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The Effect of Log Seasonality on the Reproductive Potential of *Monochamus galloprovincialis* Olivier (Coleoptera: Cerambycidae) Reared in Black Pine Logs under Laboratory Conditions

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Abstract: *Monochamus galloprovincialis* (Olivier) is the vector of the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhner) Nickle, in Europe and Asia. Reproduction is probably the most important event in the life history of insects and may be affected by a number of factors, such as seasonal changes in larval or adult nutrition. In this study the effect of season on the reproductive potential of *M. galloprovincialis* females reared in black pine logs was investigated by constructing fertility tables for each of 43 pine logs that differed only in the season that they were cut. Population parameters were compared among 3 seasonal cohorts. The intrinsic rate of increase and related population parameters of the beetles that emerged from autumn logs were mostly higher than for beetles that emerged from spring and summer logs. These results suggest that seasonal differences in the nutritional quality of the logs (for immature development) and pine twigs (for adult feeding) may have caused the observed differences in *M. galloprovincialis* survival and reproduction.

Key Words: *Pinus nigra*, fertility tables, intrinsic rate of increase, pine wilt disease, season

Laboratuvar Koşulları Altında Karaçam Kütüklerinde Beslenen *Monochamus galloprovincialis* Olivier (Coleoptera: Cerambycidae)'in Üreme Potansiyeli Üzerine Kütüklerin Mevsimlik Değişiminin Etkisi

Özet: *Monochamus galloprovincialis* (Olivier), Avrupa ve Asya'da Çam Odun Nematodunun, *Bursaphelenchus xylophilus* (Steiner and Buhner) Nickle, vektörüdür. Böceklerin yaşam döngüsü içerisinde en önemli olgulardan biri olan üreme larva ya da ergin besinlerinin mevsimlik değişimi gibi bazı faktörlerden etkilenebilir. Bu çalışmada, karaçam kütüklerinde beslenen *M. galloprovincialis* dişilerinin üreme potansiyeli üzerine mevsimin etkisini belirlemek için farklı mevsimlerde kesilen 43 adet çam kütüğünün herbiri için oluşturulan üretkenlik tabloları kullanılmıştır. Populasyon parametreleri 3 farklı mevsimsel kohort arasında karşılaştırılmıştır. Sonbahar kütüklerinden çıkan böceklerin populasyon artışının gerçek oranı ve ilişkili populasyon parametreleri ilkbahar ve yaz kütüklerinden çıkanlara göre genellikle daha yüksek bulunmuştur. Bu sonuçlar, ergin olmayan dönemin gelişiminde kütüklerin ve ergin beslenmesinde de çam sürgünlerinin besinsel değerlerindeki mevsimlik değişimlerin *M. galloprovincialis*'in hayatta kalma ve üremesinde gözlenen farklılıklara neden olduğunu önermektedir.

Anahtar Sözcükler: *Pinus nigra*, üretkenlik tabloları, populasyonun gerçek artış oranı, çam kuruma hastalığı, mevsim

Introduction

The pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhner 1934), Nickle 1970, is the causal agent of pine wilt disease. The nematode is vectored between host trees by cerambycid beetles in the genus *Monochamus* (Coleoptera: Cerambycidae) (Linit, 1988). The pinewood nematode was detected in Portugal for the first time in Europe in 1999 (Mota et al., 1999). Following this detection, *Monochamus galloprovincialis*

(Olivier) was reported as a vector of the pinewood nematode in Portugal (Sousa et al., 2001). *M. galloprovincialis* is widely distributed in Europe and some parts of Asia (Hellrigl, 1971; Francardi and Pennacchio, 1996).

Monochamus species colonize coniferous trees that are weakened, dying, and freshly felled (Baker, 1972) in response to volatile chemical exposure (Ikeda et al., 1980a; 1980b). These beetles are considered a

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secondary pest in forests. After this association with the pinewood nematode was established, the importance of *Monochamus* species has increased. Numerous studies have been carried out, particularly in North America and East Asia. In response to the detection of the pinewood nematode in Europe, the number of studies on *M. galloprovincialis* has recently increased (Pajares et al., 2004; Naves et al., 2006a, 2006b, 2007).

Turkey occupies an important transitional geographic area between Europe and Asia, which may increase the possibility of the inadvertent introduction of the pinewood nematode from infested regions like Asia and Europe (e.g., Portugal). In Turkey, the only known potential vector of the pine wood nematode is *M. galloprovincialis* and no published information is available, except for some general descriptive details (Çanakçıoğlu and Mol, 1998; Özdikmen et al., 2005). Determination of the reproductive potential of *M. galloprovincialis* is important for understanding the population dynamics and for predicting the population growth of *M. galloprovincialis* in Turkey.

Several studies were conducted on the reproductive potential of *Monochamus* species in North America and Japan (Togashi and Magira, 1981; Togashi, 1997; Nakayama et al., 1998; Zhang and Linit, 1998; Akbulut and Linit, 1999a; 1999b). In Europe, only a few studies related to the reproductive traits of *M. galloprovincialis* are available (Francardi and Pennacchio, 1996; Naves et al., 2006a).

