk.) tend to be mutually inhibited (summarized in Byers, 1989). An advantage of small body size is that a wider range of phloem thicknesses can be inhabited than would be the case for large-bodied species, and the compact gallery structure and shorter development time of *I. latidens* (Miller & Borden, 1985) may allow this species to reproduce successfully amongst the galleries of the larger species.

If habitat is more available for *I. latidens* than for other *Ips* species, male residence times might be expected to be shorter in this species (Reid & Roitberg, 1995). Prolonged male residence in *Ips* has the benefit of increasing the reproductive rate of mates and reducing gallery intrusions by predators, but it limits access to additional males (Reid & Roitberg, 1994). Male residence time data are sparse, but it appears that male *I. latidens* deserted their galleries earlier relative to their mates than is the case for *I. pini*, a polygynous species. In *I. latidens*, the gallery age at which 50% of males had left (24 days) was 67% of the age of galleries at which 50% of females had left (36 days). In contrast, male *I. pini* abandon their galleries only a few days before their mates (Reid & Roitberg, 1994). Thus, these preliminary data are consistent with the idea that *I. latidens* has greater habitat availability that favours shorter male residence times than in other *Ips* species.

Interestingly, another guild of North American bark beetles appears to show relationships between body size, mating system, and breeding habitat use parallel to those of *I. latidens* and its sympatric species. The other very small *Ips*, *I. avulsus* (Eichhoff) (≈ 2 mm length), seems to have a similar mating system and breeding ecology to *I. latidens*, although they do not appear to be in the same taxonomic group (Hopping, 1963, 1964; Cognato *et al*., 1995). Monogamy in *I. avulsus* is indicated by an even sex ratio of breeding adults and by the observations that most dissected galleries contained either a male and female pair or a single female, although galleries had multiple arms (Cook *et al*., 1983). *Ips avulsus* occupies a wider range of tree diameters than cohabiting species of bark beetles that include the polygynous *I. calligraphus* (Germar) (Paine *et al*., 1981), and it is attracted to the pheromones of cohabiting species (Birch *et al*., 1980). By contrast, the larger *I. calligraphus* (≈ 5 mm length) has a 3:1 female-biased sex ratio at breeding sites (Cook *et al*., 1983), a narrower niche breadth than *I. avulsus* (Paine *et al*., 1981), and is inhibited by the pheromones of cohabiting species such as *I. avulsus*. The

similarities between *I. latidens* and *I. avulsus*, and the contrasts between *I. avulsus* and *I. calligraphus,* reinforce the notion that mating systems in bark beetles may be driven, at least in part, by habitat availability that in turn influences the breeding sex ratio.

Although the two smallest species of *Ips*, *I. latidens* and *I. avulsus*, are monogamous, small size does not necessarily predict mating system. Within the Tribe Ipini, for example, *Pityogenes* and *Pityophthorus* are as small or smaller than *I. latidens* and *I. avulsus*, yet are highly polygynous (S. L. Wood, 1982; Kirkendall, 1983). Instead, small size may be important only insofar as it increases the range of habitat available. Thus, the focus of further work on the diversity of mating systems in bark beetles should include the effects of habitat availability.

Acknowledgements

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