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RESEARCH

Attack Pattern and Reproductive Ecology of *Tomicus brevipilosus* (Coleoptera: Curculionidae) on *Pinus yunnanensis* in Southwestern China

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ABSTRACT. *Tomicus brevipilosus* (Eggers) (Coleoptera: Curculionidae, Scolytinae) was recently discovered as a new pest of Yunnan pine (*Pinus yunnanensis Franchet)* in Yunnan Province in southwestern China. However, little was known on its reproductive biology and pattern of trunk attack on Yunnan pine. The objectives of this study were to better understand the reproductive biology of *T. brevipilosus* by investigating the seasonality of trunk attacks by parent adults for the purpose of reproduction (i.e., breeding attacks) and the within-tree pattern of these attacks. Our results showed that *T. brevipilosus* breeding attacks in *P. yunnanensis* generally started in early March and ended in early June in Anning County, Yunnan. *T. brevipilosus* exhibited two general patterns of infestation. From early March to mid-April, *T. brevipilosus* bred preferentially in the trunks of Yunnan pine trees that were already infested by *Tomicus yunnanensis* Kirkendall and Faccoli and *Tomicus minor* (Hartig), colonizing spaces along the trunk (mostly in the mid- and lower trunk) that were not already occupied by the other two *Tomicus* species. Later, from about mid-April to early June, when there were no Yunnan pine trees newly infested by *T. yunnanensis* and *T. minor*, *T. brevipilosus* attacked Yunnan pine by itself, infesting the lower parts of the trunk first and then infesting progressively upward along the trunk into the crown. Infestation by *T. brevipilosus* extends the total period that *P. yunnanensis* trees are under attack by *Tomicus* beetles in southwestern China, which helps explain why Yunnan pine has suffered high levels of tree mortality in recent decades.

Key Words: *Tomicus brevipilosus, Tomicus yunnanensis, Tomicus minor,* pine shoot beetle, within-tree attack pattern

Bark beetles in the genus *Tomicus* (Coleoptera: Curculionidae, Scolytinae), with the exception of *Tomicus puellus* (Reitter) that infests primarily *Picea* trees, are well-known pests of pine (*Pinus*) trees in most Eurasian countries where pine is native (Bakke 1968, Ye 1991, Faccoli 2007, Kirkendall et al. 2008, Li et al. 2010, Lieutier et al. 2015). These univoltine bark beetles are commonly called shoot beetles because the newly emerged adults feed inside living shoots of their host trees during the summer months as they become sexually mature, which often results in death of the infested shoots (Långström 1983, Ye 1994a, Kohlmayr et al. 2002). The Palaearctic genus *Tomicus* contains eight recognized species worldwide, of which five occur only in Asia, one only in Europe, and two in Eurasia (Kirkendall et al. 2008, Li et al. 2010, Lieutier et al. 2015). The Eurasian species, *Tomicus piniperda* (L.) is the only *Tomicus* species to be introduced beyond its native range, being first found in the Great Lakes region of North America in 1992 (Czokajlo et al. 1997, Haack and Poland 2001, Lieutier et al. 2015).

Tomicus brevipilosus (Eggers) is native to Asia where it has been reported to occur in China, India, Japan, Korea, and Philippines (Kirkendall et al. 2008, Lu et al. 2014). This bark beetle has been recorded to infest several species of *Pinus*, including *Pinus yunnanensis* (Franchet), *Pinus koraiensis* Siebold & Zucc., and *Pinus kesiya* Royle ex Gordon, but severe damage has seldom been reported (Murayama 1959, Kirkendall et al. 2008, Lu et al. 2014). In China, *T. brevipilosus* has been generally regarded as a secondary pine pest, mainly infesting pine trees weakened by drought, defoliation, and other environmental stressors (Kirkendall et al. 2008, Lu et al. 2014). However, since the late 1990s, *T. brevipilosus* along with *Tomicus yunnanensis* Kirkendall and Faccoli and *Tomicus minor* (Hartig) have reached outbreak levels, resulting in widespread tree mortality with more than 200,000 ha of infested *P. yunnanensis* forests in southwestern China (Ye 1991, Duan et al. 2004, Liu et al. 2010, Lu et al. 2014).

In Yunnan, *T. brevipilosus* completes its life cycle in Yunnan pine (*P. yunnanensis*) (Lu et al. 2014). After exiting the host material in which the brood developed, newly emerged adults fly to the crowns of nearby pine trees, usually beginning in June, where they feed in shoots for the next 9–10 mo and become sexually mature (Lu et al. 2014). Each adult usually feeds inside and kills 3–5 shoots (Lu 2011). Extensive shoot feeding by *Tomicus* adults can cause growth loss and lower a tree's natural resistance to the point where individual trees are predisposed to infestation (i.e., breeding attacks) during the beetles' reproductive phase (Lieutier et al. 2003, Lu et al. 2014).

