Seasonal variation in leaf characteristics and food selection by larval noctuids on an evergreen Mediterranean shrub

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Abstract — Despite year round availability of foliage, abundance of generalist noctuid larvae (Lepidoptera: Noctuidae) in evergreen-dominated Mediterranean forests has a narrow, distinct spring peak. This restricted larval period has been suggested to result in part from avoidance of the nutritionally poor mature foliage, and preference for nutritionally superior spring-produced young leaves. This study examines this hypothesis by (i) documenting differences in nutritional characteristics between expanding (April) and mature (June) young leaves of the evergreen Mediterranean shrub *Daphne laureola* L. (Thymelaeaceae), and (ii) experimentally studying the feeding preferences of noctuid larvae for young leaves, old leaves (≥ 1 yr old), and developing fruits of this species in one south-eastern Spanish locality. Young leaves of *D. laureola* declined in nutrient concentration and specific dry mass from April to June. The responses of noctuid larvae, in terms of both relative preference and total consumption, to this seasonal variation in chemical and physical features of young leaves were also investigated. When noctuid larvae were simultaneously offered young leaves, old leaves and developing fruits, they exhibited similar preferences for young leaves and developing fruits, and rejected old leaves developed during the previous year. Noctuid larvae did not modify their consumption of young leaves relative to old leaves and developing fruits in response to seasonal changes. Food selection patterns exhibited by *D. laureola* noctuid herbivores, notably the rejection of old leaves in favour of young ones, are consistent with the hypothesis relating restricted larval periods of these generalist consumers with the low food value of the previous season leaves of evergreen Mediterranean plants. © 2000 Éditions scientifiques et médicales Elsevier SAS

Daphne laureola / evergreen plants / food selection / insect herbivory / Lepidoptera / Noctuidae / phenology

1. INTRODUCTION

Understanding the relationship between the phenology of insect populations and seasonality in food availability and abiotic conditions is central to our knowledge of insect life history evolution [13, 37, 39, 41]. A large number of studies conducted in a variety of ecological conditions have documented seasonal patterns in the size of herbivorous insect populations, and found close relationships between these seasonal rhythms and variation in both the quantity and quality of available food, and the abiotic environments [7, 14, 15, 29, 31]. For example, in habitats dominated by deciduous plant species, such as northern temperate forests, distinct seasonal peaks of caterpillar abundance coincide with the relatively short period when most plants are flushing new leaves. This has been interpreted as the consequence of adaptive adjustments of lepidopteran life cycles to match the peak in resource abundance and quality [9, 25]. Seasonal peaks in abundance of insect herbivores also take place in habitats dominated by evergreen plants, such as tropical rainforests [39, 40, 41] and Mediterranean forests and scrublands [43]. In these cases, fluctuations in food abundance alone cannot be the major factor responsible for the evolution of seasonality in the size of herbivore populations since foliage is available all year round. Seasonality in abiotic factors and food quality, among other factors, may be ultimately responsible for patterns of larval herbivore abundance in habitats dominated by evergreen species [10, 18].

In a study of seasonality and life cycles of woody plant-feeding noctuid moths in evergreen-dominated Mediterranean habitats of southern Spain, Yela and Herrera [43] found that the abundance of noctuid

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larvae peaked in May-June, shortly after host plants started to produce new leaves. Virtually no noctuid larvae were found on the evergreen foliage at other times of the year. These authors suggested that avoidance of low-quality mature leaves of evergreen species may be partly responsible for the restriction of the larval stage of the vast majority of noctuids to the spring period, thus eventually leading to patterns of larval herbivore abundance similar to those found in temperate habitats dominated by deciduous plants. Furthermore, developing fruits are also a food resource frequently eaten by noctuid folivores in Mediterranean habitats (C.M. Herrera, unpubl.), hence their seasonal availability could also influence larval abundance. The purpose of this paper is to provide evidence in support of these hypotheses for the particular case of the noctuid larvae associated with the evergreen shrub *Daphne laureola* in a south-eastern Spanish Mediterranean habitat. This was one of the plant species considered by Yela and Herrera [43], and the present investigation was conducted at one of their study sites. In addition to documenting differences in the physical and chemical characteristics of expanding (April) and mature (June) young leaves of *D. laureola*, the following specific hypotheses will be examined here: (i) *D. laureola* noctuid herbivores discriminate between young leaves, old leaves (≥ 1 yr old) and developing fruits when simultaneously available, and feed mainly on young leaves; (ii) relative preference for young leaves decreases along the season in response to changes in their nutritional characteristics; (iii) the efficiency of conversion of ingested food and the growth rate of larvae are also affected by leaf age.

