

Seasonality and life cycles of woody plant-feeding noctuid moths (Lepidoptera: Noctuidae) in Mediterranean habitats

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Abstract. 1. The annual cycle of noctuid moths feeding as larvae on the foliage of eighteen woody plant species (belonging to ten different families) was studied at two southeastern Spanish Mediterranean forest habitats. Two questions were addressed in this study. (1) Does the rigorous (hot and dry) summer season characteristic of the Mediterranean-type climate impose a constraint on noctuid life histories? (2) Are there detectable differences in abundance or phenological patterns between the noctuid assemblages feeding on evergreen and winter-deciduous trees and shrubs?

2. Regardless of their leaf persistence habit, the majority of woody species studied had short shoot growth and leaf production periods in spring. Abundance of noctuid larvae peaked in May–June, shortly after host plants started to produce new leaves. Virtually no noctuid larvae were found on the foliage of the woody species studied at other times of year. Abundance and seasonal pattern of occurrence of larvae were similar on evergreen and deciduous food plants.

3. In contrast with the unimodal seasonal pattern exhibited by larvae, the abundance of adult moths (assessed by light trapping) showed two distinct peaks in early summer and early autumn, and a marked minimum in mid-summer.

4. Most woody plant-feeding noctuids recorded in this study (86% of species, about 95% of individuals) were univoltine. Univoltine species fell into one of two distinct life history categories, corresponding to pre- and post-summer flight periods. These two contrasting phenologies were associated with a bimodality in the duration of the pupal stage ('short' versus 'long'), and were closely related to taxonomical affiliation at the subfamily level.

5. Within the 'short' pupal duration group, some species mate and oviposit shortly after emergence and pass the dry season in the egg stage, while others remain as potentially active, non-reproductive adults over most of the summer and mate by the end of that season. Species in the 'long' pupal duration group pass the summer in pupal or prepupal stage.

6. In the Mediterranean habitats studied, the adversity of the summer dry season seems to have led to a woody plant-feeding noctuid species assemblage almost entirely made up of univoltine species that concentrate their larval phases when suitable food (young leaves) is most abundant, and 'avoid' mid-summer as a flight time by emerging either shortly before or shortly after the adverse summer drought period. Year-round foliage availability afforded by dominant evergreen plants does not seem to have influenced the seasonal organization of noctuid cycles in any substantial way.

Key words. Evergreen plants, herbivory, Lepidoptera, life history, Mediterranean forest, Mediterranean climate, Noctuidae, phenology, seasonality.

Introduction

Noctuid moths (Lepidoptera: Noctuidae) make up the most species-rich family in the order Lepidoptera. Although estimates provided by different authors differ slightly, it seems safe to conclude that noctuid moths represent between 20% and 25% of the total number of Lepidopteran species (100,000–120,000 species; Bretherton *et al.*, 1979; Poole, 1989; Fibiger, 1990; Gaston, 1991). In addition to their worldwide diversity, noctuid moths are also characterized by their remarkable abundance and species richness in most terrestrial ecosystems, and they usually comprise a major proportion of captures at light and bait traps (e.g. Cleve, 1971; Mikkola, 1972; Persson, 1976; Löbel, 1982; Janzen, 1988a; Barlow & Woiwod, 1989; White, 1991). Noctuid larvae feed on virtually all kinds of terrestrial plants (e.g. Bergmann, 1954; Stehr, 1987), thus they presumably play a prominent role as agents of herbivory in most ecosystems. In striking contrast with their likely ecological relevance, noctuid moths (apart from intensively studied agricultural pests) are only infrequently selected as study subjects in herbivory studies, and often they are even explicitly excluded from community-wide herbivory investigations (e.g. Futuyma, 1976; Table 1). The relative neglect of this numerically most important group of Lepidopteran herbivores may probably be attributed to the practical difficulties involved in the accurate identification of larval stages at the species level (Merzheevskaya, 1989), the nocturnal and inconspicuous habits of most of these, and the poor knowledge of the basic life history aspects of the majority of species.

In this paper, we describe the seasonal pattern of abundance of noctuid moths (at both the larval and adult stages) feeding on eighteen species of woody plants at two nearby, well-preserved Mediterranean habitats of southeastern Spain. The primary aim of the study was to assess the organization of the annual cycle of woody-plant feeding noctuid species living under Mediterranean-climate conditions, and relate it to the habit (evergreen versus deciduous) of their host plants. Two questions are specifically addressed.

(1) Does the rigorous (hot and dry) summer season characteristic of the Mediterranean-type climate represent a constraint on noctuid life histories? An understanding of the relationship between the phenology of insect populations and the seasonality of food availability and abiotic conditions is central to our knowledge of insect life history evolution (Feeny, 1970; Wolda, 1978, 1988; Strong *et al.*, 1984; Janzen, 1987). The Mediterranean-type climate is characterized by the predictable occurrence of a severe summer drought lasting for several months (Aschmann, 1973). This period represents an adverse season for woody plants (Merino *et al.*, 1976; Mooney *et al.*, 1977) and at least some insect groups (Herrera, 1980; Fernández-Haeger & Jordano Barbudo, 1982; Jordano, 1984; Baz, 1986, 1989). The role of the summer drought season as a constraining factor on the life history of noctuid moths inhabiting Iberian Mediterranean habitats has been previously suggested, among others, by Calle (1974) and Yela

(1980, 1992a), but these suggestions were generally based on data for adult moths alone.

