

## Effects of temperature on the host preference of pine processionary caterpillar *Thaumetopoea wilkinsoni* Tams, 1924 (Lepidoptera: Notodontidae)

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**Abstract:** The work reported here analyzes the effects of temperature on host consumption and preference of eastern pine processionary caterpillar *Thaumetopoea wilkinsoni* (Lepidoptera: Notodontidae). Nest censuses were taken in the field and food choice tests were conducted in the laboratory. Two pine species (*Pinus nigra* and *P. brutia*) were considered. Caterpillars hatched on both pine species were collected and included in experiments that were conducted under 4 different temperature regimes (15, 20, 25, and 30 °C). Needles of both pine species were offered as food. Results showed that increasing the temperature caused an increase in the feeding amount of the caterpillars and also a blurring effect on preference. Early instar diet was found to have effects on late instar diet.

**Key words:** *Thaumetopoea*, pine processionary caterpillar, food preference, effects of temperature

### Sıcaklığın çam kese böceği tırtılı *Thaumetopoea wilkinsoni* Tams, 1924 (Lepidoptera: Notodontidae)'nin besin tercihi üzerindeki etkileri

**Özet:** Burada özetlenen çalışmada doğu çam kese böceği *Thaumetopoea wilkinsoni*'nin (Lepidoptera: Notodontidae) besin tüketimi ve tercihinin sıcaklığın etkisi araştırılmıştır. Arazide kese sayımları ve laboratuarda besin seçme deneyleri yapılmıştır. İki çam türü (*Pinus nigra* ve *P. brutia*) ele alınmıştır. Her iki ağaç türünde de yumurtadan çıkan tırtıllar toplanmış ve dört farklı sıcaklık koşulunda (15, 20, 25, 30 °C) yürütülen deneylere dahil edilmişlerdir. Tırtıllara besin olarak her iki ağaç türünden toplanmış yapraklar verilmiştir. Sonuçlar sıcaklık arttıkça tırtılların beslenme miktarının da arttığını ve aynı zamanda besin tercihinde bir belirsizleşme olduğunu göstermiştir. Erken evrelerde alınan besin tipinin ileri evrelerdeki besin tercihinin etkileyebildiği görülmüştür.

**Anahtar sözcükler:** *Thaumetopoea*, çam kese böceği, besin tercihi, sıcaklığın etkileri

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## Introduction

Temperature and food preference are among the most important factors affecting the distribution of organisms (Strong et al., 1984; Parmesan et al., 1999; Hughes, 2000; Crozier, 2002; Root et al., 2003). The joint effects of these 2 factors have an increased importance when the subject under focus is the distribution of oligophagous insects. In comparison to monophagous insects, oligophagous insects are known to have the ability to quickly find new potential hosts in new environments when temperature changes push them to shift their distribution. Therefore, these species can invade and establish themselves in new habitats fairly easily (Stastny et al., 2006, for pine processionary moth), a problem that has been termed as “invasion of unexpected hosts.”

There are numerous studies showing the effects of temperature change on herbivorous insects, either directly by affecting insect physiology and behavior, or indirectly by changing host plant abundance and quality (Ohgushi and Sawada, 1997; Harrington et al., 1999; Ayres and Lombardero, 2000; Bale et al., 2002; Johns and Hughes, 2002; Hódar et al., 2003; Hódar and Zamora, 2004; Andrew and Hughes, 2007). These kinds of studies are rising in importance as our understanding of the effects of climatic change increase. According to climatic change studies, global average surface temperatures have increased by  $0.6 \pm 0.2$  °C since the late 19th century, mostly due to anthropogenic factors. Moreover, climatic models predict temperatures to rise by 1.4-5.8 °C by 2100 (IPCC, 2001). In this context, it becomes important to evaluate the relationship between temperature change and food preference/consumption for pestiferous oligophagous insects.

Climatic change has not been the only anthropogenic factor affecting ecosystems during the last century. Mediterranean forests, for instance, have also suffered from monospecific planting (Masutti and Battisti, 1990; Driesche and Bellows, 1996; Hódar et al., 2002), since single species plantations can be more susceptible to pest invasions and disease outbreaks (Ciesla and Donaubaer, 1994). In order to reduce this risk, clustered and heterogeneous afforestation practices are recommended (Gadgil and Bain, 1999; Schönenberger, 2001). However, successful afforestation is not easy to accomplish,