Sexually mature adult beetles eventually depart the shoots to reproduce in the trunks of *P. yunnanensis* trees, primarily in April and May (Lu et al. 2014). It is not known what initiates the reproductive phase in *T. brevipilosus.* Adult females initiate attack by constructing individual longitudinal galleries in the phloem tissue and depositing eggs in niches along the gallery walls. After hatching, larvae feed transversely in individual galleries in the phloem and outer sapwood and then pupate at the ends of the galleries. Larval feeding disrupts nutrient flow within the phloem tissue (Långström 1983, Fernández et al. 1999, Ye and Ding 1999, Långström et al. 2002).

Gallery construction and reproduction by *T. brevipilosus* and at times other *Tomicus* species are regarded as the direct causes for *P. yunnanensis* tree mortality, particularly when mass attack occurs on individual trees (Ye and Ding 1999, Lu et al. 2014). As one aspect of developing a *T. brevipilosis* management program, the objective of our study was to clarify the timing and duration of the beetle's reproductive period and within-tree attack pattern, as well as other aspects of the beetle's reproductive biology. A further aim of this study was to improve

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our understanding of the reproductive ecology of *T. brevipilosus* with respect to other *Tomicus* species that infest *P. yunnanensis* in southwestern China.

Materials and Methods

Study Area. The field study was carried out (primarily by P.C., J.L., and H.Y.) in a *P. yunnanensis* stand in Anning County (24.97° N, 102.33° E, 1,800 m a.s.l), approximately 80 km west of Kunming, the capital of Yunnan, in southwestern China. The stand was along the lower slope of a hillside and covered about 300 ha. The *P. yunnanensis* trees in this stand were originally planted by aerial seeding in the mid-1970s. Most of the pine trees were 24–28 cm in diameter and 7.5–8.5 m tall at the time of this field study (2007–2009). Low numbers of *T. yunnanensis* and *T. minor* were first recorded infesting trees in this stand in the early 1990s, followed by *T. brevipilosus* within a few years (Duan et al. 2004). All these three *Tomicus* species have been active in this stand since the late 1990s (Duan et al. 2004, Lu et al. 2014). It is important to note that in Yunnan, *T. yunnanensis* was considered as *T. piniperda* due to their morphological similarities before 2008 (e.g., Ye 1991, 1994a,b, 1995; Ye and Lieutier 1997; Ye and Ding 1999; Långström et al. 2002; Lieutier et al. 2003; Duan et al. 2004), when *T. yunnanensis* was first described as a new *Tomicus* species (Kirkendall et al. 2008).

Experimental Procedures. During January to July in each year from 2007 to 2009, 3–4 *P. yunnanensis* trees with evidence of recent bark beetle breeding attacks were sampled every 10 d, for a total of 10 trees per month. Most of the sampled trees were cut from the interior portion of the stand and were among the larger trees present. We selected trees that appeared to have been recently infested based on the texture and color of the frass and resin that was present near the entry hole where the *Tomicus* beetles entered the bark along the trunk surface (Lu 2011). The sampled trees were felled by cutting the trunk near the ground with a chainsaw, and then we cut the trunk into 50-cm-long logs, starting at the base and stopping near mid-crown. The logs were marked in the field to identify from which tree and which part of the trunk they were cut and then transported to the laboratory. In the laboratory, usually within 1–2 d after cutting, we measured the surface area of each log and then carefully removed the outer bark to look for bark beetles and their galleries. We recorded several parameters related to beetle reproduction and development, including length and width of the maternal gallery using a Vernier calliper (HMCT 6202-01, Harbin, China), number of maternal galleries for each *Tomicus* species, and the number of eggs, larvae and at times pupae for each maternal gallery. All parent bark beetles were collected from the maternal galleries, placed individually into labeled plastic bags, and identified to species under a stereomicroscope (Nikon-smz 500) based on morphological characteristics of the various *Tomicus* species (Kirkendall et al. 2008, Li et al. 2010). We recorded our observations for each *Tomicus* species on a per log basis, using data from all the bark beetles galleries that were present, no matter their age.

In addition, detailed observations were made on 106 *T. brevipilosus* maternal galleries (in which the parent female was still present) at 10-d intervals from March to July 2009, from which the timing of first occurrence of eggs, larvae, and pupae were recorded. These parameters were used to estimate the duration of egg, larval, and pupal development in the field. At the same time, several other maternal gallery parameters were measured and recorded including gallery length, gallery width, and numbers of eggs or larvae present (for details see Lu 2011).

Data Analysis. Correlation analysis was conducted between the length of the maternal egg gallery and the number of eggs present in the galleries constructed by *T. brevipilosus*. Statistical analyses were performed using SPSS (version 13 for Windows) with an alpha level of 0.05. Temperature data were obtained from Yunnan Meteorological Bureau, which had a weather recording station about 8 km from our field site.

Results

Breeding Attacks. *T. brevipilosus* breeding attacks, including sister broods, on *P. yunnanensis* trees were initiated in early March and ended in early June, spanning a period of about 3 mo (Fig. 1). The timing and duration of breeding attacks were similar over the 3-yr study period from 2007 to 2009 (Fig. 1).

