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Diet switching and food delivery by shrubsteppe passerines in response to an experimental reduction in food

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DIET SWITCHING AND FOOD DELIVERY BY SHRUBSTEPPE PASSERINES IN RESPONSE TO AN EXPERIMENTAL REDUCTION IN FOOD

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ABSTRACT.—We experimentally reduced the food base of nesting Brewer's Sparrows (*Spizella breweri*) and Sage Thrashers (*Oreoscoptes montanus*) in a shrubsteppe region of south central Idaho in 1989 and 1990. Frequency and mass of "birdfood" arthropods in pitfall, sweep net, and stickyboard samples were generally lower on sites treated with a broad-spectrum insecticide (malathion) than on untreated sites though the effect varied among taxa. In 1990 *O. montanus* switched nestling diets to prey taxa not affected by the treatment. Time between nestling food deliveries was greater for *S. breweri* on the treated than untreated site in 1989. In 1990 there were no between-site differences, but there was an increase in delivery time on the treated plot after treatment; this difference was within the range of delivery times recorded on the untreated plot. Malathion applications did reduce the food base, but plasticity in passerine behavior and emergence characteristics of some prey taxa ameliorated indirect effects of food reduction to birds.

Key words: Brewer's Sparrow, Sage Thrasher, Spizella breweri, Oreoscoptes montanus, food reduction, diet switching, food delivery, malathion, insecticide.

Few investigators have experimentally reduced prey abundance in the field to determine indirect effects to birds (but see Cooper et al. 1990, Rodenhouse and Holmes 1992, Pascual 1994). Our objective was to experimentally reduce prey of nesting migratory passerines through application of malathion, a broad-spectrum insecticide, and determine what effects this perturbation would have on prey abundance, food delivery intervals, and nestling diets.

We predicted that the number (frequency) and/or mass of "birdfood" arthropods sampled with 3 different methods would decrease on the treated plot after insecticide application. Where food was reduced, time between food deliveries was predicted to increase. Furthermore, we predicted that some arthropod taxa would be reduced more than others after the application (Pfadt et al. 1985) and that adults would switch to more abundant prey types (Rotenberry 1980).

Wiens (1974, 1977, 1984) and Wiens and Rotenberry (1980) suggested that arthropod food in shrubsteppe ecosystems is "superabundant" during most years, but birds may experience an ecological crunch in those years when food is scarce. Howe et al. (1996) found no effect of food reduction on nestling survivorship but some effects on nestling size on our study site. If food were reduced but not to crunch levels during our study, we would expect to observe behavioral responses, such as diet switching and increased feeding times, as adults attempt to cope with food reduction. Changes in behavioral and physical characteristics might be expected even when no effects on adult density or productivity are evident from food reduction.

STUDY AREA AND METHODS

The study area is located in the shrubsteppe region of south central Idaho approximately 72 km north of Twin Falls at an elevation of 1450–1500 m. A single untreated plot (unsprayed) was randomly chosen for the 2-yr study, and 2 different treatment plots were chosen for 1989 and 1990. Each plot consisted of a 49-ha core area wherein all data were collected. On the treated plots we sprayed the core areas and an additional 0.8-km-wide strip around the core areas. A standard grasshopper control rate of malathion was applied on 3

June 1989 and 8 June 1990. Detailed site and treatment application descriptions can be found in Howe et al. (1996).

Spizella breweri (Brewer's Sparrows) and *Oreoscoptes montanus* (Sage Thrashers) are found throughout the shrubsteppe region of western North America (Wiens and Rotenberry 1981). Both species are primarily insectivorous during the breeding season (Wiens and Rotenberry 1979, Rotenberry 1980) and feed their young almost exclusively arthropods (Petersen and Best 1986, Petersen et al. 1986, Rotenberry and Wiens unpublished data). On our study sites *S. breweri* began hatching in late May, with peak hatching during the first 2–3 wk of June. *Oreoscoptes montanus* began hatching in early May, with 1 hatching peak during late May and another in late June.