since the complex nature of plant-herbivore interactions presents difficulties in establishing sustainable forestation strategies. The core of this interaction, namely “host use patterns,” is influenced not only by spatial variation in host plant abundance but also by host plant quality and local adaptations of insects to host populations (Kuussaari et al., 2000 and references therein). Therefore, detailed surveys of host use patterns of local insect populations are crucial for successful afforestation practices. Understanding the relationship between increasing temperature and the food preference of herbivorous insects will make an important contribution to our understanding of the highly complex nature of plant-herbivore interactions. The pine processionary caterpillar (PPC), *Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775), and its eastern vicariant *T. wilkinsoni* Tams, 1924 (Lepidoptera: Notodontidae) are 2 of the most important defoliators of both natural and man-made pinewoods around the Mediterranean Sea (Démolin, 1969; Avtzis, 1986; Battisti, 1988; Breuer and Devkota, 1990; Halperin, 1990; Avci, 2000). However, our current knowledge about the relationship between temperature and food preference of this oligophagous defoliator is poor. Such information is vitally needed for establishing reliable predictions of the future distribution of pine processionary moths in the Mediterranean basin, where the mean temperatures are expected to increase (Menzel et al., 2006). Such predictions will play an important role in restructuring control strategies under changing climatic conditions.

The work reported here examines the host preference and host use of PPCs in terms of 2 pine species (*Pinus nigra* Arnold, 1785 and *P. brutia* Tenore, 1811) under natural and laboratory conditions. Specifically, we try to deduce the effect of temperature on the feeding amount and preference of PPCs.

## Materials and methods

### Sampling and study area

Field studies and samplings were conducted mainly in the seed stands of the Forestry Service in the Asar district of Antalya, Turkey (coastal alluvial plateau on the side of the Taurus Mountains; 37°01'265"N, 30°43'632"E; 253-257 m a.s.l.). This plantation

includes separated patches of *Pinus nigra* and *P. brutia*. In addition, some extra caterpillars were collected from the Dağbeli district of Antalya (Middle Taurus; 37°13'474"N, 30°33'354"E; 850-900 m a.s.l.) for stock purposes. The only host tree species that inhabits Dağbeli is *P. brutia*. Autochthonous patches of this species are similar in age, height, and density because of the routine management practices of the Forestry Service.

The climate in the zone is coastal Mediterranean, with temperate and rainy winters and hot and dry summers. The higher altitudes have a colder climate, with frequent snows in winter. In Asar, the mean minimum temperature in the coldest month (February) is -4 °C, the mean maximum in the warmest month (July) is 45 °C, and the annual average temperature is 18.1 °C. Rainfall is concentrated mainly in the autumn and spring, with an annual rainfall of 1130.2 mm and a relative humidity of 63%. In Dağbeli, the mean minimum temperature in the coldest month (March) is -11.4 °C, the mean maximum in the warmest month (July) is 39.4 °C, and the annual average temperature is 13.5 °C. Annual rainfall is 380.5 mm and relative humidity is 58% (data from the meteorological stations in Korkuteli district and the city of Antalya, averaged for the last 30 years).

### Organisms studied

PPCs attack plants of the genus *Pinus*. Depending on the host species, larval development varies widely. Adults of this univoltine moth fly to oviposit in summer or early autumn according to prevailing environmental conditions (Démolin, 1969; Hódar et al., 2002 and references therein). In the study area, the timing of oviposition is generally around mid-August. Strongly gregarious crawling larvae hatch in mid-September, almost 1 month after oviposition, and go through 5 instars in collectively built silk nests during autumn and winter before pupation. Larvae migrate from the silk nests situated in the treetops to the ground for pupation. The procession to the ground for pupation is completed in mid-May. The pupal stage takes place underground, usually near the host tree, and lasts for at least 3 months. However, the pupation period is highly variable and may last for several years, depending on resource availability and climatic conditions.

### Time schedule

Fieldwork was carried out between May 2004 and May 2005, a study period that allowed us to observe the population in 2 consecutive years. Laboratory studies were carried out between 2004 and 2005.

### Field observations

Survival capacities of PPCs on different hosts were evaluated by nest censuses conducted in Asar, where monospecific plantations of *P. nigra* and *P. brutia* coexist. The censuses were conducted in May 2004 and February 2005, when 1200 trees were chosen at random from each monospecific plantation, and the number of nests found on each tree was recorded in the 2 consecutive years. Differences between nest counts were evaluated by means of the nonparametric Kruskal-Wallis test (STATISTICA version 7.0), since the data violated the assumption of normality.

### Sampling and rearing

Larval sampling was conducted by collecting whole nests during the day while larvae were at rest within the nests. Twigs with nests were cut using branch scissors. Some green leaves on these twigs were kept to prevent larval starvation during transportation. Collected nests were transported to the laboratory in 50-L isolated boxes. Similar boxes were used to transport the shoots of pines that were previously not attacked or defoliated by PPCs. The needles of these shoots were later used in larval rearing and preference experiments.

Collected nests were fixed to 20-cm-long stakes and established in glass boxes of 30 × 30 × 30 cm in size. The stakes allowed proper ventilation of the boxes by holding the nests in the air and thus preventing fungal infection. In addition, the box surfaces on which the box covers sat were covered with cotton strips to maintain ventilation and stop runaways.

