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Developmental rates of the Lappet Moth *Streblote panda* Hübner [1820] (Lepidoptera: Lasiocampidae) at constant temperatures

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Abstract

Streblote panda Hübner [1820] (Lepidoptera: Lasiocampidae) is a potential pest of forest, floricultural and horticultural plants. This paper reports the rate of development of this species at six constant temperatures between 16.0 and 31.0°C (3°C increments). Individuals were monitored daily and egg, larval and pupal development times recorded. The development rate was calculated as the reciprocal of the median number of days required to complete development. Linear regression methods were used to estimate lower temperature thresholds and the number of degree-days (DDs) needed for the development of each stage (and total development) under these laboratory conditions. The average hatching time was 18.0 days at 16°C and 7.2 days at 31°C; the average larval development time was 131.8 days at 16°C and 31.7 days at 31°C. The egg-to-adult development time ranged from 189.0 days at 16°C to 48.5 days at 31°C. The threshold temperatures were 7.9, 11.9, 12.5 and 11.3°C for egg, larval, pupal and egg-to-adult development respectively. Differences between larval instars were found; threshold temperatures were lower for late instars. The number of degree days (DDs) for egg-to-adult development was estimated at 1000.0 above 11.9°C. The results suggest three full generations are possible per year in SW Spain.

Additional key words: degree-days, generations, growth rate, life stages, phenology.

Resumen

Tasas de desarrollo de la especie *Streblote panda* Hübner [1820] (Lepidoptera: Lasiocampidae) a distintas temperaturas.

Streblote panda Hübner [1820] (Lepidoptera: Lasiocampidae) es una especie de distribución mediterránea, que ha sido catalogada como plaga potencial de diferentes plantas con interés forestal, ornamental o agrícola. Se estudió la influencia sobre las tasas de desarrollo de la especie a seis temperaturas constantes, desde 16,0 a 31,0°C, con 3°C de incremento. Las orugas fueron observadas diariamente, registrándose los tiempos de desarrollo para los estadios de huevo, larva y pupa. Las tasas de desarrollo se calcularon usando el inverso de la mediana de los días requeridos para completar el desarrollo. Se determinaron, mediante regresiones lineares, las temperaturas mínimas cardinales de desarrollo y los requerimientos de días-grado (DG) bajo condiciones de laboratorio para cada estadio. Los tiempos medios de desarrollo registrados para el estadio de huevo oscilaron desde 18,0 días a 16°C hasta 7,2 días a 31°C. El desarrollo larvario se completó en un tiempo medio que fluctuó entre los 131,8 días a 16°C y 31,7 días a 31°C. El desarrollo total registrado de la especie, de huevo a adulto, osciló entre los 189,0 días a 16°C hasta 48,5 días a 31°C. La temperatura mínima cardinal de desarrollo obtenida fue de 7,9, 11,9, 12,5 y 11,3°C para huevo, larva, pupa y desarrollo total respectivamente, siendo esta temperatura menor para los últimos estadios larvarios. Se encontraron diferencias significativas en el tiempo de desarrollo entre estadios larvarios. Los requerimientos de DG para el desarrollo total de *S. panda* fueron de 1000,0 DG por encima de los 11,9°C. Los cálculos de DG sugieren que son posibles tres generaciones por año en el suroeste de España.

Palabras clave adicionales: días-grado, estadios de desarrollo, fenología, generaciones, tasa de crecimiento.

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Introduction

Information on the development of pest insects under different environmental conditions is vital for forecasting, management and risk analysis. Pest management is improved by knowledge of the life stages that cause damage, and an understanding of the conditions that slow or accelerate development (Wilson and Barnett, 1983; Higley and Peterson, 1994; Waldstein and Reissig, 2001). Phenological models based on population dynamics and the environmental parameters that drive them invariably include the effect of temperature. The relationship between temperature and rate of development is a critical factor that influences pest biology, distribution and abundance (Braman *et al.*, 1984; Legg *et al.*, 2000; Tobin *et al.*, 2002, 2003).

The lappet moth *Streblote panda* Hübner [1820] is distributed throughout the southwestern Mediterranean Basin, from the southern Iberian Peninsula to the Sahara and from Morocco to Egypt. In Spain this species lives in low-lying and coastal areas from Andalusia to Catalonia (Freina and Witt, 1987; Cervelló *et al.*, 2002). Its caterpillars feed on the leaves of many evergreen plants belonging to a broad spectrum of plant families (Gómez-Bustillo and Fernández-Rubio, 1976; Gomez de Aizpurúa, 2002; Calvo, 2004; Calvo and Molina, 2004a); indeed, the species is considered a pest of forest, floricultural and horticultural plants. Younger plants can be severely defoliated, compromising their establishment and production (Zhang, 1994; Molina, 1998; Calvo and Molina, 2004b).