The attacking population of *T. brevipilosus* parent females varied from month to month, based on the total number of maternal galleries found each year for each *Tomicus* species while debarking the logs but formed an approximately normal distribution curve each year during the period from March to June (Fig. 1). Typically, breeding attacks in March accounted for about 10–25% of the annual attacks (10.25% in 2007, 24.44% in 2008, and 18.39% in 2009). From March to May, the number of attacks increased rapidly, peaking in April in 2007 and 2009, or in May in 2008 (Fig. 1). The peak month of breeding attacks in each year of study accounted for a relatively high percentage of the total annual attacks: 65.38% in 2007, 37.78% in 2008, and 58.62% in 2009. In June, when new *Tomicus* infestations ended, the June breeding attacks accounted for only 2.56% of all annual attacks in 2007, 8.89% in 2008, and 11.49% in 2009 (Fig. 1).

The daily minimum and maximum air temperatures for the recording station about 8 km from our field site are shown in Fig. 2 for 1 January through 30 June during 2007–2009. Considering areas of the world where *Tomicus* species experience cold winters, spring flight is usually initiated when air temperatures exceed 10–12°C (Bakke 1968; Salonen 1973; Långström 1983; Haack et al. 2000, 2001; Haack and Poland 2001; Ye et al. 2002; Lieutier et al. 2015). Considering a flight threshold of 12°C at our study site, it is clear from the data presented in Fig. 2 that this temperature was exceeded on almost every day from January through June during 2007–2009. Even air temperatures of 15°C were exceeded nearly every month (Fig. 2).

T. brevipilosus Breeding Attacks in Relation to Other Tomicus Species. The log dissections during this 3-yr study indicated that breeding attacks by *T. brevipilosus* occurred in *P. yunnanensis* trees both with and without coinfestation by the other two *Tomicus* species that were present in the area (Figs. 3 and 4). For example, in March, when *T. brevipilosus* commenced breeding attacks, there already existed several Yunnan pine trees that were infested by *T. yunnanensis* and *T. minor*, which had initiated breeding earlier in the year than *T. brevipilosus* (Lu et al. 2014). In this situation, *T. brevipilosus* only attacked trees that were already infested by *T. yunnanensis* and *T. minor* (Fig. 3). In April, as the number of trees newly infested by *T. yunnanensis* and *T. minor*

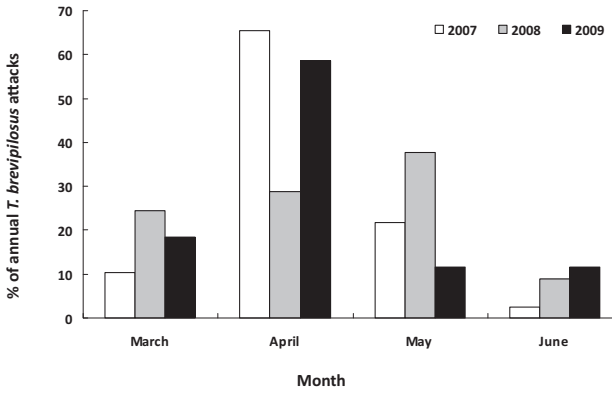


Fig. 1. Percent of annual *T. brevipilosus* breeding attacks that were initiated monthly on *P. yunnanensis* trees ($n = 10$ trees per month) that were sampled at the study site in Yunnan from January through July in 2007–2009.

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decreased, *T. brevipilosus* continued to infest pine trees in which *T. yunnanensis* and *T. minor* already occurred as well as initiated attack by itself on other pine trees (Fig 3). During May and June, when there were no other pine trees with new *T. yunnanensis* or *T. minor* breeding attacks, *T. brevipilosus* attacked only by itself on previously uninfested pine trees (Fig. 3).

Within-Tree Distribution on Breeding Attacks. *T. brevipilosus* was able to colonize the entire trunk of *P. yunnanensis* trees, usually starting about 50 cm above the ground level and reaching the mid-crown level (Fig.3). However, the colonization pattern varied dramatically, depending if the other two *Tomicus* species were already present on the tree trunks or not. In those cases when both *T. yunnanensis* and *T. minor* were already present along the trunk at the time of *T. brevipilosus* infestation, which usually happened in March to April (Fig. 3), *T. brevipilosus* tended to colonize the open spaces of inner bark (phloem) where the other two *Tomicus* species and their brood had not already occupied. In most cases, *T. yunnanensis* appeared to be the first species to colonize the trees, occupying primarily the upper portions of the trunk, whereas *T. minor* tended to colonize trees already infested by *T. yunnanensis,* infesting primarily the lower portions of the trunk (Ye