*Pinus brutia* needles from Asar and *P. nigra* needles from Ankara (Beytepe Campus) were collected on twigs as larval food and put into 5-L plastic containers filled with water. These containers were exposed to daily insolation in the laboratory garden to keep the needles fresh.

## Laboratory experiments

The effect of temperature on dietary preferences and food consumption was evaluated using the following experiment: 10 petri dishes, each containing 3 larvae, were placed in climatic chambers at 15, 20, 25, and 30 °C. Each petri dish contained both *P. nigra* and *P. brutia* needles, which were offered as food. To control for the effects of the host tree of origin, 2 replicate groups were set up. Replicate group 1 contained larvae collected from *P. brutia* and replicate group 2 contained larvae collected from *P. nigra*. Second to third instar and fourth to fifth instar larvae were used in the experiments. Three larvae per dish were used to maintain maximum feeding with minimum larvae as recommended by Hóðar et al. (2002). Offered needles were weighed before placing them in the dishes as food. The larvae were monitored for 10 days. Food consumption and preference was determined by weighing the needles each day and calculating the daily weight loss, which is a good indicator of food consumption. In addition, a control group consisting of only pine needles was placed in each temperature treatment and those needles were also weighed on a daily basis, enabling us to take into account weight loss due to evaporation (Figure 1).

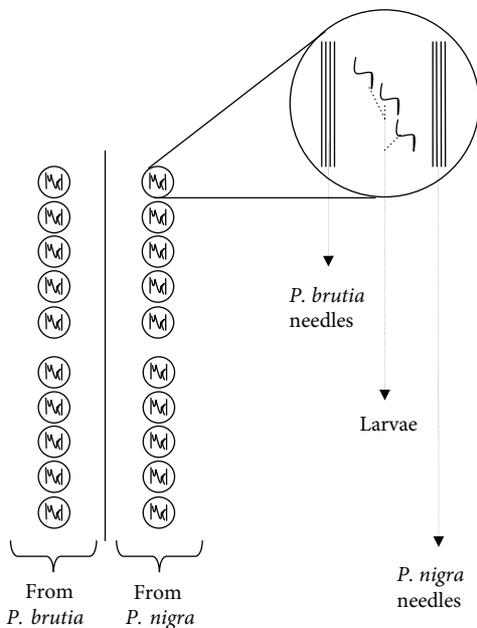


Figure 1. Schematic illustration of dietary experiments.

All of the rearing and experiments were conducted under a 12:12 photoperiod and 60% relative humidity.

The effects of temperature, food, and time (days) on food consumption were analyzed using a mixed-model ANOVA design in which temperature was entered as a fixed effect, and food and time were treated as random variables. All analyses were conducted using STATISTICA version 7.0.

We presented the caterpillars with the 2 food sources simultaneously in order to see which food source they would consume the most of if both were equally available. As in the above experiment, we measured the daily consumption of *P. nigra* and *P. brutia* needles and compared them in order to evaluate which had been consumed the most. However, when both food sources are presented simultaneously, we can no longer treat the food source as a fixed factor since we do not know in advance which food source the caterpillars will consume. Therefore, the factor of food source in our experiments was not treated as a fixed factor, but rather as a random factor, in order to take into account our prior uncertainty of which food source would be consumed. In addition, food consumption and food choice varied from day to day and also between temperature regimes. Therefore, to take into account all of these factors, we conducted a mixed-model ANOVA, where the amount of *P. brutia* and *P. nigra* consumed was taken as the dependant variable, temperature regime was treated as a fixed factor, and “food source” and “day” were treated as random factors. We also checked for the interactions between food source × temperature and food source × day in order to evaluate whether the choice of food (i.e. the amounts of consumed *P. nigra* and *P. brutia*) changed daily or between temperature regimes.

## Results

### Field censuses

The results of the nest censuses showed a clear difference in the number of nests found within *P. brutia* and *P. nigra* stands in the seed plantations of Asar. In both years, the mean number of nests found per tree in *P. brutia* stands was significantly higher than in *P. nigra* stands ( $H(1, N = 2400) = 47.12815$ ;  $P = 0.000$ ). Yearly differences per tree species were also statistically significant (for *P. brutia*  $H(1, N = 1200)$

= 536.4114;  $P = 0.000$ ; for *P. nigra*  $H(1, N = 1200) = 61.58960$ ;  $P = 0.000$ ). The mean number of nests per tree dropped from 6.07 to 0.62 between 2004 and 2005 in the *P. brutia* stand, but increased slightly in *P. nigra* from 0.8 in 2004 to 1.7 in 2005 (Figure 2).

