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Population dynamics of *Monochamus galloprovincialis* **Olivier (Coleoptera: Cerambycidae) in two pine species under laboratory conditions**

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Abstract The study of the life history dynamics of the pine sawyer beetle *Monochamus galloprovincialis* (Olivier) is important because the beetles vector the pinewood nematode. The objectives of this study were to investigate differences in beetle life history parameters between the two common host tree species in Turkey, *Pinus sylvestris* and *Pinus nigra*. Relationships between the number of oviposition sites, holding time (time between log cut and oviposition), log moisture content, log volume and area, and adult survivorship were evaluated. No significant differences were found between the two tree species except adult density per m^2 . The holding time did not influence the number of oviposition sites, larval entry holes or adults for *P. sylvestris*. There was a negative correlation between the holding time and the number of oviposition sites for *P. nigra*. The number of adults emerged per log was correlated with the number of larval entry holes only for *P. sylvestris*. Only 12 and 15% of the initial cohort completed development and emerged as adults for *P. sylvestris* and *P. nigra*, respectively. Both tree species are equally suitable hosts for *M. galloprovincialis* development. We conclude that the

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high within-log mortality of beetles is a combination of resource quality and quantity factors and intraspecific competition and cannibalism during larval development.

Keywords Egg density · Generation survivorship · Pine sawyer · *Pinus nigra* · *Pinus sylvestris* · Pine wilt

Introduction

Pine wilt disease, caused by the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer [1934;](#page-6-0) Nickle [1970](#page-6-1)) is an important threat to susceptible conifer forests of the world. The nematode is vectored primarily by *Monochamus* species beetles (Coleoptera: Cerambycidae). Pinewood nematode was first detected in Europe in Portugal in 1999 (Mota et al. [1999\)](#page-6-2). Consequently, it has become a crucial issue to determine possible vector species of the nematode in Europe. The pine sawyer beetle, *Monochamus galloprovincialis* (Olivier), was reported as the vector of the pinewood nematode in Portugal (Sousa et al. [2001](#page-6-3)). Following the detection of this association between the nematode and the beetle, a number of studies on the ecology and biology of *M. galloprovincialis* have been initiated (Naves et al. [2006a](#page-6-4), [b](#page-6-5), [2007](#page-6-6)).

According to Hellrigl ([1971](#page-6-7)), five species of *Monochamus* are present in Europe; *M. galloprovincialis*, *M. sartor* (Fabricius), *M. sutor* (Linnaeus), *M. urussovi* (Fischer) and *M. saltuarius* (Gebler). *Monochamus* species are considered to be secondary pests and colonize weakened, dying or recently cut conifer trees (Baker [1972](#page-6-8)).

The life cycle of the beetle may extend up to 2 years. Adults mate on the bole and females deposit eggs underneath the bark of pine trees. Early larval instars develop entirely in the subcortical zone, consuming mainly phloem

and cambium (Pershing and Linit [1986\)](#page-6-9). Later instars construct galleries in the sapwood and also continue to forage in the phloem and cambium (Pershing and Linit [1986](#page-6-9)). Pupation occurs at the terminus of the larval gallery. Newly formed adult beetles emerge from the trees and fly to healthy trees for maturation feeding.

The most important host of *M. galloprovincialis* in Europe is Scots pine, *Pinus sylvestris* Linnaeus, one of the most widely distributed pine species in Europe (Hellrigl [1971](#page-6-7)). In Turkey, there are three widely distributed native pine species; *P. brutia* Tenore, *P. nigra* Arnold and *P. sylvestris*. Adults and larvae of *M. galloprovincialis* have been found in both trees and cut logs of *P. nigra and P. sylvestris*. A laboratory colony of *M. galloprovincialis* was established at Duzce University in Turkey using the laboratory rearing technique of Linit [\(1985](#page-6-10)). Observations of the beetle colonies developing in *P. sylvestris* and *P. nigra* logs showed similarities and differences in the number of eggs and the number of adults emerging from logs of each tree species. We also observed that within-log generation survivorships were very low for both tree species.

