Interaction of foliage and larval age influences preference and performance of a geometrid caterpillar

Lauren Pinault[1,2]

Population Ecology Group, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 6C2

Graham Thurston

Population Ecology Group, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 6C2, and Atlantic Forestry Centre, Canadian Forest Service, Natural Resources Canada, P.O. Box 4000, Regent Street, Fredericton, New Brunswick, Canada E3B 5P7

Dan Quiring

Population Ecology Group, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 6C2

Abstract—In two recent studies it was reported that feeding on foliage of multiple age classes can improve insect fitness, but it was not determined whether the increase in fitness was due to larvae obtaining a more balanced diet (the balanced-diet hypothesis) or to a difference in the nutritional requirements between young and old larvae (the ontogenetic hypothesis). To test these two hypotheses, we examined the foraging behaviour and performance of young (second or third to fourth instar) and old (third or fourth to fifth instar) larvae of the pale-winged gray moth, *Iridopsis ephyraria* (Walker) (Lepidoptera: Geometridae), on different-aged foliage of eastern hemlock, *Tsuga canadensis* (L.) Carrière (Pinaceae), during an outbreak in southwestern Nova Scotia. Defoliation attributed to *I. ephyraria* was highest on current-year foliage and gradually declined with foliage age. Young larvae were only observed feeding on current-year shoots but old larvae fed on foliage of all ages. When forced to feed on foliage of specific ages in manipulative field studies, survival rates of young and old larvae were highest on current-year and old (≥1 year old) foliage, respectively. However, both young and old larvae had higher survival rates when provided with access to foliage of all age classes than when they were forced to feed on only young or old foliage. Thus, this study supports both the balanced-diet and ontogenetic hypotheses.

Résumé—Deux études récentes indiquent que l'alimentation sur du feuillage appartenant à plusieurs classes d'âge peut augmenter la fitness des insectes, mais elles ne mentionnent pas si l'amélioration de la fitness est due à un régime alimentaire mieux équilibré chez les larves (hypothèse du régime équilibré) ou à des besoins nutritifs différents chez les larves jeunes et âgées (hypothèse ontogénique). Afin de tester ces deux hypothèses, nous avons examiné le comportement de recherche de nourriture et la performance chez des larves jeunes (de second ou troisième à quatrième stades) et âgées (troisième ou quatrième à cinquième stades) de l'arpenteuse à taches, *Iridopsis ephyraria* (Walker) (Lepidoptera: Geometridae), sur du feuillage d'âges différents de la pruche, *Tsuga canadensis* (L.) Carrière (Pinaceae) durant une épidémie dans le sud-ouest de la Nouvelle-Écosse. La défoliation attribuée à *I. ephyraria* est maximale sur le feuillage de l'année courante et elle décline graduellement en fonction de l'âge du feuillage. Les jeunes larves se nourrissent seulement des pousses de l'année courante, alors que les larves âgées s'alimentent de feuillage des tous les âges. Lorsque forcées de s'alimenter sur du feuillage d'âge donné lors de

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[1] Corresponding author (e-mail: lauren.pinault@gmail.com).
[2] Present address: Department of Biological Sciences, Brock University, St. Catharines, Ontario, Canada L2S 3A1.

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manipulations de terrain, les jeunes larves survivent mieux sur du feuillage de l'année courante et les larves âgées sur du feuillage plus vieux (≥1 an). Néanmoins, les larves, jeunes et âgées, ont une survie plus grande lorsqu'elles ont accès à du feuillage de tous âges que lorsqu'on les force à se nourrir seulement de feuillage jeune ou vieux. Notre étude appuie donc à la fois l'hypothèse du régime équilibré et l'hypothèse ontogénique.

