

Influence of habitat and climate on the capture of male pine processionary moths

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Abstract

In the Aspromonte National Park (Calabria, Southern Italy), data were collected over 3 years on the flight of male pine processionary moths (PPM), as determined by pheromone traps, to determine the effect of habitat characteristics and climatic factors on male PPM flight. A variety of parameters, such as tree density, host tree species and the position of the traps, were investigated to analyze their effect on PPM catches in relation to weekly minimum temperatures and accumulated precipitation. The characteristics of the forest stands had a variable effect on moth catches. The abundance of PPM males caught was related to host *Pinus* species and to the size of patches, with a noticeable positive effect of temperature and a negative effect of precipitation. The host *Pinus nigra*, particularly when associated with other host species, such as *Pinus sylvestris* and *Pinus insignis*, smaller sized patches and lower density forests, positively affected moth flight. Flying males were caught above a threshold of a mean weekly temperature of 14 °C in combination with a photoperiod of >13.5 h of light with the flights in advance at higher altitudes. The relationship between the number of moths caught and nest density was evident in only 1 year, suggesting that the estimate of the population density based on the number of moths caught in the traps is possible only above a certain population density. A logistic model for all years is proposed to describe the relationships between the time scale and the cumulative percentage of flights.

Key words: Lepidoptera, *Pinus*, habitat, *Thaumetopoea pityocampa*, forest pest, generalized linear model, climate, logistic model.

Introduction

The pine processionary moth (PPM) *Thaumetopoea pityocampa* (Denis et Schiffermuller) (Lepidoptera Notodontidae Thaumetopoeinae) is a phytophagous insect that generally feeds on trees of the genus *Pinus* L. (Avtzis, 1986; Devkota and Schmidt, 1990; Zhang and Paiva, 1998) and, to a lesser degree, on other conifer species (Demolin, 1970). The species is widespread in the pine forests of the Mediterranean, including southwestern Europe, the Balkan Peninsula and Northern Africa (Huchon and Démolin, 1971). Outbreaks of the species in areas previously uninhabited by the insect can be favored by the presence of secondary hosts (Stastny *et al.*, 2006) or related to climate warming (Goussard *et al.*, 1999; Hodar and Zamora, 2004; Battisti *et al.*, 2005; 2006; Robinet *et al.*, 2007).

PPM infestation impairs the vitality of pine forests (Devkota and Schmidt, 1990; Masutti and Battisti, 1990; Hodar *et al.*, 2003; Carus, 2004) and affects humans and animals in direct contact with an infested tree. The urticant hairs produced and released by the larvae are responsible for allergic pathologies (Ducombs *et al.*, 1981; Lamy *et al.*, 1990; Werno and Lamy, 1994; Artola-Bordás, 2008; Battisti *et al.*, 2011).

Adult moths commonly emerge from the soil between mid-June and mid-August and their dispersal mainly depends on flight (Salvato *et al.*, 2005; Kerdelhué, 2006). Female PPMs are short lived and have limited flight capabilities, whereas adult males disperse more widely (Démolin, 1969).

The ability of PPMs to attack pine forests mainly depends on the environmental conditions of a forest. Different factors contributing to PPM infestations; in par-

ticular, the widespread, often monospecific planting of the preferred host, *Pinus nigra* (Carus, 2010) at different altitudinal ranges favors PPM spread. These plantation forests constitute a simplified ecosystem that reduces the spatial heterogeneity that can affect the ability of PPM to spread throughout a habitat (Salamens and Rossi, 2011).

Insect flight and its dispersal is generally affected by habitat (Einhorn, 1983), atmospheric factors, such as wind, air temperature and rainfall (Isard *et al.*, 1999; Elliot *et al.*, 2000; Walters *et al.*, 2006; Bonsignore and Bellamy, 2007) and the health of the insect (Chaput-Bardy *et al.*, 2010). Similarly to other lepidopteran species, the flight activity of PPM can be affected by insect age, mating status and other internal factors (Agwu, 1972; Hurtrel and Thiéry, 1999; Hughes and Dorn, 2002).

The flight of male PPM can be surveyed by using traps baited with sex pheromone. Such traps have been widely used following the identification of a specific PPM sex pheromone (Guerrero *et al.*, 1981). The sex pheromone shows activity similar to that displayed by virgin females in a wind tunnel (Quero *et al.*, 1997) and provides a suitable tool for monitoring PPM populations (Tiberi and Niccoli, 1984; Jactel *et al.*, 2006).

In the current study, we investigated the effects of habitat characteristics, the time of year and a variety of environmental parameters (i.e. climate variables) on PPM flight in an area where PPMs are generally and historically distributed. We also assessed the relations of these factors with the flight activity of male PPM. Based on our observations, we developed a model to estimate the flight activity of adult male PPM depending on the Julian Day (JD).

Materials and methods

Study area

The study was carried out over 3 years (2003-2005) in the National Park of Aspromonte (Calabria Region, South Italy), which extends from 38°23'N to 38°15'N and from 16°11'E to 15°59'E, where PPMs are currently widespread (figure 1). Aspromonte is the southernmost mountain of the Calabrian peninsula, located in the central Mediterranean Basin; the mountain is characterized by a heterogeneous topography and altitudes up to 2000 m above sea level. Precipitation shows a strong seasonal variability, as a consequence of a Mediterranean climate. Maximum precipitation occurs during winter (550 mm), followed by autumn (450 mm) and spring (320 mm), and is very low during summer (100 mm). The cold season (October 1-March 31) accounts for >80% of the total annual precipitation (Federico *et al.*, 2009).

The Aspromonte forest is Mediterranean in type, containing both natural and introduced species. The forest comprises various species of pine that are PPM hosts, growing both in monoculture and associated with other tree species. Large forest areas are dominated by *P. nigra*, followed by *Pinus pinaster*, *Pinus halepensis*, *Pinus pinea*, *Pinus strobus* and *Pinus insignis (radiata)*. Other areas of the Aspromonte Park are dominated by oak *Quercus* spp., beech *Fagus sylvatica* and shrubs.