Several laboratory studies also reported low values of within-log generation survivorships of *Monochamus* species. In North America, researchers found that the withinlog generation survivorship of *M. carolinensis* (Olivier) ranged from 6 to 15% (Linit [1985;](#page-6-10) Akbulut and Linit [1999](#page-6-11); Akbulut et al. [2004\)](#page-6-12). Alya and Hain [\(1985](#page-6-13)) reported withinlog generation survivorship as 15% for *M. carolinensis* and *M. titillato*r (Fabricius) in logs maintained in outdoor cages in North Carolina. The high mortality of beetles within the logs suggested that either intraspecific competition and/or interspecific competition occurred among larvae within logs (Akbulut et al. [2004\)](#page-6-12).

Turkey is located at an important transitional geographic area between Europe and Asia and imports wood products from different countries every year. Consequently, possible introduction of the pinewood nematode and other exotic pests is a constant threat for Turkey. The presence of *M. galloprovincialis*, the vector of the pine wood nematode in Europe, was reported previously from a number of different sites in Turkey (Özdikmen et al. [2005\)](#page-6-14). The biology and ecology of *M. galloprovincialis* in different pine species are unknown in Turkey. It is important to study the dynamics of a laboratory colony of *M. galloprovincialis* in different host trees which could lend insight into the population dynamics of wild populations of beetles in different forest stands of *P. nigra* and *P. sylvestris.*

The goals of this study were: (1) to investigate the relationship between the number of eggs laid and larval and adult survival, (2) to investigate whether log factors such as log age prior to oviposition and log volume and area affect the number of oviposition sites, the survival of larvae, and the number adult beetles emerging from each log and (3) to investigate differences in life history parameters of *M. galloprovincialis* between the two common host tree species in Turkey, *P. sylvestris* and *P. nigra*.

Materials and methods

A laboratory colony of *M. galloprovincialis* founded from infested black pine, *P. nigra*, at Duzce Forest District, Düzce, Turkey was used to get oviposition on experimental logs. Every 2–3 weeks in 2003 and 2004, we felled a healthy Scots pine and black pine and the boles of the trees were cut into logs (45–60 cm long and 10–20 cm diameter). The ends of each log were dipped in hot liquid paraffin to slow desiccation. Two holes (each 1.3 cm diameter by 3 cm deep), one hole on each end and opposite side of the log, were drilled through the bark and into the wood. Two grams of wood chips without bark pieces from each log were collected from these two holes to determine moisture content (%). The holes were plugged with styrofoam and sealed with petroleum jelly. The moisture content of wood chips was calculated as follows: [wet weight $(g) - dry$ weight (g)]/wet weight \times 100. Dry weight was determined after placing the wood chip samples in an oven at 120°C for 48 h.

Log length, diameter and bark thickness at the midpoint were measured, and log volume and surface area were determined from these measurements. Each log of both tree species was held in the lab for 0–25 days (70–80% RH, 24– 26°C) until placed in an oviposition cage containing an average of 20 sexually mature beetles of each sex and fresh pine twigs for feeding. Two oviposition cages were used; one for *P. sylvestris* and another for *P. nigra*. The number of days between the cutting of a tree and placement of a log in the oviposition cage (holding time) was recorded for each log. Each log was removed from the oviposition cage after 2–5 days. Oviposition start date and end date were recorded for each log. The number of oviposition sites was counted before transferring the log to a growth chamber. The logs were held at 24–26°C, 70–80% RH, and a photoperiod of 14:10 (L:D) h during beetle development. Starting about 70–80 days after oviposition, each log was placed in a PVC container and emerging adult beetles were collected daily.

Beetle emergences were considered to be completed if no adult beetles emerged for 6 weeks following the last adult beetle emergence. After beetle emergence ended, the bark of each log was removed and the number of larval entry holes (oval for larval entry into the xylem) and adult exit holes (round for adult emergence from the xylem) were counted (Pershing and Linit [1986\)](#page-6-9). Each larval entry hole was considered to be an evidence of the survival of one early instar larva.