The most important host of *M. galloprovincialis* in Europe is the Scots pine, *Pinus sylvestris* L. (Hellrigl, 1971). In Turkey, there are 3 widely distributed native pine species: *P. brutia* Ten., *P. nigra* Arnold, and *P. sylvestris*. Adults and larvae of *M. galloprovincialis* have been found in both trees and cut logs of *P. nigra* in Turkey.

Female beetles deposit eggs underneath the bark. Larval and pupal stages complete their development in the wood. Early larval instars initiate feeding in the subcortical zone, consuming mainly phloem and cambium (Pershing and Linit, 1986). Later instars enter the sapwood, but continue to forage in the phloem and cambium. These tissues contain high levels of carbohydrate, lipids, minerals, nitrogen, and water (Cowling and Merrill, 1966; Haack and Slansky, 1987), and their amounts vary seasonally (Hepting, 1945; Fischer and Höll, 1992).

Leather (1995) suggested that reproduction of insects may be affected by a number of factors, such as ovariole number, larval nutrition, adult size, adult nutrition, adult longevity, and host plant quality and its seasonal changes. The development of insects is affected by the nutritional quality of their host plants (Dixon, 1971; Hosking and Hutcheson, 1979; Leather, 1995). The effect of host plant quality and seasonal changes in host plant quality on insect reproduction have been documented. In general, increasing host quality positively affects the reproduction of insects (Hough and Pimental, 1978; Gruber and Dixon, 1988; Leather, 1995). Seasonal changes in host plant quality also have a noticeable effect on the reproductive potential of insects (Dixon, 1971).

The main goal of this study was to investigate the effect of season on the reproductive potential of *M. galloprovincialis* reared in black pine logs. The specific objective was to compare the intrinsic rate of increase and associated population parameters of 3 cohorts of *M. galloprovincialis* reared in black pine logs that differed only in the season in which they were cut.

Materials and Methods

Laboratory techniques and calculations were adopted from Akbulut (1998). A laboratory colony of *M. galloprovincialis* that originated from beetle-infested black pine, *Pinus nigra* Arnold, of Düzce Forest District, Düzce, was used to obtain oviposition on experimental logs. Every 2-3 weeks in 2004, a healthy black pine was felled, the boles of the trees were cut into logs (45-60 cm long, 10-20 cm diameter), and the logs were brought into the laboratory. The lower portion of the bole was not used because of thick bark, which inhibits *Monochamus* oviposition. The cut ends of each log were waxed with hot liquid paraffin to retard desiccation. Length, diameter, and bark thickness of each log were measured. Then, 2 holes were drilled into the log: 1 hole at the top of one end and 1 hole at the bottom of the other end. From each log, 2 g of wood chips without bark pieces were collected from these 2 holes to determine the log's moisture content (%). The holes were plugged with Styrofoam and sealed with petroleum jelly. The moisture content of the wood chips was calculated as follows: $[\text{wet weight (g)} - \text{dry weight (g)}] / \text{wet weight} \times 100$. Dry weight was determined after placing the wood chip samples in an oven at 120 °C for 48 h.

Each experimental log was placed in an oviposition cage (68 × 60 × 60 cm) containing an average of 20 beetles of each sex to receive oviposition. Fresh pine twigs were also provided for adult feeding. To reduce variation in the intraspecific competition among beetle larvae within the experimental logs, each log was removed from the oviposition cage when it had 35-60 oviposition sites. This usually occurred within 24-48 h. The oviposition start and end dates were recorded for each log. The number of oviposition sites of each log was counted. Then, the log was put into its own PVC container during beetle development. This experiment was carried out under constant laboratory conditions; 24-26 °C, 70%-80% relative humidity, and a photoperiod of 14:10 h (L:D).

These procedures were replicated with a total of 43 logs collected during the spring, summer, and autumn of 2004. Each seasonal batch consisted of 15 logs (except spring, 13 logs) to assure a sufficient number of emerged beetles for each season. Logs cut from trees between March and May were considered the spring treatment, those cut from trees between June and August the summer treatment, and those cut from trees between September and November the autumn treatment.

Newly emerged beetles were collected daily from each log and the age of the beetles, from egg deposition to adult emergence, was noted. The weight of each beetle was recorded (mg) and was marked on the elytra using a binary numbering technique to maintain the beetle identity (Humphry and Linit, 1989).

Each female beetle, together with a male partner, was put into its own plastic container (21 cm high × 26 cm diameter) with screen lids and maintained under the constant experimental conditions as stated previously. Male beetles were rotated among their female partners on a 5-day basis to eliminate differences in sperm quality or the quantity females received. When the male beetle died before its female partner, it was replaced with another male beetle of the same age. Each pair was provided with fresh black pine twigs for feeding every 48 h and small bolts for oviposition (10-16 cm long, 7-12 cm diameter) every 5 days. These bolts were taken from the upper parts of black pine. Every 5 days, each bolt was replaced with a fresh one and all oviposition sites were identified and examined by removing the bark around each site with a knife. The number of eggs for each site was counted. This process continued until the death of each female. The total number of eggs was determined by

calculating the number of eggs oviposited by each female during her life span.