[Traduit par la Rédaction]

Introduction

The nutritional quality of foliage for herbivorous insects often changes rapidly with foliage age and consequently most insects specialize on either young or old foliage (*e.g.*, Reichle *et al.* 1973; Root 1973; Rausher 1981; Damman 1987; Carisey and Bauce 1996). However, some insects consume foliage of a variety of ages. For example, sawfly larvae (Hymenoptera) (Ikeda *et al.* 1977; Jensen 1988; Moreau *et al.* 2003; Parsons *et al.* 2003) and the ramie moth, *Arcte coerulea* (Guenée) (Lepidoptera: Noctuidae) (Ide 2006), consume foliage of a mixture of older age classes. Presumably, a mixed diet of foliage of different ages could allow larvae to obtain a better balance of water and nutrients while minimizing the uptake of harmful allelochemicals (Cates 1980; Schroeder 1986; Moreau *et al.* 2003). It was recently reported from both a laboratory study with a caterpillar (Carroll 1999) and a manipulative field study with a sawfly (Moreau *et al.* 2003) that herbivore performance was improved by feeding on conifer foliage of multiple age classes (the balanced-diet hypothesis). Feeding on foliage of different ages might also allow larvae to avoid natural enemies at certain times of the day (Damman 1987; Hunter 2003).

Alternatively, a mixed diet of foliage of different ages might result from variations in the feeding patterns of younger *versus* older larvae (the ontogenetic hypothesis). Young and old instars might have different nutritional requirements with respect to water, nutrients, and toxin content in foliage (Cates 1980; Schroeder 1986), or young larvae might be limited to younger foliage because of the physical feeding barrier presented by toughened, older foliage (Bernays *et al.* 1991; Hochuli 2001). Some Lepidoptera, such as the New England buck moth, *Hemileuca lucina* Hy. Edwards (Saturniidae), and the hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenée) (Geometridae), feed on the young foliage of current-year shoots as young instars but consume a mixed diet as older instars (Stamp and Bowers 1990; Raske *et al.* 1995).

In this study we evaluated both the balanced-diet and ontogenetic hypotheses using field surveys and manipulative field experiments with the pale-winged gray moth, *Iridopsis ephyraria* (Walker) (Lepidoptera: Geometridae), an indigenous defoliator of eastern hemlock, *Tsuga canadensis* (L.) Carrière (Pinaceae), that feeds on both current-year and older foliage. If the balanced-diet hypothesis is valid, larvae should feed on foliage of multiple age classes and larval fitness should be highest when they feed on a mixed diet. If the ontogenetic hypothesis is valid, young larvae should primarily feed and attain their highest fitness on young foliage, and older larvae should primarily feed and attain their highest fitness on old foliage. However, the balanced-diet and ontogenetic hypotheses are not mutually exclusive.

Materials and methods

Study insect

Iridopsis ephyraria caterpillars were well suited for study of the balanced-diet and ontogenetic hypotheses because preliminary observations suggested that they consume foliage of all ages. In preliminary observations, young larvae appeared to feed primarily on current-year foliage, whereas later instars consumed foliage of a mixture of older ages. The pale-winged gray moth severely defoliated stands of eastern hemlock in southwestern Nova Scotia between 2001 and 2003, after which the population gradually declined. There is no previous record of an outbreak of *I. ephyraria* in the refereed literature, although the species is widely distributed from Alberta to Nova Scotia and south to Texas (Ferguson 1954; McGuffin 1977). In Nova Scotia, larvae emerge in May or June, pass through five instars, and pupate in mid-July (Pinault *et al.* 2007). Adults are active in early August, when females lay eggs singly on the boles of mature eastern hemlocks. Larvae consume a wide variety of plants, most notably eastern hemlock (Pinault *et al.* 2007).

The range of eastern hemlock extends from southeastern Canada south to Georgia and west to Minnesota (Godman and Lancaster 1990). In Nova Scotia, eastern hemlocks produce new, brightly coloured shoots between May and July (L. Pinault, personal observation). Needles of different ages along a branch are distinguished by bud scars along the main axis of the branch as well as by a slight change in branch direction.

Foraging behaviour of larvae in nature

The locations of larval feeding on a branch were observed at four study sites in 2004 at Kejimkujik National Park and National Historic Site (KNP; 44°23′N, 65°13′W) in southwestern Nova Scotia, Canada. At each site, one upper and one lower crown branch were tagged on each of 10 small (<3 m tall), understory eastern hemlock (hereinafter hemlock) trees prior to egg hatch. Current-year to 3-year-old foliage on study branches was carefully searched for feeding larvae. The position of larvae on the branch was recorded on 18 June, 28 June, and 15 July, when most were second, third, and fifth instars, respectively.