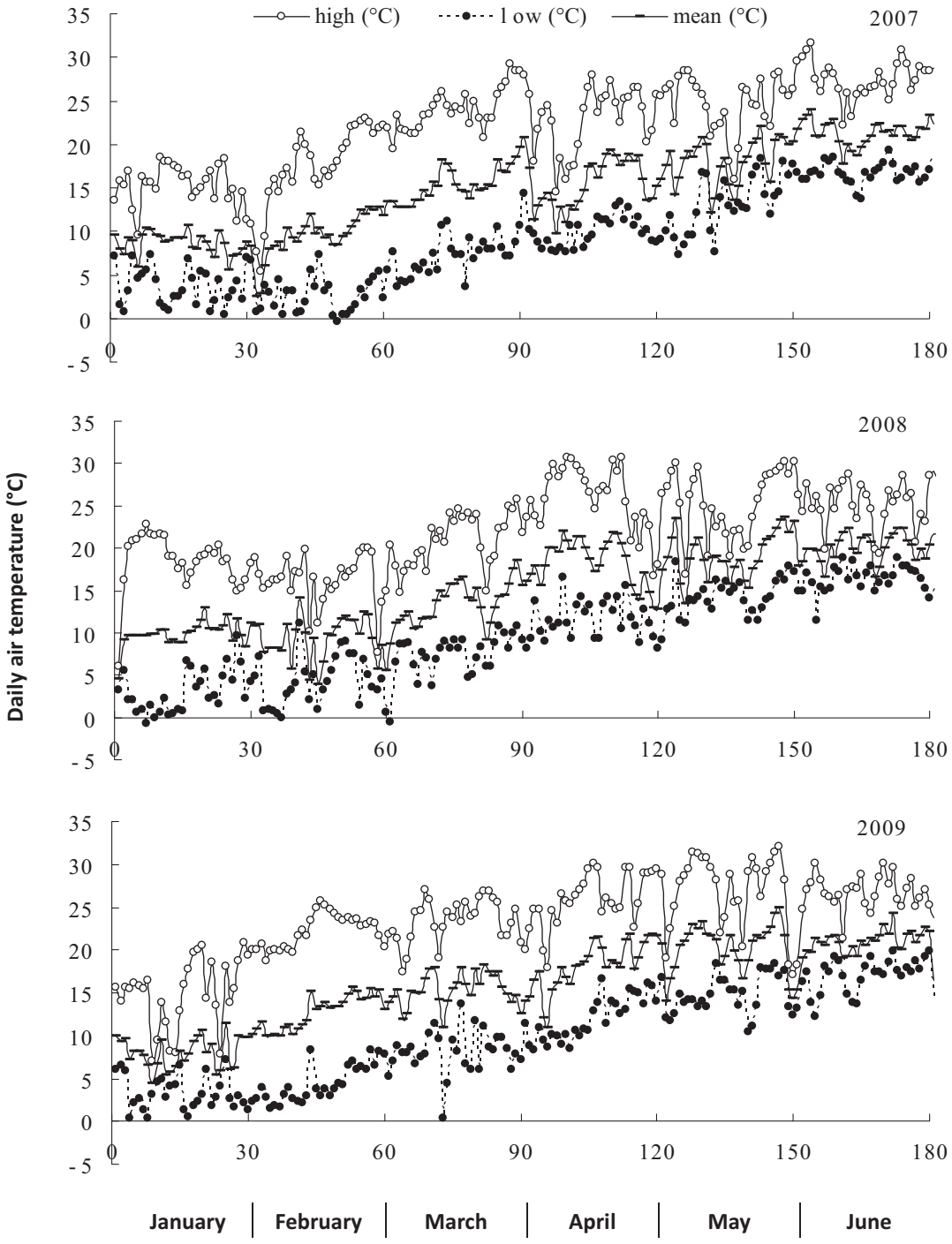


Fig. 2. Maximum, minimum, and mean daily air temperatures from 1 January through 30 June in 2007–2009 in Anning County (24.97°N, 102.33°E, 1800 m a.s.l) that were recorded at an official weather station about 8 km from our study site.

