SIZE-MEDIATED PERFORMANCE OF A GENERALIST HERBIVORE FEEDING ON MIXED DIETS

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ABSTRACT—Mixed diets can allow generalist insect herbivores to obtain nutritionally balanced resources or dilute toxins from specific foods, but also present the generalist with greater challenges in decision-making and require a greater ability to detoxify a wide range of plant defensive compounds. Young and small generalist larvae can have different nutritional requirements, ability to detoxify compounds, and mobility compared to older and larger larvae. In this field study, I asked how larval size affected performance of the woolly bear (*Platyprepia virginalis*), a generalist herbivore, on a uniform diet of bush lupine (*Lupinus arboreus*) compared to a mixed diet including bush lupine. Large larvae had greater survival on the mixed diet treatment compared to the lupine-only diet, but survival of small larvae did not vary with diet. Larval size also influenced growth on each diet, but this effect varied with year. In 1997, large larvae had higher growth on a lupine-only diet compared to a mixed diet, whereas small larvae had equivalent growth on both diets. In 1998, larvae of each size did not differ in their response to diet treatments. In the field, large larvae apparently eat a more diverse diet than small larvae, which contrasts with the growth result for 1997. This suggests that factors other than growth, such as parasitism or predation, might influence choice of host plants.

RESUMEN—Una dieta mixta puede permitir a los herbívoros obtener recursos nutritivamente balanceados o diluir toxinas de alimentos específicos, pero también presentan más retos para el herbívoro al tomar decisiones y requieren de una mayor capacidad para neutralizar una mayor cantidad de compuestos defensivos de las plantas. Larvas generalistas jóvenes y pequeñas pueden tener diferentes requerimientos nutricionales, capacidades para neutralizar compuestos, y movilidad en comparación con larvas más viejas y grandes. En este estudio de campo, investigué cómo el tamaño de la larva afecta la función de la oruga *Platyprepia virginalis,* un herbívoro generalista, con una dieta uniforme de lupino arbusto, *Lupinus arboreus,* comparada con una dieta mixta que incluye lupino. Larvas grandes sobrevivieron mejor con la dieta mixta que la dieta de solamente lupino, aunque la supervivencia de larvas pequeñas no varió con dieta. El tamaño de la larva también influyó el crecimiento con cada dieta, pero esto dependió en el año. En 1997, larvas grandes tuvieron más crecimiento con la dieta de sólo lupino comparada con la dieta mixta, mientras que la dieta no afectó el crecimiento de larvas pequeñas. En 1998, la dieta no tuvo efecto sobre las larvas de ninguno de los tamaños. Bajo condiciones naturales parece que las larvas grandes tienen una dieta más diversa que las larvas pequeñas, lo que difiere con los resultados de crecimiento de 1997. Esto sugiere que existen otros factores aparte del crecimiento, tales como el parasitismo o la depredación, que pueden influir en la elección de la planta hospedera.

One might expect an organism with a broad diet to be at a selective advantage to one with a narrow diet simply due to increased resource availability (Futuyma and Moreno, 1988). For generalist herbivores, consuming a mixed diet rather than a uniform diet also can provide more balanced nutrition (Pulliam, 1975; Westoby, 1978; Rapport, 1980) or a means for diluting toxins from specific plant species (Freeland and Janzen, 1974). For an insect, being a generalist also can contribute to escape from predators or parasites by having a less predictable odor (De Moraes et al., 1998) or location.