To assess caterpillar preference for a particular age of foliage in mature trees, we measured defoliation attributable to *I. ephyraria* at 7 study sites in 2005 and 19 sites in 2006. All sites were located within 30 km of KNP. At each site, 30 mature hemlock trees, each separated by at least 7 m, were selected along 1–3 linear transects. Using binoculars, one observer estimated defoliation of current-year to 3-year-old foliage along the main axis of one haphazardly chosen midcrown branch. The mature hemlock trees were too tall to permit the use of more traditional sampling methods, such as pole pruning. Natural needle fall occurred at 4 years of age and older, therefore these foliage ages were not included in the analysis. Defoliation estimates were categorized into 10% defoliation classes as in Parsons *et al.* (2003) and Pinault and Quiring (2008). Seasonal percent defoliation was calculated by taking the difference between estimates from late July (following pupation) and early June (prior to egg hatch).

To assess caterpillar preference for a particular age of foliage in immature trees, small (<3 m tall), understory hemlock trees, each separated by at least 3 m, were selected along a linear transect at four (2004) or five (2005) of the sites described above. Ten trees per site were selected in 2004; this number was increased to 30 trees per site in 2005. Defoliation along the main axis of a randomly chosen midcrown branch was visually estimated as in Pinault and Quiring (2008).

Performance of larvae on different-aged foliage

To assess the performance of larvae that fed on foliage of different ages, we caged larvae on midcrown branches of 25 small (<3 m tall) hemlock trees at a site in KNP with little (<10%) previous defoliation in 2006. On each study tree, three branches were each enclosed in a nylon mesh sleeve cage and randomly assigned to one of three dietary treatments: current-year foliage only, old (1–6 years) foliage only, or a mixed diet of foliage of different ages (*i.e.*, the entire branch, which included current-year to 6-year-old foliage). Five second-instar (hereinafter young) larvae were collected from nearby hemlock foliage and placed in each sleeve cage and the cage was closed with twist ties attached around the outside. First instars were not used in this experiment because of the difficulty of locating adequate numbers of the extremely small larvae (<1 mm in length; Pinault *et al.* 2007) when field densities are low, as they were in 2006. Larvae in the current-year foliage treatment were restricted to current-year foliage by placing a twist tie around the outside of the cage on the border between the current-year and 1-year-old foliage. Larvae in the old-foliage treatment were excluded from the current-year foliage in the same way. Larvae were monitored throughout development to ensure that foliage of at least 50% of age classes remained (*i.e.*, was not consumed). When the majority of larvae were in the third or fourth instar (approximately halfway through larval development; Pinault *et al.* 2007), all larvae were removed and survival was determined for early instars. Five new third- or fourth-instar (hereinafter old) larvae were collected from nearby trees and placed in a study cage on the same branch. Cages were removed after adult eclosion had finished and inspected for survivors, and survival until pupation (late-instar survival) was determined for each cage. Each period spent in the cage was approximately 2 weeks in duration for both young and old instars. Pupal survival was not recorded because *I. ephyraria* larvae pupate in soil, and pupae in the sleeve cages desiccated quickly. Gender and wing length were determined for adults that emerged in the

Table 1. Summary of nested ANOVA assessing the influence of date (D), foliage age (F), tree (T), and site (S) on the locations where *Iridopsis ephyraria* larvae were observed feeding.

	df			
Source of variation	Numerator	Denominator	F	P
S	3	36	9.94	<0.001
T (S)	36	480	1.96	<0.001
F	3	9	17.11	<0.001
D	2	6	2.59	0.150
S × F	9	108	9.83	<0.001
S × D	6	72	22.53	<0.001
F × D	6	18	3.88	0.012
F × T (S)	108	480	1.96	<0.001
D × T (S)	72	480	1.06	0.350
S × F × D	18	216	20.83	<0.001
F × D × T (S)	216	480	1.09	0.220
Error	480			

sleeve cages and had undamaged wings when collected.

Statistical analysis

The numbers of larvae observed on foliage of different ages were compared using a four-way analysis of variance (ANOVA) with site and tree (nested within site) as random factors and date and foliage age as fixed factors, as well as all possible interactions.

For both mature and small trees, percent defoliation along a branch was assessed with a split-plot analysis of covariance (ANCOVA) because foliage ages were grouped by branch nested within site with foliage age, site, and the interaction between the two as testable factors. Previous percent defoliation was included as a covariate because this influenced the amount of foliage initially available to be consumed. Defoliation was assessed repeatedly between years at some sites, so separate analyses were conducted for each year. Defoliation of mature trees in 2005 was power-transformed ($X^{0.11}$) and defoliation of small trees in 2005 was log-transformed to meet the assumption of homogeneity of variances.