Several population parameters were determined for beetles emerging from each experimental log based only on survival and reproduction data of females. The sex ratio of eggs was assumed to be 0.50 (female/total number of beetles) based on the number of adults of both sexes that emerged in the current study. The initial female egg density for each log was estimated as follows: the number of oviposition sites × sex ratio × the number of eggs per oviposition site (1.01). This constant (1.01) was determined in a preliminary study in which 2128 oviposition sites were dissected and the number of eggs counted for each oviposition site. Within-wood survival rate (egg to adult emergence) was calculated as the ratio of the total number of emerged female beetles to the estimated number of female progeny from each log. This is the best estimate of immature survivorship for these cryptic life stages of the beetle. Cohort survivorship at the time of first adult emergence was calculated after adult emergence was complete. Only immature individuals that survived to the adult stage were considered alive.

A fertility table (Birch, 1948) was constructed for the beetles that emerged from each log by collecting age-specific survivorship and fecundity data. The age-specific survival rate of adults (l_x), the proportion of females alive at time x and the age-specific fecundity (m_x), and the expected number of female progeny per female at age x were calculated for each time interval ($x = 5$ days). After calculating of these components of the fertility tables, several population parameters of each treatment group (season) were calculated for each replicate (an experimental log). The net reproductive rate ($R_0 = \sum l_x m_x$), the number of times the population multiplied in 1 generation, mean generation time ($T = \sum l_x m_x x / \sum l_x m_x$), mean time passed between the birth of parents and the birth of offspring, and the intrinsic rate of increase ($\sum e^{-rx} l_x m_x$), and the rate of increase per capita per time period (a measure of population growth) were calculated for each experimental log within a season. In addition, adult female longevity and age-specific egg deposition rates were determined for each season. Beetles that emerged from logs cut during the same season were pooled into a single population to plot the temporal pattern of egg deposition, adult survivorship, the number of live adult female beetles, and the age-specific fecundity pattern curves.

Analysis of variance (ANOVA) and least square means tests were used to compare mean values of variables associated with beetle biology and fertility table parameters (l_x , m_x , R_o , T , and r) between seasons. Variables associated with beetle characteristics were tested by using each beetle within a season as an observation. Variables associated with log moisture content and fertility table parameters were tested by using each log within a season as an observation. Correlation analysis was used to analyze the relationships between the number of eggs deposited and the number of adults that emerged, between adult longevity and the total number of eggs deposited, and between the intrinsic rate of increase and the independent variables (moisture content of logs, immature survival rates, and total age specific fecundities). Statistical procedures were performed using the Statistical Analysis System (SAS Institute 1999-2000). Beetles that emerged from each seasonal log batch were defined as the spring, summer, or autumn cohort.

Results

The moisture content of the logs (%) differed significantly between seasons ($F = 9.65$; $df = 2, 40$; $P = 0.0004$). The lowest moisture content was found in summer logs (Table 1). Spring and autumn logs had similar moisture content. The mean numbers of oviposition sites were similar for each season ($F = 0.99$; $df = 2, 40$; $P = 0.3817$), but the number of females that emerged per log differed significantly ($F = 7.70$; $df = 2,$

40 ; $P = 0.0015$). The highest mean number of females emerged from autumn logs (Table 1). In total, 131 female beetles emerged from 43 experimental logs. There was an insignificant positive correlation between the moisture content of logs and the number of adult females that emerged from spring ($r = 0.34634$; $P = 0.2464$; $n = 13$) and autumn logs ($r = 0.05777$; $P = 0.8380$; $n = 15$), whereas the relationship between the moisture content of logs and the number of adult females that emerged from summer logs was negative ($r = -0.05545$; $P = 0.8444$; $n = 15$)

Immature survivorship differed significantly between seasons ($F = 3.25$, $df = 40$, $P = 0.0491$). The survivorship rate of the spring cohort was lower than that of the summer and autumn cohorts (Table 1). There was a significant negative correlation between the immature survivorship rate and number oviposition sites per log only for summer logs ($r = -0.66419$; $P = 0.0069$; $n = 15$), while this relationship was not significant for the spring ($r = -0.05706$; $P = 0.8531$; $n = 13$) or autumn cohorts ($r = -0.09419$; $P = 0.7385$; $n = 15$). Mean beetle weight was similar for each season ($F = 1.97$; $df = 2, 128$; $P = 0.1435$). Females that emerged from spring logs were heavier than those that emerged from summer and autumn logs (Table 2). Immature age of females (age at emergence) did not differ significantly between seasons ($F = 2.04$; $df = 2, 128$; $P = 0.1337$), but females that emerged from logs cut during the spring had a shorter within-wood development period than those that emerged from summer and autumn logs (Table 2).

Table 1. Mean \pm SD log moisture content, number of oviposition sites per log, number of females that emerged per log, and within-wood survivorship at the time of first female emergence for logs cut during spring, summer, and autumn.