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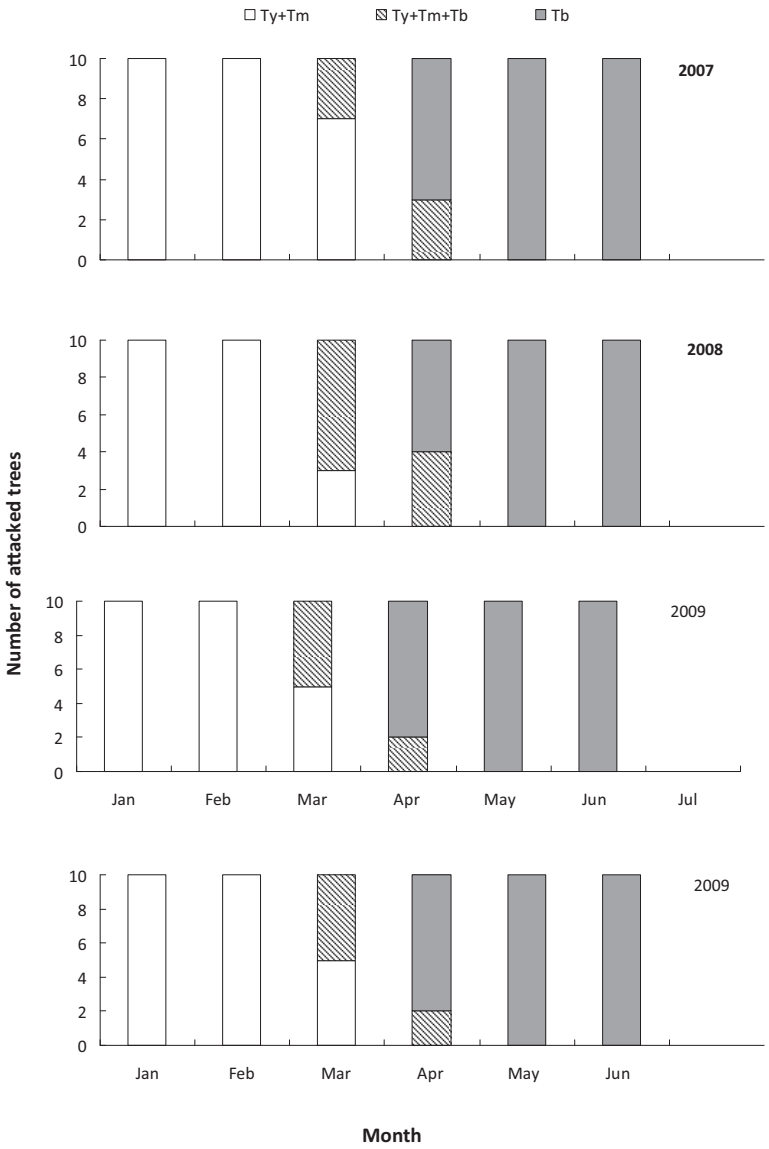


Fig. 3. Number of *P. yunnanensis* trees with recent attacks by various combinations of three *Tomicus* species (*T. brevipilosus,* Tb; *T. minor,* Tm; *T. yunnanensis,* Ty) based on sampling 10 trees per month in Yunnan that were cut from January to July, 2007–2009.

and Ding 1999) (Fig. 4A). There was some overlap of both *T. yunnanensis* and *T. minor* in the mid-trunk region of most trees (Fig. 4A). Given this situation, the early-season *T. brevipilosus* attacks were scattered along the entire trunk between the gallery systems of the two other *Tomicus* species but being concentrated mostly in the mid- and lower-trunk samples (Figs. 1 and 4A). Therefore, during the early portion of the *T. brevipilosus* flight season, *T. brevipilosus* attacks tended to overlap mostly with *T. minor* galleries in the lower trunk and to a much lesser degree with *T. yunnanensis* galleries in upper trunk and with both of these *Tomicus* species in the mid-trunk sections (Fig. 4A).

In those cases where *T. brevipilosus* was the only *Tomicus* species present to initiate attack, which usually happened from mid-April to early June (Fig. 3), *T. brevipilosus* tended to initiate attack along the lower trunk first and then move progressively upward along the trunk (Fig. 4B). When the tree trunks were fully colonized by *T. brevipilosus*, the attack density was broadly similar over much of the trunk surface area (Fig. 4B).

Reproduction. *T. brevipilosus* adult females initiated oviposition within a few days of starting gallery construction on the trunks of *P. yunnanensis* trees given that the first eggs were observed in early March. Overall, considering all *T. brevipilosus* breeding attacks observed in 2009, oviposition occurred from early March to early June (Table 1), about 3–3.5 mo, peaking in April to May. The period of active oviposition closely matched the period of tree colonization (i.e., breeding attacks; Fig. 1).

In 2009, the first *T. brevipilosus* eggs were found in early March and the first larvae in mid-March, indicating that the egg incubation period was less than 2 wk in the field during March. The first pupae were recorded in early May, with most pupating by mid-May, when average daily air temperature was about 18°C (Fig. 2). Therefore, *T. brevipilosus* larvae appeared to require about 40–50 d to complete larval development. The pupation period lasted about 10–20 d at the study site. Callow adults of *T. brevipilosus* were first observed under the bark of the sampled trees in late May, with emergence of the new brood adults starting in early June and peaking during mid- to late June (Table 1).