The covariate of previous percent defoliation was not independent of foliage age and so we also performed a repeated-measures multivariate analysis of variance (MANOVA) with each foliage age as a separate variable, followed by polynomial orthogonal contrasts to compare defoliation levels between foliage ages. Because the results from the MANOVA were similar to those from the ANCOVA, only the ANCOVAs and the polynomial orthogonal contrasts are described.

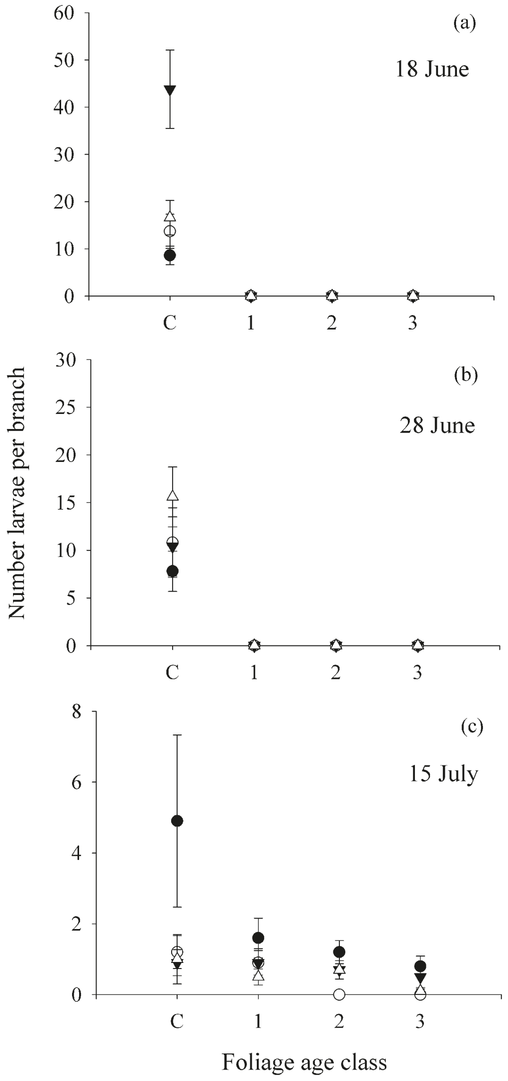
The performance of larvae in sleeve cages was compared using a split-plot ANOVA because study branches were grouped within tree with larval age (young or old), foliage age, and the interaction of the two as factors. Proportion surviving was power-transformed ($X^{0.25}$) to meet the assumption of homogeneity of variances. Variation in adult wing length was assessed using a two-way ANOVA with foliage age and moth gender as factors.

Results

Foraging behaviour of larvae in nature

Foliage age explained a significant proportion of the variation in the locations where larvae were observed feeding in nature (Table 1), with most caterpillars found on current-year shoots (Fig. 1). On the first two sampling dates, second and third instars were only observed feeding on current-year foliage (Figs. 1*a*, 1*b*). On 15 July, older instars consumed foliage of a mixture of ages (Fig. 1*c*), resulting in a significant interaction between foliage age and date (Table 1). We observed higher numbers of late-instar larvae on current-year foliage at only one site (Fig. 1*c*), leading to a significant foliage age × date × site interaction (Table 1). Site, tree, and site × foliage age, site × date, and foliage age × tree interactions all explained some of the variation in larval density (Table 1), likely reflecting a high natural variability among trees and sites.

Fig. 1. Number of *Iridopsis ephyraria* larvae per branch (mean ± SE) feeding on different-aged foliage (current (C) and 1–3 years old) on small, understory eastern hemlock trees at four sites at Kejimkujik National Park and National Historic Site, Nova Scotia, on three dates in 2004. Different symbols represent different sites. Note the differences in *y*-axis scales.