(2) Are there detectable differences in abundance or phenological patterns between the noctuid assemblages feeding on evergreen and winter-deciduous trees and shrubs? Prevalence of evergreen species is one prominent feature of Mediterranean forests and shrublands, and evergreenness has been long interpreted as an adaptation of woody plants to the Mediterranean-type climate (Mooney & Dunn, 1970a, b). Apart from the obvious difference of leaf longevity, leaves of evergreen and deciduous woody perennials differ in several respects, including photosynthetic rate, toughness, and water and nutrient content (Mooney & Gulmon, 1982; Margaris *et al.*, 1984; Puttick, 1986; and references therein). Margaris *et al.* (1984), for instance, reported a higher average N and P content for evergreens in a large sample of species from Greek shrublands. Nutritional differences between the foliage of deciduous and evergreen species probably have important implications for plant–herbivore interactions in Mediterranean habitats (Puttick, 1986), and it has been suggested that deciduous plants tend to support a greater abundance of lepidopteran larvae than do evergreen plants (Blondel *et al.*, 1991; Blondel & Dias, 1992).

Study sites and methods

This study was carried out from April 1991 to March 1992 at two sites located in the Sierra de Cazorla (Jaén province, southeastern Spain). Study sites were in the Guadahornillos valley (Reserva de Navahondona-Guahornillos), a 2500 ha watershed characterized by species-rich, well-preserved Mediterranean montane forests and tall shrublands (see J. Herrera, 1984; C. M. Herrera, 1989, for descriptions of the vegetation). Climate of the area is typically Mediterranean, with a distinct summer dry season. Mean annual rainfall at the nearest weather station (Vadillo-Castril, 1000 m elevation) is 1188 mm ($N = 30$ years), only 9% of which falls between June and September. Mean temperature of the hottest (August) and coldest (January) months at that station were 21.1°C and 4.0°C, respectively ($N = 17$ years).

The 'Hoyos de Muñoz' site (HM hereafter) was at 1045 m elevation on an east-facing slope vegetated by tall shrubland and mixed forest (height of vegetation mostly between 3 and 15 m). Dominant tree species were *Quercus rotundifolia*, *Pinus pinaster*, *Phillyrea latifolia* and *Arbutus unedo*. Dominant shrubs were *Rosmarinus officinalis*, *Viburnum tinus* and *Pistacia lentiscus* (Table 1). The 'Camino del Agracea' site (CA hereafter; 6.5 km to the south of HM) was at 1235 m elevation on a north-facing slope vegetated by mature mixed forest with an understorey of sparse shrubs and juvenile trees (height of vegetation up to 25 m). Dominant tree species were *Quercus rotundifolia*, *Pinus nigra*, *Phillyrea latifolia*, *Q. faginea* and *Juniperus oxycedrus*. *Rubus ulmifolius*, *Crataegus monogyna* and *Rosa canina* dominated in the shrub layer (Table 1). Due

Table 1. Relative importance (per cent cover) of woody species at the two study sites (based on intercepts along ten 20 m long transects at each site). Figures do not sum up to 100 because some rare species were omitted. Plus signs in parentheses denote species sampled for noctuid larvae at each site. Some of these were not recorded in the transects (marked with asterisks).

Plant species	HM site	CA site
Evergreen		
<i>Arbutus unedo</i>	11.3 (+)	* (+)
<i>Daphne laureola</i>		1.2 (+)
<i>Erica arborea</i>	1.7 (+)	
<i>Juniperus oxycedrus</i>	1.6 (+)	7.0 (+)
<i>Juniperus phoenicea</i>		* (+)
<i>Phillyrea angustifolia</i>	2.5 (+)	
<i>Phillyrea latifolia</i>	12.8 (+)	8.7 (+)
<i>Pinus nigra</i>		22.3
<i>Pinus pinaster</i>	13.7	
<i>Pistacia lentiscus</i>	3.0 (+)	
<i>Quercus rotundifolia</i>	14.5 (+)	34.5 (+)
<i>Rosmarinus officinalis</i>	16.9	
<i>Rubus ulmifolius</i>	0.2 (+)	3.5 (+)
<i>Viburnum tinus</i>	10.9 (+)	
Deciduous		
<i>Acer granatense</i>		0.1 (+)
<i>Berberis hispanica</i>		1.3 (+)
<i>Craeaegus monogyna</i>		2.9 (+)
<i>Pistacia terebinthus</i>	1.6 (+)	0.1
<i>Quercus faginea</i>	6.6 (+)	8.4 (+)
<i>Rosa canina</i>	* (+)	2.4 (+)
<i>Sorbus torminalis</i>	1.7 (+)	5.5 (+)

to its higher elevation and north-facing orientation, the CA site is cooler and humid than HM, and this difference is reflected in a lower relative contribution of evergreens to total woody plant cover (77% in CA, 89% in HM; Table 1).