2. METHODS

2.1. Study site

This investigation was carried out during April–June 1996 in the Sierra de Cazorla (Jaén province), in south-eastern Spain. We studied a marked population of *D. laureola* located in the Roblehondo area, at 1 235 m elevation. This was the 'CA site' of Yela and Herrera [43], and descriptions of the site may be found in previous studies [1, 2, 43].

2.2. Study organisms

Daphne laureola L. is an evergreen shrub that, in the Mediterranean region, occupies preferentially the undergrowth of mixed mountain forests [28]. This species has a strongly monopodial growth pattern, and shoot elongation takes place during several consecu-

tive seasons without branching [27]. Leaves are found only at the distal portion of each branch, forming a single well-defined rosette ('leaf whorl' hereafter). In the study region, flowering begins in early February, a few weeks before new leaves begin to grow. Expansion of new leaves is rather slow and takes place from mid-March to mid-May. Once leaf expansion has started, fruits (single-seeded drupes) begin to develop and they ripen in early/mid-June. Plants shed their oldest leaves in early summer, when the expansion of new leaves has finished. Hence during spring, leaf whorls simultaneously bear actively expanding new leaves ('young leaves' hereafter), leaves developed during the previous year ('old leaves' hereafter) and developing fruits.

In the study area, larvae of noctuid moths were the only herbivores recorded feeding on the foliage of *D. laureola* plants from late winter to early summer during three consecutive field seasons (1994–1996; C. Alonso, unpubl.). The species involved were *Trigonophora flammea* Esper., *Noctua janthe* Bkh., *Pseudenargia ulicis* Staud. and *Noctua fimbriata*. Like most species in the Noctuidae [12, 26], these are generalist consumers which also feed on a variety of other plants in the study area (e.g. *Narcissus longispathus*, *Paeonia broteroi*, *Helleborus foetidus*, *Primula vulgaris*). They have nocturnal habits, feeding on *D. laureola* leaf whorls during the night and spending daytime on the ground, hidden in the litter [2].

2.3. Leaf physical and chemical characteristics

Physical properties and chemical composition of *D. laureola* leaves were assessed on samples of both expanding (in late April) and fully expanded (in early June) young leaves collected from each of 28 marked individuals. On each sampling occasion, four to five leaf whorls were randomly selected on each plant, and three to four intact (i.e. without signs of herbivory) leaves were collected from each whorl, up to a total of eighteen leaves per plant. Leaves were removed with scissors, placed into sealed plastic bags and kept in a portable cooler to minimise water loss during transport to the field station. Individual leaves were fresh weighed, pressed flat, dried at 45 °C until constant mass, and then re-weighed. Leaves were then photocopied, their images digitised using a scanner, and their areas were subsequently measured using the NIH Image program (version 1.59 written by Wayne Rasband, US National Institutes of Health). Water percentage and specific leaf mass (mg·mm^{-2}) based on fresh and dry leaf mass were determined for April and June leaves.

In each sampling period (April and June), dry leaves from the same plant were pooled into a single sample and ground in a coffee mill. Chemical analyses were

conducted on these combined samples and, thus, two sets of analytical results, corresponding to April and June leaves, were obtained for each individual plant sampled. Analyses of N, P, K, Mg, Ca, Na, Cu, Fe, Mn and Zn concentrations were performed at the laboratories of the 'Instituto de Recursos Naturales y Agrobiología, Consejo Superior de Investigaciones Científicas', in Sevilla. Total N concentration was determined by the Kjeldahl method using a Technicon BD-40 Digestor Block for mineralization and Technicon AutoAnalyzer II for determination. For the other elements, samples were incinerated before analysis. K and Na concentrations were determined by flame spectrophotometry, vanadate-molibdate spectrophotometry was used for P determination, and atomic spectrophotometry for the other elements [8, 30].