Foliage age explained a significant proportion of the variation in percent defoliation on mature trees in 2006 but was marginally insignificant in 2005 (Table 2). Larvae consumed a greater proportion of current-year than older foliage (Fig. 2). Polynomial orthogonal contrasts from the repeated-measures MANOVA indicated that for foliage of all ages, defoliation levels were significantly different in 2006, except for current-year foliage *versus* 2-year-old (t_{551} = 0.046, P = 0.276) and 3-year-old foliage (t_{551} = –0.015, P = 0.730). Previous defoliation explained most of the variation in defoliation levels (Table 2), because previous high defoliation levels resulted in less older (*i.e.*, ≥1 year) foliage being available for consumption (Fig. 2). In both years, percent defoliation varied among sites and was influenced by the interaction between site and foliage age (Table 2), the latter probably resulting from variations in the defoliation pattern at some of the study sites.

As with the mature trees, *I. ephyraria* larvae consumed a higher proportion of the current-year than old foliage on small understory trees (Fig. 3). However, presumably because of previous high levels of defoliation that varied among sites, the interaction between foliage age and site, but not the main effect of foliage age, was significant (Table 3). Site and previous percent defoliation also explained a significant proportion of the variation in defoliation levels (Table 3).

Performance of larvae on different-aged foliage

Foliage age explained a significant proportion of the variation in larval survival ($F_{2,48}$ = 24.56, $P < 0.001$). Both young and old larvae survived best on a mixed diet, *i.e.*, foliage of different ages (Fig. 4). Although the survival rates of young and old larvae were similar ($F_{1,24}$ = 3.14, P = 0.09), there was a significant interaction between larval age and foliage age ($F_{2,48}$ = 6.08, $P < 0.005$). This was due to differences in responses to foliage of different ages by young *versus* old larvae and perhaps to the higher rate of survival of young than of old larvae when feeding on a mixed diet. When forced to feed on only young or old foliage, the rate of survival of young larvae was higher on young foliage, whereas that of old larvae was higher on old foliage (Fig. 4).

Wing lengths of adults that had developed on old foliage or on the mixed diet were not influenced by foliage age ($F_{1,31}$ = 0.37, P = 0.49), gender ($F_{1,31}$ = 0.01, P = 0.92), or the interaction of the two ($F_{1,31}$ = 0.77, P = 0.39). Wing lengths of adults from the treatment cages with current-year foliage were not analyzed because we obtained only three adults with undamaged wings from this treatment.

Table 2. Summary of split-plot ANCOVAs evaluating the influence of foliage age on defoliation by *Iridopsis ephyraria* larvae on mature eastern hemlock trees during each of two years.

	2005			2006		
Source of variation	df	*F*	*P*	df	*F*	*P*
Between plots						
Site	6	12.22	<0.001	18	5.06	<0.001
Error [tree (site)]	203			551		
Within plots						
Foliage age	3	2.89	0.064	3	8.08	<0.001
Site × foliage age	18	4.41	<0.001	54	5.80	<0.001
Error [foliage age × tree (site)]	608			1652		
Previous defoliation	1	145.37	<0.001	1	463.96	<0.001

Note: Data from 2005 were power-transformed ($X^{0.11}$) prior to analysis.

Fig. 2. Percent defoliation (mean + SE) of current (C) and 1- to 3-year-old foliage on mature eastern hemlock trees near Kejimkujik National Park and National Historic Site in 2005 (7 sites) (*a*) and 2006 (19 sites) (*b*). Previous defoliation (solid bars) and final defoliation (open bars) were measured just before and after feeding by *Iridopsis ephyraria* larvae, respectively. Seasonal defoliation is the difference between the two measurements.