Some information on this species e.g., its development, nutritional ecology and fecundity etc., has been published (Calvo and Molina, 2004a,b; 2005). However, many aspects of its biology and ecology are still confusing or unknown, especially with respect to the number of generations that can be produced in one year, the stage when diapause occurs, and its thermal requirements, etc. Generally, adults and larvae are found year round, with two to four generations thought possible per year (Huertas, 1980; Freina and Witt, 1987; Calvo, 2004).

This study was conducted to assess the development rate of *S. panda* at different temperatures. The aim was to determine the number of days and degree-days (DD) required for each stage to complete development, and to determine the same for overall egg-to-adult development. The determination of developmental rates at different temperatures could provide clues regarding the success of this species in different thermal environments.

Material and Methods

Rearing. The eggs and larvae used in this study were obtained from a colony maintained at the CIFA «Las Torres-Tomejil» Research Station (Alcalá del Río, Seville, Spain). These were the offspring of mature larvae captured on blueberry plants *(Vaccinium* × *corymbosum* L., Ericaceae) in Moguer (Huelva, SW Spain). Eggs were obtained from several matings. Four to five egg masses (mean number of eggs per egg mass = 258.6 ± 22.6 SE) were placed in Petri dishes sealed with Parafilm® and placed in growth chambers at different temperatures between 16 and 31°C (3°C increments; light source white fluorescent lamps; photoperiod 16 h light, 8 h darkness). For the assay at 25.0°C, however, 15 egg masses were used.

After hatching, four groups of 10 larvae were randomly selected from the neonates for rearing under each temperature regime. These larvae remained in their groups until reaching the fourth instar, at which time they were isolated from one another. Fifteen 4th instar larvae per temperature treatment were randomly chosen and their development individually monitored. From hatching to pupation, all larvae were maintained on strawberry tree leaves *(Arbutus unedo* L., Ericaceae), one of this moth's most common host plants in SW Andalusia. Caterpillars were placed in 100 ml plastic cages with perforated covers, and supplied with fresh twigs inserted into Eppendorf tubes filled with distilled water, as described by Calvo (2004). Only totally expanded leaves were offered to larvae; any non-expanded leaves were removed from the twigs. Petri dishes containing eggs, as well as boxes with larvae, were examined daily and developmental stage changes recorded (a moult was considered to occur after an associated exuvium was observed).

The DegDay program (Higley and Peterson, 1994; Snyder, 2002) was used to calculate the number of DDs accumulated in Moguer, employing the single sine method.

Maximum and minimum temperatures were recorded by an experimental station in this locality (UTM 29SPB92).

Statistical methods. Several methods have been proposed to calculate and describe the relationship between insect developmental rate and temperature (Higley *et al.*, 1986; Higley and Peterson, 1994; Kontodimas *et al.,* 2004). Of these, linear approximation enables the calculation of the lower threshold for development and the thermal constant within a limited temperature range. This method is the most widely used in pest management (Wilson and Barnett, 1983; Pedigo and Zeiss, 1996), and has been shown a fairly reliable predictor of development (Got *et al.,* 1996). The mean and median development time (days) required to complete each life stage, plus the overall egg-to-adult period, was calculated for each temperature regime. Mean developmental data were subjected to analysis of variance (ANOVA). Means were compared using the Student-Newman-Keuls multiple range test (Dent and Walton, 1997). Significance was set at P=0.05. The developmental rate of each immature life stage was calculated as the reciprocal (1/days) of the median number of days required to complete that life stage. Median values were selected for calculations since phenological predictions based on these seem to be more accurate than those based on means (Pedigo and Zeiss, 1996; Legg *et al.,* 2002). The relationship between developmental rate and temperature was then described by linear regression using the Pedigo and Zeiss methods (1996; see also Campbell *et al.*, 1974). The threshold temperature (T_0) for each preimaginal stage was determined from the linear regression of the developmental rate at constant temperature. Once a lower threshold for each life stage was determined, the number of DDs required to complete development was estimated for each life stage and for the entire egg-to-adult period from the reciprocals of the fitted regression line (b) (DD = 1/b). Standard errors associated with estimations of both DD and T_0 were calculated using the mathematical relationships of Campbell *et al.* (1974). All statistical analyses were performed using Statistix 4.1 package (Analytical Software, 1996).

