

Birds have no impact on folivorous insect guilds on a montane willow

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We examined the impact of avian predators on the community of insects feeding on Lemmon's willow, *Salix lemmonii*, at Carman Valley, California. *Salix lemmonii* supports a diverse assemblage of insect species that feed in either a concealed or an exposed manner on leaves by mining, tying, curling, galling, skeletonizing, or chewing. We tested the hypothesis that there are guild specific differences in the effects of avian predators on concealed and exposed-feeding folivores. We compared the feeding damage and frequency of each guild in the presence and absence of avian predators. Contrary to most studies of the effects of avian predators on folivorous insects, birds failed to reduce significantly the frequency of or feeding damage caused by exposed-feeding insects during 1999 and 2000. Chewing insects, which accounted for the majority of foliar damage by exposed-feeding insects, inflicted slightly more damage and skeletonizing insects slightly less damage in the presence of birds. We also observed no reduction in the frequency of concealed-feeding insects in the presence of avian predators; rather three out of four guilds were slightly more common in the presence of avian predators. While the abundance of foliage gleaning birds at the study site was slightly lower than the average for the past nine years, we interpret our results to indicate a true lack of an effect of avian predators on the community of folivorous insects on *S. lemmonii*. Future inquiry into the effects of avian predators on folivorous insects should focus on determining under what circumstances birds will or will not suppress guilds of folivorous insects.

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Several studies have shown that birds can suppress the abundance of and feeding damage caused by folivorous insects (Atlegrim 1989, Marquis and Whelan 1994, Floyd 1996, Greenberg et al. 2000, Strong et al. 2000, Sanz 2001). However, most studies that have excluded birds from host plants to test for effects of avian predation have done so only for insect guilds that feed exposed on the exterior of foliage, and many have only examined the exposed-feeding Lepidoptera (Holmes et al. 1979, Campbell et al. 1983, Damman 1987, Atlegrim 1989, Marquis and Whelan 1994, Floyd 1996, Greenberg et al. 2000, Strong et al. 2000). Only a few studies have tested the impact of

avian predators on insects in concealed-feeding guilds that leaf mine, form galls, roll leaves, or tie leaves together (Tscharntke 1992, Connor et al. 1999, Sipura 1999). Previous studies that examined the role of predation in suppressing guilds of concealed-feeding insects relied on multiple decrement life tables and have not distinguished between avian and invertebrate predation (Cornell and Hawkins 1995, Connor and Taverner 1997). While life table studies indicate that predation can account for a substantial fraction of larval and pupal mortality among insects in concealed-feeding guilds, the contribution of avian predators is still unknown.

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Avian insectivores might not only suppress or regulate folivorous insect populations, but may also serve as a selective force leading to adaptations to avoid predators. Birds are important insectivores since they are highly selective visual predators that can develop search images for their prey (Tinbergen 1960, Holmes et al. 1979). The damage that an insect causes to the host plant while feeding may serve as potential cues for visually hunting birds (Heinrich 1979, 1993, Heinrich and Collins 1983, Murakami 1999).

Insects consume foliage in a variety of ways that may confer different degrees of protection from predators. Insect larvae could avoid avian predation by feeding cryptically on the exterior of a leaf or by feeding internally within a leaf, a gall, rolled leaf, or multiple leaves tied together. The success of both concealed and exposed-feeding habits may be limited by trade-offs between feeding efficiency and predation risk (Damman 1987, Bergelson and Lawton 1988, Connor and Taverner 1997). For example, an exposed-feeding insect may have higher mobility and access to resources of better quality, but may consequently increase its vulnerability to desiccation, parasitism, and predation (Connor and Taverner 1997). Conversely, an internal-feeding insect such as a leaf miner or gall former, may be more successful at avoiding the risks of predation or desiccation, but must remain confined to a single leaf, or to a leaf-tie, for the entirety of its larval development. In general, such limited mobility is associated with smaller body size, lower fecundity, and a greater risk of incomplete development and death from premature leaf abscission (Faeth et al. 1981, Kahn and Cornell 1989, Cornell 1990, Preszler and Price 1993, Connor et al. 1994). Although concealed-feeding insects are sedentary and therefore potentially easy targets for avian predators, they may not be energetically profitable because of their size (6 mm or less). Furthermore, the difficulty of localizing prey within its shelter can increase search and handling time, and most birds do not possess the physical ability or musculature to open a gall, leaf tie, leaf curl, or leaf mine (Connor et al. 1999). Therefore, we hypothesize that guilds of exposed-feeding insects experience a greater degree of suppression by avian predators than do guilds of concealed-feeding insects.

To determine if avian predators suppress exposed-feeding more than concealed-feeding guilds of folivorous insects, we excluded birds experimentally and compared the frequency of occurrence of exposed and concealed-feeding insects, and the feeding damage caused by exposed-feeding insects in the presence and in the absence of avian predators. We examined the impact of avian predators on seven guilds of insects on the willow, *Salix lemmonii*.

Methods

Study site

Our study was conducted in Knuthson Meadow a section of larger meadow known as Carman Valley, California in the Sierra Nevada Mountains at 1700 m (39° 41.55' N, 120° 27.22' W). The study site is bordered on two sides by mixed conifer forest and is approximately 5.2 hectares in area. Willow comprises about 25–30% of the vegetative cover. The remaining vegetation consists of grasses, sedges, forbs, and sage brush (*Artemisia* sp.).