A total of eighteen woody species (thirteen at each study site) were chosen for sampling of noctuid larvae (Table 1). Eight of these occurred at both sites. Most species sampled at HM were evergreen, while deciduous and evergreen species contributed roughly similar proportions at CA (Table 1). Sampling for noctuid larvae was carried out at both sites from April to October 1991. With only minor exceptions, two separate sampling sessions (daytime and night-time) were carried out every week at each study site. In each session, the foliage from accessible parts of three individuals (selected haphazardly) of each plant species was beaten with a wooden stick at three different height intervals (0–1 m, 1–2 m and 2–3 m above the ground) according to a standardized procedure (following Harris *et al.*, 1972, a three-tree sample was considered acceptable for assessing larval abundance). Each height interval was beaten ten times in rapid succession (=1 sampling unit, 's.u.' hereafter), and falling insects were collected on a 0.25 m² sheet of white cloth placed directly beneath the beaten vegetation volume (roughly equalling 0.25 m³). Each sampling session involved 117 s.u. in each site when all height levels were represented in all

sampled plants (13 plant species × 3 individuals × 3 height levels). In addition to this regular sampling scheme, and depending on time availability, some additional sampling sessions were conducted occasionally (following the same method) on the most rewarding (from the viewpoint of noctuid larvae yield) plant species. Results of this supplementary sampling will be combined with those from regular sampling. The combined sampling effort over the study period on the eighteen plant species studied was 6602 and 6107 s.u. in HM and CA, respectively. Noctuid larvae obtained in the course of sampling sessions were identified to species in the field whenever possible, or raised on host plant foliage for later identification and additional observations on feeding behaviour.

The number of larvae recovered per sampling unit (all plant species, sites and dates combined) exhibited a clumped distribution among sampling units (frequencies departed significantly from those predicted from a Poisson distribution; Chi-square = 21.69, df = 1, $P < 0.001$). This fact, and the reduced number of larvae recovered per sampling unit (mean = 0.028 larvae/s.u.), led us to analyse patterns of larval abundance by examining variations in the frequency of occurrence of samples yielding at least one larva ('positive' samples hereafter), rather than counts of individual larvae per sampling unit. The nominal nature of the dependent variable (presence/absence of larvae in a sampling unit) requires the application of analytical methods specific to categorical data, and linear models based on logistic regression (SAS Institute, 1988) will thus be used to assess patterns of larval abundance.

Adult moths were sampled at the two study sites (one trap per site) from April 1991 to March 1992 by means of blacklight, Heath-type traps (Heath, 1965), as modified by Fernández-Rubio (1985). Each trap consisted of a single 8 W superactinic fluorescent lamp (Philips TL 8W/05) placed 30 cm above the ground, just above a metallic funnel leading to a bucket half-filled with pieces of corrugated cardboard. An open vial containing 1,1,2,2-tetrachloroethane, a slowly evaporating anaesthetic, was placed on the bucket's floor. Moths attracted to the light fell into the bucket and became anaesthetized. Lamps were powered by 12 V car batteries, and were automatically switched on (at dusk) and off (at dawn) by means of a photoelectric device.

A total of twenty-six light-trapping sessions were carried out at each study site, totalling 109 and 107 sampling nights at HM and CA, respectively. Traps were operated for 2–6 days on each sampling session (4.1 days on average). Light-trapping sessions were deliberately concentrated on the period of putatively greatest adult moth abundance (April–October), and were more widely spaced during late autumn and winter (November–March). To account for differences among light-trapping sessions in sampling effort, captures will be standardized to individuals/day for the analyses. As these average figures are based on spaced sampling periods of short duration, we expect that they are largely unaffected by local removal effects (White, 1988), and thus reasonably reflect seasonal variations in adult moth abundance. The

indirect and selective nature of light trapping may lead to biased estimates of adult moth abundance and species diversity (Yela, 1992a, and references therein). Nevertheless, no other method has proven so consistently successful in capturing large numbers of a broad variety of night-flying moths (Muirhead-Thomson, 1991). A significant correlation was found in this study between larval and adult (as revealed by light trapping) abundance of individual moth species in the habitats studied, thus pointing to the reliability of light trapping results (see below).

Nomenclature of noctuid species used in this paper follows Yela (1992a). For discussion on the taxonomical status of some of the species dealt with here, the reader is referred to Yela & Sarto i Monteys (1990) and Yela (1992a).

Results

Patterns of larval abundance

A total of 361 noctuid larvae were collected in the course of the study (182 in HM, 179 in CA), 326 of which (90.3%) could be determined to species. At least forty-eight species and twenty-seven genera were represented among collected larvae (Appendix 1). At both sites, abundance of noctuid larvae in the foliage of the woody species sampled was very low for most of the study period. Only 2.5% of sampling units ($N=12709$ s.u., both sites combined) yielded some larvae, and 91.5% of these positive samples yielded single individuals.

The effects of time of year, study site, host plant habit (deciduous versus evergreen), and time of sampling (day-time versus night-time), on the occurrence of larvae in samples (the categorical, dependent variable) were tested simultaneously using a linear model based on logistic regression and maximum likelihood estimation (procedure CATMOD in the SAS package; SAS Institute, 1988). All variables were treated as categorical except for time of year, which was treated as a continuous variable. For each sample, time of year was coded as the number of half-month periods elapsed from the start of the study (first half of April = 1, second half of October = 14). To account for the non-linearity of the effect of time of year on the frequency of occurrence of positive samples (Fig. 1), (time of year)² was also included in the model. Results of the analysis are summarized in Table 2. The fit of the model to the data was statistically significant, as shown by the non-significance of the likelihood ratio.