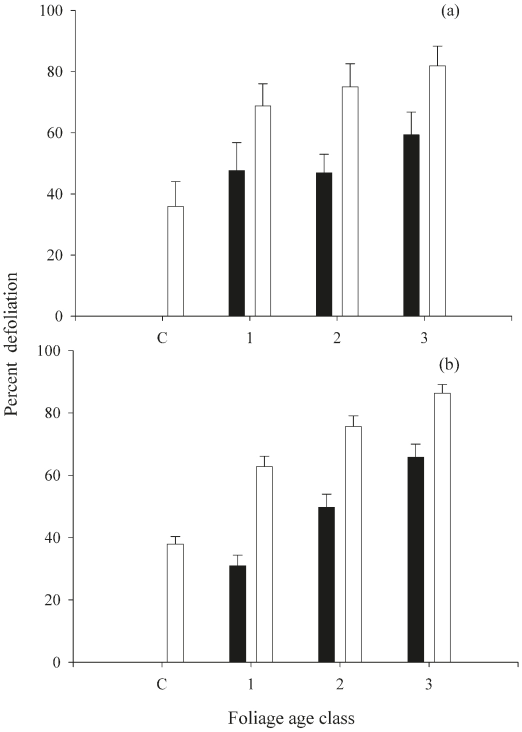


Fig. 3. Percent defoliation (mean + SE) of current (C) and 1- to 3-year-old foliage in small, understory eastern hemlock trees near Kejimkujik National Park and National Historic Site in 2004 (4 sites) (*a*) and 2005 (5 sites) (*b*). Previous defoliation (solid bars) and final defoliation (open bars) were measured just before and after feeding by *Iridopsis ephyraria* larvae, respectively. Seasonal defoliation is the difference between the two measurements.

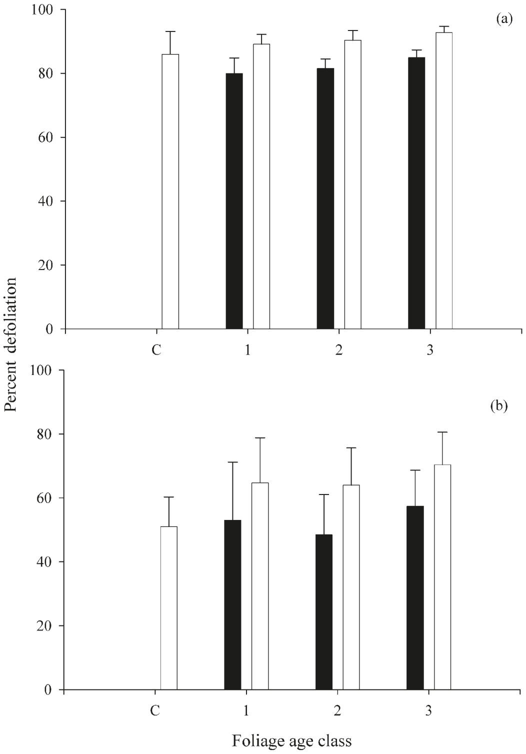
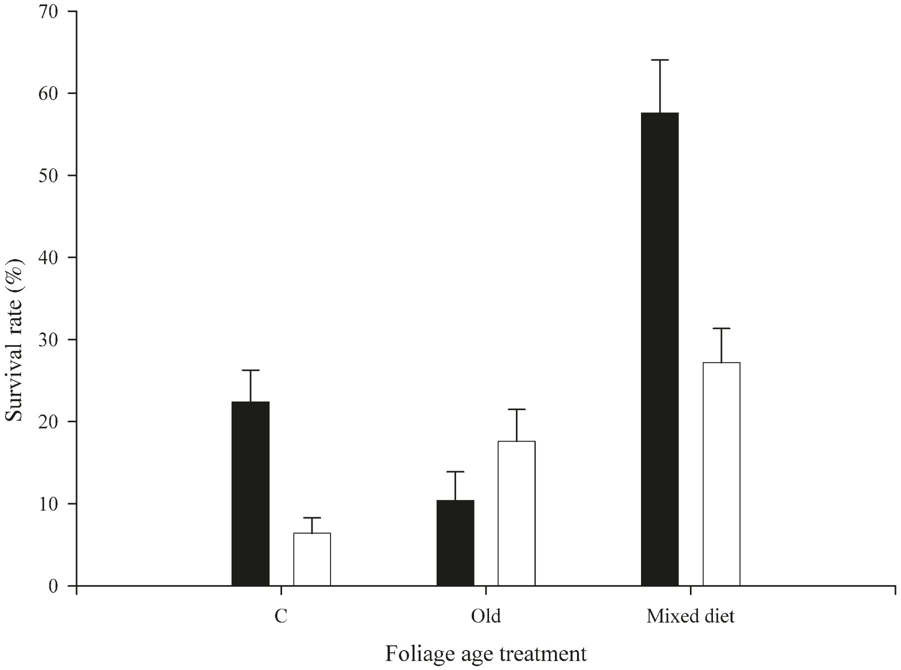


Table 3. Summary of split-plot ANCOVAs evaluating the influence of foliage age on defoliation by *Iridopsis ephyraria* larvae on small, understory eastern hemlock trees during each of two years.