The typical maternal gallery of *T. brevipilosus* is a single longitudinal tunnel with an entrance hole at the bark surface that leads to a slightly enlarged mating chamber and then a single gallery in which eggs are deposited along the gallery walls. The average length of

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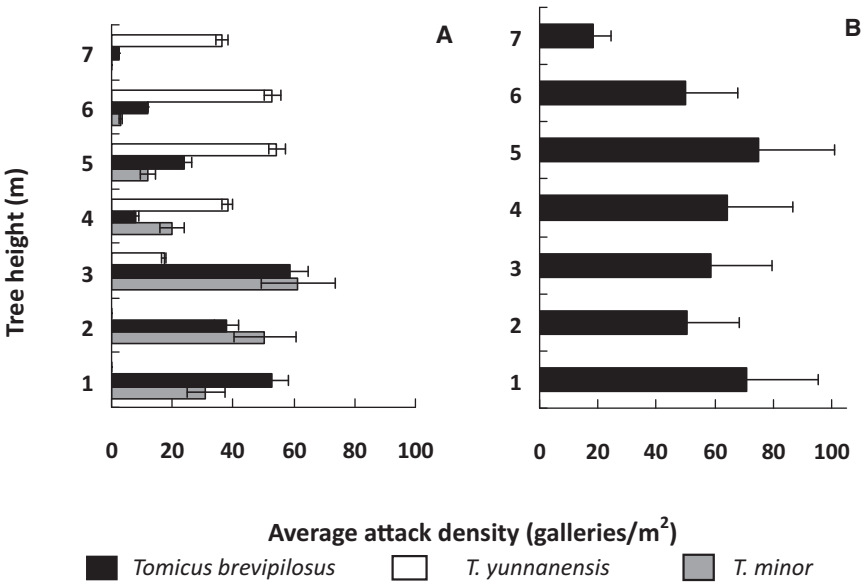


Fig. 4. Average attack density of *T. brevipilosus*, *T. minor,* and *T. yunnanensis* at various heights along the main trunk of *P. yunnanensis* trees in Yunnan when sampled monthly from January through June 2007–2009. (A) The vertical distribution for the three *Tomicus* species individually when all three species were present on the same trees (March and April). (B) The vertical distribution for *T. brevipilosus* when it was the only beetle present on the sampled trees (April–June). The data were pooled for all months and years.

Table 1. Typical life cycle of *T. brevipilosus* in Anning County (24.97° N, 102.33° E, 1,800 m a.s.l), Yunnan, China, based primarily on field work conducted in 2009

Life stage	Jan F M L	Feb. F M L	Mar. F M L	April F M L	May F M L	June F M L	July F M L	Aug. F M L	Sept. F M L	Oct. F M L	Nov. F M L	Dec. F M L
Adult	+ + +	+ + +	+ + +	+ + +								
Egg			0 0 0	0 0 0	0 0 0	0						
Larva			– –	– – –	– – –	– – –						
Pupa					¤ ¤ ¤	¤ ¤	¤ ¤					
Adult					+	++ +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +

F, first 10-d period of month; M, middle 10-d period; L, last 10-day period.

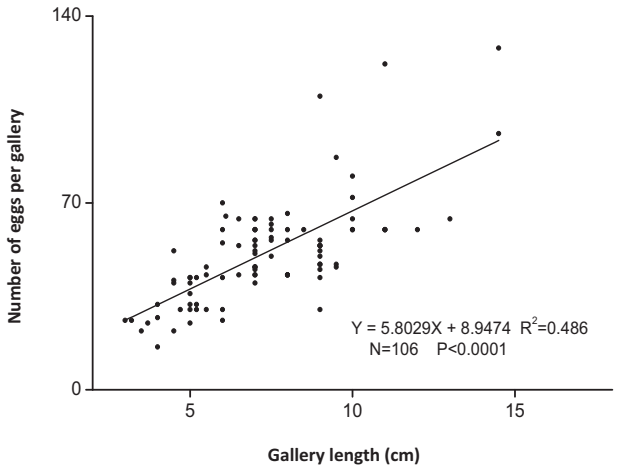


Fig. 5. Linear relationship between number of eggs within a single *T. brevipilosus* maternal gallery and the length of the corresponding maternal gallery.

apparently fully constructed *T. brevipilosus* maternal galleries was 7.2 ± 2.3 (mean ± SE, $n = 106$) cm long (14.0 cm maximum) and varied in width from 4.7 to 5.4 mm. The average number of eggs laid per gallery was 50.9 ± 18.7 (mean ± SE, $n = 106$) and ranged from 22 to 128 eggs. The number of the eggs per gallery was significantly and positively correlated with maternal gallery length ($R^2 = 0.486$, $n = 106$, $P < 0.0001$) (Fig. 5).

Discussion

The presence of two *Tomicus* species co-occurring in the same pine forest has been commonly reported in many Eurasian countries (Bakke 1968, Långström 1983, Ye and Ding 1999), but the co-occurrence of three *Tomicus* species infesting the same pine trees has seldom been reported in the world (Lu et al. 2014). In Yunnan, in southwestern China, where three *Tomicus* species can coexist in the same *P. yunnanensis* forest, it was not known how these three *Tomicus* species would interact. That is, would they compete with each other for the same resource or would they reduce competition by partitioning their breeding resource either spatially or seasonally (Paine et al. 1981, Flamm et al. 1987, Wilkinson and Haack 1987, Haack et al. 1989, Amezaga and Rodríguez 1998, Ayres et al. 2001)? Obviously, answering this question will help in understanding the damage potential caused by the various *Tomicus* species in southwestern China.