Results

Streblote panda completed development at all temperatures between 16 and 31°C (Table 1). The lower

Table 1. Mean ± SE and median development time (days) of *S. panda* reared at a range of constant temperatures (±1°C) under cool white fluorescent lamps (photoperiod 16 h light, 8 h darkness). Means in the same row followed by the same letter do not differ significantly (P < 0.05; ANOVA, Newman-Keuls multiple range test).

Temperature (°C)	16	19	22	25	28	31
Egg	18.0 ± 0.0a (18.0)	15.7 ± 1.7b (16.0)	12.6 ± 2.1c (12.0)	9.3 ± 0.9d (9.0)	8.08 ± 0.8d (8.0)	7.2 ± 0.9e (7.0)
L_1	17.4 ± 0.3a (19.0)	14.7 ± 0.3b (12.0)	10.9 ± 0.3c (10.0)	6.2 ± 0.3d (6.0)	5.0 ± 0.0e (5.0)	6.0 ± 0.0d (4.0)
L_2	14.4 ± 0.2a (14.0)	9.2 ± 0.3b (7.0)	7.2 ± 0.3c (10.0)	4.7 ± 0.3d (4.0)	3.6 ± 0.1e (4.0)	3.0 ± 0.0f (3.0)
L_3	17.3 ± 0.6a (17.0)	11.0 ± 0.3b (9.0)	8.0 ± 0.2c (10.0)	4.9 ± 0.4d (5.0)	4.3 ± 0.1d (4.0)	4.0 ± 0.0d (3.0)
L_4	21.3 ± 0.7a (21.0)	12.9 ± 0.4b (14.0)	8.8 ± 0.2c (9.0)	5.3 ± 0.4e (5.0)	6.6 ± 0.3d (6.0)	10.7 ± 0.7c (7.0)
L_5	34.1 ± 4.6a (24.0)	20.0 ± 0.7b (21.0)	14.3 ± 0.7c (15.0)	8.7 ± 0.5d (10.0)	10.5 ± 0.4d (12.0)	8.8 ± 0.3d (10.0)
L_6*	43.7 ± 1.5 (45.5)	26.8 ± 1.7 (23.0)	26.7 ± 1.7 (21.0)	17.8 ± 0.75 (15.0)	—	14.6 ± 3.8 (12.0)
L_7*	31.0 ± 0.0 (31.0)	30.5 ± 2.5 (35.0)	—	—	—	—
Larva	131.8 ± 3.7a (140.5)	79.7 ± 5.7a (121.0)	98.3 ± 1.5a (75.0)	50.66 ± 1.2a (45.0)	30.5 ± 0.7b (41.0)	31.7 ± 0.9b (39.0)
Pupa	39.2 ± 8.2a (48.0)	26.7 ± 1.1ab (28)	22.5 ± 1.3b (23.0)	14.7 ± 0.3c (15.0)	12.1 ± 0.2cd (12.0)	9.6 ± 0.6d (10.0)
Egg-to adult total	189.0 (206.5)	122.1 (165.0)	133.4 (110.0)	74.7 (69.0)	50.7 (61.0)	48.5 (56.0)

* Data not included in ANOVA analysis due to small sample size.

temperatures significantly delayed the development of all life stages. For instance, complete development took 189.0 days at 16°C and 48.5 days at 31°C. This trend was matched through all stages of development. For the eggs and pupae, the maximum developmental rate was observed at 31°C; the maximum rate for larval development was observed at 28°C. Five instars were recorded for these larvae (Fig. 1a).

Survival varied across temperatures and developmental stages. Hatch success varied between 60.96% and 79.85%, with high variability at each temperature. Larval survival was 100% at all temperatures tested. Pupal and adult survival was 100% for temperatures above 22°C (Table 2).

Extrapolation of the temperature-dependent development curves allowed the estimation of developmental threshold temperatures for eggs, larval instars, pupae and total development. Developmental rates (1/d) for the egg-to-adult period showed a linear relationship with temperature (Fig 1b). Similar trends were seen for the larval and pupal stages. Based on regression analysis of development rate at all temperatures, a minimum temperature threshold between 7.9°C and 12.5°C was estimated, depending on life stage (Table 3, Fig. 1a,b). The lowest minimum threshold was for egg development while the highest minimum threshold was for the pupal stage. Threshold