Season	N	Moisture content (%)	No. of oviposition sites	No. of females that emerged	Within-wood survivorship
Spring	13	55.85 \pm 8.25 a	51.46 \pm 11.21 a	2.23 \pm 1.10 a	0.09 \pm 0.04 a
Summer	15	45.67 \pm 4.88 b	46.20 \pm 10.04 a	2.67 \pm 1.50 a	0.13 \pm 0.12 ab
Autumn	15	55.67 \pm 8.05 a	49.00 \pm 8.51 a	4.07 \pm 1.28 b	0.16 \pm 0.05 b

Means within each column followed by the same letter did not differ according to Fisher's LSD ($\alpha = 0.05$).

Table 2. Characteristics of *M. galloprovincialis* females that emerged from logs cut during spring, summer, and autumn (mean \pm SD).

Season	N	Adult wt. (mg)	Within-wood development ^a	Fecundity ^b	Adult longevity ^c	Total longevity ^d
Spring	29	0.36 \pm 0.08 a	210.38 \pm 62.66 a	73.31 \pm 59.62 a	41.41 \pm 24.29 a	252.28 \pm 57.18 a
Summer	41	0.32 \pm 0.07 a	231.63 \pm 38.90 a	20.59 \pm 31.56 b	18.39 \pm 15.45 b	250.15 \pm 41.69 a
Autumn	61	0.32 \pm 0.09 a	227.05 \pm 38.29 a	77.38 \pm 73.32 a	39.21 \pm 26.94 a	266.13 \pm 45.57 a

Means within each column followed by the same letter did not differ according to Fisher's LSD ($\alpha = 0.05$).

^a Within-wood development (the number of days from egg deposition to adult emergence).

^b Fecundity (the total number of eggs deposited per female).

^c Adult longevity (the number of days from beetle emergence to death).

^d Total longevity (the number of days from egg to adult death).

The age-specific pattern of egg deposition differed between seasons (Figure 1). Beetles that emerged from spring logs started to deposit eggs earlier than beetles that emerged from summer and autumn logs (Figure 1). The total number of eggs deposited (fecundity) by beetles differed significantly between seasons ($F = 12.06$; $df = 2$, 128; $P = 0.0001$). Beetles that emerged from logs cut during the autumn had the highest fecundity (Table 2).

The longevity of adult females ($F = 12.05$; $df = 2$, 128; $P = 0.0001$) was significantly different between seasons, but the total longevity (egg to adult death) was similar ($F = 1.68$; $df = 2$, 128; $P = 0.1900$). The greatest adult longevity was exhibited by beetles that emerged from spring logs, followed by beetles that emerged from autumn logs (Table 2). The beetles that emerged from autumn logs had the greatest total longevity (Table 2). The beetles of the spring cohort emerged earlier from the logs and lived longer as adults than those that emerged from the summer and autumn logs (Table 2). The mean

percentage of the beetles' life spans spent as adults was greater for individuals that emerged from spring logs (17.8%) than for individuals from summer (7.3%) or autumn logs (14.3%). In addition, there was a significant correlation between adult longevity and the number of eggs laid by the spring ($r = 0.57152$; $P = 0.0413$; $n = 13$), summer ($r = 0.71838$; $P = 0.0026$; $n = 15$) and autumn cohorts ($r = 0.73480$; $P = 0.0018$; $N = 15$).

Beetles that emerged from autumn logs had longer adult survivorship than beetles that emerged from both spring and summer logs (Figure 2). The longest adult survivorship was observed for the spring cohort because of early emergence (Figure 2). The number of live adult females was low for all 3 cohorts in the first part of the graph (Figure 3). There was a sudden increase in the number of live adult females in the second part of the graph (Figure 3). Beetles in the spring cohort emerged earlier and started to contribute to reproduction earlier than beetles in the summer and autumn cohorts.

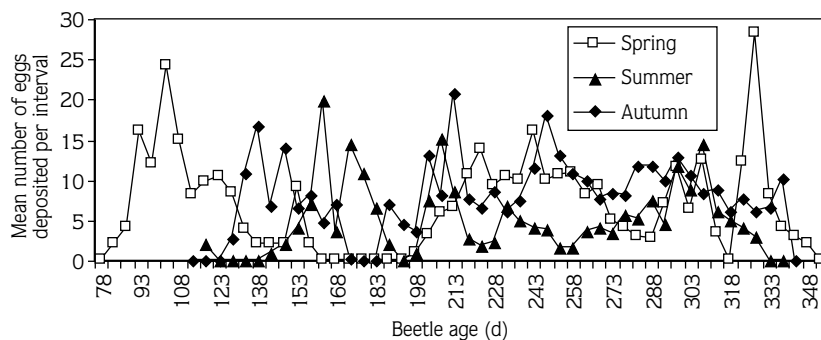


Figure 1. Age-specific patterns of egg deposition for *M. galloprovincialis* females that emerged from spring (\square), summer (\blacktriangle), and autumn (\blacklozenge) experimental logs.



Figure 2. Adult survivorship curves for *M. galloprovincialis* females that emerged from spring (□), summer (▲), and autumn (◆) experimental logs.

