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Instar Numbers, Development, Flight Period, and Fecundity of *Dendroctonus valens* (Coleoptera: Curculionidae: Scolytinae) in China

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ABSTRACT The red turpentine beetle, Dendroctonus valens LeConte (Coleoptera: Curculionidae: Scolytinae), is one of the most destructive invasive forest pests in China. Little is known about the biological characteristics of red turpentine beetle. Analysis of the frequency distribution has shown that red turpentine beetle's larvae have five instars with head capsule width 0.64, 0.83, 1.16, 1.45, and 1.99 mm, respectively. The ratio of increase of head capsule width is 1.33, which is consistent with Dyar's rule. The duration of egg, larval, and pupal is ≈10, 84, and 10 d, respectively. After its emergence, the callow adult darkens to the typical reddish brown by the time it is ready to leave the tree; beetles begin to "fly out" at the 10th day and continue for 20 d, with the peak flight taking place on the 21st day. Pairs of red turpentine beetles introduced into pine bolts produced 106 offspring. Such basic information is important for developing management strategies to combat this invasive bark beetle in China.

KEY WORDS Dendroctonus valens, instar number, development, flight period, fecundity

The red turpentine beetle *Dendroctonus valens* Le-Conte (Coleoptera: Curculionidae: Scolytinae), native to North America, was introduced into Shanxi Province in China in the early 1980s when unprocessed logs were imported from the west coast of the United States (Yan et al. 2005). The bark beetle has spread rapidly to other provinces (Hebei, Henan, Shaanxi, Inner Mongolia, and Beijing; Sun et al. 2004, Pan et al. 2010). *D. valens* infests most pine species (Smith 1971). In western North America, the red turpentine beetle is considered a secondary pest, usually attacking only weakened or dying pines and freshly cut stumps and logs (Cibrián-Tovar et al. 1995, Owen et al. 2010). However, in China, red turpentine beetles attack healthy pines and thus are a primary pest (Britton and Sun 2002, Miao et al. 2003, Liu et al. 2008). Since its introduction, the red turpentine beetle has killed >6 million trees of the Chinese red pine *Pinus tabuliformis* Carrière (Sun et al. 2004), which was widely planted throughout China during reforestation efforts.

Since the first outbreak in Shanxi in 1999, most studies of the red turpentine beetle have focused on understanding the pest's attack behavior and chemical communication (Sun et al. 2004, Zhang et al. 2009, Shi and Sun 2010, Liu et al. 2011). In its native range in western North America, the red turpentine beetle is known to use host odors and kairomones to find and select *Pinus ponderosa* Douglas ex C.Lawson hosts

(Vité and Gara 1962, Wood 1982, Hobson et al. 1993, Rappaport et al. 2001, Erbilgin et al. 2007); it is thought to do the same to find and select the Chinese pine *P. tabuliformis* (Sun et al. 2004, Liu et al. 2011).

D. valens is monogamous, in that a female will mate with only one male in the gallery she bores into the tree (Liu et al. 2006, Owen et al. 2010). Successfully attacking females release pheromones, which attract large numbers of both females and males, resulting in a mass attack that overcomes a tree's resistance (Z.D.L., unpublished data). The mass attack lasts about 2 wk. The beetles make galleries in the cambial layer of trees where mating and oviposition occur. Broods develop successfully only if part or the entire tree is killed (Owen 1990). Two symptoms distinguish red turpentine beetle infestation from the infestation of other bark beetles: the presence of large light pink to reddish–brown pitch tubes (≈1–2 in. in diameter) around the base of the trees and piles of pink or white feces on the ground (Smith 1971, Liu et al. 2008).

Little is known about the life history of *D. valens* (Smith 1971, Miao et al. 2001, Owen et al. 2010). The purpose of this study was to determine the number of instars, the duration of the life stages, flight periodicity, and the fecundity of *D. valens* as a basis for developing pest management strategies. First, the number of instars was determined by analyzing the frequency distribution. According to Dyar's rule (1890), head capsule width increases geometrically, with the ratio between instars being ≈1.4, which we tested with our data. Second, larvae were reared on

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artificial diet in the laboratory to record the development times from hatching to adult emergence and to estimate when adult flight occurs. Finally, fecundity was determined by inoculating fresh bolts of *P. tabuliformis* with paired beetles.