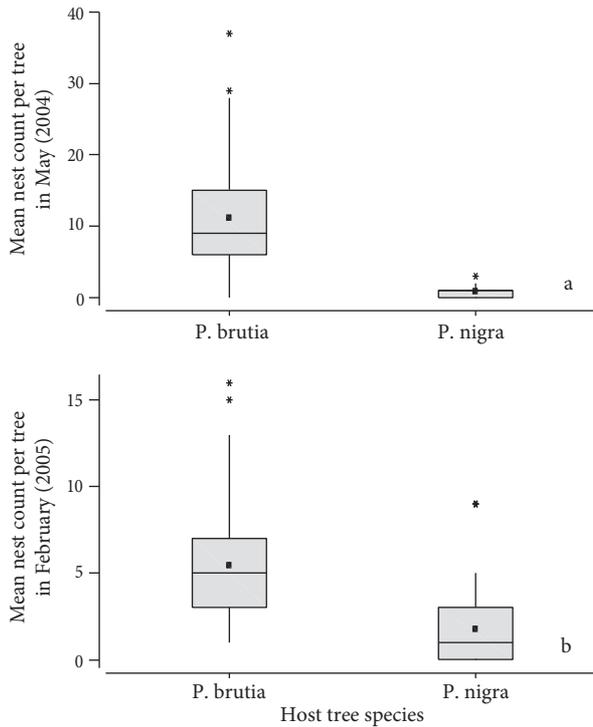


Figure 2. Comparison of nest quantities counted on *P. brutia* and *P. nigra* in a) May 2004 and b) May 2005.

### Laboratory experiments

Mixed-model ANOVA results of food consumption for larvae collected from *P. nigra* and *P. brutia* are given in Tables 1 and 2, respectively. According to our results, temperature and day had a significant effect on larval food consumption in larvae collected from *P. brutia* (Table 1), while only the effect of days was significant in larvae collected from *P. nigra* (Table 2). In larvae collected from *P. brutia*, overall food consumption increased with increasing temperatures, although a drop in food consumption was recorded at 25 °C (Figures 3a and 3b). However, the control thermometer in the 25 °C chamber recorded a fluctuation between 25 and 30 °C, which means that this chamber failed to hold a constant temperature. In larvae collected from *P. nigra*, food consumption rates varied slightly between temperature regimes, but no apparent trend was observed (Figures 4a and 4b).

In both replicate groups, overall consumption of *P. nigra* needles was higher than that of *P. brutia* needles for all temperature regimes (Figures 3a and 4a). However, the effect of food source on larval consumption was statistically significant only in larvae collected from *P. nigra* (Table 2). Larvae collected from *P. nigra* had a clear preference for *P. nigra* needles over *P. brutia* needles, but no statistically significant trend was observed for larvae collected from *P. brutia* (Figures 3a and 4a).

Table 1. Mixed-model ANOVA detailing the effects of temperature, day, and food source on the consumption rate of *T. wilkinsoni* larvae collected from *P. brutia*.

	Effect (F/R)	SS	DF	MS	Den. Syn. Error DF	Den. Syn. Error MS	F	P
<b>Intercept</b>	Fixed	3844.150	1	3844.150	3.4273	6.729761	571.2164	0.000062
<b>Temp.</b>	Fixed	16.508	3	5.503	3.0000	0.085461	64.3870	0.003196
<b>Day</b>	Random	42.784	9	4.754	9.0000	0.849445	5.5964	0.008593
<b>Food</b>	Random	3.359	1	3.359	3.5698	0.469745	7.1508	0.062662
<b>Temp. × Food</b>	Random	0.256	3	0.085	474.0000	0.463819	0.1843	0.907097
<b>Food × Day</b>	Random	7.645	9	0.849	474.0000	0.463819	1.8314	0.060460
<b>Error</b>		219.850	474	0.464				

Table 2. Mixed-model ANOVA detailing the effects of temperature, day, and food source on the consumption rate of *T. wilkinsoni* larvae collected from *P. nigra*.

	Effect (F/R)	SS	DF	MS	Den. Syn. Error DF	Den. Syn. Error MS	F	P
<b>Intercept</b>	Fixed	7262.281	1	7262.281	1.5344	70.76145	102.6305	0.021774
<b>Temp.</b>	Fixed	13.632	3	4.544	3.0000	1.05890	4.2913	0.131280
<b>Day</b>	Random	132.646	9	14.738	9.0000	0.67394	21.8691	0.000045
<b>Food</b>	Random	56.920	1	56.920	1.2541	0.72412	78.6057	0.043896
<b>Temp. × Food</b>	Random	3.177	3	1.059	566.0000	1.01373	1.0446	0.372338
<b>Food × Day</b>	Random	6.065	9	0.674	566.0000	1.01373	0.6648	0.741055
<b>Error</b>		573.769	566	1.014				