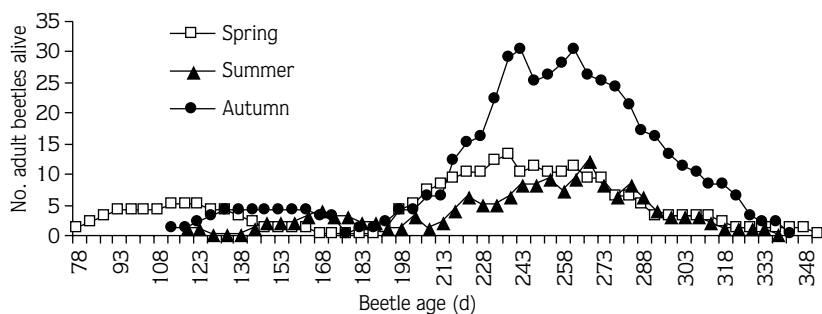


Figure 3. The number of live adult *M. galloprovincialis* females that emerged from spring (□), summer (▲), and autumn (●) experimental logs.

The total age-specific fecundity (Σm_x) ($F = 14.29$; $df = 2, 40$; $P = 0.0001$) differed significantly between seasons (Table 3). Contributions to m_x began earliest for the spring cohort and latest for the summer cohort (Figure 4). Total age-specific fecundity is a function of the age-specific egg deposition rate (Figure 1) and cohort survivorship (Figures 2 and 3).

The net reproductive rate (R_0) ($F = 28.66$; $df = 2, 40$; $P = 0.0001$) and the intrinsic rate of increase (r) differed significantly ($F = 12.82$; $df = 1, 40$; $P = 0.0001$) between seasonal cohorts; however, mean generation time (T) ($F = 0.16$; $df = 2, 40$; $P = 0.8504$) was similar.

The intrinsic rate of increase correlated significantly with the immature survival rate for the summer cohort ($r = -0.55151$; $P = 0.0331$; $n = 15$), but not for the spring ($r = -0.08604$; $P = 0.7799$; $n = 13$) or autumn ($r = 0.10470$; $P = 0.7104$; $n = 15$) cohorts. There was a significant correlation between the intrinsic rate of increase and the number of eggs laid (fecundity) for the

spring ($r = 0.55033$; $P = 0.0513$; $n = 13$), summer ($r = 0.79024$; $P = 0.0005$; $n = 15$), and autumn ($r = 0.75934$; $P = 0.0010$; $n = 15$) cohorts.

Beetles that emerged from autumn logs had higher reproductive parameter values (for most variables) and shorter generation times than those that emerged from spring and summer logs (Table 3).

Discussion

Reproduction is probably the most important event in the life history of insects and may be affected by larval nutrition, adult nutrition, and seasonal changes in host plant quality (Leather, 1995). The intrinsic rate of increase, a measure of the rate of population growth, can be used to compare the reproductive potential of different species or populations of a single species under different environmental or physical conditions (Birch, 1948). In the current study, the reproductive potential of *M. galloprovincialis* reared in *P. nigra* logs cut during

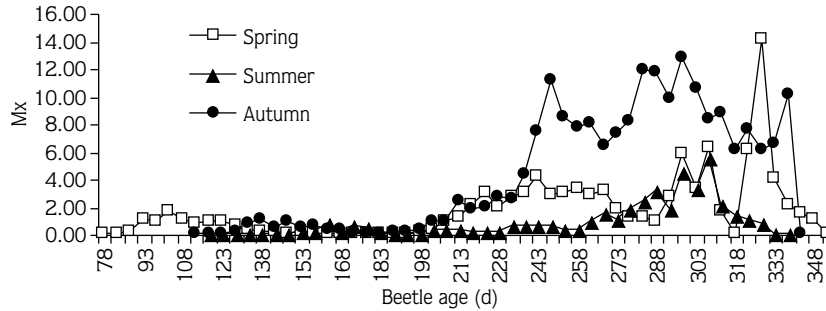


Figure 4. The age-specific fecundity patterns for *M. galloprovincialis* females that emerged from spring (□), summer (▲), and autumn (●) experimental logs.

Table 3. Reproductive parameters of *M. galloprovincialis* females that emerged from logs cut during spring, summer, and autumn (mean \pm SD).

Season	N	Age-specific fecundity (Σm_x)	Net reproductive rate (R_0)	Mean generation time (T)	Intrinsic rate of increase (r)
Spring	13	54.13 \pm 30.80 a	3.35 \pm 1.61 a	42.56 \pm 12.48 a	0.02 \pm 0.03 a
Summer	15	15.54 \pm 15.61 b	1.09 \pm 1.10 b	44.87 \pm 10.87 a	-0.02 \pm 0.04 b
Autumn	15	75.37 \pm 41.18 a	6.54 \pm 2.78 c	42.52 \pm 14.77 a	0.05 \pm 0.03 a

Means within each column followed by the same letter did not differ according to Fisher's LSD ($\alpha = 0.05$).

different seasons was compared under laboratory conditions by using the intrinsic rate of increase and related population parameters.