Materials and Methods

Insect Collection and Rearing. Field trapping was conducted in a natural stand of *P. tabuliformis* at Beishe Mountain, in the foothills of the Luliang Mountains (37° 48′ N, 111° 57′ E, mean elevation 1,400 m), west of Gujiao City, Shanxi Province, China, where the first *D. valens* outbreak was recorded in 1999 (Sun et al. 2004). This site is dominated by a plantation of 30-yr-old *P. tabuliformis*. Eight Lindgren funnel traps baited with the kairomone attractant (3-carene; Lvzhou Bio-control Company, Taiyuan, Shanxi, China; Sun et al. 2004, Erbilgin et al. 2007) were used to trap adult *D. valens* as they "flew out" from their overwintering sites from early May to early June in 2009 and 2010. Traps were checked daily; *D. valens* were collected, and the sexes separated and stored in plastic boxes with holes for ventilation (≈200 adults per box). Males were distinguished by the stridulation sounds they made when stressed (McGhehey 1968), and females cannot release this stridulation sound. To avoid mistaking males for females, we checked the sound three times for each beetle.

In July 2008, *D. valens* eggs and larvae were collected at the Beishe Mountain site mentioned above by carefully dissecting naturally infested pine trees and stumps of *P. tabuliformis* with the characteristic piles of pink or white feces around the base of the tree. The 70 largest field-collected larvae and the collected eggs were allowed to develop in the laboratory. All other larvae were placed in ethanol (EtOH) for the later measurement of head width.

Instar Number. The 70 large larvae collected in field were reared individually in 2-ml Eppendorf tubes on the artificial diet and checked daily until pupation to ensure they were in their final instar; their head capsules were then preserved in EtOH. The eggs collected in the field were allowed to hatch and checked every day. Newly hatched larvae were placed in EtOH. Those samples, which were kept in EtOH, included variously sized larvae collected in field, newly hatched larvae, and the head capsules of the final instars, were used to determine the instar number by measuring the width of the head capsules to the nearest 0.01 mm with a microscope (Olympus, Tokyo, Japan). The sample size was 518, including 74 neonates and 39 capsules of final instars. After head capsules were measured, the frequency distribution of head capsules was made to determine the instar numbers.

Developmental Duration. Pairs of *D. valens* collected in the field were inoculated into pine bolts to obtain eggs for the developmental experiment in the laboratory. Three large *P. tabuliformis* pines (30 cm diameter at breast height [DBH]) were felled, and the tree trunks were cut into bolts ≈100 cm in length

(three bolts per tree were cut from the ground level). Bolts were placed upright in a temperature-controlled room (20°C) with natural light. The cut ends were coated with melted wax to retard moisture loss. A pair of red turpentine beetles, one female and one male, was inoculated into each of the eight holes drilled with a 1.0-cm-diameter cork borer in each bolt. The predrilled holes made it easier for red turpentine beetles to bore into the bark. One week after inoculation, the bolts were dissected for eggs, as females usually begin to lay eggs 1 wk after mating with a male (personal observation). Eggs were transferred to an artificial diet made of pine phloem powder (water 250 ml, phloem 100 g, and agar 6 g) modified from Wallin and Raffa (2000) and Kopper et al. (2005) and kept in the climate chamber at 20°C in the dark until adults emerged. The duration from egg to adult emergence was recorded daily. Those pupae from the 70 large larvae from which head capsules of final instars were obtained, as mentioned above, were pooled together with pupae reared from eggs in the laboratory to determine the duration of the pupal stage. In total, 574 neonates, 310 second-instar, 102 third-instar, 34 fourth-instar, 17 fifth-instar, and 85 pupae were measured.