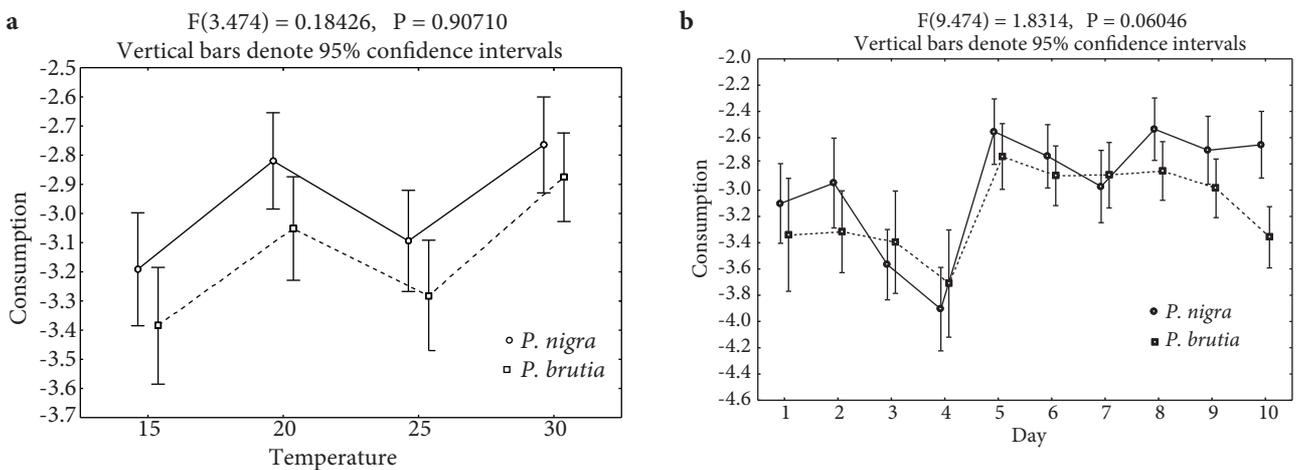


Figure 3. Consumption by *T. wilkinsoni* collected from *P. brutia*: a) least square means for consumption of *P. nigra* and *P. brutia* at different temperatures, b) least square daily means for consumption of *P. nigra* and *P. brutia* with consumption rates, in g/day, given as ln values.

The effect of temperature on food preference (as deduced by the temperature × food interaction) was not significant in either replicate group (Tables 1 and 2); however, a weak interaction was observed in larvae collected from *P. nigra*, where the difference between *P. nigra* and *P. brutia* consumption dropped significantly at higher temperatures (Figure 4a). No such interaction was observed in larvae collected from *P. brutia* (Figure 3a).

No significant interaction of temperature with days was observed in the food consumption of the

larvae in either replicate group (Tables 1 and 2), although food consumption varied from day to day (Figures 3b and 4b).

## Discussion

The use of 2-choice tests with 2 different plant species yields results that can develop in several different ways depending on whether larvae change their behavior to consume 1 or the other plant species, or both (de Boer, 2004). The leading process that produces

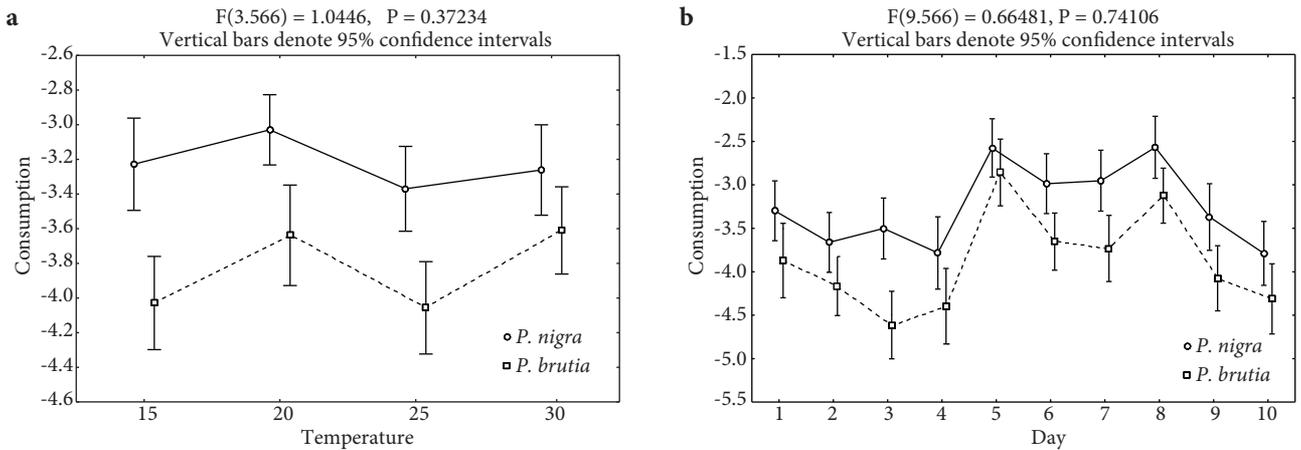


Figure 4. Consumption by *T. wilkinsoni* collected from *P. nigra*: a) least square means for consumption of *P. nigra* and *P. brutia* at different temperatures, b) least square daily means for consumption of *P. nigra* and *P. brutia* with consumption rates, in g/day, given as ln values.