2.4. Feeding experiments

Discrimination by caterpillars among different aged leaves and developing fruits of *D. laureola* was determined experimentally. Caterpillars used for trials were collected at night from *D. laureola* plants at the study population and placed individually into 15-cm Petri dishes. Larvae were deprived of food for 24 h before starting the experiments, which were conducted at night to resemble the normal activity period of these species. In each trial, we put in every Petri dish, one young *D. laureola* leaf (i.e. produced during the current season), one old leaf of similar area (i.e. produced the previous year), and three to five developing fruits. All vegetal structures in the same Petri dish were collected from the same individual plant and leaf whorl, to avoid the possible influence on results of intra-plant, among-whorl variation in food quality. Leaves and fruits used had no signs of herbivory.

Experiments were conducted at the same two dates as the collections of *D. laureola* leaves (late April and early June, 'April' and 'June' hereafter) to determine the effect of seasonal variation in young leaf characteristics on feeding preferences. Caterpillars were not sufficiently abundant in the field to perform feeding trials using plant parts from each of the 28 marked *D. laureola* plants, thus only a subsample of plants was used (five and two plants in April and June experiments, respectively). At the beginning of each experiment, we recorded the fresh mass of the offered leaves and fruits, and of each experimental caterpillar. Caterpillars were singly placed in the centre of the Petri dish and equidistant from the two leaves, which were in contact by one of their extremes. Developing fruits were placed between the two leaves. Room temperature during trials was ~ 13 °C in April and ~ 17 °C in June. This increase in temperature resembled the natural increment of temperature during the spring season. Larvae were allowed to feed for 4 h, then were

re-weighed and returned to the plants where they had been collected. At the end of each experiment, leaves and fruits were re-weighed. We also estimated the surface consumed by caterpillars from each type of leaf using a reticulated paper, and recorded the number of fully or partially eaten fruits. Five control Petri dishes, where no caterpillar was included, were added to the experiment and handled in the same way to estimate water loss rate of different plant structures during the experimental period. Regression models without intercept were conducted separately for each structure and used to determine the expected mass after the experiment when there was no consumption. The regression coefficients (± SE) obtained were 0.953 (± 0.004) for fruits, 0.954 (± 0.004) for young leaves, and 0.933 (± 0.004) for old leaves. These were used to compute expected post-experiment mass of structures in absence of consumption. The difference between real and expected mass was used as a quantitative estimate of consumed biomass.

We also analysed the variation in relative biomass consumption (RC = total biomass consumed/initial larval body mass), the efficiency of conversion of ingested food (ECI = [final – initial larval body mass]/total biomass consumed), and the growth relative to the initial body mass (RG = [final – initial body mass]/initial body mass) in relation to the type of food consumed and date of the experiment.

All the results shown in this paper refer to the $n = 38$ and 19 caterpillars that fed during the trials in April and June, respectively.

2.5. Data analysis

All analyses were performed using the SAS statistical package [33]. Variables related to leaf physical properties (area, fresh and dry mass, water percentage and specific mass) and mineral composition (concentration of individual nutrients) all reasonably satisfied the requirement of normality. Analyses of temporal variation in leaf characteristics at the population level were performed using mixed-model analyses of variance (Proc MIXED), and modelling the leaf characteristics data from the same plant on different collection dates as repeated measurements. Collection date (April vs. June) was the only fixed effect included in the models. The covariance structure was defined as compound symmetry for each individual plant, i.e. the plant random effect was defined as the subject term [19]. Individual leaf measurements of physical properties were nested within plants in these analyses.

The statistical significance of differences between experimental dates (April and June) in feeding preference and food consumption rate were tested by fitting generalized linear models (Proc GENMOD) to results from the feeding experiments. Variation in consump-

tion between dates was analysed using identity as the link function, since total consumed biomass was normally distributed. Preference for young leaves was modelled as the probability that one biomass unit eaten was from a young leaf. Accordingly, the dependent variable used in the model was the ratio of young leaf biomass consumed to total biomass consumed (%YOUNG hereafter), with binomial error distribution and probit link function. Over-dispersion problems associated with the binomial distribution models were controlled by estimating the dispersion parameter as Pearson's chi-square [33]. In the analyses of seasonal differences in both consumption rate and feeding preference, 'Date' (April vs. June) was the only effect tested in the models, and it was treated as a fixed effect. Caterpillar body mass, recorded just before starting feeding trials, was incorporated in the models as a covariate.