The intrinsic rate of increase differed between seasons. Beetles that emerged from autumn logs had a greater rate of increase than those that emerged from spring and summer logs. Significant differences in the intrinsic rate of increase between seasons were caused by differences in the rate of immature survivorship and length of the immature developmental period, the survival pattern and longevity of adult stage beetles, and the number of offspring produced per female per time interval. These factors may have been affected by differences in the larval and adult nutritional quality of the host trees (logs and twigs) cut during different seasons of the year.

In this study, the survival rates of immature stages differed between seasons. The lowest immature survival rate was unexpectedly observed in beetles that emerged from spring logs, which could have been related to the number of oviposition sites. Logs cut during the spring

had the most oviposition sites and there was an insignificant negative correlation between the number of oviposition sites and the immature survival rate for the spring cohort. The spring and summer cohorts produced an almost equal low number of adults, while the autumn cohort produced a significantly higher number of adults. Log properties (nutritional quality, moisture content, etc.) probably affected the immature survival rate of each cohort. Log properties affected the length of the immature developmental period (the number of days from egg to adult emergence), but did not differ significantly between seasons. Adult beetles that emerged from spring logs required fewer days to develop from the egg stage to adult emergence. The longest immature developmental period was observed in summer logs. This result suggested that logs cut during the spring and autumn were more suitable for the development of immature stages than were summer logs.

Birch (1948) stated that early egg deposition makes an important contribution to the value of r . Togashi and Magira (1981) also reported that early-emerged females

had higher fecundity than late-emerged females of *M. alternatus*. In the current study, the spring cohort emerged earlier and started egg deposition earlier than did the summer and autumn cohorts. To have equivalent r values, the summer and autumn cohorts with slow immature development would have needed to have a greater total fecundity than the spring cohort, which reached reproductive age in less time. The autumn cohort had a higher rate of immature survivorship and fecundity than the spring cohort, which increased the r value even though the autumn cohort had a slow immature development period. The combination of immature survivorship rate, fecundity, and adult longevity yielded the highest intrinsic rate of increase for the autumn cohort.

The age-specific pattern of egg deposition differed slightly between seasons only at the beginning part of the graph (Figure 1). The total longevity was similar, but adult longevity differed between seasons. The summer cohort had the shortest total longevity, while the autumn cohort had the longest. Spring beetles emerged earlier and lived longer as adults and thus spent more time in reproduction. On the other hand, summer beetles spent more time in immature development and spent less time as adults. The mean generation time (T), the mean time passed between the birth of parents and the birth of offspring, did not differ between seasons.

The effect of host plant quality and its seasonal changes on insect reproduction have been documented. Hough and Pimental (1978) reported that the larvae of *Lymantria dispar* L. that feed on hosts with low nitrogen levels were less fecund as adults than those reared on nitrogen-rich hosts. Nitrogen concentration influenced the rate of reproductive development of the pine weevil, *Hylobius abietis* L., which feeds on conifers (Wainhouse et al., 2004). Seasonal changes in host plant quality also have a noticeable effect on the reproductive potential of insects. The bird cherry-oat aphid, *Rhopalosiphum padi* L., responded to the seasonal patterns of nitrogen content of its host plants. When nitrogen levels were low, reproductive performance of the aphid was also low (Dixon, 1971).

Adult nutrition may affect the reproduction and longevity of insects. Longevity and egg production of the butterfly, *Colias philodice eurytheme* Boisduval, and the moth, *Euxoa messoria* Harris, increased with carbohydrate intake (Stern and Smith, 1960; Cheng, 1972) during the adult stage. Leather (1984) reported a

significant relationship between longevity and the availability of adult food in the pine beauty moth, *Panolis flammea* D and S. The moth, *Zeiraphera canadensis* Mut and Free, lived longer and was more fecund when fed a sugar solution than when fed only water (Carroll and Quiring, 1992).

There are seasonal differences in the amount of accumulated carbohydrates in conifers. In general, the level of soluble sugars is high in winter and low in summer, whereas the starch level is high in spring and autumn (Fischer and Höll, 1992). Starch content of Scots pine sapwood was reported to be low from January to March, to increase in April, to remain high through June, and then to decrease during the following months to a minimum winter value (Fischer and Höll, 1992). Food reserves of shortleaf pine, *Pinus echinata* Mill, stems reached a maximum between April and June. After June, reserves were maintained at a more or less constant but lower level until the following March, with a minimum occurring in mid-August (Hepting, 1945).

The moisture content of wood can also influence larval growth and survival. Haack and Benjamin (1980) reported that the phloem feeder *Agrilus bilineatus* Weber failed to complete larval development when infested host tree moisture content dropped rapidly. In the current study, wood moisture content of logs differed significantly between seasons. Wood moisture content was the highest and the immature developmental time (egg to adult emergence) was the shortest in logs cut during the spring.

Nutritional analysis of the phloem and cambium of the experimental logs was not conducted because of logistical constraints; however, we conclude that the nutritional quality of the phloem and cambium, as well as the differences in moisture content of the xylem fed upon by larvae, and the quality of the subcortical tissue consumed by adult beetles that were fed twigs may have contributed to the differences in the life processes and reproductive parameters associated with the seasonal cohorts of the beetles.