The frequency of occurrence of noctuid larvae in samples exhibited a distinct peak in the first half of June and declined abruptly afterwards (Fig. 1). During most of the summer, noctuid larvae were not recovered from the foliage of studied plant species despite extensive sampling effort. The two study sites did not differ significantly with regard to the seasonal course of larval abundance, as revealed by the nonsignificance of the interaction Site \times Time of Year in the model (Table 2). Sites were also similar in overall frequency of occurrence of larvae in samples (Table 2).

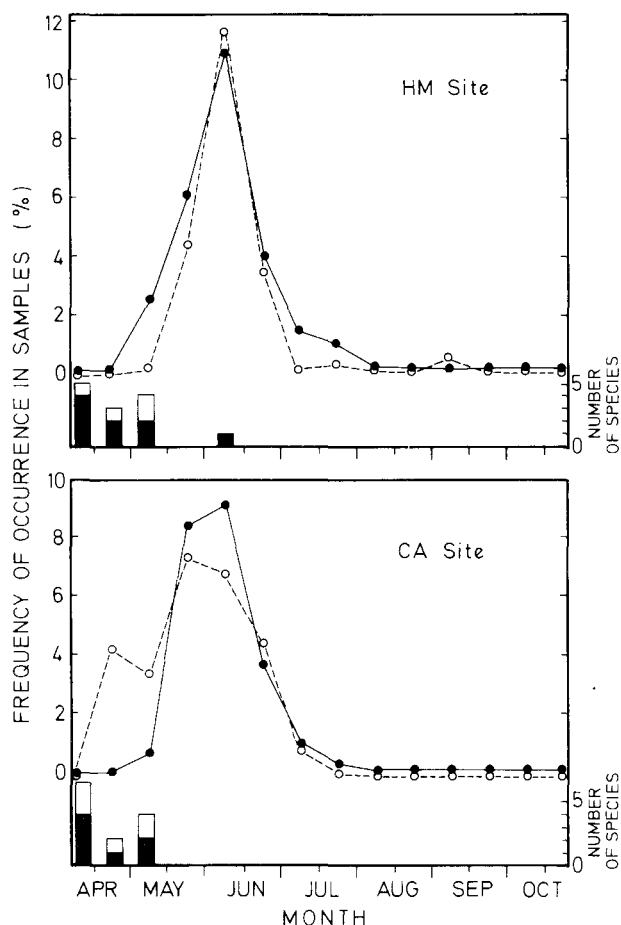


Fig. 1. Seasonal variation in the frequency of occurrence of noctuid larvae in samples from deciduous (open dots, dashed line) and evergreen woody species (filled dots, solid line) at the two study sites, April–October 1991. Within each leaf persistence category, data from all host species sampled were grouped into half-month periods for computations of frequencies of occurrence. Bars at bottom of each panel denote the number of plant species (among those sampled for noctuid larvae) starting to produce new leaves in each half-month period (filled bars, evergreen species; open bars, deciduous species).

At both sites, the seasonal pattern of larval occurrence in samples was remarkably similar on deciduous and evergreen plant species (Fig. 1). There were no significant differences in the seasonal pattern of larval abundance on evergreen and deciduous host plants, as revealed by the nonsignificance of the interaction Habit \times Time of Year in the model (Table 2). The dates of initiation of shoot growth and production of new leaves by the plant species sampled are shown in Fig. 1 for comparison with the seasonal course of larval abundance. Most plant species started to produce new leaves during April and the first half of May. No important differences existed in the study year between evergreen and deciduous plant species with regard to the timing of production of new leaves at any site. The shoot growth and leaf flush periods were relatively short (1–2 months) in all plant species studied (fitting into

Table 2. Analysis of variance table for the linear model (based on logistic regression) for the effects of time of year (half-month periods), study site, host plant habit (deciduous versus evergreen), and time of day (daytime versus night-time), on the occurrence of noctuid larvae in samples. The analysis was performed using procedure CATMOD in SAS (SAS Institute, 1988) and maximum likelihood estimation. All variables except time of year were treated as categorical (see text for further details).

Effect	df	Chi-square	P
Intercept	1	110.98	<0.0001
Study site (S)	1	1.82	0.1773
Host plant habit (H)	1	1.42	0.2327
Time of Day (TD)	1	0.73	0.3927
Time of Year (TY)	1	77.02	<0.0001
(TY) ²	1	88.14	<0.0001
TY × S	1	1.87	0.1713
TY × H	1	1.45	0.2292
TY × TD	1	2.16	0.1414
Likelihood ratio	92	75.89	0.8878

the 'Quercus type' of Hoffmann & Lyr, 1973), with the exceptions of *Rosa canina* and *Rubus ulmifolius* (up to 5 months). Local peaks of larval abundance occurred shortly after the period during which most plant species started to produce new leaves.

The proportional occurrence of positive samples from evergreen and deciduous host plant species at the two study sites is shown in Table 3. The frequency of positive samples ranged from 0% in *Juniperus phoenicea* and *Viburnum tinus*, to 7.2% in *Erica arborea* (all dates combined). The logistic regression model did not reveal significant differences between evergreen and deciduous species with respect to frequency of occurrence of larvae in samples (Table 2).

Time of sampling (daytime versus night-time) had no significant effect on the probability of occurrence of larvae in samples, and this pattern was independent of time of year (Table 2).