In a previous study, the mean number of eggs per oviposition site was found to be 1.01 (\pm 0.45 SD, max = 4, min = 0, $n = 2,128$). In this study, 2,128 oviposition sites created by sexually mature females were dissected and the number of eggs counted for each oviposition site. A total of 2,151 eggs were counted. Of the 2,128 oviposition sites, 175 contained no egg, 1,780 contained one egg, 152 contained two eggs, 17 contained three eggs, and 4 contained four eggs. This constant number was multiplied by the number of oviposition sites to obtain an estimated egg number per log. Each adult exit hole was considered to be an evidence of the survival of one adult. Generation survivorship was calculated by dividing the number of adult emergence holes by the estimated number of eggs for each log and the resulting percentages were averaged for the entire tree. Apparent survivorship between the egg stage and the initiation of larval galleries was computed by dividing the number of larval entry holes in the xylem by the number of eggs laid and was expressed as a percentage. Apparent survivorship between the latter larval stages and adults was computed by dividing the number of adult emergence holes by the number of larval entry holes and was expressed as a percentage. Generation time from egg deposition to adult death was determined by adding time to adult emergence and adult age for each individual beetle.

A t test was used to determine differences between the two tree species (*P. sylvestris*, *P. nigra*) in all variables including the number eggs, larvae, adults, log volume, log area, holding time, moisture content, generation survivorship, apparent survivorships (from egg to larvae and from larvae to adult), and adult density per square meter. Regression analysis and subsequent equations of the best-fit lines were used to investigate the relationship between the number of oviposition sites, the number of larval entry holes and the number of adults emerged from each log. Additional regressions were made between the holding time of each log and egg number, log measurements, the number of larvae, and the number of adults emerged. Data from logs were combined and regression analyses were calculated on the means on a per tree basis. All statistical analyses were performed using the statistical analysis system (SAS Institute [1992\)](#page-6-15). All statistical differences were reported at $P = 0.05$.

Results

Comparisons of two host trees' variables

Data from 141 and 72 rearing logs, from 16 and 7 trees of *P. sylvestris* and *P. nigra*, respectively, were used in this experiment. Log volume averaged ca. $8,216$ and $4,580$ cm³ for *P. sylvestri*s and *P. nigra*, respectively (Table [1\)](#page-2-0). Moisture content of logs ($F = 0.10$, $df = 22$, $P = 0.7520$) and holding time, the length of time a log was held before oviposition ($F = 0.27$, $df = 22$, $P = 0.6075$) did not differ significantly between tree species; the means were very similar (Table [1\)](#page-2-0). The bark of *P. nigra* was significantly thicker than *P. sylvestris* $(F = 4.47, df = 22, P = 0.048)$. Although female beetles laid more eggs on average (82.5) on *P. sylvestris* than *P. nigra* (53.8), the differences were not significant $(F = 2.92, df = 22, P = 0.1021)$.

An average of 12 larvae per log ($F = 0.03$, $df = 22$, $P = 0.8630$) survived to tunnel into the xylem of both tree

Table 1 Summary statistics for moisture $(\%)$, number of days logs were held before oviposition (holding time), log metrics [area (cm²) and volume (cm³)], numbers of eggs laid, larval entry holes constructed, and adults emerged for *Monochamus galloprovincialis* for *Pinus sylvestris* and *P. nigra*