Sampling

SuperGreen traps (Intrachem Bio, Italy) baited with a specific sex pheromone [(Z)-13-hexadecen-11-yn-1-ol acetate] were positioned in pine forests throughout the 3-year study period. The traps were checked for moths on a weekly basis and the sex pheromone dispensers were replaced every 30 days. The traps at the end of the flight period were removed in cases where no moths had been found for 2 consecutive weeks. The monitoring was performed in forest patches between 80 and 200 ha in size. At the sampling sites, traps were hung on three trees positioned at the vertexes of a triangle, with a distance of 100 m between each one. Each tree hosting a pheromone trap constituted a node of sampling. In total, 207 traps in 32 patches of forest were placed in the same position during all 3 years (figure 1).

The position of each trap was georeferenced using a GPS instrument (Trimble Geo-XH). The recording of data in field was done using a palmar computer with operating system Windows Us and the ArcPad™ application of ESRI, which integrates a GPS receiver. Trap characteristics, such as details of its patch, position (internal or edge) in the forest, the type of species and the density of the trees, were recorded. In 2004 and 2005, the number of PPM nests found in January in a linear transect of 25 *Pinus* plants in each patch was counted.

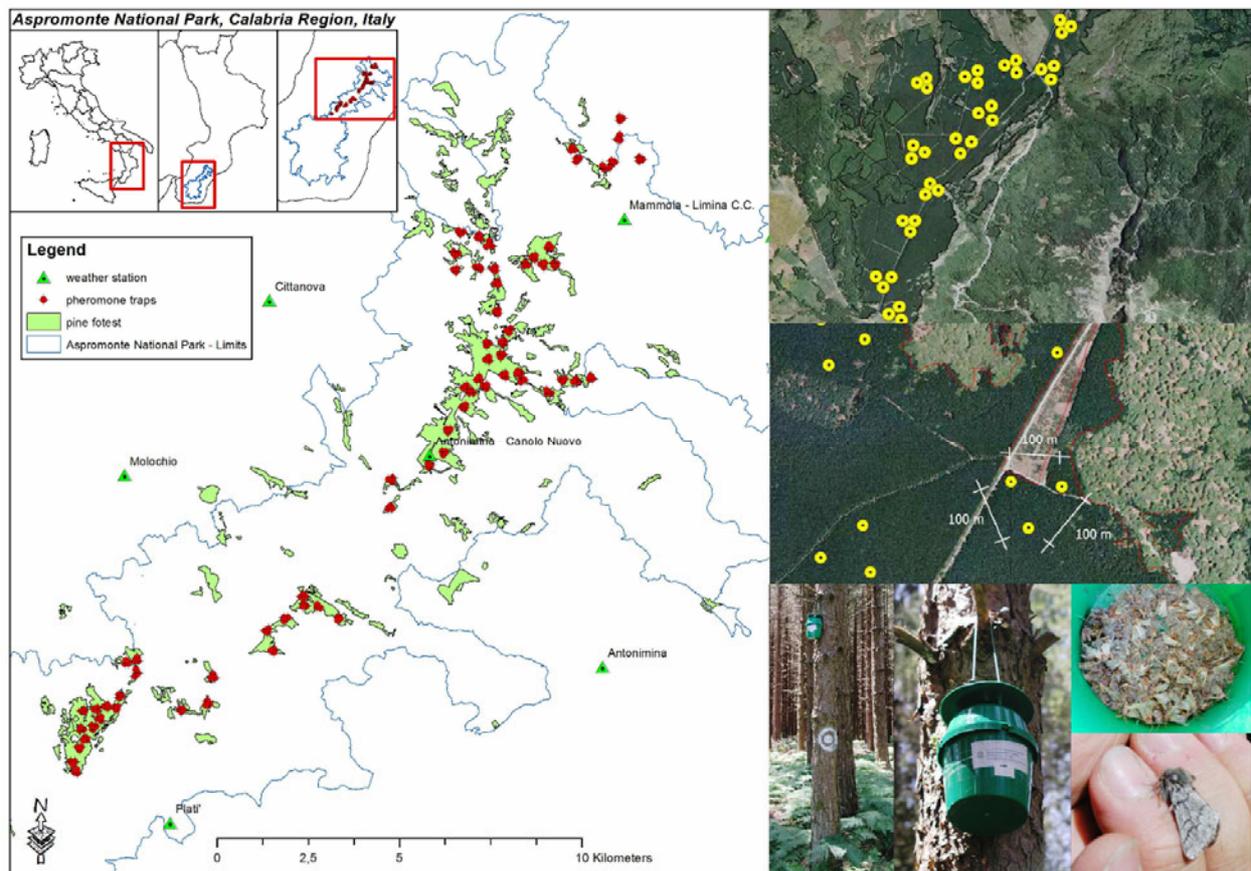


Figure 1. The spatial distribution of the 207 traps and the Aspromonte meteorological stations of the Regional Agency for Environmental Protection.

Meteorological data were taken from the surface station network provided by the Regional Agency for Environmental Protection. The spatial distribution of the Aspromonte meteorological stations is homogeneous and covers all of the area (figure 1). The minimum weekly temperature and the accumulated weekly precipitation for the period from January 1 to the end of the moth-capture period were calculated by the Institute of Atmospheric and Climate Sciences – Italian National Research Council (ISAC – CNR) for each year. The meteorological data were extrapolated to each trap by interpolating measurements from the nearest station (no further than 10 km from the traps). Kriging interpolation was used to represent the spatial variability of the precipitation in the study area (Federico *et al.*, 2009). Temperature was interpolated by weighting temperature averages, with the weights accounting for the distance and height differences between the trap position and surrounding stations. Both the Kriging and the distance-based weighting methods have been widely used to interpolate climatic data (Legates and Willmont, 1990). Each interpolation technique was compared on the basis of bias, mean absolute error (MAE) and mean squared error (MSE).