M. galloprovincialis completes its generation in 1-2 years. The flight period of the beetles starts in May in Turkey (Çanakçıoğlu and Mol, 1998). Adults may be seen in the wild until September. Thus, beetles can colonize available host trees between May and September. According to the results of the present study, the colonization of trees during different seasons affected the

length of within-wood development and reproductive potential of *M. galloprovincialis*. The results of this study indicate that beetles that colonize host trees during the autumn and spring would have a greater reproductive potential than those that colonize trees during summer. Similar results were found for *M. carolinensis* in the US (Akbulut and Linit, 1999b). Thus, the time of colonization of new host trees and the quality of twigs during adult feeding may play important roles in the reproductive success and population dynamics of *M. galloprovincialis*.

References

- Akbulut, S. 1998. Effect of *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae) Fourth Stage Dispersal Juveniles and Log Seasonality on Life Processes of *Monochamus carolinensis* (Coleoptera: Cerambycidae). PhD dissertation. University of Missouri-Columbia, p. 146.
- Akbulut, S. and M.J. Linit. 1999a. Reproductive potential of *Monochamus carolinensis* (Coleoptera: Cerambycidae) with respect to pinewood nematode phoresis. *Environ. Entomol.* 28: 407-411.
- Akbulut, S. and M.J. Linit. 1999b. Seasonal effect on reproductive performance of *Monochamus carolinensis* (Coleoptera: Cerambycidae) reared in pine logs. *J. Economic Entomol.* 92: 631-637.
- Baker, W.L. 1972. Eastern Forest Insects. USDA For. Serv. Misc. Pub., USA.
- Birch, L.C. 1948. The intrinsic rate of natural increase an insect population. *J. Animal Ecol.* 17: 15-26.
- Çanakçıoğlu, H. and T. Mol. 1998. Orman Entomolojisi: Zararlı ve Yararlı Böcekler. İstanbul Üniversitesi Yayını.
- Carroll, A.L. and D.T. Quiring. 1992. Sucrose ingestion by *Zeiraphera canadensis* Mut. and Free. (Lepidoptera: Tortricidae) increases fecundity and lifetime fecundity, but not oviposition rate. *Can. Entomol.* 124: 335-340.
- Cheng, H.H. 1972. Oviposition and longevity of the dark-sided cutworm, *Euxoa messoria* (Lepidoptera: Noctuidae) in the laboratory. *Can. Entomol.* 104: 919-925.
- Cowling, E.G. and W. Merrill. 1966. Nitrogen in wood and its role in wood deterioration. *Can. J. Bot.* 44: 1539-1554.
- Dixon, A.F.G. 1971. The life cycle and host preferences of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) and their bearing on the theories of host alternation in aphids. *Ann. Appl. Biol.* 68: 133-139.
- Fischer, C. and W. Höll. 1992. Food reserves of Scots pine (*Pinus sylvestris* L.). II. Seasonal changes and radial distribution of carbohydrate and fat reserves in pine wood. *Trees.* 6: 147-155.
- Francardi, V. and F. Pennacchio. 1996. Note sulla bioecologia di *Monochamus galloprovincialis galloprovincialis* (Olivier) in Toscana e in Liguria (Coleoptera: Cerambycidae). *Redia.* 2: 153-169.
- Gruber, K. and A.F.G. Dixon. 1988. The effect of nutrient stress on development and reproduction in an aphid. *Entomol. Exp. Appl.* 47: 23-30.
- Haack, R.A. and D.M. Benjamin. 1980. Influence of time of summer felling of infested oak trees on larval development and adult emergence of the two lined chestnut borer, *Agrilus bilineatus*. *Univ. Wisc. For. Res. Notes.* 236.
- Haack, R.A. and F. Slansky Jr. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera and Hymenoptera. In: *Nutritional Ecology of Insects, Spiders and Related Invertebrates* (Eds.: F. Slansky Jr. and J.G. Rodriguez), Wiley, New York, pp. 449-486.
- Hellrigl, K.G. 1971. Die bionomie der Europäischen *Monochamus*-arten (Coleopt., Cerambycidae) und ihre bedeutung für die forst- und holzwirtschaft. *Redia.* 52: 367-509.
- Hepting, G.H. 1945. Reserve food storage in shortleaf pine in relation to little-leaf disease. *Phytopathol.* 35: 106-120.
- Hosking, G.P. and J.A. Hutcheson. 1979. Nutritional basis for feeding zone preference of *Arhopalus ferus* (Coleoptera: Cerambycidae). *New Zealand J. For. Sci.* 9: 185-192.
- Hough, J.A. and D. Pimentel. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. *Environ. Entomol.* 7: 97-102.
- Humphry, S.J. and M.J. Linit. 1989. Effect of pinewood nematode density on tethered flight of *Monochamus carolinensis* (Coleoptera: Cerambycidae). *Environ. Entomol.* 18: 670-673.
- Ikeda, T. K. Oda, A. Yamane and N. Enda. 1980a. Volatiles from pine logs as the attractant for the Japanese pine sawyer *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). *J. Jpn. For. Soc.* 62: 150-152.
- Ikeda, T. N. Enda, A. Yamane, K. Oda and T. Toyoda. 1980b. Attractants for the Japanese pine sawyer, *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). *Appl. Entomol. Zool.* 15: 358-361.