this change can be diet-induced food preference (Bernays and Weiss, 1996; Bernays, 1999), which can be described as a change in food preference in favor of food that has been previously eaten exclusively for 24 h or more (Jermy et al., 1968). To observe this effect, food preference experiments were repeated for larvae that fed on different host trees during early instar stages. In our experiments, *P. nigra* needles were consistently preferred over *P. brutia* needles irrespective of the host tree of origin (i.e. whether the larvae came from *P. brutia* or *P. nigra*). However, there were still noticeable differences between food preference and consumption of larvae collected from *P. nigra* and *P. brutia*. The larvae that were collected from *P. nigra* showed a higher and statistically significant preference for *P. nigra* needles than larvae collected from *P. brutia*. Similarly, larvae from *P. brutia* showed relatively lower *P. nigra* preference (Figures 3 and 4). Thus, there is some support for the hypothesis that a diet-induced food preference exists in PPCs.

Numerous factors could have contributed to the higher consumption of *P. nigra* needles over *P. brutia* needles in both replicate groups. Variation in toughness between *P. nigra* and *P. brutia* needles, relative proportion, and types of secondary metabolites within *P. nigra* and *P. brutia* needles can all affect consumption rates and preferences of larvae.

However, the *P. nigra* needles that were offered to the larvae in our study were collected from the campus forest of Hacettepe University, and the geographical location of the campus (Ankara, middle Anatolia) is completely free of pine processionary moths (PPMs). On the other hand, *P. brutia* needles were collected from the same area in which PPCs were collected. It is well known that induced resistance can develop in plants under herbivory pressure (Battisti, 1988; Hódar et al. 2004 and references therein). Thus, it is not surprising that *P. nigra* needles that have grown in a herbivory-free environment are preferred over *P. brutia* needles that have grown and evolved under heavy herbivory pressure and presumably developed a potent resistance against herbivory. However, to understand the exact mechanisms underlying the preference toward *P. nigra* needles in this study, detailed analysis and information on the chemical and physical properties of *P. brutia* and *P. nigra* needles are needed.

The direct effects of temperature on insects are likely to differ among species, depending on their life-history strategies in their current environment and their overall ability to adapt to changing conditions (Bale et al., 2002). Two conclusions can be drawn from this study about the effects of temperature on food consumption and preference (data from the 25 °C chamber were ignored, because we could not

maintain a constant temperature in this chamber, but we did not remove this chamber's results). First, food consumption showed a steady increase with increasing temperature in experiments conducted with larvae collected from *P. brutia*. Interestingly, this trend was not observed in larvae collected from *P. nigra* stands, which stayed relatively constant between temperature regimes. The increased trend observed in larvae collected from *P. brutia* stands is not surprising, since feeding amount, digestion, and growth rate are proportional to temperature (Casey et al., 1988; Gotthard et al., 2000). These results could indicate, at least for PPCs resident on *P. brutia* stands, that increasing temperature can produce new optimums. A higher consumption rate with increasing temperature can result in vertical and horizontal range expansions, such as those recorded by Hódar et al. (2004), Hoch et al. (2005), Roques et al. (2005), and Stastny et al. (2006). These results also have important implications for future PPM management strategies, which will have to deal with difficulties brought on by higher resource consumption rates. An increase in food consumption with an increasing temperature usually results in higher rates of development (for various examples in different taxa see, e.g., Kinne, 1970; Mackey, 1977; Watts et al., 1982; Johnson et al., 1992; Otterlei et al., 1999; Tun-Lin et al., 2000; Harrington et al., 2001) and an earlier time of descent underground for pupation. This reduction in developmental time and a quicker life-cycle will mean that larvae are less exposed to natural enemies, which might result in an increase in proportional damage to trees. Therefore, changes in temperature will not only affect the total area infested by PPCs but also the severity of damage caused by these pests.

Secondly, although temperature did not have a significant effect on food consumption rates of larvae collected from *P. nigra* stands, it did have a noticeable effect on food preference. In feeding trials conducted under a temperature regime of 30 °C, consumption rates of *P. brutia* increased significantly in larvae collected from *P. nigra* stands, and a decrease in the difference between *P. brutia* and *P. nigra* needle consumption was observed. This result leads us to assume that an increase in temperature can result, at least for the PPM populations in the study area, in a decrease in host selectivity, and thus the less-

preferred pine species could face an increased risk of infestation and damage. It can also be speculated from this result that PPMs can expand their range to secondary less-preferred hosts under changing climatic conditions. However, more detailed studies on the life history strategies of PPMs are needed to gather further evidence for this speculation.