The other measurable variables considered were the altitude of each trap and JD from January 1 of each study year. The relation between altitude and the number of moths caught was also analyzed in more detail to determine whether and how altitude affects the emergence of PPM adults.

Statistical analysis

Given the variability in the count data across the study years, which was the result of the different rate of infestation by PPM between years, and also the fact that the data relating to the number of catches did not reach the assumption of normality, the flight activity was analyzed by regression for counting data, using a generalized linear model (GLM). In this study, Gaussian models for time series, consisting of counts, were inappropriate and it was necessary to use nonlinear models; when abundances are low and there are many zeros in the data, such data sets can show non-normal distributions (Seavy *et al.*, 2005; Davis and Wu, 2009).

For the analysis of data from each year, the choice between Poisson regression and negative binomial regression was based on the lowest Akaike information criterion (AIC) values (Akaike, 1973). For any given data set, model selection is important in data analysis, and the information obtained from AIC values was used to choose between the two regression analyses (Ver Hoef and Boveng, 2007; Lee and Ghosh, 2009).

The following factors were added as variables: tree species, forest density [ranked by three classes (high, intermediate and low) according to the density of forest patch] and the position of traps or node (internal or external in the forest patch). Patch size in hectares (ha), minimum weekly temperature (°C), altitude above sea level (asl) and total weekly precipitation were added as covariates to the model. For the years 2004 and 2005, the mean number of nests for each patch was added to model.

A correlation analysis between PPM catches and size patches for each year was performed to observe the direction of the effect of this variable.

To evaluate the dynamics of flight during the period when adult moths were present across the 3 study years, a logistic equation (four-parameter), commonly used for phenology modeling (Manel and Debouzie, 1997; Meagher and Delph, 2001; Regniere *et al.*, 2007) was used. Equation 1 was applied to the cumulative percentage of male moth flights at different JD and was fitted for all years of data:

$$y(x) = y_0 + \frac{a}{1 + (x/x_0)^b} \quad [1]$$

where y is the cumulative percentage of adults, x is JD, and a , b , x_0 and y_0 are constants. The parameter x_0 was found to have biological meaning and represented the JD of 50% of moth flights.

To explore possible relations between JD and altitude and to verify their independent effects on male flight, Pearson's chi-square test (χ^2) test in a contingency table was performed on the percentages of total catches for each year. In this case, the altitude and JD variables were ranked into five and six categories, respectively (<800; 800-900; 901-1000; 1001-1100; >1100 m asl for altitude, and 150-175; 176-200; 201-225; 226-250; 251-275; 276-300 for JD). If the proportions of individuals in the different columns varied significantly between rows (or vice versa) in the contingency table, one could conclude that there was a contingency between the two variables.

All analyses were performed using SPSS 19 (2010 SPSS Inc., Chicago, USA). To highlight that the effect of accumulated weekly precipitation on flights was related to weekly temperature, two-dimensional graphs were used that included flights for all years with temperatures that ranged from 13 to 15 °C.

Results

The negative binomial regression model was used for all 3 years because of the lower values of AIC estimates with respect to the Poisson model (2003: 3946.41 vs. 4429.21; 2004: 5847.74 vs. 7136.12; and 2005: 14227.35 vs. 24074.73).

The regression analysis model highlighted the factors that influenced the number of catches of PPM males for each study year (table 1). The number of catches was significantly related to the tree species present and patch size ($P \leq 0.001$) in all study years and forest density (but only in 2005; $P = 0.045$). Weekly minimum temperature had a significant effect on the number of moths caught in all years ($P < 0.001$), followed by weekly precipitation ($P < 0.001_{2003}$), altitude ($P < 0.001_{2004-2005}$) and nest density ($P < 0.001_{2005}$) (table 1). The position of the trap relative to the forest edge (internal and external) had no effect on the number of PPM males caught.

The density of PPMs differed between the years of observation and most PPM males were caught during 2005 (figure 2). Patch composition influenced the number of trapped males, with more being caught in tree stands where *P. nigra* was present (figure 3). In terms of

Table 1. Generalized linear model with negative binomial distribution results evaluating the effect of different variables on PPM captures. Likelihood Ratio χ^2 for 2003 was 284.18 (df = 17; $P < 0.001$) and for 2004 and 2005 were 1214.72 (df = 18; $P < 0.001$) and 2464.19 (df = 18; $P < 0.001$), respectively.

| Source | df (2003) | Wald χ^2 (2003) | P (2003) | df (2004) | Wald χ^2 (2004) | P (2004) | df (2005) | Wald χ^2 (2005) | P (2005) |
|----------------------------------|-----------|----------------------|------------|-----------|----------------------|------------|-----------|----------------------|------------|
| Intercept | 1 | 22.89 | <0.001 | 1 | 268.13 | <0.001 | 1 | 444.36 | <0.001 |
| Species | 9 | 44.11 | <0.001 | 9 | 146.11 | <0.001 | 9 | 494.49 | <0.001 |
| Wood density | 2 | 0.586 | 0.75 | 2 | 4.99 | 0.082 | 2 | 6.20 | 0.045 |
| Position of traps | 1 | 0.038 | 0.57 | 1 | 1.09 | 0.295 | 1 | 1.44 | 0.23 |
| Patch size | 1 | 24.28 | <0.001 | 1 | 10.66 | 0.001 | 1 | 132.14 | <0.001 |
| Minimum temperature | 1 | 53.22 | <0.001 | 1 | 575.33 | <0.001 | 1 | 999.97 | <0.001 |
| Weekly accumulated precipitation | 1 | 31.26 | <0.001 | 1 | 1.37 | 0.242 | 1 | 1.44 | 0.231 |
| Altitude | 1 | 0.01 | 0.91 | 1 | 533.34 | <0.001 | 1 | 169.94 | <0.001 |
| Nest density | | | | 1 | 0.22 | 0.642 | 1 | 18.41 | <0.001 |