	2004			2005		
Source of variation	df	*F*	*P*	df	*F*	*P*
Between plots						
Site	3	4.11	0.013	4	4.98	<0.001
Error [tree (site)]	36			145		
Within plots						
Foliage age	4	0.99	0.450	3	0.34	0.800
Site × foliage age	12	6.93	<0.001	12	5.23	<0.001
Error [foliage age × tree (site)]	143			434		
Previous defoliation	1	68.89	<0.001	1	132.02	<0.001

Note: Data from 2005 were log-transformed prior to analysis.

Fig. 4. Rates of survival (mean + SE) of young (solid bars) and old (open bars) *Iridopsis ephyraria* larvae feeding on current-year (C) or old (1–6 years) foliage or on both current-year and old foliage (mixed diet) on eastern hemlock trees near Kejimkujik National Park and National Historic Site in 2006.



Discussion

The results of this study support both the balanced-diet and ontogenetic hypotheses. The superior performance of both young and old larvae on a mixed diet supports the balanced-diet hypothesis. Similarly, the higher rate of survival of young larvae on current-year than on old foliage, combined with the opposite result for old larvae, supports the ontogenetic hypothesis.

Superior performance on a mixed diet may be due to the uptake of an optimal amount of nutritional components, such as nitrogen, while minimizing the uptake of growth-limiting toxins often present in foliage at specific ages (Cates 1980; Schroeder 1986; Moreau *et al.* 2003). In future studies it might be useful to examine the different dietary requirements of young *versus* old larvae that might lead to the consumption of a balanced diet.

The higher rates of survival of young larvae on current-year than on old foliage may be due to higher water content and nitrogen concentration in young leaves (Cates 1980; Schroeder 1986;

Hatcher 1990). Foliage water content had the strongest effect on growth of another geometrid caterpillar (Haukioja *et al.* 2002). Alternatively, leaf toughness may have reduced the performance of young larvae feeding on old foliage. Early instars, which have smaller mouthparts and muscles, may have difficulty piercing the epidermis of old foliage (Hochuli 2001). As well, more bites are necessary to consume tougher food (Bernays *et al.* 1991), and therefore more energy is expended to eat a similar amount of leaf tissue.

The higher rates of survival of old larvae when feeding on old than on current-year foliage may be due to their ability to overcome the physical barrier presented by toughened needles (Hochuli 2001). Some larvae specialize on old foliage to reduce the threat from natural enemies (Damman 1987), although natural enemies were excluded from the sleeve cages in the present study.

Generally, survival rates were low for both early and late instars in our study. Although similarly low survival rates for *I. ephyraria* larvae were reported in a previous study, where most mortality was attributed to fungal infection or parasitism (Pinault *et al.* 2007), we observed no mortality due to natural enemies.

Our field surveys of defoliation by *I. ephyraria* larvae demonstrated that larvae feed on foliage of all age classes. However, observations of larvae feeding on small trees suggest that this is due in large part to the feeding habits of old larvae. Young larvae were only observed to feed on current-year shoots, whereas older instars were observed feeding on both current-year and older foliage. It is probable that some young larvae fed on older foliage at times other than the few minutes when they were observed during our field surveys, because the rates of survival of young larvae in the manipulated sleeve cage studies were highest when they were allowed access to both young and old foliage.

Defoliation levels also varied significantly among sites. This was expected because sites were chosen to represent a range of caterpillar densities, and previous defoliation levels varied significantly among sites. Thus, previous defoliation (Karban and Myers 1989), other environmental conditions (*e.g.*, soil quality or abundance of natural enemies), tree genotype, or genotype–environment interactions may explain among-site variations in defoliation level. Whatever their cause, these among-site variations also influenced the relative differences in defoliation levels among foliage age classes (see the interactions in Tables 2 and 3).

In summary, the results of this study support the hypothesis that juvenile insects that feed on foliage of a variety of age classes do so to maximize fitness (Carroll 1999; Moreau *et al.* 2003). Our study has advanced earlier work by showing that feeding on foliage of different age classes can maximize fitness by improving juvenile nutrition in two ways: (1) larvae of different ages have different nutritional requirements (ontogenetic hypothesis) and (2) by feeding on foliage of different age classes, a larva can obtain a more balanced diet during early- or late-instar development (balanced-diet hypothesis).

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