Experimental design

To determine if avian predators differentially suppress guilds of folivorous insects, we compared the frequency of and feeding damage caused by exposed and concealed-feeding insects on willow shrubs that were either enclosed with netting to exclude birds or left un-enclosed to permit access by avian predators. In 1999, we conducted a within-subjects experiment estimating the effects of avian predators by comparing adjacent enclosed and un-enclosed regions of individual shrubs. In 2000, to insure that the proximity of enclosures to our samples of un-enclosed foliage did not result in reduced foraging by birds, we estimated the effects of avian predation in a between-subjects design. In the 2000 experiment, different shrubs were either enclosed or not enclosed, so the treatments were spatially separated.

A within-subjects experimental design was used in 1999 to avoid the confounding effects of environmental and genotypic differences between subjects (Simms and Fritz 1991, Roche and Fritz 1997, Strauss and Agrawal 1999). By excluding birds from only a portion of each subject, each subject serves as a control for itself. Each subject consisted of a region of a willow shrub enclosed in a cage constructed of PVC pipe and nylon bird netting (16 × 19 mm mesh opening) and an adjacent similar-sized region of the same willow shrub not enclosed in netting. Enclosures varied in size, but were generally 2–3 m in each linear dimension. Individual willow shrubs were between 3–8 m in diameter and 3–4 m in height. Enclosures were erected on 24 May 1999, and shrubs were sampled four times (24 June, 26 July, 19 August, and 17 September 1999). One hundred leaves were sampled from each portion of each subject. Since species of *Salix* are dioecious and there may be sex-based variation in the abundance and feeding damage caused by folivores, we used only female plants (Boecklen et al. 1990, Åhman 1997).

We set our targeted level of replication for the exclusion experiment by calculating the sample size necessary to detect a 75% reduction in the frequency of or feeding damage caused by insects with a Type II error rate of

20% and a Type I error rate of 5%. We chose an effect magnitude of 75% since this falls within the range of effects reported in previous studies (Atlegrim 1989, Marquis and Whelan 1994, Floyd 1996). We used preliminary data from *S. lemmonii* in Carman Valley from 1998 to estimate the expected between shrub variability. Based on these variances, a sample size of 16 would be necessary to detect a reduction in frequency of 75% for all insect guilds (Cohen 1977). Due to constraints on cage construction, we constructed 14 cages rather than the 16 intended, which increased the detectable effect to 78%.

In 2000, we used a between-subjects design so that any inadvertent reduction in avian impact caused by the proximity of the enclosures to the un-enclosed foliage could be removed from the experiment. Female *S. lemmonii* were selected and assigned at random to either the enclosed or un-enclosed treatment. Enclosures similar in size and materials to those built in 1999 were erected on 25 May and sampled three times (19 June, 17 July, and 14 August). In the 2000 experiment, we reallocated our sampling effort increasing the number of un-enclosed subjects to 18 while the number of enclosed subjects remained at 14.

Estimating guild specific frequencies and feeding damage

During each sampling period in 1999, we randomly selected eight branches per subject, four each from within the enclosed and adjacent un-enclosed foliage. We excluded branches adjacent to the netting to prevent any confounding effects due to avian foraging across the netting. For each branch, we examined and recorded data from the first 25 leaves terminal to the point at which the branch was grasped. In 2000, only 3 branches were randomly sampled from each subject, but all other methods were identical to those used in 1999. By sub-sampling from the data collected in 1999, we determined that estimates of treatment averages and standard errors based on samples of 75 leaves per subject did not differ from those based on samples of 100 leaves. We did not sample in September 2000 since willow leaves were yellowing and abscising at high rates.

We categorized all foliar feeding damage as being caused by one of seven feeding guilds: four concealed-feeding guilds (leaf mining, gall forming, leaf tying, and leaf curling) and three exposed-feeding guilds (large skeletonizing, pit skeletonizing, and external chewing). We assigned insects that feed all or partially enveloped by leaf tissues to concealed-feeding guilds, and insects that feed on the exterior on the leaf surface or leaf edge to exposed-feeding guilds. The feeding guilds were distinguished by the size and nature of the feeding damage they caused. The pit-skeletonizing guild takes small

bites from either the upper or lower surface of the leaf creating small pits, 1 mm or less in diameter.

Because of the variety of feeding damage caused by different guilds, we used two metrics to estimate the guild specific impact of avian predators. The frequency of insects in each feeding guild was estimated by recording the number of leaves with feeding damage characteristic of each guild per 100 leaves. For exposed-feeding insects, we also estimated the amount of foliar damage caused by each guild. To estimate the area damaged on each leaf by the large-skeletonizing and external-chewing insects, we placed a transparent plastic grid (3 mm²) over each area of feeding damage and counted the number of grid squares intercepted by the feeding damage. For pit-skeletonizing insects, we counted the number of "pits" on each leaf and multiplied by the average surface area of a single pit (0.36 mm²).

The avian predators

Birds were mist-netted and banded between May and August of each year following the protocol of the Monitoring Avian Productivity and Survivorship Program (MAPS, DeSante et al. 1995). Nets were set in narrow flyways between willow clumps, and run every 10 days from 06:00 to 11:00 am. To establish the potential predation pressure that birds represent each year and to determine if our study years were unusual relative to other years, the abundance of foliage-gleaning birds was estimated using closed population models for each year from 1992 to 2000. Twenty-three of the bird species netted at the study site were classified as members of the foliage-gleaning guild (Table 1). Using the model selection algorithm in the program Capture, we selected appropriate models to estimate the abundance of foliage-gleaning bird species (Otis et al. 1978, White et al. 1978). Tests for closure of the population indicated that it was reasonable to assume closure only for the month of June, since recapture probabilities were very low during July and August. Therefore, only capture histories from June of each year were used in a four-period model for each year to estimate the abundance of foliage-gleaning birds. The average number of captures per net-day is also reported to permit inter-annual comparisons of potential avian predation pressure for the months of July and August.