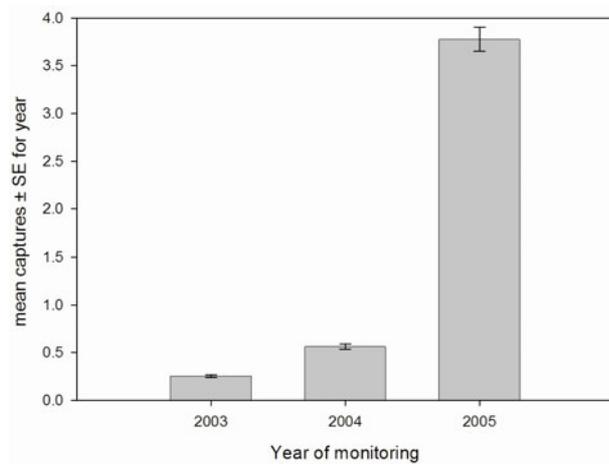


Figure 2. Mean captures per trap ($N = 207$) for each week in each year of monitoring.

the other variables, tree density was the other factor to affect the number of PPMs caught but only during 2005, when the intermediate tree density showed the highest number of PPM males caught.

There was a negative relation (Pearson correlation) between patch size and the number of males caught. The parametric correlation was significant for all years, being more significant with a higher density of PPM [$r_{(2003)} = -0.09$, $P < 0.001$, $N = 3312$; $r_{(2004)} = -0.046$, $P = 0.007$, $N = 3519$; $r_{(2005)} = -0.16$, $P < 0.001$, $N = 3510$]; however, in 2004, although significant, the relation was not as clear.

As shown in figure 4, weekly mean temperature was related to the value of cumulative percentage of flights. Temperatures were higher in 2003 compared with 2005 and 2004. Flights were observed as soon as the minimum weekly temperature was above 14 °C, in combination with a photoperiod of >13.5 h of light.

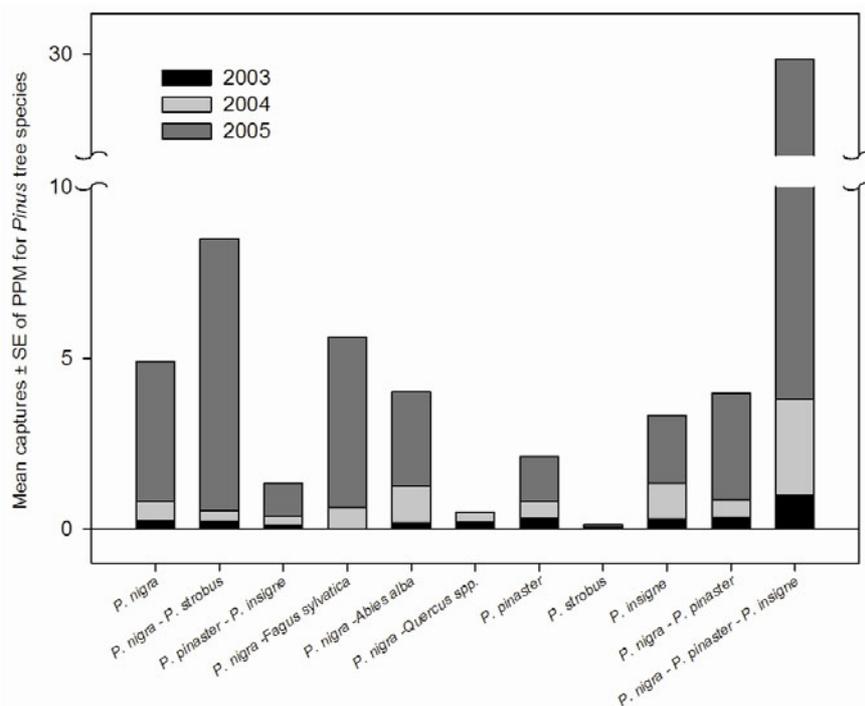


Figure 3. Comparison of mean male PPMs captured over 3 years in areas of different tree species.

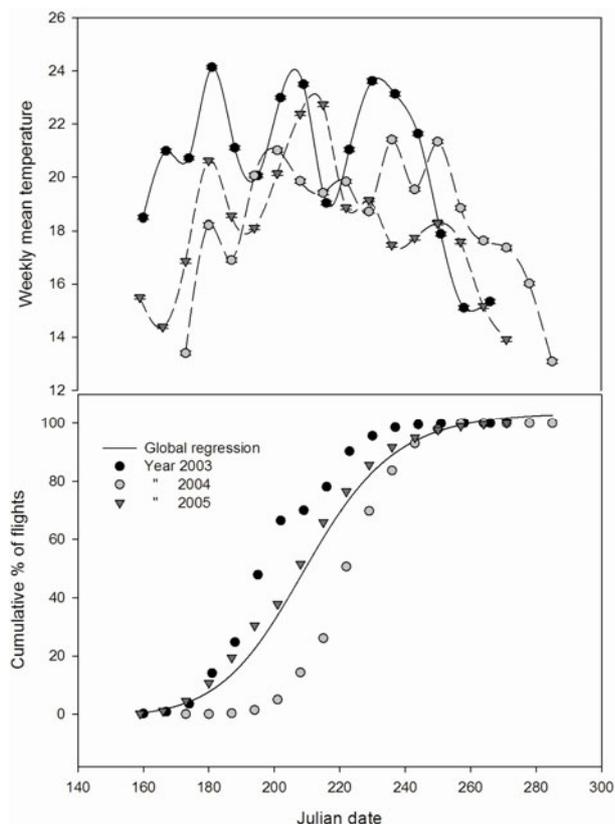


Figure 4. Cumulative percentage of adult male PPM flights and weekly mean temperature (2003-2005). The solid line refers to overall regressed data with a logistic equation where parameters are as follows: a , 104.7629; b , -15.55; x_0 , 210.17; y_0 , -0.98; R^2 , 0.9064.