Despite the benefits of a broad diet, most insect herbivores are specialists that use only a few species of host plants for feeding and oviposition (Bernays and Graham, 1988; Jaenike, 1990). The relative scarcity of generalist species suggests that the costs of being a generalist might outweigh the potential benefits. Some generalists incur metabolic costs associated with switching foods (Schoonhoven and Meerman, 1978; Scriber, 1979). Generalists can lack the cues that specialists use to find food and take longer to locate food, be less decisive once feeding, switch plants more frequently, or incur greater ecological risks (Bernays, 1999*a*, 1999*b*; Bernays and Funk, 1999; Bernays, 2001). Although there are many proposed benefits of a mixed diet rather than uniform diet, no overall pattern emerges from studies. Orthopterans benefit from a mixed diet compared to a uniform diet (reviewed in Bernays and Minkenberg, 1997), as do many non-insect herbivores (Pennings et al., 1993). However, other insect taxa, such as lepidopterans and hemipterans, generally perform as well or better with a uniform diet of a preferred food compared to a mixed diet (Stoyenoff et al., 1994; Bernays and Minkenberg, 1997; Ballabeni and Rahier, 2000; Singer, 2001).

Larval age can affect the costs and benefits of being a generalist. Larval age can influence performance when eating mixtures of plant defensive compounds (Yang et al., 1996) or performance on previously damaged hosts (Krause and Raffa, 1995). In several lepidopteran larvae, the activity of mixed-function oxidases increases with age (reviewed in Brattsten, 1979). In gypsy moths, another broad generalist, midgut pH increases with larval age, providing greater ability to dissociate tannin-protein complexes (Schultz and Lechowicz, 1986). Thus, older larvae might have a greater ability to cope with a mixed diet due to increased ability to detoxify secondary compounds. Many microlepidopteran larvae change feeding habit as they grow, so they can incur both costs and benefits of a wider range of environmental and nutritional conditions (Gaston et al., 1991). Larger larvae also can be more mobile and encounter a greater range of potential host species (Scriber and Slansky, 1981). Fox and Morrow (1981) pointed out that even generalists at the species level are not always generalists at the population or individual level. It is possible that even within an individual, costs and benefits of being a generalist might vary with the age or size of the larvae.

The woolly bear *Platyprepia virginalis* (Lepidoptera: Arctiidae) is a suitable species to study how age affects performance on mixed diets. This species is a broad generalist known to feed on a wide diversity of taxa (English-Loeb et al., 1993). However, young larvae at the Bodega Bay Marine Laboratory feed primarily upon a single host, bush lupine (*Lupinus arboreus*: Fabaceae). As larvae become larger and more mobile, they also feed on other plants, including *L. nanus* (Fabaceae), *Amsinckia menziesii* (Boraginaceae), *Conium maculatum* (Apiaceae), *Plantago lanceolata* (Plantaginaceae), *Iris* (Iridaceae), and various grass species (Poaceae) (English-Loeb et al., 1993). Thus, I hypothesized that larger larvae would perform better than small larvae on a mixed diet compared to a uniform diet of bush lupine.

In this study I asked how diet and larval size affect performance (measured as survival and growth) of the woolly bear *P. virginalis*. The question of how larval size affects performance on mixed diets compared to uniform diets has not been previously addressed in a field study. Because age and size covary, these experiments are a test of larval age as much as size. For simplicity, I will use the term ''size'' hereafter with the understanding that age is confounded with size.

METHODS—Adult moths of *P. virginalis* are univoltine at Bodega Bay and oviposit in May or June. Eggs hatch in the summer and remain as first or second instar larvae until late winter, when they begin to feed rapidly (English-Loeb et al., 1993). Early instars at Bodega Bay live at the base of bush lupines and move little. In the spring, larvae crawl into the foliage and are evident feeding on bush lupines, and a diversity of other foliage, until pupation in April or May (Karban, 1998).