Variable	<i>Pinus slyvestris</i> (tree species 1)				<i>Pinus nigra</i> (tree species 2)			
	\boldsymbol{n}	Mean \pm SD	Min.	Max.	n	Mean \pm SD	Min.	Max.
Moisture $(\%)$	16	50.0 ± 6.2	34.6	59.7	7	50.8 ± 4.9	43.3	58.3
Holding time (days)	16	9.2 ± 5.8	0.0	24.8	7	10.4 ± 2.9	6.7	14.2
Eggs (n)	16	82.5 ± 43.3	20.2	210.4	7	53.8 ± 7.8	43.2	68.2
Larvae (n)	16	12.6 ± 2.8	6.0	17.1	7	12.8 ± 3.1	7.9	16.1
Adults (n)	16	6.8 ± 1.9	3.0	10.0	7	7.4 ± 2.4	4.1	11.3
Log area cm^2)	16	$2,208.1 \pm 676.5$	1,392.0	3,958.4	7	$1,676.2 \pm 174.0$	1,465.8	2,000.7
Log volume $(cm3)$	16	$8,216.5 \pm 4,976.0$	3,351.1	22,266.0	τ	$4,580.0 \pm 915.5$	3,473.2	6,419.8
Generation survival $(\%)$	16	11.8 ± 5.3	3.0	23.8	7	14.8 ± 4.9	9.2	22.6
Egg to larva survival $(\%)$	16	20.9 ± 7.4	5.7	31.3	7	25.7 ± 5.5	17.2	32.0
Larva to adult survival $(\%)$	16	56.4 ± 14.2	36.4	83.3	7	56.2 ± 13.2	39.4	72.3
Generation time (days)	16	235.5 ± 47.3	137.4	289.5	τ	252.5 ± 34.1	178.7	296.0
Adults per $m2$	16	$1,093.0 \pm 566.2$	179.6	2,116.3	7	$1,667.2 \pm 670.1$	953.0	2,565.1
Bark thickness (cm)	16	3.7 ± 1.6	1.2	9.0	7	5.2 ± 1.5	2.0	10.0

Generation time, generation survivorship (% survivorship from egg to adult), and apparent survivorship (number of individuals dying as a percentage of those that entered the stage) of eggs to late-stage larvae (those entering the xylem, most likely second instar and older) and apparent survivorship (%) of late-stage larvae to adults are included in this table, and the number of adults per m^2 (Adens, m^2), as well

species (Table [1](#page-2-0)). The number of adults emerged per log was also very similar between tree species $(F = 0.35,$ $df = 22$, $P = 0.5618$ (Table [1\)](#page-2-0). Apparent survivorship between the egg stage and the initiation of larval galleries was a mean of 20.93 and 25.70% for *P. sylvestris* and *P. nigra*, respectively and did not differ significantly $(F = 2.33, df = 22, P = 0.1419)$. Apparent survivorship between the larval stages and adult emergence was double that of egg to larvae survivorship but did not differ significantly between tree species ($F = 0.00$, $df = 22$, $P = 0.9806$) (Table [1\)](#page-2-0). Within-log generation survivorship [egg-stage to adult emergence (survive)] was also similar $(F = 1.81)$, *df* = 22, *P* = 0.1928) between *P. sylvestris* and *P. nigra* $(Table 1)$ $(Table 1)$. Log volume approached significance, indicating that the logs of *P. sylvestris* were unintentionally larger than that of *P. nigra* (*F* = 3.59, *df* = 22, *P* = 0.0719). Bark volume also differed significantly with greater values for *P. sylvestris* (*F* = 5.14, *df* = 22, *P* = 0.0340). The number of adult beetles per cubic meter (density) differed significantly $(F = 4.49, df = 22, P = 0.0461)$ with greater numbers for *P. sylvestris* (Table [1\)](#page-2-0). Generation time from egg to adult death averaged 246.6 and 258.0 days for beetles from *P. sylvestris* and *P. nigra*, respectively, and did not differ significantly $(F = 0.69, df = 22, P = 0.6426)$.

Beetle life history on *P. sylvestris*

The holding time did not influence the number of eggs laid $(r = 0.1919, P = 0.4764, n = 16)$, larval entry into the xylem $(r = 0.1639, P = 0.5441, n = 16)$ or the number of adults emerging $(r = 0.1864, P = 0.4893, n = 16)$ for beetles on *P. sylvestris*. The number of eggs was not significantly correlated with bark thickness when analyzed on a per tree basis ($r = 0.0798$, $P = 0.1516$, $n = 16$), but was negatively and significantly correlated with bark thickness when analyzed on a per log basis ($r = -0.2081$, $P = 0.0130$, $n = 141$) (Fig. [1\)](#page-3-0). The number of larval entry holes into the xylem, an indicator of early larval instar survival, was significantly and positively correlated with log moisture content (*r* = 0.4975, *P* = 0.0499, *n* = 16) (Fig. [2](#page-3-1)). The number of adults emerging was significantly and positively correlated $(r = 0.4969, P = 0.0502, n = 16)$ with the number of larval entry holes into the xylem (Fig. [3](#page-4-0)). The number of adults was significantly and negatively correlated with log volume $(r = -0.5323, P = 0.0337, n = 16)$ (Fig. [4](#page-4-1)) and area $(r = 0.5047, P = 0.0462, n = 16).$