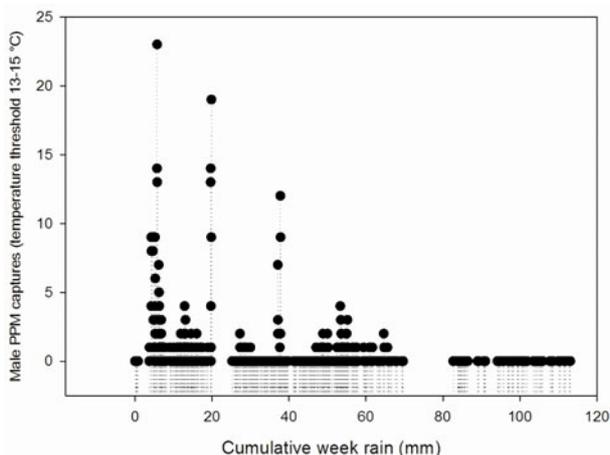


Figure 5. The relationship between cumulative weekly precipitation and PPM catches for 3 years. The cumulative precipitation data relate to the monitoring data collected above a temperature threshold of 13-15°C.

Applying the logistic equation for flight to data of all study years resulted in parameter values of 210.17 ± 2.92 (JD) for x_0 (time of 50% all flights) (figure 4), ranging between 196.57 ± 1.18 (JD) (2003) and 222.34 ± 0.22 (JD) (2004), and with a value of 206.47 ± 0.57 for 2005. The relation between weekly temperature and the value

of cumulative percentage of flights was significant for 2003, when temperatures were higher compared with 2005 and 2004. Across the 3 years of observation, adult PPM males were present from the second week of June (JD = 160) to mid-September in 2003, from the second week of June (JD = 173) to the third week of September in 2004 and from the third week of June (JD = 183) to the end of September in 2005. The longest period of flight was recorded in 2005 and the shortest in 2003.

The χ^2 test to analyze the independence in the contingency table of the variables altitude and JD on the percentage number of males caught shows contingency between the two variables for 2 years. The associations between altitude and JD were significant for 2003 and 2004 ($\chi^2 = 42.40$, $P < 0.01$, $df = 20$, for 2003; $\chi^2 = 42.30$, $df = 20$, $P < 0.01$, for 2004), but not for 2005 ($\chi^2 = 21.73$, $df = 20$, $P > 0.25$). The higher the altitude, the earlier flights were initiated. In particular, the flights were more anticipated for 2003 with 65% vs. 47% (value expected; 176-200 JD; 26 June-19 July, at >1100 m) and 63% vs. 50% of total flights expected for 2004 (201-225 JD; 20 July-15 August at >1100 m). The percentages of monitored and expected flights in the contingency table corresponded throughout the 2005. The negative effect of precipitation on flight illustrated by figure 5 was particularly pronounced for traps located at higher altitudes, where temperatures were relatively low.

Discussion

Dispersal is a fundamental part of spatially extended population dynamics (Bullock *et al.*, 2002), and the structure of a heterogeneous landscape can have profound effects on the persistence of a species over a vast distribution area (Salamens and Rossi, 2011). Trap catches in our study and, thus, flight patterns of PPM males were differentially affected by the environmental factors examined during the 3-year study period. The number of captured males was higher where *P. nigra* was present with other species, noticeably *P. pinaster* and *P. insignis*. Of interest were male PPM catches in mixed forests of deciduous and pine trees, as in the case of *P. nigra-F. sylvatica* and *P. nigra-Abies alba*. In both cases, catches were larger than those in areas of *P. nigra-Quercus* spp., which usually occur at lower altitudes. Areas of forest comprising *P. nigra*, *P. pinaster* and *P. insignis* were those in which most moths were caught, and were significantly more than in areas of each species alone. This indicates that PPMs could spread to forest areas where the preferred tree host is present alongside other species of tree. Hodar *et al.* (2002) underline that PPM females do not select hosts for egg laying owing to their limited flight abilities, at least within one restricted group of host tree species (Kerdelhue *et al.*, 2006); our results suggest that this is also the case for male PPMs.

The presence of nonhost species can involve a chemical barrier for host localization and, in complex forest compositions (e.g. *P. nigra*, *P. pinaster* and *P. insignis*), monoterpenes can have a role in the selection of hosts for egg laying (Niccoli *et al.*, 2008).

In addition to tree species composition, the number of trapped males also depended on patch dimension and tree density, albeit less so; these effects were evident with the higher density of adults recorded in 2005. The male adults swarmed on those trees that showed areas of variability in the landscape, in particular where tree density was not high.

With regard to dispersal mode, Einhorn *et al.* (1983) reported a higher number of PPM males at edges of pine stands and that climatic conditions along edges (e.g. temperature) were more favourable compared with within-stand conditions. Although in our study there were no differences in catches between internal and external traps, this previously reported edge effect could be related to a preference of PPM for oviposition sites, as suggested by the distribution of overwintering nests (Salamens and Rossi, 2011) and also pupation sites (Bonsignore, unpublished data).

Although the relation between the number of PPM caught and the level of PMM infestation is not always evident (Devkota *et al.*, 1992; Baronio *et al.*, 1994), this relation in 2005 with nest density was evident, suggesting that the estimate of the population density based on the number of moths caught in the traps is possible only above a certain population density (for details, see Jactel *et al.*, 2006). Trap catches of PPM males were recorded above a threshold of a minimum weekly temperature of 14 °C and a photoperiod >13.5 h of light. This finding is in agreement with results of Battisti *et al.* (2006), who suggested a temperature threshold of 14 °C for flight take-off. Increasing temperatures allow for longer flight times by these moths (Arnaldo *et al.*, 2011) and, thus, can be associated with longer migration distances (Ishiguri and Shirai, 2004; Sparks *et al.*, 2005). The observed positive relation between flight activity and temperature underlines the role of temperature as a limiting factor for male dispersal and, consequently, for species distribution.