The occurrence of PPCs in any monospecific plantation is the direct result of female preference for oviposition. Larval preference does not contribute to the existence of PPCs in different hosts, but larval survival does. If we evaluate nest censuses as an index of larval survival, it is possible to say that larval survival is higher in *P. brutia* stands than in *P. nigra* stands. When this inference is evaluated together with results showing an increase in *P. brutia* consumption with increasing temperature, we can say that warming due to climatic change can amplify the harshness of the interaction between PPCs and *P. brutia*, the main pine species in the study area.

To conclude, this study points out that increasing temperature can, in some situations, cause shifts in food preference patterns of PPMs, and the direct effects of increasing temperature on PPM populations can result in increased damage to the hosts. However, the complex nature of ecosystems can alter the direct effects of such environmental factors, so to faithfully predict how temperature changes can affect PPM populations, more detailed data on the natural enemies and life-history parameters (fecundity, survival, etc.) of PPMs are needed. Such knowledge is of vital importance if we wish to establish effective and sustainable management practices for PPM infestations.

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## References

- Andrew, N.R. and Hughes, L. 2007. Potential host colonization by insect herbivores in a warmer climate: a transplant experiment. *Global Change Biology* 13: 1539-1549.
- Avcı, M. 2000. Investigation on structure of egg-batches, parasitism and egg laying habits of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lepidoptera: Thaumetopoeidae) in various regions of Turkey. *Turk. J. Entomol.* 24: 167-178.
- Avtzis, N. 1986. Development of *Thaumetopoea pityocampa* (Lepidoptera: Thaumetopoeidae) in relation to food utilization. *Forest Ecol. Man.* 15: 65-68.
- Ayres, M.P. and Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Total Environ.* 262: 263-286.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. and Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperatures on insect herbivores. *Glob. Change Biol.* 8: 1-16.
- Battisti, A. 1988. Host-plant relationships and population dynamics of the pine processionary caterpillar *Thaumetopoea pityocampa* (Denis & Schiffermüller). *J. Appl. Entomol.* 105: 393-402.
- Bernays, E.A. 1999. Plasticity and the problem of choice in food selection. *Ann. Entomol. Soc. Am.* 92: 944-958.
- Bernays, E.A. and Weiss, M.R. 1996. Induced food preferences in caterpillars: the need to identify mechanisms. *Entomol. Experiment. Appl.* 78: 1-8.
- Breuer, M. and Devkota, B. 1990. Control of *Thaumetopoea pityocampa* (Den. & Schiff.) by extracts of *Melia azedarach* L. (Meliaceae). *J. Appl. Entomol.* 110(2): 128-135.
- Casey, T.M., Joos, B., Fitzgerald, T.D., Yurlona, M. and Young, P. 1988. Synchronized group feeding, thermoregulation, and growth of eastern tent caterpillars in relation to microclimate. *Physiol. Zool.* 61: 372-377.
- Ciesla, W.M. and Donaubaue, E. 1994. Decline and Dieback of Trees and Forests: A Global Overview, FAO Forestry Paper 120. FAO, Rome.
- Crozier, L. 2002. Climate change and its effect on species range boundaries: a case study of the Sachem Skipper butterfly, *Atalopedes campestris*. In: *Wildlife Responses to Climate Change* (Eds. T.L. Root and S.H. Schneider), Island Press, Washington, DC, pp. 57-91.
- De Boer, G. 2004. Temporal and developmental aspects of diet-induced food preferences in larvae of the tobacco hornworm, *Manduca sexta*. *Entomol. Experiment. Appl.* 113: 197-204.
- Démolin, G. 1969. Comportement des adultes de *Thaumetopoea pityocampa* Schiff. Dispersion spatiale, importance écologique. *Ann. Sci. Forest.* 26: 81-102.
- Driesche, R.G. and Bellows, T.S. 1996. *Biological Control*. Chapman & Hall, New York.
- Gadgil, P.D. and Bain, J. 1999. Vulnerability of planted forests to biotic and abiotic disturbances. *New Forests* 17: 227-238.
- Gotthard, K., Nylin, S. and Wiklund, C. 2000. Individual state controls temperature dependence in a butterfly (*Lasiommata maera*). *Proc. Royal Soc. London B* 267: 589-593.
- Halperin, J. 1990. Life history of *Thaumetopoea* spp. (Lepidoptera: Thaumetopoeidae) in Israel. *J. Appl. Entomol.* 110(1): 1-6.
- Harrington, R., Fleming, R.A. and Woiwod, I.P. 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? *Agri. Forest Entomol.* 3: 233-240.
- Harrington, R., Woiwod, I. and Sparks, T. 1999. Climate change and trophic interactions. *Trends in Ecology and Evolution* 14: 146-150.
- Hoch, G., Netherer, S., Pennerstorfer, J., Baier, P., Battisti, A. and Schopf, A. 2005. Range expansion of the pine processionary moth in Europe II: Activity and survival of *Thaumetopoea pityocampa* (Lep.: Thaumetopoeidae) during the winter months in an alpine valley. In: *Proceedings of the 16th U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and Other Invasive Species*, GTR-NE-337, p. 42.
- Hódar, J.A., Castro, J. and Zamora, R. 2003. Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biol. Cons.* 110: 123-129.
- Hódar, J.A., Zamora, R. and Castro, J. 2002. Host utilisation by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species. *Ecol. Entomol.* 27: 292-301.
- Hódar, J.A., Zamora, R., Castro, J. and Baraza, E. 2004. Feast and famine: previous defoliation limiting survival of pine processionary caterpillar *Thaumetopoea pityocampa* in Scots pine *Pinus sylvestris*. *Ac. Oecol.* 26: 203-210.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Tr. Ecol. Evol.* 15: 56-61.
- Intergovernmental Panel on Climate Change. 2001, Third Assessment Report. IPCC, Geneva. Available at [http://www.grida.no/publications/other/ipcc\\_tar/](http://www.grida.no/publications/other/ipcc_tar/).
- Jermy, T., Hanson, F.E. and Dethier, V.G. 1968. Induction of specific food preference in lepidopterous larvae. *Entomol. Experiment. Appl.* 11: 211-230.
- Johns, C.V. and Hughes, A. 2002. Interactive effects of elevated CO<sub>2</sub> and temperature on the leaf-miner *Dialectica scariella* Zeller (Lepidoptera: Gracillariidae) in Paterson's Curse, *Echium plantagineum* (Boraginaceae). *Glob. Change Biol.* 8: 142-152.
- Johnson, J.A., Wofford, P.L. and Whitehand, L.C. 1992. Effect of diet and temperature on development rates, survival, and reproduction of the Indianmeal moth (Lepidoptera: Pyralidae). *J. Econ. Entomol.* 85(2): 561-566.