Leaf abscission

Since herbivory may cause premature leaf abscission, sampling only the foliage remaining attached to the host plant might lead to an underestimate of the frequency of and feeding damage caused by each guild (Pritchard and James 1984, Williams and Whitham

Table 1. Foliage gleaning bird species captured at Carman Valley, CA in 1999 and 2000. An x indicates that a species was captured in a particular month. Six additional foliage gleaning species were captured between 1992 and 1998, but absent in 1999–2000.

Species	Common name	1999			2000		
		June	July	Aug	June	July	Aug
<i>Parus gambeli</i>	mountain chickadee	x	x	x	x	x	x
<i>Vireo solitarius</i>	solitary vireo		x	x	x	x	x
<i>Vireo gilvus</i>	warbling vireo	x	x		x	x	x
<i>Vermivora celata</i>	orange-crowned warbler	x	x	x	x	x	x
<i>Vermivora ruficapilla</i>	Nashville warbler	x	x		x	x	x
<i>Dendroica coronata</i>	Audubon's warbler	x	x	x	x	x	
<i>Dendroica petechia</i>	yellow warbler	x	x	x	x	x	x
<i>Dendroica occidentalis</i>	hermit warbler	x	x		x		x
<i>Geothlypis trichas</i>	common yellowthroat				x	x	
<i>Oporornis tolmiei</i>	McGillivray's warbler	x	x	x	x	x	x
<i>Carduelis pinus</i>	pine siskin	x	x				
<i>Pipilio erythrophthalmus</i>	spotted towhee			x			
<i>Junco hyemalis</i>	Oregon junco	x	x	x	x	x	x
<i>Spizella breweri</i>	Brewer's sparrow	x	x	x	x		x
<i>Melospiza lincolnii</i>	Lincoln sparrow	x	x	x	x	x	
<i>Melospiza melodia</i>	song sparrow	x	x	x	x	x	x
<i>Passerella iliaca</i>	fox sparrow	x	x		x	x	

1986, James and Pritchard 1988, Stiling and Simberloff 1989). To determine the effect of leaf abscission on our test for the effect of avian predators, we estimated the rate of leaf abscission within and outside enclosures in 1999. We placed a 0.25 m² leaf-litter basket (constructed from PVC pipe and 1 mm² mesh screening) within each enclosure and under the adjacent unenclosed foliage beginning on 24 June 1999. We counted the number of leaf petioles trapped each month from June through August.

Data analysis

In 1999, data for each feeding guild were analyzed separately using a 2-factor (time by predation treatment), fixed-effects, full within-subjects ANOVA. In 2000, data for each guild were analyzed separately using a two-factor, fixed-effects, partial within-subjects ANOVA (with the predation treatment estimated between subjects). Frequency and damage were approximately normally distributed without transformation. To determine if avian predators differentially affect concealed and exposed-feeding insects, we performed a 3-factor fixed-effects ANOVA (predation treatment, time, and feeding habit) of the frequency of concealed and exposed-feeding insects after pooling the data for individual guilds by "feeding habit" (concealed or exposed). In 1999, this 3-factor ANOVA was a full within-subjects model, and in 2000 it was a partial within-subjects model with the effect of the predation treatment estimated between subjects. The number of leaf petioles abscised each month was examined using a 2-factor, fixed effects, within-subjects ANOVA. All hypothesis tests are univariate tests with the degrees of freedom of the within-subjects tests corrected for non-

sphericity of the variance-covariance matrix using the Huyhn-Feldt ϵ (O'Brien and Kaiser 1985, Brown et al. 1997).

We estimated the effect magnitudes for the predator exclusion treatment for each guild and the combined effects of the exposed and the concealed-feeding guilds using Cohen's d for within- and between-subjects designs (Rosenthal 1994). We then converted these estimates of d to a common metric, Fisher's z -transformed values of r , and combined the effects sizes using meta-analysis to determine if the average effect of predation among our 1999 and 2000 experiments differed significantly from zero (Shadish and Haddock 1994).

Results

Avian predation and guild-specific frequencies and feeding damage

We found no statistically significant effect of avian predation on the frequency of or feeding damage caused by folivorous insects either for any individual feeding guild, or for the aggregate of the concealed or exposed-feeding guilds in either 1999 or 2000 (Table 2–4, Fig. 1–4). Two exposed-feeding guilds, the large and pit-skeletonizing guilds, were consistently slightly lower in frequency and caused less feeding damage in the presence of avian predators in both 1999 and 2000 (Fig. 1, 2 and 4). However, on average, external-chewing damage was slightly more frequent and extensive higher in the presence of birds (Fig. 1, 2 and 4). The frequencies of three of the four concealed-feeding guilds were slightly higher in the presence of avian predators than in their absence (Fig. 3 and 4). Nevertheless, we detected no statistically significant difference

Table 2. Analysis of variance of feeding damage (surface area damaged, mm²) for each guild of exposed-feeding insects. Results reported for 1999 are univariate tests with degrees of freedom adjusted for non-sphericity of the variance-covariance matrix using Huyhn-Feldt ϵ .