Seasonality of adult moths

A total of 2461 noctuid moth adults (811 in HM, 1650 in CA), belonging to 136 species and seventy-five genera, were trapped at light from April 1991 to March 1992. Only 847 of these moths (320 in HM, 527 in CA; 34.4% of total) belonged to species whose larvae had been collected during the foliage-beating sampling scheme. We will deal exclusively with this subset of light-trap catches (forty-eight species; Appendix 1), as these species may confidently be categorized as feeding on woody plants during part or all of their larval stage. In this set of species there was significant consistency at both sites in the rank order of abundances of individual species as larvae and adults (HM: $r_s = 0.483$, $N = 31$ species, $P = 0.006$; CA: $r_s = 0.396$, $N = 39$ species, $P = 0.013$). This result suggests that the species composition of adult samples was not too seriously

Table 3. Frequency of occurrence of noctuid larvae in samples from the woody plant species studied. Entries are proportions (%) of total sampling units on a given plant species (in parentheses) that yielded at least one noctuid larva, all dates combined.

Plant species	HM	CA
Evergreen species		
<i>Arbutus unedo</i>	2.84 (776)	1.39 (288)
<i>Daphne laureola</i>		3.31 (242)
<i>Erica arborea</i>	7.16 (531)	
<i>Juniperus oxycedrus</i>	0.41 (487)	2.26 (663)
<i>Juniperus phoenicea</i>		0 (390)
<i>Phillyrea angustifolia</i>	0.47 (422)	
<i>Phillyrea latifolia</i>	2.27 (660)	1.64 (730)
<i>Pistacia lentiscus</i>	0.38 (532)	
<i>Quercus roundifolia</i>	5.90 (695)	6.51 (768)
<i>Rubus ulmifolius</i>	0.57 (352)	1.23 (407)
<i>Viburnum tinus</i>	0 (612)	
Deciduous species		
<i>Acer granatense</i>		1.87 (320)
<i>Berberis hispanica</i>		0.65 (309)
<i>Crataegus monogyna</i>		2.33 (559)
<i>Pistacia terebinthus</i>	0.71 (422)	
<i>Quercus faginea</i>	5.19 (443)	5.39 (445)
<i>Rosa canina</i>	0.93 (324)	1.85 (542)
<i>Sorbus torminalis</i>	2.05 (341)	1.17 (428)

distorted by the potential biases inherent to the light trapping method.

Moth abundance indices (moths/day, all species combined) were computed separately for each trapping session at each site, by dividing the total number of moths caught during the session by the number of days the trap was in operation. The seasonal cycle of adult moth captures was markedly bimodal, with distinct peaks occurring in early summer (mid-July) and early autumn (late September to early October) (Fig. 2). The middle of the summer was characterized by a dearth of adult moths at light traps. This was particularly marked at HM, where two consecutive trapping sessions (on 11–15 and 18–22 August) yielded no adult moths of the species considered here. The relative magnitudes of the early-summer and early-autumn abundance peaks differed among sites. The early-summer peak was most marked at CA, while the reverse occurred at HM. At both sites the seasonal course of species richness (number of species per light-trapping session) paralleled that of moth abundance (Fig. 2).

Life cycles

The set of woody plant-feeding species considered in this study was characterized by a marked prevalence of univoltine taxa, in terms of both number of species (42/48 species) and the number of individuals (95.8% of larvae, 94.6% of adults, the two sites combined) (Appendix 1). The contrast between the seasonal patterns of abundance of larvae and adults (Figs 1 and 2) thus indicates that two distinct life cycles are represented among the woody plant-

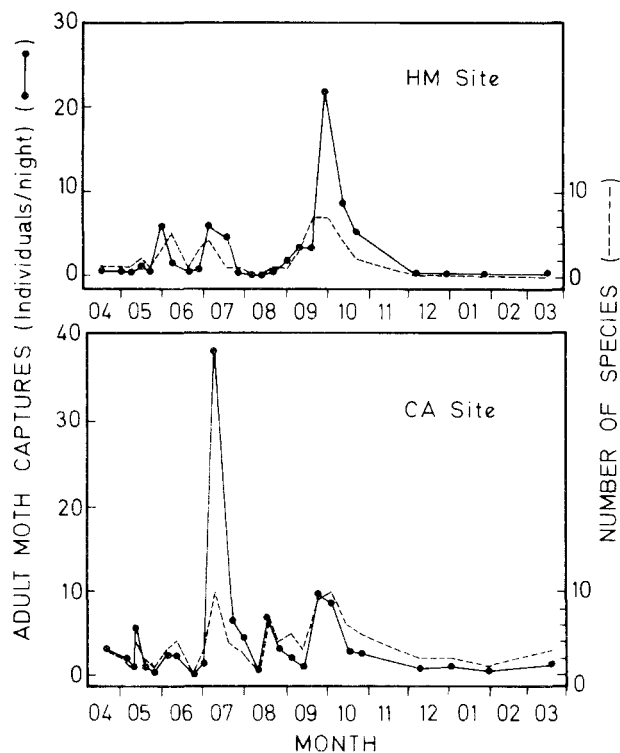


Fig. 2. Annual variation in abundance (filled dots, solid line) and number of species (dashed line) of adult noctuid moth captures in light traps at the two study sites, April 1991 to March 1992. Only species whose larvae were collected from some of the woody species studied were included in the computations. Each data point corresponds to a separate light trapping session.

feeding univoltine noctuids of the habitats studied. While all species were similar in having larval stages spanning a short period during spring, a noticeable dichotomy existed with respect to timing of adult emergence. Some species completed the pupal stage rapidly and the adults emerged in early summer (e.g. some *Catocala*, *Noctua*), whereas others spent the summer in the prepupal or pupal stages and adult emergence was delayed until the next autumn (e.g. *Agrochola*) or, less frequently, winter (e.g. *Conistra*) or early next spring (e.g. *Orthosia*). Individual univoltine species could thus be readily classed into either the 'short' (16 species; 37.9%) or 'long' (26 species; 62.1%) pupal stage groups (i.e. adults emerging before or after the summer, respectively) (Appendix 1). The emergence of adults belonging to each of these groups was responsible for the two major seasonal pulses of adult moth captures shown in Fig. 2.