This study, along with the results presented by Lu et al. (2014), indicated that the three *Tomicus* species that coexist in *P. yunnanensis* forests are in large part separated seasonally in their reproductive cycles, and when they do overlap seasonally, they partition themselves spatially along the main trunk. For example, Lu et al. (2014) noted that *T. yunnanensis* reproduces from early November to March of the next year, whereas *T. minor* started to reproduce about 1–2 wk later, from

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late November to late March or early April, and usually only infested trees already under attack by *T. yunnanensis* (Ye and Ding 1999, Chen et al. 2010). In contrast, breeding duration of *T. brevipilosus* was primarily from early March to early June, thus overlapping with that of the other two *Tomicus* species by only about 1 mo (Fig. 3). These differences in the peak breeding season for the above three *Tomicus* species in Yunnan likely reduce interspecific competition among these *Tomicus* species on the one hand but also lengthen the total period of time that pine trees can be under attack by *Tomicus* beetles each year and thereby can result in more serious damage to Yunnan pine stands (Lu et al. 2014).

The initiation of *Tomicus* breeding attacks in northern latitudes that experience cold winters is closely related to maximum daily air temperatures. For example, in northern Europe and North America, *T. piniperda* typically initiates flight and breeding attacks when daily air temperatures reach 10–12°C, and *T. minor* when temperatures reach 12–14°C(Bakke 1968; Salonen 1973; Långström 1983; Schlyter and Löfqvist 1990; Haack et al. 2000, 2001; Haack and Poland 2001; Ye et al. 2002). In northeastern Italy, *Tomicus destruens* (Wollaston) initiates spring flight when daily mean temperatures exceed 12°C (Faccoli et al. 2005), but in central Italy, *T. destruens* flies to breeding sites in October and November when the maximum daily temperatures are 18–22°C and daily minimum temperatures are 7–14°C (Sabbatini Peverieri et al. 2008).

In contrast, in Yunnan, little is known about the circumstances that trigger spring flight in the four local *Tomicus* species. In the case of *T. yunnanensis*, adults initiate breeding attacks in November apparently by simply departing the shoots and walking along the branches to the main trunk of the same tree on which they shoot fed (Liu et al. 2010). Later, usually beginning in January, *T. yunnanensis* adults will fly to new hosts after first experiencing periods of cold and then having mean maximum air temperatures once again reaching or exceeding 12°C (Liu et al. 2010). The threshold temperature for spring flight of *T. minor* has not been studied in Yunnan, but it is likely slightly higher than that of *T. yunnanensis* given that *T. minor* initiates spring flight soon after *T. yunnanensis* (Lu et al. 2014).

The threshold temperature for spring flight of *T. brevipilosus* is not known, but it is likely considerably higher than that of *T. yunnanensis* and *T. minor* given that *T. brevipilosus* spring flight starts about 2 mo later, in March (Lu et al. 2014; Fig. 3). Perhaps initiation of *T. brevipilosus* spring flight is more closely linked to daily mean temperature rather than the daily maximum as reported for *T. destruens* in Italy (Faccoli et al. 2005). An examination of the temperature data in Fig. 2 shows that in March of each year, the daily mean air temperature ranged over 11.8–19.6°C in 2007, 8.7–18.5°C in 2008, and 11.9–18.2°C in 2009. If we consider a mean air temperature of 15°C as an arbitrary threshold value for *T. brevipilosus* flight, then there were 15 d that could have supported flight in March and 16 d in April 2007, 10 and 25 d in 2008, and 18 and 26 d in 2009, respectively. Of course, other factors besides simply air temperature could influence initiation of spring flight in *T. brevipilosus*, such as day length, ovarian development, or some physiological change within the host tree that is detected by adults as they overwinter in the shoots.

As shown in Fig. 1, *T. brevipilosus* peak flight was apparently shifted 1 mo later in 2008 when compared with 2007 and 2009. It is not clear if this shift is simply an artifact of the trees that were sampled in the different years or if this apparent shift reflects some major temperature differences among the three sampling years. If the difference in the flight season is related to temperature, it is difficult to identify a major difference in the 2008 temperature data shown in Fig. 2 when compared with the data from 2007 and 2009. One difference, as mentioned above, is that there were fewer days in March 2008 when the mean daily temperature exceeded 15°C when compared with March in 2007 or 2009. However, mean temperatures in April 2008 were broadly similar to April 2009 but warmer than April 2007. Such year to year variation in the timing of the initial spring flight of overwintering *Tomicus* adults is common and has been shown to be related to annual differences in spring temperatures (Bakke 1968; Salonen 1973; Långström 1983, 1986; Haack and Lawrence 1995; Haack et al. 2000; Faccoli et al. 2005).