The lack of laboratory experiments investigating the presence of a thermal threshold for male PPM flight, has limited attempts to develop a phenological forecasting model, as generally adopted for other lepidopteran pest species (Damos and Savopoulou-Soultani, 2010). Based on our data collected over a 3-year period, we can infer that there is a dynamic flight period characterized by an increase in total flights linked to an increase in population density. The increase in host availability and a possible increase in the average temperature (global warming) pave the way to the future success of the species in new areas.

The weekly accumulated precipitation had a negative effect on the number of PPM flights. This is likely to be correlated with low temperatures prevailing in wet soil layers and possible effects on pupal development in the soil (Markalas, 1989; Murray and Zalucki, 1990; Hulthen and Clarke, 2005). For the Calabria Region, several studies (Federico *et al.*, 2007, Federico *et al.*, 2009) have shown that the interaction between the orography and mesoscale circulations leads to a precipitation gradient between the Tyrrhenian and Ionian side of the peninsula and in the Aspromonte Park; that is, precipitation is enhanced in favourably exposed areas (Tyrrhenian side) and suppressed in sheltered areas (Ionian side). The

yearly precipitation maximum is recorded over the Aspromonte mountain (>1400 mm/y). Severe weather conditions and heavy precipitation can significantly influence PPM catches. Statistics based on over 30 years of data (Federico *et al.*, 2009) reveal that Aspromonte has the largest occurrence of torrential rainfall (>25 events with precipitation >100 mm/day) in the region.

In 2003, 65% of the total flights of the year were realized before 200 JD (20 July) compared with 2005, where 50% of the total flights occurred from the 226 to 250 JD. These results suggest that flight is bound not only to a minimum thermal threshold, but also to the pupal stage formation and its duration before flight. The summer of 2003 was one of the hottest recorded in Europe (Chase *et al.*, 2006). Earlier emergence and flight might improve survival and would result in earlier egg laying and faster appearances of the larvae and, therefore, to more hours available for feeding, leading to a greater probability of winter survival (Buffo *et al.*, 2007); however, at lower altitudes, early flight does not necessarily lead to an increase in PPM fitness, because eggs and young larvae can be killed by high temperatures. Future climatic scenarios simulated by climatic models (Arnaldo *et al.*, 2011) forecast that the period for PMM emergence will expand, resulting in earlier flight activity.

Overall, the current study confirms the efficacy of pheromone traps for providing information on the flight activity of male PPMs, as already successfully adopted for other species, such as *Thaumetopoea processionea* (L.) (Breuer, 2003). Pheromone-baited traps provide a suitable tool for monitoring PPMs and for determining the effects of the environment on their activity. The traps also provide useful information about the adaptability of this species in the Mediterranean area.

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References

- AGWU S. I., 1972.- Flight activity of *Leucoptera spartifoliella* (Lepidoptera, Lyonetiidae).- *Entomologia Experimentalis et Applicata*, 1: 97-104.
- AKAIKE H., 1973.- Information theory and an extension of the maximum likelihood principle, pp. 267-281. In: *2nd International Symposium on Information Theory* (PETROV B. N., CSAKI F., Eds), Budapest, Akademiai Kiado.
- ARNALDO P. S., OLIVEIRA I., SANTOS J., LEITE S., 2011.- Climate change and forest plagues: The case of the pine processionary moth in northeastern Portugal.- *Forest Systems*, 20: 508-515.
- ARTOLA-BORDÁS F., ARNEDO-PENA A., ROMEU-GARCÍA M. A., BELLIDO-BLASCO J. B., 2008.- Outbreak of dermatitis caused by pine processionary caterpillar (*Thaumetopoea pityocampa*) in schoolchildren.- *Anales del sistema sanitario de Navarra*, 3: 289-293.