Larval RC, RG and ECI were analysed in relation to type of diet consumed and date of the experiment. Diet was classed into three non-overlapping categories, depending on whether the caterpillar fed on 'only young leaf', 'only developing fruits', or 'young leaf + fruits'. No caterpillar ate only old leaf during the feeding experiments, and the four individuals that consumed other combinations of food were excluded to reduce the diet classes to only the three most representative ones. Both diet and date were considered as fixed factors in the respective models. The interaction between diet and date was not statistically significant in any of the three models fitted, thus it was omitted.

3. RESULTS

3.1. Seasonal variation in leaf characteristics

Expanding (April) and final-sized (June) leaves of *D. laureola* differed significantly in all the physical properties considered (*table I*). Fresh and dry mass, leaf area, and water percentage increased, and dry and fresh specific mass declined, as leaves aged from April to June. Nutrient concentration of leaves also varied significantly between collection dates (*figure 1*). Only sodium and zinc concentrations did not vary significantly between dates. Nitrogen, phosphorus and iron were the elements exhibiting the most marked declines, and potassium and calcium the most marked increases, from April to June leaves.

3.2. Feeding experiments

The species composition of the caterpillars used in the experiments depended solely on their availability in the field. Most individuals used belonged to three species (twenty *Noctua janthe*, twelve *Pseudenargia ulicis* and twenty-two *Trigonophora flammea*). A fourth species (*N. fimbriata*) was scarce with only three individuals being used in the analyses. These species did not differ significantly in the type of selected diet when it was assessed by the amount of eaten biomass of different structures ($P = 0.44$; Fisher's exact-probability test). These results were also supported by an independent data set obtained in 1995 (data not shown). As there was no evidence of interspecific difference in food selection patterns, data from all the species will be combined in the analyses below.

3.2.1. Food preferences

In the feeding experiments, 59.6 % of the larvae consumed most biomass from developing fruits, 38.6 % from young leaves, and only 1.8 % from old leaves. Furthermore, no individual ate only old leaves during the feeding experiments. Thus, *D. laureola* leaves produced the previous season were clearly rejected by noctuid caterpillars. Apart from this discrimination, the proportions of caterpillars eating only young leaf, only fruits, or mixed diets did not differ

Table I. Seasonal variation in the physical characteristics of young (first year) *Daphne laureola* leaves. Values shown are model-corrected means and 95 % confidence limits (in parentheses) from the repeated-measures mixed-model ANOVA based on data from 28 individual plants (see Methods: Data analysis section). Wald's χ^2 and P values refer to tests of significance for between-date differences.

Variable	Collection date		Wald's χ^2	P
	April	June		
Fresh mass (mg)	197.2 (172.8–221.5)	395.2 (371.0–419.5)	1 153.1	< 0.0001
Dry mass (mg)	40.8 (35.5–46.0)	74.2 (68.9–79.4)	1 007.3	< 0.0001
Water percentage	78.9 (78.2–79.7)	81.1 (80.3–81.8)	236.3	< 0.0001
Leaf area (cm^2)	6.07 (5.49–6.67)	12.61 (12.0–13.19)	1 545.8	< 0.0001
Fresh specific mass (mg·mm^{-2})	0.33 (0.31–0.34)	0.31 (0.30–0.32)	53.2	< 0.0001
Dry specific mass (mg·mm^{-2})	0.069 (0.065–0.073)	0.059 (0.055–0.063)	279.5	< 0.0001