Source		1999			2000		
		df (num, denom)	F	p	df (num, denom)	F	p
Large-skeletonizing Guild	Time	2.307, 29.99	3.486	0.038	1.730, 51.886	0.126	0.854
	Predation	1, 13	4.454	0.055	1, 30	1.294	0.264
	Time \times Predation	2.988, 38.847	1.151	0.341	1.730, 51.886	0.255	0.744
Pit-skeletonizing Guild	Time	1.546, 20.093	15.433	0.000	1.782, 53.452	0.681	0.494
	Predation	1, 13	2.735	0.122	1, 30	0.160	0.692
	Time \times Predation	2.978, 38.708	1.033	0.388	1.782, 53.452	0.88	0.438
External-chewing Guild	Time	1.189, 15.46	16.650	0.001	2, 60	4.547	0.014
	Predation	1, 13	0.487	0.498	1, 30	0.180	0.674
	Time \times Predation	2.842, 36.949	0.194	0.891	2, 60	1.035	0.361
External guilds (pooled)	Time	1.166, 15.162	16.366	0.001	2, 60	4.106	0.021
	Predation	1, 13	1.019	0.331	1, 30	0.073	0.789
	Time \times Predation	2.779, 36.127	0.165	0.908	2, 60	1.075	0.348

Table 3. Analysis of variance of frequency (number of occurrences/100 leaves) for each guild of exposed-feeding insects. All tests are univariate tests with degrees of freedom adjusted for non-sphericity of the variance-covariance matrix using Huyhn-Feldt ϵ .

Source		1999			2000		
		df (num, denom)	F	p	df (num, denom)	F	p
Large-skeletonizing Guild	Time	2.323, 30.194	5.136	0.009	2, 60	6.275	0.003
	Predation	1, 13	0.492	0.496	1, 30	0.017	0.898
	Time \times Predation	3, 39	2.191	0.104	2, 60	0.307	0.736
Pit-skeletonizing Guild	Time	1.812, 23.551	24.482	0.000	2, 60	0.225	0.799
	Predation	1, 13	2.484	0.139	1, 30	0.018	0.893
	Time \times Predation	3, 39	0.593	0.623	2, 60	0.614	0.544
External-chewing Guild	Time	1.947, 25.308	13.257	0.000	1.636, 49.094	58.402	0.000
	Predation	1, 13	0.161	0.695	1, 30	0.526	0.474
	Time \times Predation	2.765, 35.944	0.864	0.461	1.636, 49.094	0.678	0.484
External guilds (pooled)	Time	1.670, 21.715	17.265	0.000	1.774, 53.221	38.702	0.000
	Predation	1, 13	1.603	0.228	1, 30	0.158	0.694
	Time \times Predation	3, 39	0.211	0.888	1.774, 53.221	0.162	0.826

Table 4. Analysis of variance of frequency (number of occurrences/100 leaves) for each guild of concealed-feeding insects. All tests are univariate tests with degrees of freedom adjusted for non-sphericity of the variance-covariance matrix using Huyhn-Feldt ϵ .

Source		1999			2000		
		df (num, denom)	F	p	df (num, denom)	F	p
Leaf-mining Guild	Time	2.529, 32.88	12.554	0.000	1.291, 38.741	9.660	0.002
	Predation	1, 13	2.519	0.136	1, 30	0.017	0.896
	Time \times Predation	1.882, 24.461	0.250	0.768	1.291, 38.741	0.007	0.966
Gall-forming Guild	Time	2.993, 38.906	8.394	0.000	2, 60	0.911	0.408
	Predation	1, 13	0.907	0.358	1, 30	0.017	0.896
	Time \times Predation	2.969, 38.597	1.043	0.384	2, 60	0.079	0.924
Leaf-curling Guild	Time	1.649, 21.441	1.165	0.322	2, 60	3.832	0.027
	Predation	1, 13	0.113	0.742	1, 30	2.109	0.157
	Time \times Predation	3, 39	0.819	0.491	2, 60	0.953	0.391
Leaf-tying Guild	Time	1.409, 19.318	96.691	0.000	1.227, 36.809	11.299	0.001
	Predation	1, 13	1.982	0.183	1, 30	0.307	0.584
	Time \times Predation	1.241, 16.135	0.373	0.595	1.227, 36.809	0.190	0.717
Concealed guilds (pooled)	Time	3, 39	59.273	0.000	2, 60	0.245	0.784
	Predation	1, 13	3.157	0.099	1, 30	0.934	0.342
	Time \times Predation	2.308, 30.007	0.725	0.511	2, 60	0.363	0.697