- AVTZIS N., 1986.- Development of *Thaumetopoea pityocampa* Schiff. (Lepidoptera:Thaumetopoeidae) in relation to food consumption.- *Forest Ecology and Management*, 15: 65-68.
- BARONIO P., ROCCHETTA G., BALDASSARI N., 1994.- Una stima delle popolazioni di *Thaumetopoea pityocampa* (Den. & Schiff.) (Lepidoptera: Thaumetopoeidae) in alcune vallate dell'Appennino forlivese.- *Bollettino dell'Istituto di Entomologia "Guido Grandi" della Università degli Studi di Bologna*, 48: 11-17.
- BATTISTI A., STASTNY M., NETHERER S., ROBINET C., SCHOPF A., ROQUES A., LARSSON S., 2005.- Expansion of geographic range in the pine processionary moth caused by increased winter temperatures.- *Ecological Applications*, 15: 2084-2096.
- BATTISTI A., STASTNY M., BUFFO E., LARSSON S., 2006.- A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly.- *Global Change Biology*, 12: 662-671.
- BATTISTI A., HOLM G., FAGRELL B., LARSSON S., 2011.- Urticating hairs in Arthropods: Their nature and medical significance.- *Annual Review of Entomology*, 56: 203-220.
- BONSIGNORE C. P., BELLAMY C., 2007.- Daily activity and flight behaviour of adults of *Capnodis tenebrionis* (Coleoptera: Buprestidae).- *European Journal of Entomology*, 104: 425-431.
- BREUER M., KONTZOG H. G., GUERRERO A., CAMPS F., DE LOOF A., 2003.- Field trials with the synthetic sex pheromone of the oak processionary moth *Thaumetopoea processionea*.- *Journal of Chemical Ecology*, 29: 2461-2468.
- BUFFO E., BATTISTI A., STASTNY M., LARSSON S., 2007.- Temperature as a predictor of survival of the pine processionary moth in the Italian Alps.- *Agricultural and Forest Entomology*, 9: 65-72.
- BULLOCK J. M., KENWARD R. E., HAILS R. S., 2002.- *Dispersal ecology*.- Blackwell, Oxford, UK.
- CARUS S., 2004.- Impact of defoliation by the pine processionary moth (*Thaumetopoea pityocampa*) on radial, height and volume growth of Calabrian pine (*Pinus brutia*) trees in Turkey.- *Phytoparasitica*, 32: 459-469.
- CARUS S., 2010.- Effect of defoliation by the pine processionary moth (PPM) on radial, height and volume growth of Crimean pine (*Pinus nigra*) trees in Turkey.- *Journal of Environmental Biology*, 31: 453-460.
- CHAPUT-BARDY A., GRÉGOIRE A., BAGUETTE M., PAGANO A., SECONDI J., 2010.- Condition and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*.- *PLoS ONE*, 5 (5): e10694. doi:10.1371/journal.pone.0010694.
- CHASE T. N., WOLTER K., PIELKE SR R. A., RASOOL I., 2006.- Was the 2003 European summer heat wave unusual in a global context?- *Geophysical Research Letters*, 33: L23709. doi:10.1029/2006GL027470.
- DAMOS P. T., SAVOPOULOU-SOULTANI M., 2010.- Development and statistical evaluation of models in forecasting moth phenology of major lepidopterous peach pest complex for Integrated Pest Management programs.- *Crop Protection*, 29: 1190-1199.
- DAVIS R. A., WU R., 2009.- A negative binomial model for time series of counts.- *Biometrika*, 96: 735-749.
- DÉMOLIN G., 1969.- Bioecología de la "Procesionaria del pino" *Thaumetopoea pityocampa* Schiff. Incidencias de los factores climáticos.- *Boletín del Servicio de Plagas Forestales*, 12: 9-24.
- DEVKOTA B., SCHMIDT G. H., 1990.- Larval development of *Thaumetopoea pityocampa* (Den. and Schiff.) (Lep., Thaumetopoeidae) from Greece as influenced by different host plants under laboratory conditions.- *Journal of Applied Entomology*, 109: 321-330.
- DEVKOTA B., BREUER M., SCHMIDT G. H., 1992.- Observations on the flight activity of the pine processionary moth *Thaumetopoea pityocampa* (Den. and Schiff.) in Greece using synthetic sex-pheromone and light traps (Insecta: Lepidoptera: Thaumetopoeidae).- *Bollettino di Zoologia Agraria e di Bachicoltura*, 24: 147-157.
- DUCOMBS G., LAMY M., MOLLARD S., GUILLARD J. M., MALEVILLE J., 1981.- Contact dermatitis from processional pine caterpillar (*Thaumetopoea pityocampa* Den. and Schiff. Lepidoptera).- *Contact Dermatitis*, 7: 287-288.
- EINHORN J., MENASSIEU P., MICHELOT D., RIOM J., 1983.- The use of sex-traps baited with synthetic attractants against the pine processionary, *Thaumetopoea pityocampa* Schiff. (Lep. Notodontidae). First experiments in southwestern France.- *Agronomie*, 3: 499-505.
- FEDERICO S., AVOLIO E., BELLECCI C., LAVAGNINI A., WALKO R. L., 2007.- Predictability of intense rain storms in the Central Mediterranean basin: sensitivity to upper-level forcing.- *Advances in Geosciences*, 12: 5-18.
- FEDERICO S., AVOLIO E., PASQUALONI L., DE LEO L., SEMPREVIVA A. M., BELLECCI C., 2009.- Preliminary results of a 30-year daily rainfall data base in southern Italy.- *Atmospheric Research*, 94: 641-651.
- GOUSSARD F., SAINTONGE F. X., GERI C., AUGER-ROZENBERG M. A., PASQUIER-BARRE F., ROUSSELET J., 1999.- Increasing risks of damage by the pine processionary *Thaumetopoea pityocampa* Denis & Schiff. in Region Centre following climatic change.- *Annales de la Société Entomologique de France*, 35: 341-343.
- GUERRERO A., CAMPS F., COLL J., RIBA M., EINHORN J., DESCOINS C., LALLEMAND J. Y., 1981.- Identification of a potential sex pheromone of the processionary moth *Thaumetopoea pityocampa*.- *Tetrahedron Letters*, 22: 2013-2016.
- HODAR J. A., ZAMORA R., 2004.- Herbivory and climatic warming: a Mediterranean outbreaking caterpillar attacks a relict, boreal pine species.- *Biodiversity and Conservation*, 13: 493-500.
- HODAR J. A., ZAMORA R., 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.- *Ecological Entomology*, 27: 292-301.
- HODAR J. A., CASTRO J., ZAMORA R., 2003.- Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat of relict Mediterranean Scots pine forests under climatic warming.- *Biological Conservation*, 110: 123-129.
- HUCHON H., DEMOLIN G., 1971.- La bioécologie de la processionnaire du pin. Dispersion potentielle dispersion actuelle.- *Phytoma*, 23: 11-20.
- HUGHES J., DORN S., 2002.- Sexual differences in the flight performance of the oriental fruit moth, *Cydia molesta*.- *Entomologia Experimentalis et Applicata*, 103: 171-182.
- HULTHEN A. D., CLARKE A. R., 2005.- The influence of soil type and moisture on pupal survival of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae).- *Australian Journal of Entomology*, 45: 16-19.
- HURTREL B., THIÉRY D., 1999.- Modulation of flight activity in *Lobesia botrana* Den. & Schiff. (Lepidoptera: Tortricidae) females studied in wind tunnel.- *Journal of Insect Behavior*, 12: 199-211.
- ISARD S. A., NASSER N. A., SPENCER J. L., LEVINE E., 1999.- The influence of the weather on western corn rootworm flight activity at the borders of a soybean field in east central Illinois.- *Aerobiologia*, 15: 95-104.
- ISHIGURI Y., SHIRAI Y., 2004.- Flight activity of the peach fruit moth, *Carposina sasakii* (Lepidoptera: Carposinidae), measured by a flight mill.- *Applied Entomology and Zoology*, 39: 127-131.