The two major life cycles exhibited by univoltine species are significantly related to taxonomic affiliation at the subfamilial level. Life cycles are unevenly distributed among the five subfamilies contributing univoltine taxa to the species sample (Catocalinae, Cuculliinae, Ipimorphinae, Hadeninae, Noctuinae; Appendix 1). With only minor exceptions, short pupal periods are characteristic of species in the Catocalinae, Cuculliinae and Noctuinae,

Table 4. Duration of the pupal stage and taxonomic affiliation of univoltine noctuid moths considered in this study (see Appendix 1 for information on individual species). Adults of species with 'short' pupal stages emerge in early summer, while the emergence of species with 'long' pupal periods is delayed until early autumn, winter or next spring (see text). There is significant heterogeneity among subfamilies in the relative occurrence of these two life cycles ($P \ll 0.001$, Fisher exact probability test).

Subfamily	Pupal stage	
	Short	Long
Catocalinae	7	1
Cuculliinae	2	0
Ipimorphinae	2	19
Hadeninae	0	5
Noctuinae	5	1

while long pupal periods are mainly found among the Ipimorphinae and Hadeninae (Table 4).

Discussion

Average abundance of noctuid larvae on shrubs and trees was very low at both study sites. Even during the period of peak abundance, it was unusual to collect more than a few (two to four) larvae from a single tree or shrub, and these instances always involved *Catocala nymphagoga*, a species monophagous on oaks that exhibits episodic local outbreaks (Yela, 1989, and references therein). The possibility exists that low noctuid larval density recorded in this investigation is an uncommon situation in the habitats studied. The study year was characterized by an unusually cool and dry spring, and these weather conditions could have adversely affected the size of larval populations directly or via their influence on the phenology of plant growth. Limitations of the sampling method could also partly account for the low larval abundance observed. Although larvae of most noctuid species associated with woody plants seems to occupy preferentially the lowermost parts of the host plants (some particular examples are discussed by, e.g., Bergmann, 1954; Forster & Wohlfahrt, 1971), larvae of strictly tree-dwelling species (e.g. some *Agrochola*, *Acrontia* and *Catocala* species) living in tree crowns >3 m above the ground may have been missed by our sampling procedure.

Dominant evergreen plants provide abundant, year-round availability of foliage to herbivores at our study sites. Nevertheless, this study has shown that noctuid herbivory on evergreen hosts was not more extended in time than on co-occurring deciduous ones. Regardless of the leaf persistence habit of host plants, larvae were present on shrubs and trees only during a relatively short period in spring, when all host species (both evergreen and deciduous) were producing new leaves and exhibiting vigorous shoot growth (see also Templado, 1975, 1990).

Evergreen and deciduous species at the habitats studied did not differ appreciably in timing of leaf production in 1991, and larval phenology of woody plant-feeding noctuids tended to match closely the phenology of their host plants. From the viewpoint of noctuid larvae, therefore, evergreen and deciduous hosts represent similarly ephemeral food resources in the habitats studied. Average abundance of larvae (as assessed by frequency of occurrence in samples) did not differ significantly between evergreen and deciduous hosts within sites, and between habitat types differing in the relative importance (cover) of the two host plant types. This result contrasts with the findings of Blondel *et al.* (1991) and Blondel & Dias (1992), who found a greater abundance of lepidopteran larvae (all major groups combined) on deciduous host plants.

Leaf age has been repeatedly shown to be one of the most important attributes determining food selection by a variety of vertebrate and invertebrate herbivores. Water content, toughness and secondary chemistry, among other parameters, change with leaf age (Crawley, 1983). A decrease in maturing leaves of the nitrogen and water content, and an increase in structural (e.g. cellulose) and secondary compounds (e.g. resins, tannins), occur in many woody perennials (Feeny, 1970; Schweitzer, 1979; Niemelä & Haukioja, 1982; Janzen & Waterman, 1984; Johnson *et al.*, 1984). Young leaves probably are a superior larval food for most lepidopteran herbivores (Feeny, 1970; Schweitzer, 1979; Niemelä *et al.*, 1982; Mauffette & Oechel, 1989), and this may probably help to explain the spring peak in noctuid larval abundance found in this study. Mature leaves of temperate woody plants, however, are used regularly as food by larvae of many lepidopteran species (Niemelä & Haukioja, 1982; Niemelä *et al.*, 1982; Mauffette & Oechel, 1989). In our study habitats, second generation larvae of some of the bivoltine species recorded seem to feed on the mature leaves of evergreen and deciduous plants in summer (e.g. *Dysgonia algira*, *Eutelia adulatrix*, *Phlogophora meticulosa*). There were, however, only a few of such bivoltine species, and most of them were also comparatively scarce. This observation is consistent with the notion that the low food value of mature leaves of most Mediterranean woody plants may restrict the larval period of noctuids to the spring period, when the availability of young leaves is greatest. Furthermore, physiological changes induced by summer water stress on host plants may additionally contribute to limit larval growth and survival during the dry season (Watt, 1986; but see Miles *et al.*, 1982). It seems difficult to accept, however, that food chemistry alone can explain the virtual absence of noctuid larvae from woody plants during the summer. The unfavourableness of the physical or biotic environment is probably an important contributing factor (Janzen, 1985a, b). The dry and hot weather characteristic of the Mediterranean summer probably limits larval life during that adverse period. In support of this hypothesis is the observation that the proportion of bivoltine and multi-voltine noctuid species (with larval periods encompassing the summer) in riparian Mediterranean environments having more favourable summer microclimate is higher