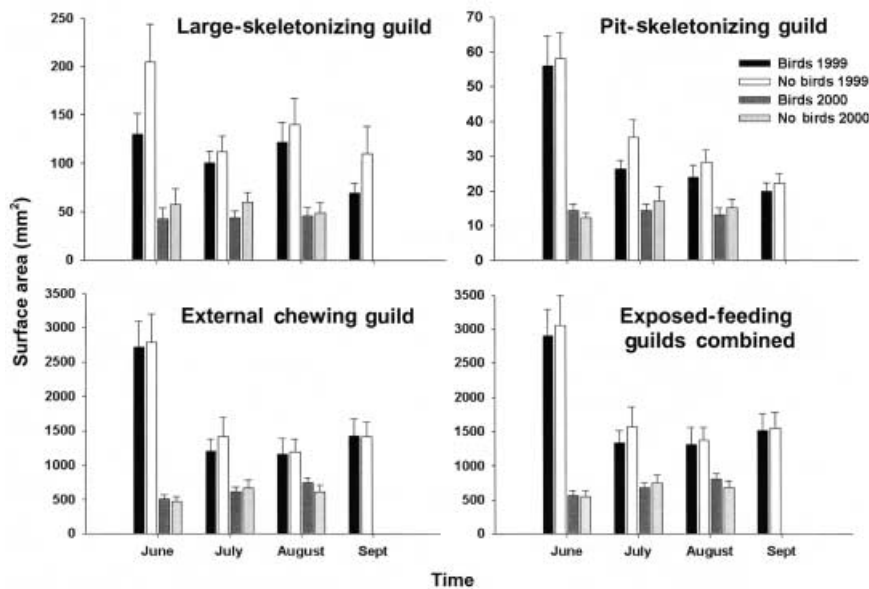


Fig. 1. Surface area damaged (mm^2) by guilds of exposed-feeding insects on *Salix lemmonii* during 1999 and 2000 (mean \pm standard error per 100 leaves). Note: y-axes are not identical in scale.

in the effects of avian predators on the frequency of concealed in comparison to exposed-feeding insects (test for the interaction of predation and feeding habit: Table 5, Fig. 5).

Temporal pattern of guild-specific frequency and damage levels

The frequencies of all guilds and damage levels were higher in 1999 than in 2000 (Fig. 1–3). Among all the guilds external-chewing insects accounted for the greatest proportion of leaf surface area damaged (Fig. 1). Overall, concealed-feeding guilds occurred in lower frequencies than exposed guilds (Fig. 3 and 5). Among the concealed feeding guilds, gall-forming insects were most common.

We detected statistically significant seasonal differences in frequency and feeding damage for most guilds in both years (Table 2–4). The frequencies of all guilds except leaf-mining insects were highest in June 1999 and declined steadily throughout the year. However, in 2000 no peak in frequency in June was observed for most guilds (Fig. 1–3).

Leaf abscission

The number of petioles caught in litter baskets was lower in the absence of avian predators ($\bar{x}_{\text{enclosed}} = 265.6 \pm 69.7$ and $\bar{x}_{\text{un-enclosed}} = 421.5 \pm 65.6$), but not significantly so ($F_{1,12} = 3.323$; $p = 0.091$). In both years, we observed high levels of leaf abscission throughout the season, as well as secondary leaf production.

Abundance of foliage-gleaning birds

The years 1999 and 2000 ranked lowest and fourth lowest, respectively, in the abundance of foliage-gleaning birds since 1992 (Fig. 6A). The number of captures in July and August was less than the average for the years 1992–2000 (Fig. 6B). Recapture rates were low in July and August compared to June. The general pattern over the whole summer is for an individual bird to be caught once and never recaptured. Those caught in June were most likely to be recaptured in June, with a few recaptured in July or August. Of the 23 species of foliage gleaning birds previously caught at the study site, only 15 were captured in 1999 and 2000 (Table 1).

Discussion

Our results suggest that foliage-gleaning birds do not suppress the frequency of and feeding damage caused by folivorous insects on *S. lemmonii*. We observed no suppression of exposed-feeding insects by avian predators averaging among years and guilds. By no suppression, we mean that the treatment magnitude was essentially zero (Fig. 5). We also found no evidence that foliage-gleaning birds suppress the frequency of concealed-feeding insects. On the contrary, when averaged among years and guilds, concealed-feeding insects were slightly more common in the presence of birds than in their absence (Fig. 5).

The effects we found are similar to those reported by Sipura (1999) for concealed-feeding and exposed-feeding insects on *Salix phylicifolia* and *S. myrsinifolia* in southeast Finland. For *S. myrsinifolia*, Sipura (1999) found that insectivorous birds exerted no effect on the

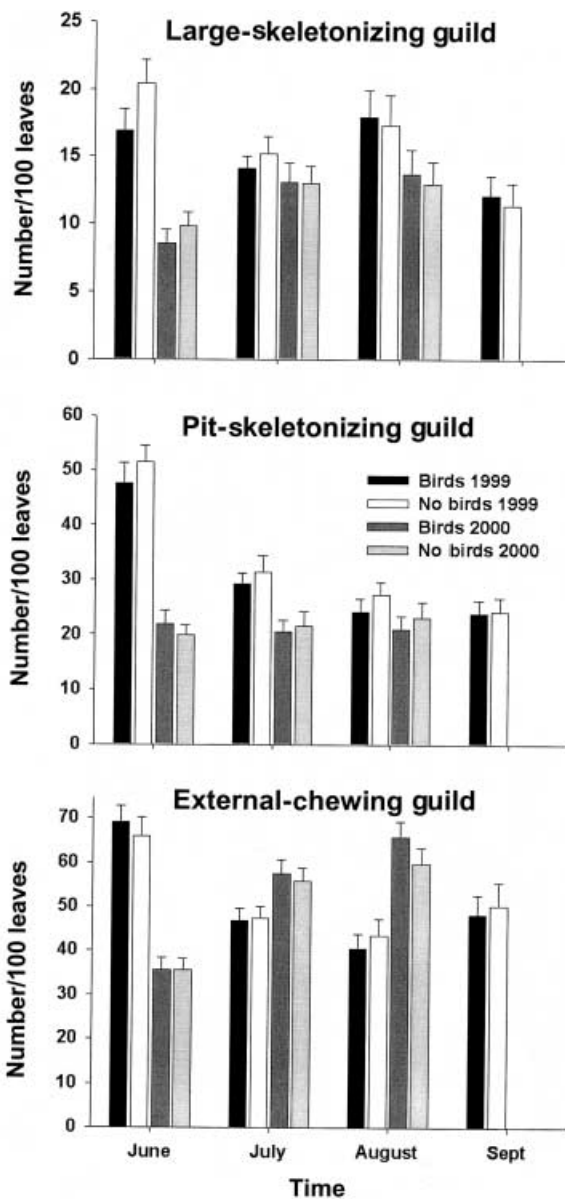


Fig. 2. Frequency of damage caused by guilds of exposed-feeding insects on *Salix lemmonii* during 1999 and 2000 (number/100 leaves: mean \pm standard error). Note: y-axes are not identical in scale.