Beetle life history on *P. nigra*

The number of eggs deposited was correlated significantly and negatively with the bark thickness $(r = -0.2683,$ $P = 0.0227$, $n = 72$) (Fig. [1](#page-3-0)) and holding time ($r = -0.8905$, $P = 0.0072$, $n = 7$) (Fig. [5\)](#page-4-2). The moisture content of logs

Fig. 1 Scatter plot of the number of eggs laid versus bark thickness for *P. nigra* and *P. sylvestris*. Each *point* represents mean data from a single log. *Lines* represent the regression equations. The regression coefficient (r^2) for *P. sylvestris* was significant at $\alpha = 0.05$ $(y = 100.6 - 6.29 x, r^2 = 0.044^*$, $P = 0.0130$). The regression coefficient for *P. nigra* was significant at $\alpha = 0.05$ ($y = 73.38 - 3.81x$, *r* ² = 0.072*, *P* = 0.0227)

Fig. 2 Scatter plot of the number of larval entry holes versus pine moisture content for *P. nigra* and *P. sylvestris*. Each *point* represents mean data from all logs of a single tree. *Lines* represent the regression equations. Only the regression coefficient (r^2) for *P. sylvestris* was significant at $\alpha = 0.05$ ($y = 1.403 + 0.224x$, $r^2 = 0.194^*$, $P = 0.0499$)

was not correlated with any variables. The number of adults emerging approached significance and tended towards positive correlation $(r = 0.7241, P = 0.0658, n = 7)$ with the number of larval entry holes into the xylem (Fig. [3\)](#page-4-0).

Discussion

The life history of *M. galloprovincialis* was very similar between the two tree species; *P. sylvestris* and *P. nigra*. The only significant differences were found in the number of adult emergence holes per square meter and bark thick-

Fig. 3 Scatter plot of the number of adults versus the number of larvae for *P. nigra* and *P. sylvestris*. Each *point* represents combined data from all logs of a single tree. *Lines* represent the regression equations. Only the regression coefficient (r^2) for *P. sylvestris* was significant at $\alpha = 0.05$ (*y* = 2.607 + 0.333*x*, $r^2 = 0.193$ ^{*}, *P* = 0.0502)

Fig. 4 Scatter plot of the number of adults versus log volume. Each *point* represents mean data from all logs of a single tree. *Lines* represent the regression equations. Only the regression coefficient (r^2) for *P. sylvestris* was significant at $\alpha = 0.05$ ($y = 8.459 - 0.0002x$, $r^2 = 0.232$ ^{*}, *P* = 0.0337)

ness of logs. Even though mean holding time was similar, the number of eggs laid on *P. sylvestris* logs was greater than the number of eggs laid on *P. nigra*. Egg deposition may have been related to the log size and bark thickness, considering the generally larger size and thinner bark of *P. sylvestris* logs. Francardi and Pennacchio [\(1996](#page-6-16)) found a negative correlation between bark thickness and density of beetles, and Naves et al. [\(2006b](#page-6-5)) suggested *M. galloprovincialis* preferred *P. sylvestris* over several other native Portuguese pine species because of *P. sylvestris*' thinner bark. Moisture content of logs, the other very important tree characteristic that may affect oviposition preferences, were very similar between host trees. The number of larvae,

Fig. 5 Scatter plot of the number of eggs versus holding time. Each *point* represents mean data from all logs of a single tree, consequently data points may fall between measured whole day (24 h) time intervals. *Lines* represent the regression equations. Only the regression coefficient (r^2) for *P. nigra* was significant at $\alpha = 0.05$ ($y = 78.851 - 2.398x$, *r* ² = 0.752*, *P* = 0.0072)

adults, apparent survivorship (egg to larvae and larvae to adult), generation survivorship (egg to adult) were similar for both host trees, although the values were slightly, but not significantly, higher for *P. nigra*. This may be related to the number of eggs deposited because there is a negative, but non-significant, correlation between the number of eggs and apparent survivorship (egg to larvae and larvae to adult) and generation survivorship (egg to adult). The logs of *P. nigra* received less oviposition than that of *P. sylvestris* which may have lead to higher survivorship rates. Intraspecific competition among *Monochamus* larvae is considered a primary mortality factor for the larvae (Dodds et al. [2001](#page-6-17)).