Preflight Period. Callow adults are tan, but they rapidly darken to a reddish–brown (Smith 1971). The new adults remain in the gallery for a few days to several months (Smith 1971). As mentioned in the previous experiment, pupae were checked for emergence every day. In this experiment, newly emerged adults were defined as 0 d old and placed on a bed of artificial diet in petri dishes (10 cm in diameter by 2 cm in height), which were kept in a cone-shaped collector (25 cm in diameter by 50 cm in height; simulating conditions under the bark) to observe when they flew out. The three-legged stainless steel cone-shaped collector had a collection hole (3 cm in diameter) at the bottom (Fig. 1). When *D. valens* adults flew into the container, they contacted the metal surface and fell into the collection cup through the hole at the bottom. Adults emerging on the same day were placed in the cone-shaped container; there were checked every day to see how many beetles had fallen in (135 samples tested). Males were distinguished by the stridulation sounds they made (McGhehey 1968).

Fecundity. The aim of this experiment was to see how many offspring a red turpentine beetle female could produce. To simulate beetle attack in the field, five trees ranging in size from 16 to 30 cm in DBH were felled and cut into bolts 100 cm in length (five bolts from each tree). Bolts were placed upright at 20°C in a temperature-controlled room with natural light, and their cut ends were coated with melted wax to avoid moisture loss. A pair of red turpentine beetles, one female and one male, was introduced into the hole drilled in the bolts (136 replicates). One month after inoculation, the bolts were dissected to check for the presence of eggs or larvae. The fecundity (total numbers of eggs and larvae) of each pair was recorded.

Fig. 3. Head capsule widths of each instar of *D. valens*. The regression line ($y = 0.4805e^{0.2827x}$; $R^2 = 0.9972$; $F = 1077.97$; $P < 0.0001$) shows the ratio of head capsule width increase is $e^{0.2827}$, that is, 1.33. Scale bars ($\pm$SE) indicate mean responses and SEs, and different letters above bars indicate significant differences at $P \leq 0.05$ with Bonferroni multiple comparison (ANOVA).

Fig. 1. The cone-shaped collector.

Statistical Analysis. Data were collected on the width of head capsule, the duration of each larval stage and pupal period and tested whether they fit to normal distribution before analysis. If they did, ANOVA was used to analyze and means were separated by multiple comparisons of the Bonferroni by the software SPSS (1999). If the data did not fit a normal distribution, a nonparametric test was carried out. Moreover, the head width was regressed with stages by exponential growth by software SPSS. Data on preflight period were accumulated at intervals of 5 d. To reflect the fecundity of red turpentine beetles, the fecundity of
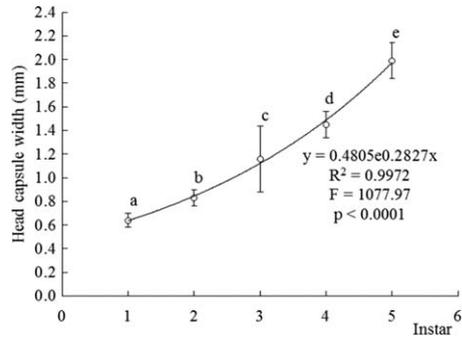
those beetles that bored into the bold and laid eggs were analyzed by the SPSS software (SPSS 1999).

Results

Number of Instars. Altogether, 518 head capsules were measured and the frequency distribution of head capsule width was graphed (Fig. 2). Five peaks in width were evident, indicating *D. valens* has five instars. The head width grew exponentially with the larval instar ($y = 0.4805e0.2827x$; $R^2 = 0.9972$; $F = 1077.97$; $P < 0.0001$). The ratio of increase in head capsule width was $e^{0.2827} = 1.33$, with a significant difference between the widths of head capsules at each instar ($F = 512.074$; df = 4, 285; $P < 0.0001$; Fig. 3).