exposed or concealed-feeding insects. In addition, Sipura (1999) reports that insectivorous birds had no effect on the abundances of concealed insects, but significantly reduced abundances of exposed-feeding insects on *S. phyllifolia*. On the other hand, our results are in stark contrast to the effects observed in other studies where birds have been shown to reduce the abundance of and feeding damage caused by exposed-feeding guilds by 50% or more (Atlegrim 1989, Marquis and Whelan 1994, Floyd 1996, Greenberg et al. 2000, Sanz 2001).

The lack of statistically significant effects in our study is not due to a lack of power. An increase in sample size would reduce the standard errors, but not alter the treatment means for our metrics of impact. In other words, the small effect size we observed for the predator exclusion treatment would be unaffected by increasing the level of replication. Moreover, our results were not altered by the increase in sample size in the experiment performed in 2000. Instead, our results indicate that avian predators truly have no effect on guilds of both exposed and concealed-feeding insects on *S. lemmonii* in Carman Valley.

Most studies use abundance as a metric to estimate the impact of avian predators on exposed-feeding insects, but we used the frequency of and feeding damage caused by insects to estimate the impact of avian predators. While it is possible that our results differ from those previously reported because we used different measures of impact, we think this is unlikely. Many of the studies that estimate the impact of avian predators using insect abundance also report results using feeding damage. In studies reporting data on both abundance and feeding damage the effects detected are similar in all instances (Marquis and Whelan 1994, Sipura 1999, Strong et al. 2000, Sanz 2001). Furthermore, Sanz (2001) also found that effects detected for frequency of occurrence were identical to those for feeding damage. In a recent review of carnivore removal studies and their effects in trophic cascades, Schmitz et al. (2000) reports that the effect of removing carnivores on plant damage did not differ from the direct effect of carnivore removal on herbivore density.

Having assumed that the frequency of and feeding damage caused by insects would increase in the absence of avian predators, we had hypothesized that the number of leaves abscised in response to herbivory might also be higher. Had this been true, estimates of the frequencies of and feeding damage caused by insects based on inspecting the leaves remaining on the shrub would be underestimates. If our sampling protocol was biased towards underestimating frequency or feeding damage in the absence of avian predators, then this could account for our not observing a statistically significant level of suppression of exposed-feeding guilds. However, we found that the number of leaf petioles trapped in leaf baskets was higher in the presence of birds, not in their absence as expected. Therefore, our sampling protocol could not have been biased towards underestimating the effect of avian predators because of herbivore induced leaf abscission. Rather, the smaller number of leaves captured in leaf baskets inside the enclosures probably resulted from reduced lateral wind-blow due to the netting material.

Of the previous studies that report that birds significantly suppress insect populations, most provide no estimate of the abundance of foliage-gleaning birds at their study site (Holmes et al. 1979, Campbell et al.

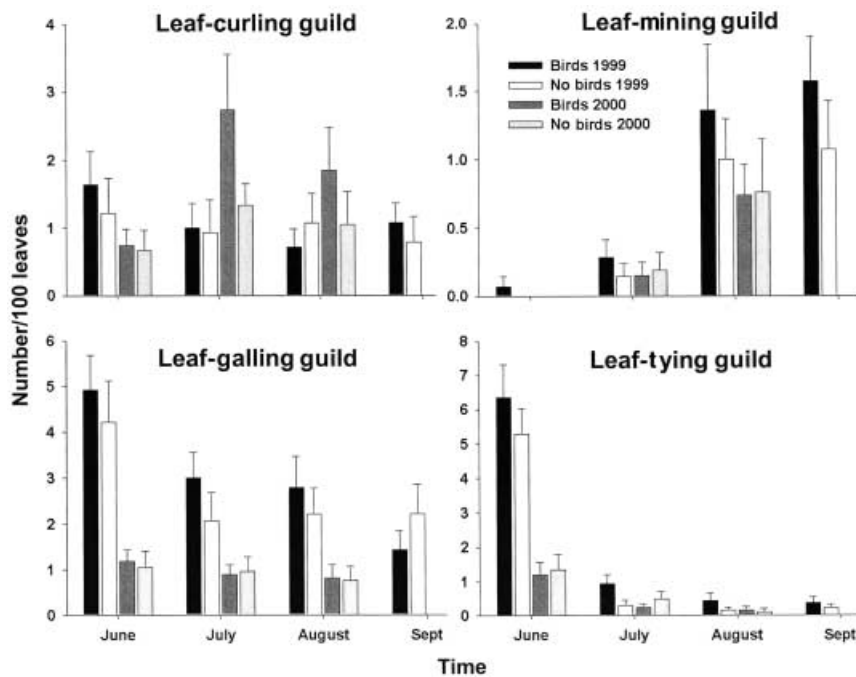


Fig. 3. Frequency of guilds of concealed-feeding insects on *Salix lemmonii* during 1999 and 2000 (number/100 leaves: mean \pm standard error). Note: y-axes are not identical in scale.