Several studies have been carried out to determine the life history parameters of *Monochamus* species (Linit [1985;](#page-6-10) Alya and Hain [1985](#page-6-13); Akbulut and Linit [1999;](#page-6-11) Akbulut et al. [2004](#page-6-12)). These studies suggested that within-log survivorship ranged from 6 to 15% for both *M. carolinensis* and *M. titillator* in laboratory colonies and in field-maintained logs. Our results for *M. galloprovincialis* indicated similar low within-log survivorship: 12 and 15% for *P. sylvestris* and *P. nigra*, respectively. Beetles that developed in logs of *P. nigra* had slightly higher within-log survivorship than that of *P. sylvestris*, which could be related to the number of eggs deposited. Low within-log survivorship may have been the result of substrate degradation and desiccation or competition and cannibalism among *M. galloprovincialis* larvae. Interspecific competition was not considered to be a mortality factor because the logs were obtained from healthy apparently insect-free pine trees, only *M. galloprovincialis* were allowed to access for oviposition, and no other insect species emerged from the logs.

Dodds et al. [\(2001\)](#page-6-17) reported that cannibalism occurred between larvae of *M. carolinensis* in artificial phloem sandwiches. Cannibalistic behaviour of *Monochamus* larvae in other species has also been reported (Anbutsu and Togashi [1997](#page-6-18); Rose [1957;](#page-6-19) Victorsson and Wikars [1996](#page-6-20)). Togashi [\(1990](#page-6-21)) reported larval cannibalism in the third and fourth stage larvae of *M. alternatus* Hope, the Japanese vector of the pine wood nematode, in naturally infested logs. We found no evidence of disease or parasitism in the insects. We suspect that intraspecific competition, cannibalism and resource quality affected within-log survivorship of *M. galloprovincialis*. Once gallery construction was initiated by the later instars, intraspecific competition decreased because of the lower density of mature larvae within the log and the greater volume of habitat available in the xylem, with a concomitant lower rate of conspecific encounter.

In general, log desiccation through time also could have contributed to low within-log survivorship even though cut ends of logs were dipped in hot paraffin and the logs were kept under high humidity to prevent desiccation. Wood moisture content was determined before oviposition and both tree species had a similar percentage of moisture. No correlation was found between wood moisture content and other variables for *P. nigra*, but wood moisture content before oviposition was correlated significantly and positively with the number of larval entry holes for *P*. *sylvestris*, suggesting wood quality parameters such as moisture content influenced early instar survival. The holding time, the length of time a log was held before being subjected to oviposition, did not affect the number of eggs laid, the number of larval entry holes, the number of adults, or larval or adult survivorship for *P. sylvestris*. Similar results were found for *P. nigra*, except for a significant and negative correlation between holding time and the number of eggs oviposited into logs. This relationship indicated that holding time may have had some negative influence on the attractiveness of logs for oviposition of females, at least for *P. nigra*.