I conducted experiments over 2 years at Horseshoe Cove and Mussel Point at the Bodega Bay Marine Laboratory in Sonoma County, California (38°19′N, 123°04′W). In both years, I used enclosures to create diet treatments. Enclosures consisted of chicken-wire cylinders approximately 10 cm high and 20 to 25 cm in diameter, with the wide end of a conical spun polyester bag wrapped underneath. I secured chicken-wire cylinders to the ground with 4 metal U-shaped stakes and tied the top narrow end of the conical bag with plastic flagging. I placed enclosures either around a small bush lupine with all other vegetation removed from the enclosure (lupine only treatment) or around a diverse mix of vegetation that included 1 bush lupine (mixed diet treatment). The exact mixture of plants in the mixed diet treatment varied among enclosures, but estimates from a pilot study at Horseshoe Cove (Adler, unpubl. data) indicated that the most common species, comprising over 88% of the ground cover, were various grasses (Poaceae), *Plantago lanceolata* (Plantaginaceae), *Rumex acetosella* (Polygonaceae), and *Lupinus arboreus* and *L. nanus* (Fabaceae). Other taxa were *Eschscholzia californica* and *Platystemon californicus* (Papaveraceae), *Triphysaria pusilla* (Scrophulariaceae), *Anagallis arvensis* (Primulaceae), *Acaena pinnatifida* and *Rubus* (Rosaceae), *Erodium cicutarium* and *Geranium molle* (Geraniaceae), *Claytonia perfoliata* (Portulacaceae), *Stachys rigida* (Lamiaceae), *Nemophila menziesii* and *Phacelia distans* (Hydrophyllaceae), *Achillea millefolium* and *Hypochoeris radicata* (Asteraceae), *Trifolium* (Fabaceae), *Carex* (Cyperaceae), and *Daucus carota* (Apiaceae). Enclosures from the pilot study ($n = 60$) had an average of 4.6 ± 0.2 species and a range of 2 to 8 species.

I collected woolly bear larvae on 23 and 24 March 1997. I recorded host plant during collection and stored all larvae in a refrigerator in paper cups with bush lupine leaves until the beginning of the experiment. On 25 March, all larvae were individually weighed and placed in separate enclosures. Seven replicates were used for each larval size (small or large) and treatment (mixed diet or lupine-only diet) combination, for a total of 28 enclosures. While this is a small sample size ($n = 7$), I found statistically significant differences even when considering this year of data alone, suggesting that samples sizes were sufficient to detect treatment effects. Larvae under 0.40 g were considered small and were typically second or third instars, judging by their color patterns (R. Karban, pers. comm.). Larvae above 0.75 g were considered large and were typically fourth or fifth instars, although this category might have included some large third instar larvae. Larvae weighing 0.40 to 0.75 g were not used. Larvae were collected, weighed, and returned to their enclosures on 30 March, 4 April, 9 April, 14 April, and 27 April. The status of each larva (alive, dead, missing, or pupated) was recorded on each date. On 9 April, damage to all plants in the mixed diet treatment was recorded to determine whether larvae were truly consuming a mixed diet.

The same methods were repeated in 1998. Bush lupines of the appropriate size were rare at Horseshoe Cove during this year due to efforts to control bush lupine seedlings in the grasslands at Bodega Bay (P. G. Connors, pers. comm.). The experiment was therefore conducted at a nearby area on the opposite side of the station with similar vegetation (on the Mussel Point side of the station, approximately 0.28 km north of the 1997 site). Woolly bears were weighed and placed in enclosures on 3 March and then weighed and returned to their enclosures on 7 March, 12 March, 21 March, 28 March, and 4 April. Larvae under 0.27 g (second-third instar) were considered small, and larvae above 0.60 g (fourth-fifth instar) were considered large. Fifteen replicates were used per larval size and treatment combination, for a total of 60 enclosures.

The effect of diet treatment, larval size, and year on larval weight was determined using repeated measures 3-way ANOVA, with initial weight as a covariate and treatment, year, and larval size as main effects. All interaction terms were included in the model. Using initial weight as a covariate and final weight as a response is essentially analyzing relative growth rate but without using ratios; I will refer to this response as growth. Due to missing cells caused by larval escape, pupation, or death, only data from the first 2 weighing dates (5-d and 10-d periods in 1997 and 4-d and 9-d periods in 1998) were used in this analysis.