1983, Atlegrim 1989, Tschardtke 1992, Marquis and Whelan 1994, Floyd 1996, Sipura 1999, Greenberg et al. 2000). However, Strong et al. (2000) suggest that decreased avian abundance might account for the relatively small effect of avian predators on Lepidoptera that they observed on *Acer saccharum*. In our study, avian abundance in 1999 was the lowest it had been for the last nine years. However, despite the increase in

abundance of avian predators in 2000, we observed no impact of avian predators on folivorous insects. Therefore, our observations of no effect of foliage-gleaning birds on folivorous insects is not solely due to an unusually low abundance of birds (Fig. 6A), but that avian predators do not suppress guilds of folivorous insects on *S. lemmonii*.

Strong et al. (2000) suggest that the relatively weak effects of avian predation that they detected might be caused by low insect abundance. Underlying Strong et al.'s (2000) idea is the conjecture that avian impact on herbivorous insects is density dependent. However, in their two-year study Strong et al. (2000) found no evidence of avian suppression of exposed-feeding Lepidoptera in the year with higher insect densities. On the other hand, Sipura (1999), in a study with two host plant species, found significant levels of suppression of exposed-feeding insects on the host species with higher insect densities. Our study is most comparable to Sipura's (1999), since he studied two willow species. If we use the average area of a *S. lemmonii* leaf (2.5 cm²) to convert our estimates of frequency and feeding damage to the scale used by Sipura (1999), then our estimates for *S. lemmonii* are comparable or higher than the values reported by Sipura (1999) on *S. phlyicifolia*, the species for which he reports avian suppression of exposed-feeding insects. Therefore, we argue that low insect abundance is unlikely to be responsible for the absence of an effect of avian predators on folivorous insects on *S. lemmonii*.

Other causes of mortality, such as arthropod predators, parasitoids or host plant defenses could compen-

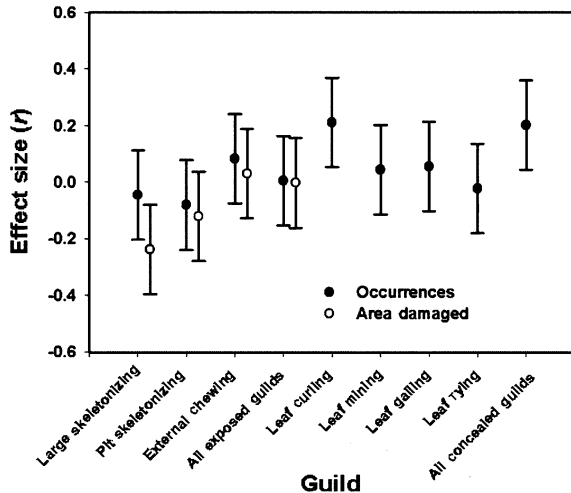


Fig. 4. The average effect of avian predation on the frequency of and feeding damage caused by guilds of concealed and exposed feeding insects on *Salix lemmonii* during 1999 and 2000 ($r \pm$ standard error). Positive values of r indicate that frequency or feeding damage was higher and negative values of r indicate that frequency or feeding damage was lower in the presence avian predators.

Table 5. Analysis of variance (Time \times Predation \times Feeding habit) of the frequency (per 100 leaves) for each feeding habit (concealed or exposed). All tests are univariate tests with degrees of freedom adjusted for non-sphericity of the variance-covariance matrix using Huynh-Feldt ϵ .

Source	1999			2000		
	df (num, denom)	F	p	df (num, denom)	F	p
Time	1.702, 22.123	21.361	0.000	1.803, 54.079	35.388	0.000
Predation	1, 13	0.565	0.466	1, 30	0.283	0.599
Feeding habit	1, 13	619.195	0.000	1, 30	1072.815	0.000
Time \times Predation	3, 39	0.165	0.919	1.803, 54.079	0.179	0.814
Habit \times Predation	1, 13	3.326	0.091	1, 30	0.066	0.798
Time \times Habit	1.650, 21.454	13.237	0.000	1.761, 52.838	40.427	0.000
Time \times Habit \times Predation	2.745, 35.681	0.331	0.785	1.761, 52.838	0.153	0.832

sate for the mortality lost when avian predators are reduced in abundance (Tscharnke 1992, Marquis and Whelan 1994). If such compensation occurred within our study enclosures, it could explain the small effect of removing avian predators that we observed. During many hours of field observation, we noticed no increase in the abundance of spiders, ants, or other arthropod predators within our enclosures. Also, in the one study specifically designed to determine if the effect of arthropod predators on folivorous insects is greater in the absence of birds, no effect was detected (Floyd 1996). Given our within-subjects experimental design in

1999 it is also unlikely that rates of host-plant mediated mortality differed between adjacent enclosed and un-enclosed portions of the same individual shrub.