Developmental Duration. After eggs hatched, larvae were reared until adult emergence, and the du-
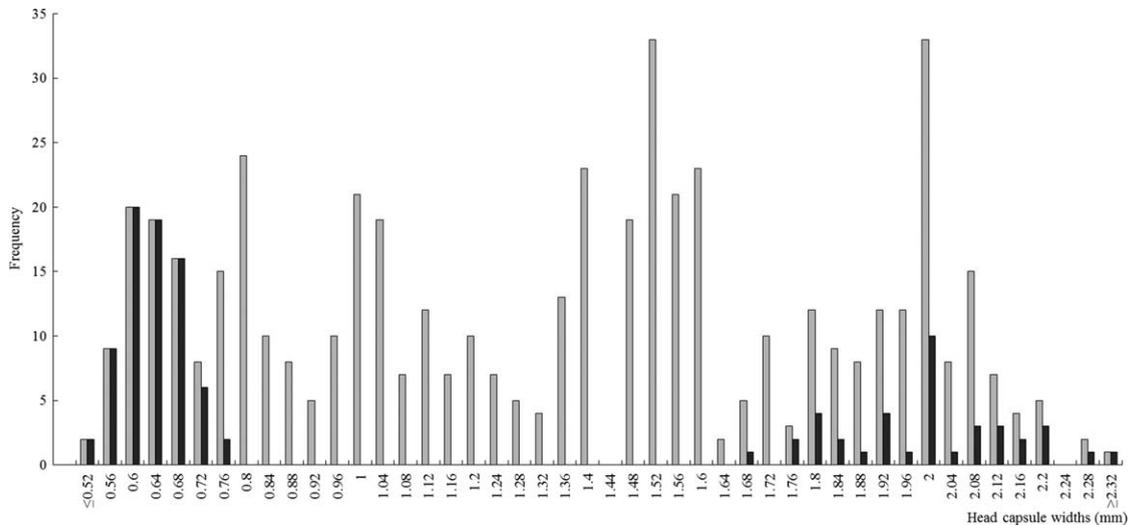

Fig. 2. Frequency distribution of the widths of head capsules of *D. valens*. The gray and the black column show the distribution of all 518 samples and standard head capsules from neonates and final instar, respectively.
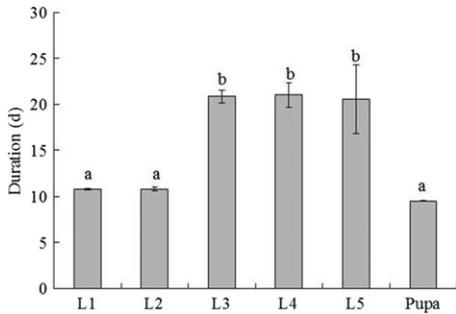
Fig. 4. Developmental duration of each stage of *D. valens*. L1, L2, L3, L4, and L5 stands for first, second, third, fourth, and fifth instars, respectively. Scale bars ($\pm$SE) indicate mean responses and SEs, and different letters above bars indicate significant differences at $P \leq 0.05$ with multiple comparison of Bonferroni (ANOVA).

ration of each stage was recorded. The developmental duration of the five instars was 10.8, 10.7, 20.9, 21.0, and 20.6 d, respectively. The duration of the third, fourth and fifth instars was significantly longer than the duration of the first and second instars ($F = 223.223$; df = 4, 1032; $P < 0.0001$; Fig. 4). The pupal stage lasted 9.5 d.

Preflight Period. After its emergence, the callow adult darkens to the typical reddish brown by the time it is ready to leave the tree. Emerging adults did not begin flying until the 10th day, and the period of flight lasted 19.5 d with the peak flight taking place on the 21st day (Fig. 5).

Fecundity. Of the 136 pairs of red turpentine beetles introduced into bolts, 63 pairs successfully bored into the bark and produced offspring. The number of offspring ranged from 16 to 281 eggs, with an average of 106.

Discussion

Our study confirms that *D. valens* has five instars, with the increase ratio of head capsule width 1.33. Our results are consistent with Dyar's rule, which states that head capsule increases geometrically, that is, $\approx$1.4 (Dyar 1890). Since 1890, the application of Dyar's rule to Lepidoptera and Coleoptera has been discussed (Prebble 1933, Kaston and Riggs 1937, Kishi 1971,
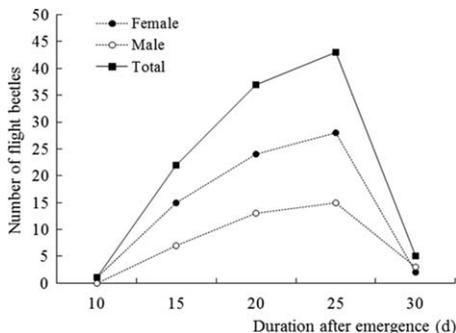

Fig. 5. Flight of *D. valens* after adult emergence.