than in the more xeric habitats studied here (Yela, 1992a, b). Heinrich (1979), Jeffries & Lawton (1984), Janzen (1985a, 1987, 1988b), Lawton (1986) and Fullard (1987), among others, have stressed the role that predators and parasitoids, in addition to the severity of the physical environment, may play in determining seasonal patterns and lepidopteran life histories. Although no information is yet available on the seasonality of the predator/parasitoid regime faced by caterpillars and adult moths at our study habitats, its influence cannot be ruled out.

In marked contrast with the unimodal seasonal pattern of larval abundance, the abundance and diversity of adults of woody plant-feeding noctuids exhibited two peaks in the course of the year. These occurred in early summer and early autumn, and were separated by a marked summer minimum. The two habitats studied differed in the relative importance of the two peaks, due mainly to the contrasting flight periods of the two species providing most captures at each site (the early autumn-flying *Ammopolia witzenmanni* was numerically dominant at HM, whereas the early summer-flying *Catocala nymphagoga* played this role at CA). This marked seasonal bimodality in noctuid adult captures has been previously reported from other Mediterranean-climate habitats at the Iberian Peninsula (e.g. Calle, 1974, 1983; Yela, 1980, 1992a, and the references therein) and thus seems to be a general phenomenon. A trend towards seasonal bimodality is also known from some mid-latitude temperate habitats (e.g. Wiltshire, 1938, 1941a, b; Hardwick, 1971; White, 1991), but is apparently absent from more northern, boreal ones (e.g. Ahola *et al.*, 1983).

In our study habitats (see also Soria, 1987, for similar results), the vast majority of (woody plant-feeding) adult moths captured belonged to univoltine species having fairly short, synchronous larval periods in spring, and species participating in each adult abundance peak differed (in those temperate habitats where seasonal bimodality occurs, it is largely originated by successive generations of numerous bivoltine species; e.g. White, 1991). This reveals the existence of two distinct life history patterns differing in the duration of the pupal stage. In the 'short pupal duration' group of univoltine species (SPD hereafter; e.g. *Catocala*, *Noctua*, *Pyramidcampa pyramidea*), larvae typically pupate in late spring or early summer, and adults emerge only 5–20 days later. Members of the 'long pupal duration' type (LPD hereafter), in contrast, also pupate (or, alternatively, enter diapause in the prepupal stage) in early summer, but remain in this stage until early autumn (e.g. *Trigonophora*, *Conistra*, *Ammopolia witzenmanni*, *Pseudenargia ulicis*) or, less frequently, next spring (*Orthosia*). Adult moths of species in the SPD group mate and start oviposition shortly after emergence in early summer (*Caerphya*, some *Catocala*, *Dicycla*, *Auchmis*), or remain as potentially active, non-reproductive adults over most of the summer, and mate by the end of that season (some *Catocala*, *Pyrois*, *Pyramidcampa*, *Noctua*). With the single exception of *Conistra*, LPD species mate shortly after emergence, in early autumn (e.g. *Agrochola*, *Lithophane*, *Allophyes*, *Dryobotodes*, *Ammopolia*) or the

next spring (*Minucia*, *Orthosia*). Species of *Conistra* emerge in autumn and do not mate until next spring.

The SPD and LPD life histories exhibited by univoltine species have in common the avoidance of summer as a flight time, and might thus be interpreted as alternative 'solutions' to get around that adverse season by entering dormancy as eggs or quiescent adults (SPD), or as prepupae or pupae (LPD). These three ways of passing the dry season have been also reported by Janzen (1987) for a tropical dry forest moth fauna, although the relative numerical importance of each modality differs from that observed in our study. A single species was reported by Janzen to spend the dry season in the egg stage, whereas as many as nine species in our much smaller species set exhibit this life history trait. This disparity may reflect different adaptive responses of moths to two contrasting ecological scenarios but also, given the strong phylogenetic component inherent in the SPD-LPD life history dichotomy documented in this study, it might simply be a consequence of contrasting taxonomic compositions of the two species assemblages.