Spizella breweri nests were observed with binoculars from elevated (1.2–2.5 m) platforms placed within 50 m of nests. Nest observations were made between ~0800 and 1200 h and 1600 h until sunset to avoid the coolest and warmest parts of the day. We conducted 2-h observations twice at each nest when nestlings were 1–3 d old (early) and 4–6 d old (late). Feeding intervals, i.e., time elapsed between consecutive feedings, were calculated and averaged for each nest over the observation period. *Oreoscoptes montanus* feeding interval data could not be obtained; if observers were within 150 m, the birds would not approach their nests.

We used the ligature method (Kuligin 1981, Henry 1982) to sample food items brought to nestlings. Ligatures were placed on each nestling in a nest for 1 h during midmorning or late afternoon. The entire amount of food brought to all nestlings within the 1-h period was considered to be a single sample. Nestling diet samples were taken from 5- and 8-d-old *O. montanus* and 5-d-old *S. breweri.* Ligature samples were not taken during food delivery observations to avoid excess disturbance. All diet samples were stored in 70% alcohol.

Arthropods were collected twice before and 3 times after treatment applications on untreated and treated plots. Timing of arthropod collections in relation to treatment varied because we avoided cold, rainy conditions. In 1989 collections were taken 13 and 2 d pretreatment and 7, 21, and 35 d posttreatment. Collections in 1990 were taken 14 and 2 d pretreatment and 11, 17, and 27 d posttreatment.

We employed 3 arthropod capture techniques: (1) pitfall traps—16-oz plastic cups buried flush with the surface with approximately 1 oz of ethylene glycol as a killing fluid; (2) sweep nets; and (3) stickyboards—pre-manufactured glue traps with approximately 190 cm^2 area per board. Twenty arthropod collection stations were selected at random on each plot. Pitfalls (2 beneath sage and 2 in the open) and stickyboards (2 high in the sage canopy and 2 near the ground) were placed at each station for 24 h during each of the 5 sampling periods. Sweep nets (50 each in shrubs and grass) were used during midmorning at each station. Pitfall and sweep net samples were also stored in 70% alcohol; while this may cause some shrinkage of samples, samples from both plots were treated identically to avoid any bias.

Arthropods from all samples were counted, measured (length), and identified to family (some families were divided into adult and larval forms). Arthropod taxa not detected in diet samples were omitted from environmental samples before analysis. Environmental samples were also truncated to reflect maximum prey size, but not minimum size (Johnson et al. 1980), found in nestling diets. Arthropod taxa found in diet samples and truncated for maximum length were considered birdfood taxa.

Mass was estimated for each arthropod using length/weight regressions (Rogers et al. 1976, 1977). Mass per sample was calculated by multiplying mass of each individual by number of individuals in each taxon.

Analysis

Our experimental design included measurement of treated and untreated subjects before and after pesticide application. We randomly assigned plots to untreated or treated groups before the 2-yr experiment and standardized measurement procedures during the experiment to control for procedure effects and experimenter bias. While it was not possible to replicate treatments within years, we were able to replicate the experiment in 2 yr. Also, we restricted our inference to the plots studied, thus avoiding pseudoreplication (Hurlbert 1984).

Unless otherwise stated, we used analysis of variance (ANOVA; SAS 1988); 1- or 2-tailed tests of significance were used depending on the comparison. Before the treatment,

between-plot comparisons (untreated vs. treated) were made with 2-tailed tests; post-treatment between-plot comparisons used 1-tailed tests. For pretreatment vs. posttreatment comparisons within plots, we used 1-tailed tests. Other between-period, within-plot comparisons used 2-tailed tests. To normalize data from both environmental and diet samples, we transformed frequency (square root) and mass (natural log) of arthropods. The alpha level for all statistical tests was 0.05.

Environmental samples from each of the 3 arthropod collection techniques were analyzed separately. We analyzed these samples first considering all birdfood taxa. A subsequent analysis was done on each arthropod taxon constituting >10% (by mass or frequency) of nestling diets; taxa making up <10% of nestling diets were lumped into an additional group—"other birdfood" (see Tables 1, 2).