Among the eight species of *Tomicus* worldwide, *T. piniperda* usually breeds in wind-blown trees, fire-damaged trees, stumps, and other severely stressed pine trees (Bakke 1968; Ye 1991; Haack et al. 2000, 2001; Kirkendall et al. 2008). *Tomicus armandii* Li and Zhang may infest weakened *Pinus armandii* Franchet trees in Yunnan (Li et al. 2010). *T. yunnanensis* is regarded as one of the most aggressive species of *Tomicus*, being able to attack and kill live, apparently healthy *P. yunnanensis* trees (Ye and Lieutier 1997, Lu et al. 2014). *T. minor* is often considered to be more of an opportunist, usually infesting host trees that are already infested by other *Tomicus* species such as *T. piniperda* or *T. yunnanensis*, which could facilitate tree death (Bakke 1968, Långström 1983, Eidmann 1992, Ye and Ding 1999, Lieutier et al. 2003, Chen et al. 2009). In this study, we discovered that *T. brevipilosus* preferred to breed in trunks of *P. yunnanensis* trees that were already infested by both *T. yunnanensis* and *T. minor*. However, later in the season, *T. brevipilosus* was able to attack apparently healthy *P. yunnanensis* trees on its own, indicating that *T. brevipilosus* is more similar to *T. yunnanensis* in its aggressiveness when compared with *T. minor* (Chen et al. 2009, 2010).

The spatial distribution of *T. brevipilosus* breeding attacks in the trunks of *P. yunnanensis* trees was greatly influenced by the presence or absence of *T. yunnanensis* and *T. minor* breeding in the same tree (Fig. 4). In trees that were already infested by the other two *Tomicus* species, *T. brevipilosus* colonized areas of the trunk that were not already occupied, resulting in a scattered distribution of *T. brevipilosus* attacks along the trunks. The ability of *T. brevipilosus* to adjust its infestation pattern in response to other *Tomicus* species likely decreases interspecific competition among *Tomicus* species, as well as better utilizes the limited inner bark resources. In addition, it is possible that the early-season attack pattern of *T. brevipilosus* could enhance the reproductive success of *T. yunnanensis* and *T. minor* by attacking unoccupied areas of the tree trunk and thereby further reducing any residual host tree resistance. However, later in the flight season, when *T. yunnanensis* and *T. minor* brood are already well advanced, the arrival of *T. brevipilosus* would likely not help much in further reducing host vigor.

In those cases when *T. brevipilosus* initiates attack by itself, the first attacks are generally located along the lower trunk with subsequent attacks occurring throughout the entire trunk. The within-tree attack pattern varies among other Chinese *Tomicus* species as well (Ye and Ding 1999). In Yunnan, the first attacks by *T. yunnanensis* tend to be along the upper trunk, whereas *T. minor* attacks are more concentrated along the lower trunk (Ye 1995, Ye and Ding 1999, Chen et al. 2010). In contrast, in northern Europe, Långström (1983) reported that *T. piniperda* tended to initiate attack along the lower trunk of local pines (mostly *Pinus sylvestris* L.), where the bark was thicker, whereas *T. minor*, which flies later, tended to colonize the upper portions of the trunk and branches where the bark is thinner. In the above two situations, it appears that *T. minor* is simply colonizing trees already infested by other *Tomicus* species but concentrating its attack on those portions of the trunk that are less occupied and thereby reducing interspecific competition. It is reasonable to assume that the attack pattern in any one world area is a reflection of the *Tomicus* and host-tree species present, as well as differences in beetle aggressiveness, threshold temperatures for flight, and adult body size (Kirkendall et al. 2008, Li et al. 2010, Lieutier et al. 2015). For the three *Tomicus* species infesting *P. yunnanensis* in Yunnan, the adult beetles are broadly similar in body size, with *T. yunnanensis* being slightly larger, and *T. brevipilosus* and *T. minor* being very similar (Kirkendall et al. 2008, Lieutier et al. 2015).

It is unclear why the attack pattern differs between *T. yunnanensis* (starting in the upper trunk) and *T. brevipilosus* (starting in the lower trunk) when each is the first bark beetle to infest the same species of pine, although such variation in attack pattern is well-recognized

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among bark beetles (Rudinsky 1962). Nevertheless, both attack patterns can result in tree death. This topic still requires further exploration.

The average length and number of eggs in *T. brevipilosus* maternal galleries reported in this study are broadly similar to findings reported for other *Tomicus* species that make longitudinal galleries (all species except for *T. minor*). For example, in comparison to the 7.2-cm-long average *T. brevipilosus* maternal gallery in this study, others have reported mean values of 4–8 cm for *T. destruens* (Faccoli 2007), 7.1–11.0 cm for *T. piniperda* (Långström and Hellqvist 1985), and 9.6–10.6 cm for *T. yunnanensis* (Ye and Ding 1999). However, an inverse relationship has been reported between attack density and average length of maternal galleries in some *Tomicus* species (Salonen 1973, Långström 1984, Faccoli 2009), but this relationship has not yet been investigated in *T. brevipilosus.* Clearly much more research is needed to fully elucidate the life history of *T. brevipilosus* and its interactions with other *Tomicus* species in Yunnan.

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