The effects of diet treatment, larval size, and year on survival were tested using a maximum likelihood analysis of variance with the categorical modeling procedure of SAS, version 8.02 (SAS Institute, Cary, North Carolina). Missing larvae were included with dead larvae, and pupated larvae were included with larvae that lived but did not pupate. Due to small sample size, it was not possible to test a full 3-way model with interaction terms. The interaction between larval size and treatment and the main effects of treatment, larval size, and year were included in the model. To determine whether lumping data across years obscured qualitative differences between years, separate *G*-tests with Yates correction for continuity (Zar, 1996:503) were used for each year and larval size combination.

Results—Eight plant taxa from 5 families were observed with damage within the enclosures in the 1997 study (*Lupinus arboreus, L. nanus,* grasses, *Plantago lanceolata, Rumex acetosella, Acaena pinnatifida, Trifolium,* and *Rubus*). Two to 5 plant species were observed with damage within each enclosure (mean ± *SD*: 2.9 ± 0.2; large larvae 3.0 ± 0.3; small larvae 2.7 ± 0.3), demonstrating that individual small and large woolly bears in the mixed diet treatment consumed a relatively mixed diet. *Lupinus arboreus* received damage in every enclosure. *Rumex acetosella,* grass, and *Plantago lanceolata* also were damaged frequently (64%, 57%, and 29% of enclosures, respectively).

Growth (final weight using initial weight as a covariate) of large larvae compared to small larvae differed between diet treatments and years of the experiment (size × diet and size × year interactions; Table 1, Fig. 1) in a repeated measures analysis. In 1997, large larvae had higher growth on a lupine-only diet compared to mixed diets, but small larvae had

TABLE 1—Effect of diet type, larval size, and year on larval weight using initial weight as a covariate for wooly bear larvae (*Platyprepia virginalis*). Repeated measures analysis with Type III sums of squares of the between-subjects effect of initial larval size, treatment, and year on subsequent larval weight.

Source	*df*	*SS*	*F*
Initial weight (covariate)	1	0.178	6.56*
Diet treatment	1	0.104	3.81[a]
Larval size	1	1.20	44.22****
Year	1	3.19	117.38****
Diet × Year	1	0.0800	2.94
Larval size × Diet	1	0.147	5.41*
Larval size × Year	1	0.323	11.89**
Diet × Larval size × Year	1	0.0800	2.93
Error	69	1.88	

* $P < 0.05$; ** $P < 0.01$; **** $P < 0.0001$
[a] $P = 0.0549$

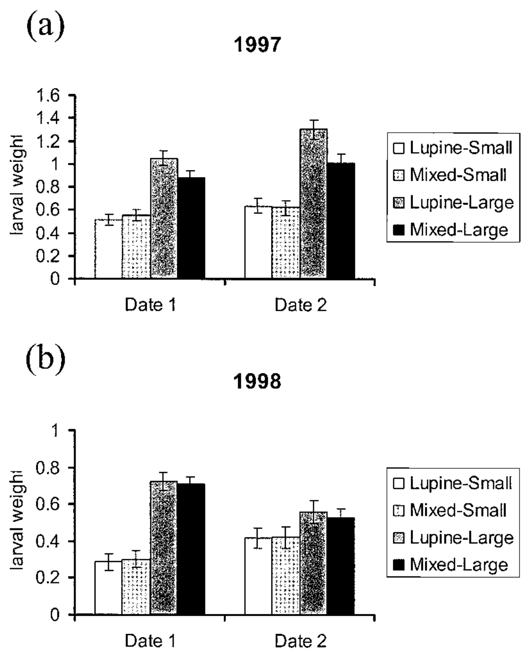

FIG. 1—The effect of diet on growth of small and large woolly bear larvae (*Platyprepia virginalis*) in (a) 1997 and (b) 1998. Lupine and Mixed refer to diet treatments, and Small and Large refer to larval size. Growth was measured as least square means of larval weight after accounting for initial weight. Dates 1 and 2 refer to 30 March and 4 April in 1997, and 7 March and 12 March in 1998. Error bars represent *SE*.

equivalent growth on each diet (Fig. 1a). In 1998, however, growth was not influenced by diet for either size of larvae (Fig. 1b). Separate 2-way ANOVAs for each year confirmed these observations, although sample size for 1997 was small (treatment × larval size interaction, 1997: $F_{1,18} = 7.33$, $P < 0.02$; 1998: $F_{1,50} = 0.65$, $P > 0.4$).