MACRONUTRIENTS

□ N
■ P
○ K
● Ca
▽ Mg
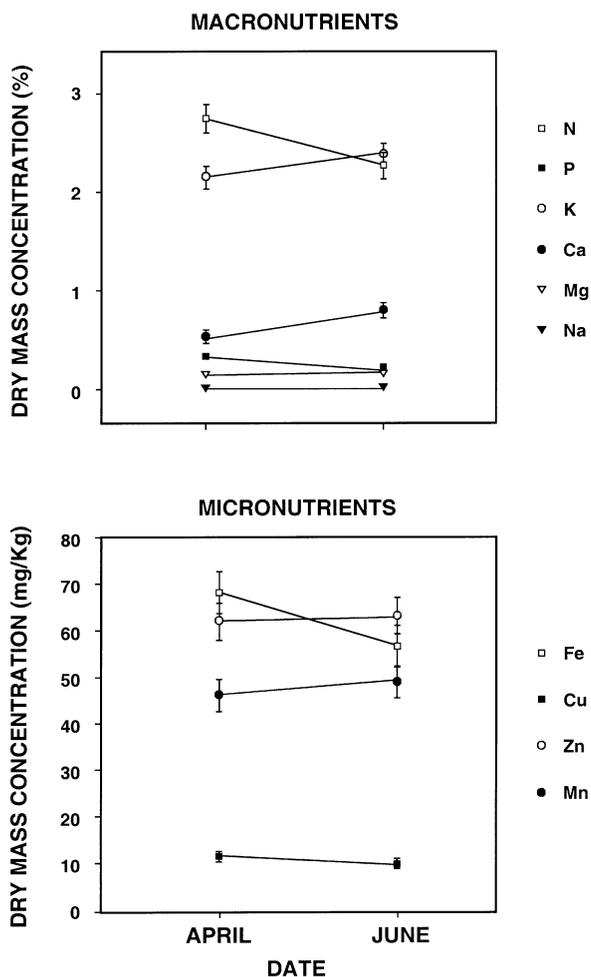▼ Na

MICRONUTRIENTS

□ Fe
■ Cu
○ Zn
● Mn

Figure 1. Variation in nutrient concentration of young *Daphne laureola* leaves collected on two different dates. Symbols represent average values for 28 individual plants, and bars the 95 % confidence intervals.

Figure 2. Frequency distribution of the proportion of young leaf (%YOUNG) consumed during experimental feeding trials ($n = 38$ and 19 for April and June, respectively).

significantly from those expected if caterpillars exhibited no selection (i.e. equal number of trials in each compared class) in the trials conducted in April ($\chi^2 = 1.0$, df = 2, $P = 0.6$). In contrast, there was a significantly higher proportion of caterpillars eating mixed diets during the trials conducted in June ($\chi^2 = 7.7$, df = 2, $P = 0.02$), suggesting a seasonal variation in diet selection.

However, when preference was modelled as a continuous binomial response variable (%YOUNG), no significant variation in this variable existed among dates (Wald's $\chi^2 = 0.92$, df = 1, $P = 0.33$) indi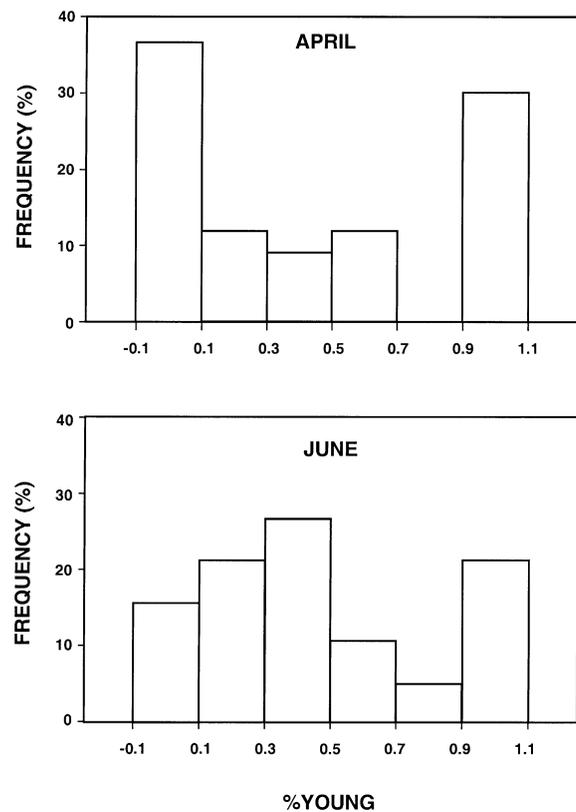cating that the proportional consumption of young leaves did not vary from April to June. Analysis of the distribution of the relative consumption of young leaf (%YOUNG) in April and June (*figure 2*) could, however, explain the apparent inconsistency of results. In April, there was a group of individuals that clearly preferred feeding on only developing fruits, a number of individuals that preferred young leaves, and a very small proportion of individuals that consumed intermediate quantities of both. In June, in contrast, the proportion of individuals with combined diets increased, even when there were also some individuals with clear preference for either fruits or young leaves (*figure 2*).