We tested for differences in food delivery intervals for three 10-d periods following the

TABLE 1. Arthropods (percent of total mass and percent of total frequency) in nestling *Spizella breweri* diets.

| Arthropod taxa[a] | | 1989 | | | 1990 | |
	N[b]	Mass[c] (%)	Freq[d] (%)	N	Mass (%)	Freq (%)
Araneida	13	8.5	11.5	9	18.5	11.5
Coleoptera larvae	3	0.5	2.0	7	15.0	53.5
Diptera	6	7.5	4.0	4	18.5	3.5
Hemiptera	6	0.5	5.0	5	6.5	7.5
Homoptera						
Cicadidae	13	53.0	11.5	—	—	—
Other	6	1.5	9.5	7	2.0	12.5
Hymenoptera	5	1.5	3.5	1	2.0	1.0
Lepidoptera						
Adults	8	3.5	7.0	1	10.5	1.0
Larvae	14	15.0	33.0	3	4.5	5.5
Neuroptera	8	2.5	8.5	—	—	—
Orthoptera	3	6.5	2.0	3	23.0	5.5

[a]Values represent total for all families within order unless specified.
[b]Number of ligature samples containing arthropod taxa, not number of individual arthropods; total number of ligature samples = 52.
[c]Percent of total diet (mass) made up of individual arthropod taxa; mass estimated using length/weight regressions (Rogers et al. 1976, 1977).
[d]Percent of total diet (frequency) made up of individual arthropod taxa.

TABLE 2. Arthropods (percent of total mass and percent of total frequency) in nestling *Oreoscoptes montanus* diets.

| Arthropod taxa[a] | | 1989 | | | 1990 | |
	N[b]	Mass[c] (%)	Freq[d] (%)	N	Mass (%)	Freq (%)
Araneida	1	<0.5	2.0	6	3.5	4.5
Coleoptera	6	1.0	11.5	4	0.5	3.0
Diptera	—	—	—	3	1.5	3.0
Hemiptera	1	1.0	3.5	1	<0.5	0.5
Homoptera						
Cicadidae	11	55.0	26.0	4	11.0	5.0
Other	—	—	—	1	<0.5	0.5
Hymenoptera	2	1.5	7.5	8	1.0	8.0
Lepidoptera						
Adults	2	3.5	3.5	—	—	—
Larvae	9	13.5	28.0	7	1.5	5.0
Orthoptera						
Acrididae	5	15.5	13.0	12	12.5	11.0
Gryllidae	2	9.0	3.5	26	69.0	58.5

[a]Values represent total for all families within order unless specified.
[b]Number of ligature samples containing arthropod taxa, not number of individual arthropods; total number of ligature samples = 51.
[c]Percent of total diet (mass) made up of individual arthropod taxa; mass estimated using length/weight regressions (Rogers et al. 1976, 1977).
[d]Percent of total diet (frequency) made up of individual arthropod taxa.

1989 treatment (insufficient data were collected to make a valid pretreatment comparison). In 1990, 1 pretreatment and 2 posttreatment periods were used. We also analyzed all between-period (within-plot) combinations in both years.

Diet samples were categorized as pre- or posttreatment. *Oreoscoptes montanus* diet samples were compared on both plots before and after treatment. Since the treatment application preceded the peak of *Spizella breweri* hatching, we made only posttreatment comparisons of their diet samples.

We calculated a posteriori power for feeding interval and arthropod frequency and mass tests which were not significant. Actual mean values were used for the untreated plot; values for the treated plot were arbitrarily set at 5 min more than the untreated plot. Power to detect 5-min differences among sampling periods within untreated and treated plots was also determined. Power to detect a 50% difference on the treated plot, compared to the actual measured value from the untreated plot, was determined (K. Burnham and G. White, Colorado State University, personal communication). We defined power as good ($\geq$0.70), moderate ($>$0.30 and $<$0.70), or poor ($\leq$0.30). Power calculations with an alpha level of 0.05 were based on 1- or 2-tailed tests of significance depending on the comparison as described above.