Mizell and Nebeker 1979). Gaines and Campbell (1935) qualified the use of frequency distributions, saying these "will give clear results only when the insects measured are fairly homogenous in rate of development and number of instars." Although Schmidt et al. (1977) and Kishi (1971) found their results were not consistent with Dyar's rule, recently, the rule was found to be consistent in the walnut twig beetle (Dallara et al. 2012). In our research, all samples collected in summer time produced five instars. Direct observation of developmental duration in the laboratory confirms these data. Whether winter populations are similar is unknown, as is whether there are any differences between geographical populations. According to the literature, the head capsules of winter larvae are larger than those of summer larvae (Mizell and Nebeker 1979). Furthermore, the possibility of geographical variation in numbers of instars has been mentioned by Raske (1976) and Schmidt and Lauer (1977). It will be worthwhile in future studies to collect samples at different times and in different locations.

The cryptic life history of *D. valens* has made estimating life history parameters difficult (Smith 1971). Some references estimated the larval stage of *D. valens* lasts about 2 mo with the pupal stage lasting $\approx$1 wk (Smith 1971, Miao et al. 2001). No experiments have been conducted under controlled conditions to measure the duration of the beetle's developmental period; our study using artificial diet is the first attempt. In the current study, the red turpentine beetle took $\approx$100 d from egg to adult emergence. In its native range in the Sierra Nevada of California, $\approx$11 wk are usually required from eggs to adult emergence (Smith 1971), less than what is usual for the population in China. We did all experiments in the dark, as *D. valens* is a group of subcortical insects that feed as larvae and adults in the phloem of trees and woody shrubs (Wood and Bright 1992) where they are covered by thick outer bark and no light is thought to penetrate. Of course, several factors could influence bark beetle development, such as temperature, food resource, humidity, and host conditions (Goldman and Franklin 1977, Coulson 1979, Fargo et al. 1979, Wagner et al. 1979). The development of *D. valens* is highly temperature dependent and larvae may grow faster at different temperatures (Smith 1971). Future studies predicting *D. valens* development in the field should consider thermal thresholds and host pine heterogeneity when devising pest management strategies.

After emergence, the callow adults cannot fly out until warm weather comes (Smith 1971, Owen et al. 2010). In warm weather, they soon bore outward through the bark and fly away to new host material. The time from adult emergence to leaving to search for a new host is critical for mass trapping with semiochemicals. In this study, we measured the intervals and showed that beetles began to fly out at the 10th day and reached their peak flight at the 20th day. Several factors could have influenced the flight date, such as temperature, precipitation, and wind. However, none of these has been studied. In the field, few red tur-

pentine beetles are trapped when it is windy or rainy (personal observation), an observation that should be investigated to develop more efficient trapping methods.

One week after mating with a male, the female begins to lay eggs (personal observation). In the red turpentine beetle's native range, North America, it is unknown how many offspring a female can produce (Smith 1971). In our experiment, we inoculated 136 pairs into bolts and 63 pairs successfully bored into the bolts and had offspring, a success rate of 46%. This percentage is reasonable, as the boring is much energy-consuming behavior and we reported paired red turpentine beetles had a success rate of ≈50% for boring into pine bolts in a previous study (Liu et al. 2006). For those red turpentine beetles that bored into the bolts and laid eggs, our study showed 106 offspring were produced, with the average ranging from 16 to 281. However, we did not consider beetle size and the diameter of bolts, both of which may affect the fecundity of *D. valens*. Body size for some insects, including bark beetles, is associated with fecundity (Reid 1962, McGhehey 1971, Amman 1972, Clarke et al. 1979, Byrne and Rice 2006, Schäfer et al. 2008). Furthermore, a recent study showed that the size of the host pine could affect the fecundity of *D. valens*, with large pine trees supporting high fecundity (Liu et al. 2011). Body size measured as weight in *D. valens* ranges from 10 to 60 mg, which could also affect the number of eggs laid (Z.D.L. et al., unpublished data).

Acknowledgments

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