A previous study by our laboratory found that the number of eggs per oviposition site of *M. galloprovincialis* averaged 1.01 for sexually mature beetles on both tree species, the same value reported by Naves et al. ([2006a](#page-6-4)) for this insect species. However, these authors reported a much lower number of egg pits with eggs (0.73 vs. 0.92), possibly because their studies were conducted under different experimental conditions on a different host (*P. pinaster*) and using newly emerged, wild collected beetles. Survivorship was low between the egg stage and the initiation of gallery construction by the larvae (21 and 26%), but higher between the later larval stages and adult emergence (56 and 56%) for *P. sylvestris* and *P. nigra*, respectively. Contrary to our findings, previous studies in North America with field-maintained logs indicated that early instar survivorship equaled $(35\%$, if logs were field-infested) or exceeded (46%, if logs were cage-infested by mating pairs of beetles) later instar survivorship (31 to 37%) for *M. carolinensis* and *M. titillator* (Alya and Hain [1985\)](#page-6-13). Similar results to the current study were reported for a colony of *M. carolinensis* (Akbulut et al. [2004\)](#page-6-12). The poor survivorship of early instar larvae in our study could be an artifact of artificially high initial egg density. Our logs averaged 0.037 and 0.032 eggs/cm² while Akbulut et al. [\(2004](#page-6-12)) found an aver-age 0.085 eggs/cm², Walsh and Linit ([1985](#page-6-22)) found an average of 0.045 eggs/cm², and Alya and Hain (1985) (1985) found an average of 0.0014 eggs/cm² in field-infested logs. Anbutsu and Togashi [\(1997](#page-6-18)) demonstrated a high rate of cannibalism (34%) in newly hatched *M. alternatus* larvae artificially inoculated pine bolts.

The positive and significant correlation between larval entry holes and log moisture content, and the lack of correlation between eggs laid and larva entry holes indicates that resource characteristics may have had a greater effect on mortality than density dependent factors early in the life history of the insect.

Adult survival was positively correlated with the number of larval entry holes, but was unrelated to egg number and log size. These results suggest that density dependent mortality factors become more important than resource quality and quantity factors in the latter parts of the beetle's life history.

Though the number of larvae and adults were unaffected by the holding time for both tree species, the number of eggs laid decreased as the age of the log increased for *P. nigra*. This finding appears counter-intuitive, considering adult beetles are attracted to dead or dying trees for mating and oviposition. Ikeda et al. [\(1980a,](#page-6-23) [b](#page-6-24)) found the increase of monoterpenes and ethanol following cessation of oleoresin exudation (due to *B. xylophilus* infestation) to closely and positively correspond to tree attractiveness and the number of oviposition scars made by *M. alternatus.* Further work is needed in this area to describe female beetle behaviour in regards to host preference and egg laying.

Results of this study suggest increasing oviposition densities on logs in a laboratory colony of *M. galloprovincialis* would not result in greater numbers of adults. Cut log age prior to oviposition (with implications for wood quality) also appeared not to be a factor in the number of adults emerging per log. Although log surface area and volume were correlated with the number of emerging adults (for *P. sylvestris*), the lack of correlations between early instars and log area and bark volume and a similar lack of correlation between log volume and later instars and pupae suggest that resource availability may play a somewhat loose role in regulating *M. galloprovincialis* numbers and suggest that other factors must play a greater role in the developmental dynamics of the beetle. Also, beetle generation time did not differ significantly between tree species, suggesting the quality and suitability of the two tree hosts were similar. Further study of the affects of phloem quantity and quality is needed to determine the precise mechanisms of the development and survivorship of *M. galloprovincialis* in trees.

In conclusion, both tree species, *P. sylvestris* and *P. nigra*, have similar effects with a few minor differences on the life history of *M. galloprovincialis*. Turkey is located at a very important transitional area between Europe and Asia. Two necessary components for the spread of pine wilt disease, a vector beetle and suitable host trees, are already present in Turkey. *Pinus nigra* and *P. sylvestris* are the second and third most widely distributed pine species in Turkey, which increases the size of susceptible areas to the pinewood nematode. According to the results of the current study, both tree species are equally suitable hosts for the development of *M. galloprovincialis*, which may increase the chance of rapid growth of the pinewood nematode's populations in the case of accidental introduction. The availability of two host species also complicates monitoring and control of accidental introduction of the nematode; the distribution of both tree species needs to be known and individuals charged with monitoring potential pine wilt outbreaks need to take into consideration the distribution and overlap of both tree species. It is important to monitor forest stands of both *P*. *sylvestris* and *P. nigra* for *M. galloprovincialis* and the presence of the pinewood nematode in Turkey.

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