RESULTS

Overall Prey Reductions

Since malathion is a broad-spectrum insecticide, we expected substantial prey taxa reductions posttreatment. And, as predicted, frequency and/or mass of birdfood arthropods from pitfall, sweep net, and stickyboard samples were lower on treated than untreated plots in most posttreatment samples in 1989 and 1990. This pattern, while variable, was evident for both *S. breweri* and *O. montanus* prey in both years of the study from all 3 sampling techniques (Figs. 1, 2). Where prey was affected, the most common posttreatment pattern observed was a lower arthropod frequency and mass on the treated plot (e.g., Fig. 2, 1990A). In a few cases (1989 sweep net samples) pretreatment differences were evident immediately before treatment; thus, posttreatment differences may have been influenced by factors other than treatment alone.

Mass and frequency of arthropods were different ($P < 0.01$) on stickyboards placed high and low in the sage canopy and were analyzed separately. Differences between microhabitats sampled by pitfall traps (open or under sage) and sweep nets (grass or sage) were not significant and did not require separate analyses.

Power to detect a 50% change in arthropod frequency and mass was consistently good for tests using pitfall and sweep net samples. Power varied more widely for tests using stickyboard samples but was generally moderate to good (Appendix A).

Spizella breweri Prey Taxa

Maximum size of prey items in *S. breweri* diets was 27 mm for Lepidoptera larvae and 23 mm for all other taxa. Prey taxa of *S. breweri* typically showed lower frequency and/or mass on the treated than untreated plot during 1 or more sampling periods after insecticide application. This pattern was evident both in 1989 and 1990. Another posttreatment pattern was also evident in 1990: a lower frequency but no detectable difference in mass (Fig. 1, 1990D). This resulted from fewer but larger prey on the treated plot.

In 1989 birdfood arthropod taxa analyzed for *S. breweri* included Araneida (arachnids), Homoptera, Lepidoptera, and "other" (a combination of taxa which individually made up <10% of nestling diet; see Table 1); these taxa were not equally affected by the insecticide (Appendix B). After treatment significantly smaller prey frequency and/or mass values were detected on the treated plot for all birdfood taxa: Araneida (both variables in pitfalls and stickyboards), Homoptera (both variables in pitfalls, frequency in sweep nets, mass in stickyboards), Lepidoptera (both variables in stickyboards), and other (mass in pitfalls). The only differences detected in these taxa immediately before treatment were in Homoptera (frequency in stickyboards) and other (both variables in sweep nets and stickyboards).