3.2.2. Variation in larval performance with diet and date

Relative food consumption (RC) was not significantly affected by date of experiment, but it was

Table II. Summary of analyses of variance testing for the effects of experimental date (April vs. June 1996) and preferred diet type ('young leaf', 'fruit', 'both') on three variables describing the performance of noctuid larvae (see text for definitions). Interactions between both factors were not significant in any of the three analyses, and were excluded from the models. Significant effects are shown in bold type.

Dependent variable	Date		Diet		Model R^2
	$F_{1,49}$	P	$F_{2,49}$	P	
Relative consumption	0.19	0.66	**13.04**	**< 0.0001**	0.35
Efficiency of conversion of ingested food	**14.97**	**0.0003**	0.05	0.95	0.28
Relative growth	**7.92**	**0.007**	**4.19**	**0.02**	0.27

significantly affected by diet type (*table II*). Larvae feeding on young leaf only had a statistically significant lower RC than those eating either fruits or mixed diets (*figure 3*). The efficiency of conversion of ingested food (ECI) was significantly affected by date but not by diet type (*table II*), with efficiency being lower in June experiments (0.20 mg larva·mg^{-1} leaf on average) than in April (0.63 mg larva·mg^{-1} leaf). Relative growth rate (RG) was significantly affected by both date and diet (*table II*). RG was lower in June experiments (mean RG = 0.08 vs. 0.18 recorded in April), and for larvae feeding on only young leaves (*figure 3*). Date and diet type explained 22.1 and 11.5 % of variance in RG, respectively.

4. DISCUSSION

Leaf age has been repeatedly shown to be one of the most important attributes determining food selection
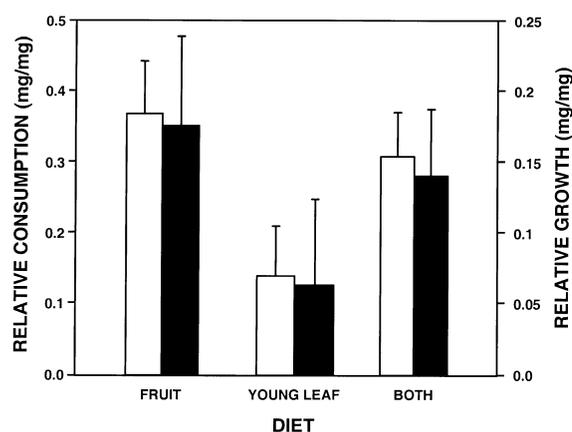

Figure 3. Consumption (white bars) and growth (black bars) relative to larval body mass on individuals feeding on young leaves, fruits or both. Columns indicate model-corrected means and bars 95 % confidence intervals.

by a variety of vertebrate and invertebrate herbivores. Water percentage, toughness, and secondary chemistry, among other parameters, change with leaf age [32]. The decrease in nitrogen concentration in maturing leaves, and the parallel increase in structural (e.g. cellulose) and secondary compounds (e.g. resins, tannins) commonly occurring in woody perennials make young leaves a superior larval food for most lepidopteran herbivores [9, 16, 17, 23, 25, 35]. This probably helps to explain the spring peak in abundance of noctuid larvae found in evergreen-dominated Mediterranean habitats despite year round foliage availability [43]. The main objective of this research was to test whether variation in food quality could be related to spring peak abundance of herbivorous insects in one evergreen species *D. laureola*.