I analyzed the effect of larval size, diet treatment, and year on death/escape compared to survival/pupation of larvae. There was substantial pupation in 1997 (10 of 22 surviving larvae), but none in 1998 (0 of 42). More larvae escaped than died during the experiment (1 death and 5 missing in 1997; 5 deaths and 13 missing in 1998). This analysis can be considered a comparison between larvae that survived in the enclosures and those that either chose to leave or died; presumably both of the latter responses indicated that the enclosures were unsatisfactory in some way. Larval size affected survival on each diet type (Table 2); large larvae were more likely to survive on the

TABLE 2—Effect of larval size, diet type, and year on survival/pupation compared to rejection/death of woolly bear larvae (*Platyprepia virginalis*) using maximum likelihood estimates of χ^2 values.

Source	*df*	χ^2	*P*
Intercept	1	14.94	0.0001
Diet treatment	1	7.30	0.0069
Larval size	1	0.65	NS
Year	1	0.81	NS
Diet × Larval size	1	3.96	0.0465

mixed diet compared to the lupine-only diet (95.5% compared to 50% survival, respectively), whereas small larvae did not differ in their survival on either diet type (77.3% survival on mixed diet compared to 68.2% on lupine-only diet). Excluding dead larvae from the analysis did not qualitatively change the results, although the diet × larval size interaction only approaches statistical significance ($P = 0.075$ rather than $P = 0.0465$, Table 2), likely due to the smaller sample size. In separate *G*-tests for each year, large larvae had significantly higher survival on mixed diet compared to lupine-only diet in 1998 ($df = 1$, $G_c = 4.52$, $P < 0.05$) and had higher survival but not significantly so in 1997 ($df = 1$, $G_c = 3.448$, $P < 0.1$), whereas small larvae did not vary in their survival on either treatment in either year (1997: $df = 1$, $G_c = 0.6064$, $P > 0.25$; 1998: $df = 1$, $G_c = 0$, $P = 1.0$).

DISCUSSION—The effect of larval size or age on performance on mixed diet compared to uniform diet has not been previously addressed in a field study. However, many studies have shown that the order in which food types are encountered can affect subsequent herbivore preference (Simmonds et al., 1992) or performance (Scriber, 1982; Taylor, 1984; Barbosa et al., 1986). Larval age affected preference for new foliage compared to mature foliage in a specialist herbivore (Stamp and Bowers, 1990). Previous herbivore damage can induce changes in plant chemistry that influence subsequent herbivory (Karban and Baldwin, 1997). In *Manduca sexta,* the costs of moving to a new plant compared to staying on an induced plant change dramatically as larvae grow. Small larvae experience high costs of moving, but large larvae have low costs of moving and are more tolerant of induced foliage (van Dam et al., 2001). Given that performance on different hosts can change as larvae mature, it is not surprising to find that the benefits of diet mixing are also influenced by larval size.

Mixed diets never resulted in higher larval growth than the lupine-only diet for any year or larval size. This result might seem surprising because woolly bear larvae are broad generalists and commonly eat a diverse diet in the field (English-Loeb et al., 1993), but it is consistent with other studies examining the benefits of mixed diet versus uniform diet for generalist herbivores. Although orthopterans, coleopterans, parasitic plants, and marine gastropods can benefit from mixed diets (e.g., Pennings and Paul, 1992; Bernays et al., 1994; Marvier, 1998; Foster et al., 1999; Ballabeni and Rahier, 2000), generalist lepidopterans typically have the highest performance on a uniform diet of a beneficial food compared to a mixed diet (Bernays and Minkenberg, 1997; Hagele and Rowell-Rahier, 1999; Singer, 2001). The mechanisms behind this taxonomic difference in response to mixed diets are not known; however, recent work has shown that costs of being a generalist include difficulty finding, choosing, and settling on a host plant, as well as increased ecological risks (reviewed by Bernays, 2001). The relative costs and benefits of generalization might vary between taxa with different physiological requirements, neural capabilities, or ecological constraints.