Several studies indicate that insectivorous birds show distinct foraging preferences based on host plant species (Holmes and Robinson 1981, Gabbe et al. 2002), and

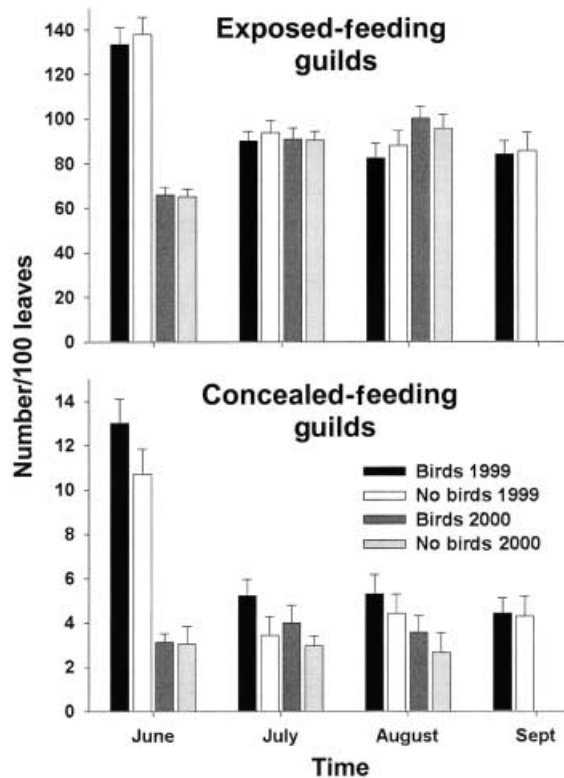


Fig. 5. Frequency of damage caused by all exposed and concealed-feeding insects on *Salix lemmonii* during 1999 and 2000 (number/100 leaves: mean \pm standard error). Note: y-axes are not identical in scale.

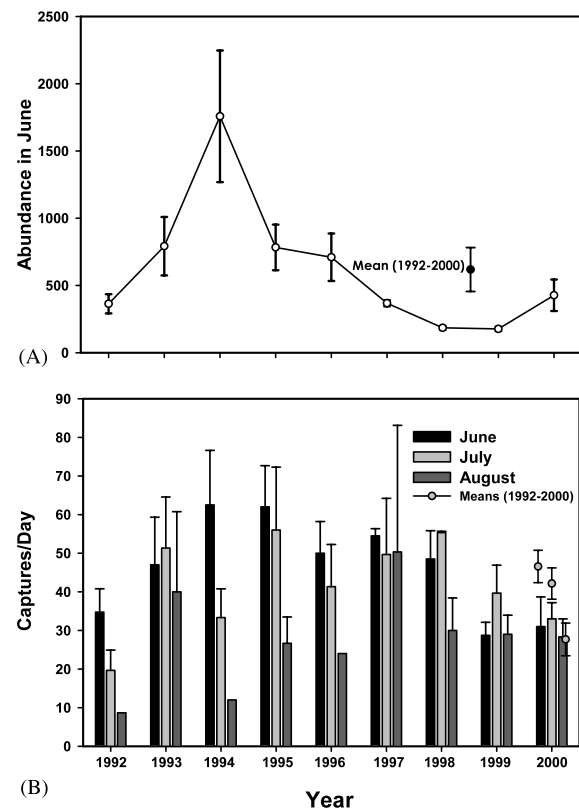


Fig. 6. Abundance of foliage gleaning birds in Carman Valley, CA 1992-2000. (A) Estimates of the abundance of foliage-gleaning birds based on captures for June of each year. Abundance estimates were derived from a variety of models $M(T)$, $M(TH)$, $M(H)$, and $M(BH)$, using the model selection algorithm in the program Capture. Error bars represent \pm standard error. (B) Estimates of the average daily capture rates for foliage-gleaning birds for each summer month. Mist nets were run for 4 days in June of each year, and for 3 days in July and August of each year. Error bars represent \pm standard error.

some suggest that these preferences are based on structural features of the plant (Robinson and Holmes 1982, 1984, Whelan 1989, Parrish 1995, Marquis and Whelan 1996). The small to non-existent effect of avian predators on willow insects reported here and by Sipura (1999) may arise because the architecture of *Salix* spp. is considerably different from the plant species examined in other studies. Willows are shrub-like plants with a dense crown of tightly packed shoots that extend vertically with high densities of narrow soft leaves. The vertical architecture, shoot density, leaf shape and size, and the flexible nature of the willow branches may prevent foliage-gleaning birds from efficiently capturing their prey. The architecture of willows could affect the foraging success of foliage-gleaning birds by impairing their movement among shoots, by affecting the conspicuousness and accessibility of prey, and also, by providing inadequate mechanical support for perching and gleaning. The plant species used in studies that report substantial effects of birds in suppressing folivorous insects are generally more arborescent or angular branching plants with broader and thicker leaves, such as bilberry (Atlegrim 1989), oak (Marquis and Whelan 1994, Sanz 2001), creosote bush (Floyd 1996), and sugar maple (Strong et al. 2000).

The complete lack of an effect of avian predators on folivorous insects that we observed represents one end of a spectrum of effects that have been reported thus far. While some studies show large effects (Holmes et al. 1979, Atlegrim 1989, Marquis and Whelan 1994), others show weaker effects, effects absent in some years, or effects absent for some host plant species (Sipura 1999, Strong et al. 2000). Thus far, the two studies that have examined concealed-feeding insects find that birds have little or no effect on their abundance or frequency (Sipura 1999 and our study). Further studies will be necessary to determine under what conditions avian predators are likely to suppress the abundance, frequency of, and feeding damage caused by guilds of exposed-feeding insects, and if the impact of avian predators is generally greater on exposed-feeding insects than on concealed-feeding insects. The current ecological literature generally supports the important role of avian predators in regulating insect community dynamics with correlated indirect effects on the host plant; however, this may reflect a possible bias for publishing significant results (Polis et al. 2000, Schmitz et al. 2000). By showing no effect we raise the issue that under some conditions maybe birds do not suppress folivorous insects and that discovering when they will and will not have an effect would be a productive line of inquiry.

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