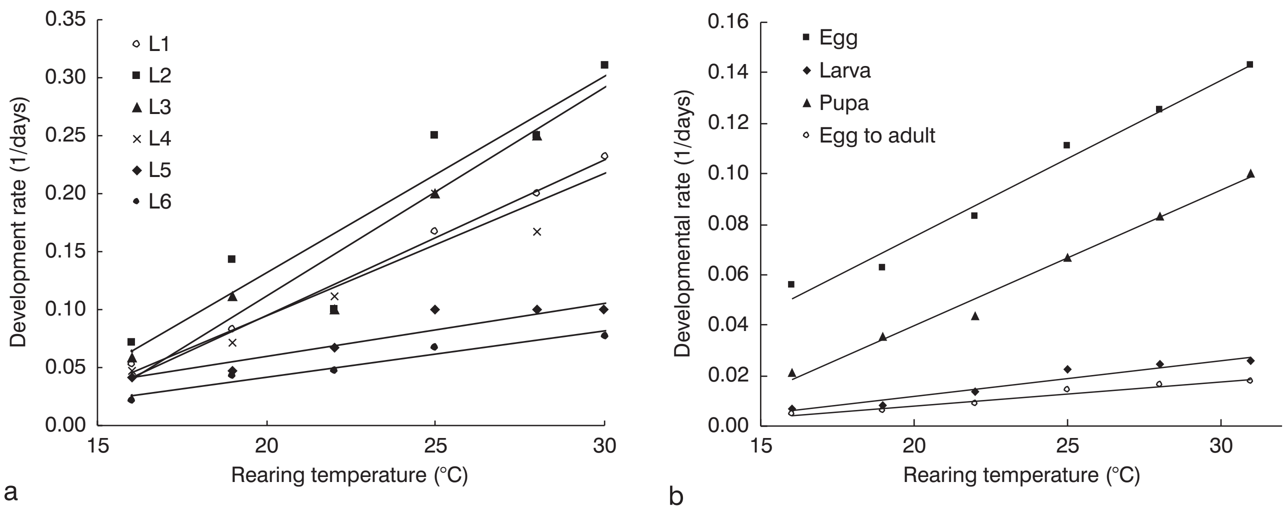

Figure 1. Temperature-dependent development rates for: a) larval instars, and b) eggs, larvae, pupae and the overall egg-to-adult period of *S. panda* Hübner [1820].

Table 2. Percentage survival of egg, pupal and adult stages of *S. panda* at six constant temperatures

		Survival (%)		
T (°C)	**n**	**Egg**	**Pupa**	**Adult**
16	15	64.8 ± 9.8 a	40.0 ± 13.1 b	40.0 ± 13.1 b
19	15	70.6 ± 8.1a	90.0 ± 5.57 a	70.0 ± 8.5 a
22	15	63.7 ± 20.7 a	100 ± 0.00 a	100 ± 0.00 a
25	15	79.8 ± 3.5 a	100 ± 0.00 a	100 ± 0.00 a
28	15	75.7 ± 2.1a	100 ± 0.00 a	100 ± 0.00 a
31	15	60.9 ± 12.1 a	100 ± 0.00 a	100 ± 0.00 a
		$F_{5,32}$ = 1.10 NS	$F_{5,99}$ = 13.43***	$F_{5,99}$ = 9.87***

Means within a column followed by different letters are significantly different (P < 0.05; ANOVA Newman-Keuls multiple range test, P < 0.05); ***: P < 0.001; NS, not significant.

Table 3. Linear regressions of median *S. panda* development rates against rearing temperature, estimates (±SE) of lower developmental threshold (T_0), and DDs required for the development of each life stage

Life stage	n	Y intercept	Slope	r^2	T_0 (°C)[a]	DD (°C day^{-1})[b]
Egg	6	–0.049	0.006	0.98	7.9 ± 0.4	161.3 ± 10.9
L_1	6	–0.172	0.013	0.98	12.8 ± 0.4	75.0 ± 5.8
L_2	6	–0.207	0.017	0.87	12.2 ± 1.0	59.0 ± 11.4
L_3	6	–0.247	0.018	0.94	13.7 ± 1.1	56.0 ± 11.5
L_4	6	–0.150	0.012	0.83	12.3 ± 1.4	82.0 ± 21.4
L_5	5	–0.032	0.005	0.87	6.9 ± 1.0	217.0 ± 41.2
L_6	6	–0.037	0.004	0.96	9.3 ± 0.7	250.0 ± 29.5
Larva	6	–0.017	0.001	0.94	11.9 ± 0.8	714.3 ± 97.2
Pupa	6	–0.067	0.005	0.99	12.5 ± 0.3	185.2 ± 10.5
Egg to adult	6	–0.110	0.001	0.96	11.3 ± 0.5	1000.0 ± 96.9

[a] The lower threshold for development was calculated as the x-intercept (–a/b) of the regression model. [b] Calculated as 1/b of the regression model.

temperatures also varied between larval instars, decreasing by 3-4°C for late instars.