- JACTEL H., MENASSIEU P., VÉTILLARD F., BARTHÉLÉMY B., PIOUS D., FRÉROT B., ROUSSELET J., GOUSSARD F., BRANCO M., BATTISTI A., 2006.- Population monitoring of the pine processionary moth (Lepidoptera: Thaumetopoeidae) with pheromone-baited traps.- *Forest Ecology and Management*, 235: 96-106.
- KERDELHUÉ C., MAGNOUX E., LIEUTIER F., ROQUES A., ROUSSELET J., 2006.- Comparative population genetic study of two oligophagous insects associated with the same hosts.- *Heredity*, 97: 38-45.
- LAMY M., 1990.- Contact dermatitis (Erucism) produced by processionary caterpillars (Genus *Thaumetopoea*).- *Journal of Applied Entomology*, 110: 425-437.
- LEGATES D. R., WILLMOTT C. J., 1990.- Mean seasonal and spatial variability in global surface air temperature, *Theoretical and Applied Climatology*, 41: 11-21.
- LEE H., GHOSH S. K., 2009.- Performance of information criteria for spatial models.- *Journal of Statistical Computation and Simulation*, 79: 93-106.
- MANEL S., DEBOUZIE D., 1997.- Modeling insect development time of two or more larval stages in the field under variable temperatures.- *Environmental Entomology*, 26: 163-169.
- MARKALAS S., 1989.- Influence of soil moisture on the mortality, fecundity and diapause of the pine processionary moth (*Thaumetopoea pityocampa* Schiff.).- *Journal of Applied Entomology*, 107: 211-215.
- MASUTTI L., BATTISTI A., 1990.- *Thaumetopoea pityocampa* (Den. & Schiff.) in Italy - Bionomics and perspectives of integrated control.- *Journal of Applied Entomology*, 110: 229-234.
- MEAGHER T. R., DELPH L. F., 2001.- Individual flower demography, floral phenology and floral display size in *Silene latifolia*.- *Evolutionary Ecology Research*, 3: 845-860.
- MURRAY D. A. H., ZALUCKI M. P., 1990.- Effect of soil moisture and simulated rainfall on pupal survival and moth emergence of *Helicoverpa punctigera* (Wallengren) and *H. armigera* (Hübner) (Lepidoptera: Noctuidae).- *Australian Journal of Entomology*, 29: 193-197.
- NICCOLI A., PANZAVOLTA T., MARZIALI L., SABBATINI PEVERIERI G., TELLINI FLORENZANO G., TIBERI R., 2008.- Further studies on the role of monoterpenes in pine host selection and oviposition of *Thaumetopoea pityocampa*.- *Phytoparasitica*, 36: 313-321.
- QUERO C., MALO E. A., FABRIAS G., CAMPS F., LUCAS P., RE-NOU M., GUERRERO A., 1997.- Reinvestigation of female sex pheromone of processionary moth (*Thaumetopoea pityocampa*): no evidence for minor components.- *Journal of Chemical Ecology*, 23: 713-726.
- REGNIERE J., LAVIGNE D., DUPONT A., CARTER N., 2007.- Predicting the seasonal development of the yellow headed spruce sawfly (Hymenoptera: Tenthredinidae) in eastern Canada.- *Canadian Entomologist*, 139: 365-377.
- ROBINET C., BAIER P., PENNERSTORFER J., SCHOPF A., ROQUES A., 2007.- Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Notodontidae) in France.- *Global Ecology and Biogeography*, 16: 460-471. doi:10.1111/j.1466-8238.2006.00302.x.
- SALVATO P., SIMONATO M., ZANE L., PATARNELLO T., MASUTTI L., BATTISTI A., 2005.- Do sexual pheromone traps provide biased information of the local gene pool in the pine processionary moth?- *Agricultural and Forest Entomology*, 7: 127-132.
- SAMALENS J. C., ROSSI J. P., 2011.- Does landscape composition alter the spatiotemporal distribution of the pine processionary moth in a pine plantation forest?- *Population Ecology*, 53: 287-296.
- SEAVY N. E., QUADER S., ALEXANDER J. D., RALPH C. J., 2005.- Generalized linear models and point count data: Statistical considerations for the design and analysis of monitoring studies.- *USDA Forest Service General Technical Reports*, PSW-GTR-191: 744-753.
- SPARKS T. H., ROY D. B., DENNIS L. H., 2005.- The influence of temperature on migration of Lepidoptera into Britain.- *Global Change Biology*, 11: 507-514.
- STASTNY M., BATTISTI A., PETRUCCO TOFFOLO E., SCHLYTER F., LARSSON S., 2006.- Host plant use in the range expansion of the pine processionary moth, *Thaumetopoea pityocampa*.- *Ecological Entomology*, 3: 481-490.
- TIBERI R., NICCOLI A., 1984.- Osservazioni pluriennali sull'impiego di trappole con il feromone sessuale di *Thaumetopoea pityocampa* (Den. et Schiff.) (Lepidoptera, Thaumetopoeidae).- *Redia*, 67: 129-144.
- VERHOEF J. M., BOVENG P. L., 2007.- Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data?- *Ecology*, 88: 2766-2772.
- WALTERS R. J., HASSALL M., TELFER M. G., HEWITT G. M., PALUTIKOF J. P., 2006.- Modelling dispersal of a temperate insect in a changing climate.- *Proceedings of the Royal Society B*, 273: 2017-2023.
- WERNER J., LAMY M., 1994.- Daily cycles for emission of urticating hairs from the pine processionary caterpillar (*Thaumetopoea pityocampa* S.) and the brown tail moth (*Euproctis chrysorrhoea* L.) (Lepidoptera) in laboratory conditions.- *Aerobiologia*, 10: 147-151.
- ZHANG Q. H., PAIVA M. R., 1998.- Female calling behaviour and male response to the sex pheromone in *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae).- *Journal of Applied Entomology*, 122: 353-360.

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