- Kinne, O. 1970. Environmental factors: temperature. In: Marine Ecology, Vol. 1 (Ed. O. Kinne), Wiley-Interscience, London, pp. 321-616.
- Kuussaari, M., Singer, M. and Hanski, I. 2000. Local specialization and landscape-level influence on host use in an herbivorous insect. *Ecology* 81(8): 2177-2187.
- Mackey, A.P. 1977. Growth and development of larval Chironomidae. *Oikos* 28: 270-275.
- Masutti, L. and Battisti, A. 1990. *Thaumetopoea pityocampa* (Den. & Schiff.) in Italy. Bionomics and perspectives of integrated control. *J. Appl. Entomol.* 110(3): 229-234.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Viet, A.J.H., Wielgolaski, F.E., Zach, S. and Züst, A. 2006. European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* 12(10): 1969-1976.
- Ohgushi, T. and Sawada, H. 1997. A shift toward early reproduction in an introduced herbivorous ladybird. *Ecol. Entomol.* 22: 90-96.
- Otterlei, E., Nyhammer, G., Folvord, A. and Stefansson, S.O. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. *Can. J. Fish. Sci.* 56: 2099-2111.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. and Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.
- Roques, A., Rousset, J., Robinet, C., Goussard, F. and Battisti, A. 2005. Range expansion of the pine processionary moth in Europe. In: Proceedings of the 16th U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and Other Invasive Species, GTR-NE-337, pp. 71-72.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.
- Schönenberger, W. 2001. Cluster afforestation for creating diverse mountain forest structures - a review. *Forest Ecol. Man.* 145: 121-128.
- Stastny, M., Battisti, A., Petrucco Toffolo, E., Schlyter, F. and Larsson, S. 2006. Host plant use in the range expansion of the pine processionary moth, *Thaumetopoea pityocampa*. *Ecol. Entomol.* 31: 481-490.
- Strong, D.R., Lawton, J.H. and Southwood, T.R.E. 1984. *Insects on Plants*. Blackwell, Oxford.
- Tun-Lin, W., Burkot, T.R. and Kay, B.H. 2000. Effects of temperature and larval diet on development rates and survival of the dengue vector *Aedes aegypti* in north Queensland, Australia. *Med. Vet. Entom.* 14: 31-37.
- Watts, S.A., Scheibling, R.E., Marsh, A.G. and McClintock, J.B. 1982. Effect of temperature and salinity on larval development of sibling species of *Echinaster* (Echinodermata: Asteroidea) and their hybrids. *Biol. Bull.* 163: 348-354.