As found for many other plant species (e.g. [18, 32]), younger developing leaves of *D. laureola* were richer in nitrogen, phosphorous and iron than older ones, with differences in nitrogen concentration around 0.6 %. This variation suggests that, from the viewpoint of herbivores, the nutritional quality of leaves declined during development (e.g. [21, 22, 36]), the only exception being the increased percentage of water in fully developed leaves. On the basis of nutritional considerations, therefore, one would have expected noctuid larvae to decrease their relative consumption from April to June if there was no compensatory feeding [24], or at least a less marked relative preference for young leaves. There was not, however, a significant effect of date on relative consumption. The same was also true for the probability of consumption of young leaves during feeding trials, that did not differ significantly among dates. The efficiency of conversion of ingested food (ECI) decreased significantly from the April to the June experiments in accordance with the decline in quality of young leaves, and might be also related to the observed increment of mixed diets. Change in tempera-

ture between experiments could have also affected the ECI; however, the expected trend was just the opposite, i.e. an increase of ECI in June when experimental temperature was higher. Thus, seasonal decline in *D. laureola* young leaf quality may negatively affect herbivores' performance through ECI and growth, but it does not constitute an advantage from the plant's point of view since relative consumption does not vary.

Other lepidopteran species feeding on evergreen plants have developed different behavioural and physiological strategies to cope with the problem of temporal variation in food availability and quality (e.g. [6, 18]). The increased frequency of trials yielding mixed diets in the June experiments (*figure 2*) indicates a seasonal change in self-selection behaviour of noctuid larvae [38], suggesting that in June (i) either young leaves, fruits or both are not considered good quality foods and, thus, caterpillars try to find better resources encouraged by absence of movement costs [5], or (ii) there is a complementary value of feeding in mixed diets [3] in last instar larvae. Both aspects must be analysed in detail to understand the nutritional reasons of larval predisposition to eating fruits. The lowest consumption and growth of larvae feeding on only young leaves (*figure 3*) suggests that effectively leaves are not the best nutritive option that *D. laureola* plants offer to noctuid caterpillars, and, apparently, their strategy would be to also include fruits in the diet.

Inferences on herbivore consumption based on preference trials such as those conducted in this study, although allowing for precise quantitative assessment of preferences, have been criticised because their artificial simplicity could modify herbivores' behaviour [4]. We used in the experiments exactly the same food that caterpillars were feeding on in the field, and larvae were field-collected rather than laboratory-raised, which makes us confident that their food selection patterns reflected their natural feeding behaviour. Nevertheless, some factors unaccounted for in our experimental design could have affected feeding behaviour, such as ambient temperature (e.g. [42]), which was slightly higher and less variable than in the field, and absence of movement costs to look for the meal [34]. There were no reasons to expect, however, that these differences affected food preference of experimental caterpillars in any major way (but see below).

The abundant consumption of developing fruits by captive caterpillars found in this study suggests one further potentially important element in the *D. laureola*-noctuid system. It must be noted, however, that regular nocturnal observations on plants conducted over several growing seasons for other investigations [1, 2] revealed noctuid larvae feeding on young leaves much more often than on developing fruits. This discrepancy between field observations and experimental results is probably related to differences in the probability of encountering the three structures in the field, in contrast with the equiprobability situation in the Petri dishes. In the field, when caterpillars reach the leaf whorls after climbing along the stems, they find first old leaves and then young leaves. Fruits are much less conspicuous, and not always present in a certain leaf whorl, thus even if larvae might prefer to feed on fruits, these are rarer in the field than in Petri dishes. In any case, consumption of developing fruits by predominantly folivorous herbivores deserves closer examination in future investigations, as plant fitness might be more strongly affected by this phenomenon than by defoliation itself [11].

Finally, noctuid larvae feeding on *D. laureola* unambiguously avoided feeding on old leaves when they were offered simultaneously with young leaves and developing fruits, suggesting the absence of natural consumption of leaves after their growing season [20], and the unsuitability of these leaves as a food source. At least in this species, evergreeness is not synonymous with year round availability of suitable food for its herbivorous insects, as old leaves remained largely unused as a food resource, and the decline of young leaf quality also affected insect's performance. Both results thus suggest that seasonal variation in the quality of food contribute to the observed seasonality of insect herbivores [43].

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