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- Leather, S.R. 1984. The effect of adult feeding on the fecundity, weight loss, and survival of the pine beauty moth, *Panolis flammea* (D and S). *Oecologia* (Berlin). 65: 70-74.
- Leather, S.R. 1995. Factor affecting fecundity, fertility, oviposition, and larviposition in insects. In: *Insect Reproduction* (Eds.: by S.R. Leather and J. Hardie). CRC, Boca Raton, FL, pp. 143-174.
- Linit, M.J. 1988. Nematode-vector relationships in the pine wilt disease system. *J. Nematol.* 20: 227-235.
- Mota, M., H. Braasch, M.A. Bravo, A.C. Penas, W. Burgermeister, K. Metge and E. Sousa. 1999. First report of *Bursaphelenchus xylophilus* in Portugal and Europe. *Nematology.* 1: 727-734.
- Nakayama, Y., S. Jikumar and K. Togashi. 1998. Reproductive traits and diel activity of adult *Monochamus saltuarius* (Coleoptera: Cerambycidae) at two different temperatures. *J. For. Res.* 3: 61-65.
- Naves, P., E.D. Sousa and J.A. Quartau. 2006a. Reproductive traits of *Monochamus galloprovincialis* (Coleoptera: Cerambycidae) under laboratory conditions. *Bull. Entomol. Res.* 96: 289-294.
- Naves, P.M., E.M. Sousa and J.A. Quartau. 2006b. Feeding and oviposition preferences of *Monochamus galloprovincialis* for certain conifers under laboratory conditions. *Entomol. Exp. Appl.* 120: 99-104.
- Naves, P.M., S. Camacho, E.M. Sousa and J.A. Quartau. 2007. Transmission of the pinewood nematode *Bursaphelenchus xylophilus* through feeding activity of *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). *J. Appl. Entomol.* 131: 21-25.
- Nickle, W.R. 1970. A taxonomic review of the genera of the Aphelenchoidea (Fuchs, 1937) Thorne, 1949 (Nematoda: Tylenchidae). *J. Nematol.* 2: 375-392.
- Özdikmen, H., Y. Özdemir and S. Turgut. (2005). Longhorned beetles collection of the Nazife Tuatay Plant Protection Museum, Ankara, Turkey (Coleoptera, Cerambycidae). *J. Entomol. Res. Soc.* 7: 1-33.
- Pajeras, J.A., F. Ibeas, J.J. Diez and D. Gallego. 2004. Attractive responses by *Monochamus galloprovincialis* (Coleoptera: Cerambycidae) to host and bark beetle semiochemicals. *J. Appl. Entomol.* 128: 633-638.
- Pershing, J.C. and M.J. Linit. 1986. Biology of *Monochamus carolinensis* (Coleoptera: Cerambycidae) on Scotch pine in Missouri. *J. Kansas Entomol. Soc.* 59: 706-711.
- SAS Institute. 1999-2000. The SAS System, version 8.1. SAS Institute Inc., Cary, North Carolina.
- Sousa, E., M. Bravo, J. Pires, P. Naves, A. Penas, L. Bonifacio and M. Mota. 2001. *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae) associated with *Monochamus galloprovincialis* (Coleoptera: Cerambycidae) in Portugal. *Nematology.* 3: 89-91.
- Steiner, G. and E.M. Buhner. 1934. *Aphelenchoidea xylophilus*, n. sp., a nematode associated with blue-stain and other fungi in timber. *J. Agric. Res.* 33: 159-164.
- Stern, V.M. and R.F. Smith. 1960. Factors affecting egg production and ovipositioning populations of *Colias philodice eurytheme* Boisduval (Lepidoptera: Pieridae). *Hilgardia.* 29: 411-454.
- Togashi, K. 1997. Life time fecundity and body size of *Monochamus alternatus* (Coleoptera: Cerambycidae) at a constant temperature. *Jpn. J. Entomol.* 65: 458-470.
- Togashi, K. and H. Magira. 1981. Age specific survival rate and fecundity of the adult Japanese pine sawyer, *Monochamus alternatus* Hope (Coleoptera: Cerambycidae), at different emergence times. *Appl. Entomol. Zool.* 16: 351-361.
- Wainhouse, D., R. Boswell and R. Ashburner. 2004. Nutrition feeding and reproductive development in adult pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). *Bull. Entomol. Res.* 94: 81-87.
- Zhang, X. and M.J. Linit. 1998. Comparison of oviposition and longevity of *Monochamus alternatus* and *Monochamus carolinensis* (Coleoptera: Cerambycidae) under laboratory conditions. *Environ. Entomol.* 27: 885-891.1.