Measurements of growth and survival provided conflicting answers regarding the benefits of a mixed diet. Large larvae had greater survival on the mixed-diet treatment compared to the lupine-only treatment in both years of this study, but small larvae were equally likely to survive on both diet types. Most of the larvae that did not ''survive'' were missing rather than dead, suggesting that larvae might have rejected the treatment. This result is consistent with field observations that large larvae tend to eat a more diverse diet than small larvae in the field (English-Loeb et al., 1993). As larvae grow and become more mobile, they might have a greater ability to choose their hosts and reject unsuitable habitat. However, growth of large larvae was greater on a uniform lupine diet than on a mixed diet in 1997 and did not differ between diet types in 1998. If growth is higher or equivalent on a lupine-only diet compared to a mixed diet, why are large larvae more likely to reject a uniform diet of lupine in enclosures, and why do they eat a broad diet in the field?

The presence of natural enemies might explain why woolly bears eat a mixed diet in the field even though they perform as well or better on a uniform diet of lupine. In the current study, all woolly bears were in enclosures that prevented the entry of predators or parasitoids. Although some woolly bears might have been harboring parasitoids when placed in enclosures, the overall risk of parasitism was presumably much lower than in natural populations. In the field, woolly bears are frequently parasitized by the tachinid fly *Thelairia bryantii* (English-Loeb et al., 1990), with an average parasitism rate over 3 years of 59% (Karban, 1998). This host-parasitoid relationship is unusual because woolly bears can survive and reproduce after parasitoid emergence (English-Loeb et al., 1990). Feeding on lupine reduced the rate of parasitism compared to feeding on poison hemlock, *Conium maculatum* (English-Loeb et al., 1993). However, parasitized larvae were more likely to survive parasitoid emergence when feeding on poison hemlock. Thus, selection might favor the use of multiple host plants to avoid parasitism when possible and to increase the chances of survival when parasitized (English-Loeb et al., 1993). It is also possible that feeding on a wider range of plants, rather than a single host species, increases the chances of not being detected by parasitoids or by predators. This benefit might outweigh the advantages of feeding on a uniform diet of a beneficial host plant.

The effect of larval age on growth also varied significantly between years. Two possible reasons for this difference are that I used a different study site, and that abiotic and biotic factors were different between years. The 1998 study was carried out at a site 0.28 km from the 1997 study. Although the 2 sites had similar vegetation, there might be differences that affected the nutritional value or herbivore resistance of plants. The extremely low growth of large larvae in 1998 might also reflect the poor quality of the foliage due to prior herbivory or high precipitation. Bush lupines had high mortality in 1998 due to heavy 1997 herbivory by the western tussock moth, *Orgyia vetusta,* combined with a wet 1998 winter (P. Connors, pers. comm.). High levels of herbivory might have affected the quality of lupine foliage relative to other host plants (Harrison and Karban, 1986; Karban and Kittelson, 1999), and high precipitation might influence host quality. The 1998 experiment also was conducted slightly earlier with somewhat smaller larvae. Any combination of these or other factors could have resulted in the differences in experiments between years. Thus, the consequences of host choice for woolly bears might be context dependent, as are many other ecological interactions (Cushman and Whitham, 1989; Thompson, 1997, 1999).

In conclusion, larval size affected survival on a mixed diet compared to uniform diet over 2 years of a field study and also influenced growth on a mixed diet compared to uniform diet. Thus, even in a highly polyphagous herbivore, the ability to cope with a broad diet changes as larvae mature. The effect of larval size on growth with different diets was qualitatively different between years, indicating that the consequences of host choice are context dependent. Large larvae are more likely to survive or remain on a mixed diet compared to a uniform diet of lupine despite having equivalent or higher growth on the uniform diet, suggesting that other factors, such as natural enemies, play a role in determining host plant range in the field.

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