This study has shown that the life cycles of woody plant-feeding noctuid moths in the Mediterranean habitats studied seem to be strongly constrained by the occurrence of a severe dry season, in a way analogous to that described by Janzen (1987, 1988a) for the whole moth species assemblage of a tropical dry forest. The adversity of the dry season's weather (directly or via their influence on plant phenological patterns) seems to have led to a species assemblage dominated (in terms of species and individuals) by univoltine species that concentrate their larval phases in spring, when young leaves are most abundant, and 'avoid' mid-summer as a flight time by emerging either shortly before or shortly after the summer drought period. A survey of previous investigations on adult noctuid moths conducted in the Iberian Peninsula indicates that the two seasonal peaks of adult abundance documented in this study occur also in other Mediterranean-climate localities, and that the more hot, dry and extended is the summer period of one locality, the more distinct and widely spaced are the two abundance peaks (Calle, 1974, 1980; Yela, 1980, 1992a; Bellavista, 1985; Olivella, 1985; Sarto i Monteyts, 1985; Palanca, 1987; Stefanescu, 1988; Garciamoreno *et al.*, 1989; Pérez López, 1989; Cifuentes, 1992), thus lending support to our interpretation. Future comparative studies on the life cycles of selected species at habitats differing in severity of the summer season should help to understand the adaptive basis of the life history traits discussed here. Of particular interest will be to discern whether the community-wide pattern of seasonal dichotomy in flight time of adult moths should be attributable to adaptations undergone by individual noctuid species in Mediterranean-climate scenarios or, alternatively, merely reflect species' exaptations (*sensu* Gould & Vrba, 1982) and have been brought about by 'ecological fitting' processes (*sensu* Janzen, 1985b). If noctuid subfamilies actually represent monophyletic groups (but see Scoble, 1992), then the strong phylogenetic component inherent in the two major life history styles described here

suggests that the latter alternative is at least a plausible possibility.

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Appendix 1. Summary of captures (number of individuals) of noctuid larvae and adults at the two study sites over the study period (April–October 1991 for larvae; April 1991 to March 1992 for adults). For adults, only those taxa with larval records were considered in this study. Duration of the pupal stage is shown only for univoltine species (S = short, L = long pupal stage, as defined in the text). Voltinism categories considered are univoltine (U) and bivoltine or potentially multivoltine (B). Subfamilial classification follows Fibiger & Hacker (1991) and Yela (1992a).

Subfamily Species	Voltinism	Pupal stage	HM site		CA site	
			Larvae	Adults	Larvae	Adults
Catocalinae						
<i>Catephia alchymista</i>	U	S	1	1		3
<i>Catocala conjuncta</i>	U	S			1	8
<i>Catocala conversa</i>	U	S	4	3	5	24
<i>Catocala dilecta</i>	U	S			1	
<i>Catocala nymphaea</i>	U	S	3	1	1	2
<i>Catocala nymphagoga</i>	U	S	49	47	48	253
<i>Catocala sponsa</i>	U	S			1	
<i>Dysgonia algira</i>	B		3	6	1	7
<i>Minucia lunaris</i>	U	L	3	10	7	8
Euteliinae						
<i>Eutelia adalatrix</i>	B		3	1		
Sarothripinae						
<i>Nycteola revayana</i> ¹	B		1	9	4	16
Acronictinae						
<i>Acronicta aceris</i>	B				1	7
Cuculliinae						
<i>Pyramidocampa pyramidea</i>	U	S	2	3	5	26
<i>Pyrois effusa</i>	U	S	1			
Ipimorphinae						
<i>Agrochola haematidea</i>	U	L	1			
<i>Agrochola helvola</i>	U	L	1	4	2	3
<i>Agrochola lychnidis</i>	U	L	3	4	1	
<i>Allophyes alfaroi</i>	U	L			5	5
<i>Ammopolia witzenmanni</i>	U	L	21	94	1	6
<i>Auchmis detersa</i>	U	S			2	
<i>Conistra alicia</i>	U	L			1	2
<i>Conistra ligula</i>	U	L			3	1
<i>Dicycla oo</i>	U	S	1		2	
<i>Dryobota labecula</i>	U	L			2	1
<i>Dryobotodes eremita</i>	U	L			1	1
<i>Dryobotodes monochroma</i>	U	L	1	2	1	8
<i>Eumichtis lichenea</i>	U	L			1	6
<i>Lithophane leautieri</i>	U	L	2		18	15
<i>Phlogophora meticulosa</i>	B		1		1	
<i>Polymixis argillaceago</i>	U	L			1	
<i>Polymixis flavicincta</i>	U	L	1			
<i>Pseudenargia ulcis</i>	U	L	2	18	5	11
<i>Spudaea ruticilla</i>	U	L	5		2	11
<i>Trigonophora jodea</i>	U	L	1		2	
<i>Trigonophora</i> spp. ²	U	L	7	66	6	39
Hadeninae						
<i>Orthosia cerasi</i>	U	L	13	2	16	9
<i>Orthosia cruda</i>	U	L	2			
<i>Orthosia gothica</i>	U	L		1	2	6
<i>Orthosia incerta</i>	U	L			2	
<i>Orthosia miniosa</i>	U	L			3	
Noctuinae						
<i>Noctua comes</i>	U	S	2	4		13
<i>Noctua fimbriata</i> ³	U	S	4		2	12
<i>Noctua janthe</i>	U	S		1	5	11
<i>Noctua pronuba</i>	U	S	2	12		13
<i>Xestia agathina</i>	U	L	37	31		
Noctuidae gen.sp.			5		17	
Total			182	320	179	527

¹ Includes *N.revayana* and *N.columbana*. ² Includes *T.flammea* and *T.crassicornis*. ³ Includes *N.fimbriata* and *N.tirrenica*.