The DD estimates for egg, total larval and pupal development were 161, 714 and 185 respectively. The overall average requirement for temperatures between 16 and 31°C was about 1000 DD (see Table 3). Using the calculated threshold temperature for total development as a base, the number of DDs accumulated in each of the past five years (1999-2003) in Moguer ranged from 2541 in 2000 to 2396 in 2002 (Fig. 2).

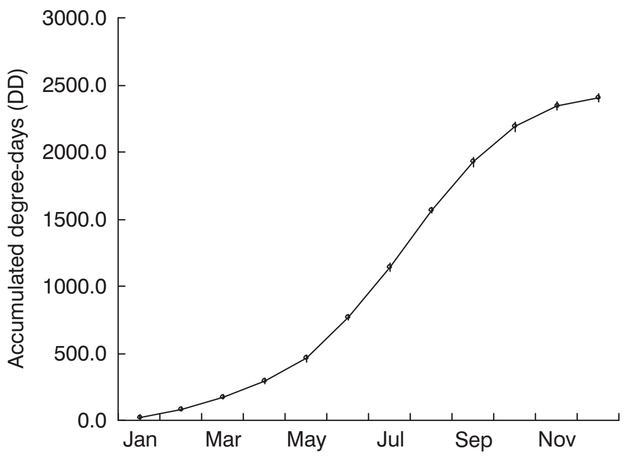

Figure 2. Mean monthly accumulation of degree-days (DDs) in Moguer (Huelva, SW Spain). Lower threshold temperature for egg-to adult development = 11.9°C. Period 1999-2003.

Discussion

The apparent adaptation of late instars to cooler temperatures, illustrated by the lower minimum threshold temperatures of instars 5 and 6, together with behavioural thermoregulation (D. Calvo, pers. obs.), facilitates the completion of larval development under cooler seasonal conditions, permitting foraging activity and the survival of larvae during the mild winters typical of the study area. Developmental differences in adaptation to temperature may also reflect behavioural and spatial segregation of the instars among microhabitats (e.g., gregarious *versus* solitary instars, exposed *versus* shaded sites, nocturnal *versus* day feeding) (Braman *et al.,* 1984). In Moguer, DDs rapidly accumulate from April to the end of August, allowing the completion of two full generations per year. In fact, mean monthly DD accumulations indicate that at least three full generations per year are possible (Fig. 2). However, differences in this basic phenological model may be expected between *S. panda* populations according to geographical location (Campbell *et al.,* 1974; Grassberger and Reiter, 2002).

Freina and Witt (1987) recorded two to four generations per year for the entire distribution area of the species. Gómez-de-Aizpurúa (2002) reported overlapping generations. Huertas (1980) observed four generations per year in SW Spain. The host plant reported by the latter author was *Retama monosperma* (L.) Boiss. (bridal broom, Fabaceae). Larval development was faster on a similar species, *R. sphaerocarpa* (L.) Heyw. than on *Arbutus unedo* (L.) (Calvo and Molina, 2004a). Individual variation in larval development has also been observed to depend on food quality (Calvo and Molina, 2004a,b). The egg-to-adult period largely determines the turnover rate of successive generations, perhaps with some influence on the part of the host or diet (Campbell *et al.,* 1974). Poorer nutritional quality leads to protracted development, as well as asynchrony between individuals of the same generation. This might explain the appearance of off-season adults.

Yearly meteorological variation seems to be a density-independent factor that limits the population dynamics of the species. This may occur directly or indirectly, acting on the phenology of the moth and the food quality of the host plants. This is illustrated by the great variability reported in the first appearance of adults (Gómez-Bustillo and Fernández-Rubio, 1976; Huertas, 1980; Freina and Witt, 1987; Gómez de Aizpurúa, 2002). The spring generation arises from eggs laid by females in the preceding late summer or early autumn (September-October). Mild winters would allow the more rapid development of the individuals of this overwintering generation, resulting in an earlier appearance of adults in the following spring. This potentially allows the completion of more generations per year. The colder conditions of late fall and winter delay development, reducing survival and slowing larval development because of indirect effects on food quality and plant phenology. This explains why larvae can be found in the field throughout the year (Calvo, 2005).

In summary, this DD model, developed from constant temperature experiments, can be used to clarify the developmental model and generation number of this species. The results of this study enhance our knowledge of *S. panda* developmental rates, temperature thresholds and DD requirements. Further studies should focus on establishing a more complete understanding of the life cycle of this species. Tests need to be performed in the field to allow the phenology of the species to be predicted more accurately under these conditions. This might assist in developing sampling protocols, the timing of insecticide applications, and the improvement of other control strategies (aimed at susceptible life stages) for different locations within the species' range.

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