In 1990 Coleoptera and Orthoptera (mass tests only) were added to the prey taxa list for *S. breweri* (see Table 1). Significantly lower posttreatment values for prey frequency and/or mass were again detected on the treated plot for all prey taxa: Araneida (mass in stickyboards), Coleoptera (frequency in pitfalls), Homoptera (frequency in pitfalls and stickyboards), Lepidoptera (mass in pitfalls and
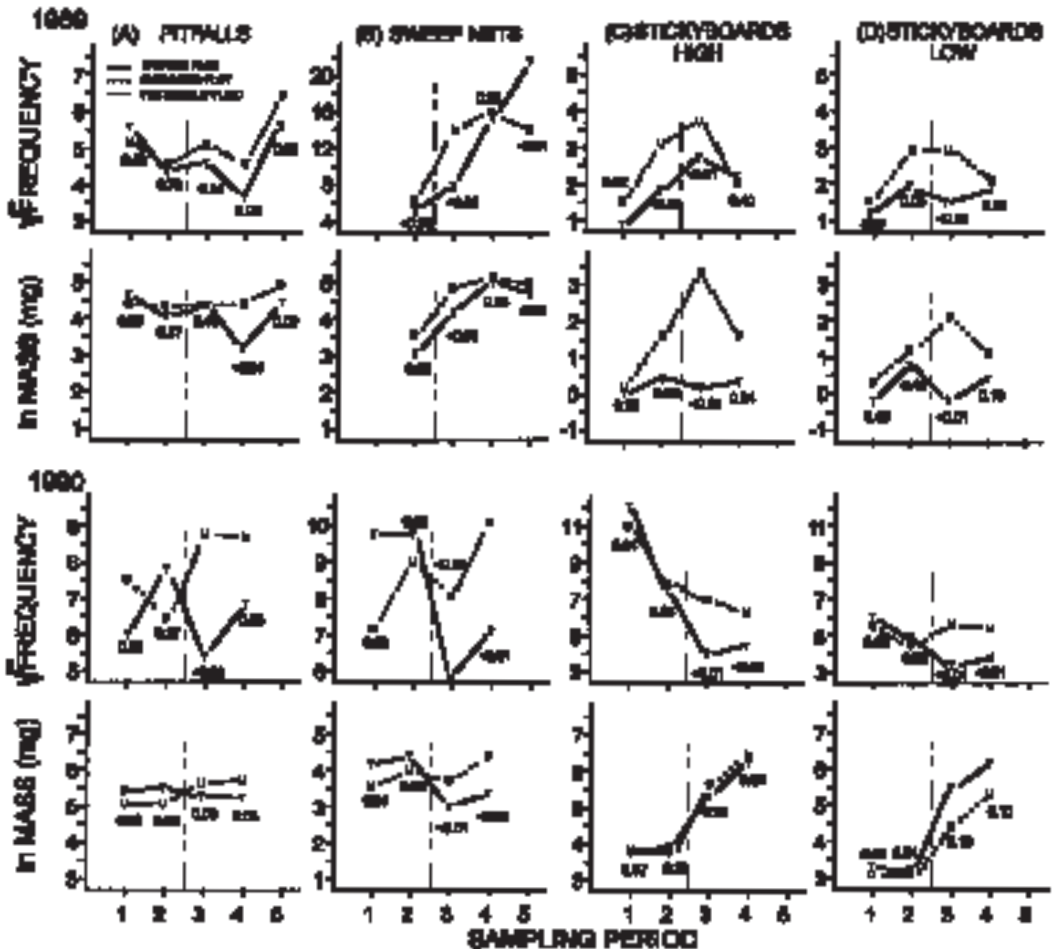
Fig. 1. *Spizella breweri* food abundance (frequency and mass of arthropods) before and after insecticide treatment in 1989 and 1990. Arthropod families were combined and represent only those taxa actually consumed by nestlings. Within figures, letters (T = treated, U = untreated) indicate means and numbers indicate probability (ANOVA) of between-plot differences occurring by chance. In 1989 sampling periods 1 and 2 were 13 and 2 d pretreatment, respectively; periods 3, 4, and 5 were 7, 21, and 35 d posttreatment, respectively. In 1990 sampling periods 1 and 2 were 14 and 2 d pretreatment; periods 3, 4, and 5 were 11, 17, and 27 d posttreatment.

stickyboards), Orthoptera (mass in pitfalls and sweep nets), and other (both variables in all 3 samples). Before treatment only Coleoptera (frequency in stickyboards) were less frequent on the treated than untreated plot; all other taxa showed either no difference or greater treatment plot values (Appendix B).

Oreoscoptes montanus Prey Taxa

Maximum size of prey in *O. montanus* diets was 32 mm for Lepidoptera larvae and 27 mm for all other taxa. Frequency and mass of *O. montanus* birdfood arthropods were generally significantly reduced on the treated but not untreated site after treatment was applied. Again, responses differed depending on taxa involved (Appendix B). In 1989 and 1990 *O. montanus* prey taxa used in analyses included Coleoptera (frequency only), Homoptera, Lepidoptera, Orthoptera, and other (Table 2).

In 1989 Coleoptera (frequency in sweep nets), Homoptera (frequency in sweep nets), Lepidoptera (mass in pitfalls, both variables in stickyboards), and other (both variables in sweep nets, frequency in stickyboards) had lower values on the treated plot after malathion application. Immediately before treatment, Coleoptera (frequency in sweep nets),
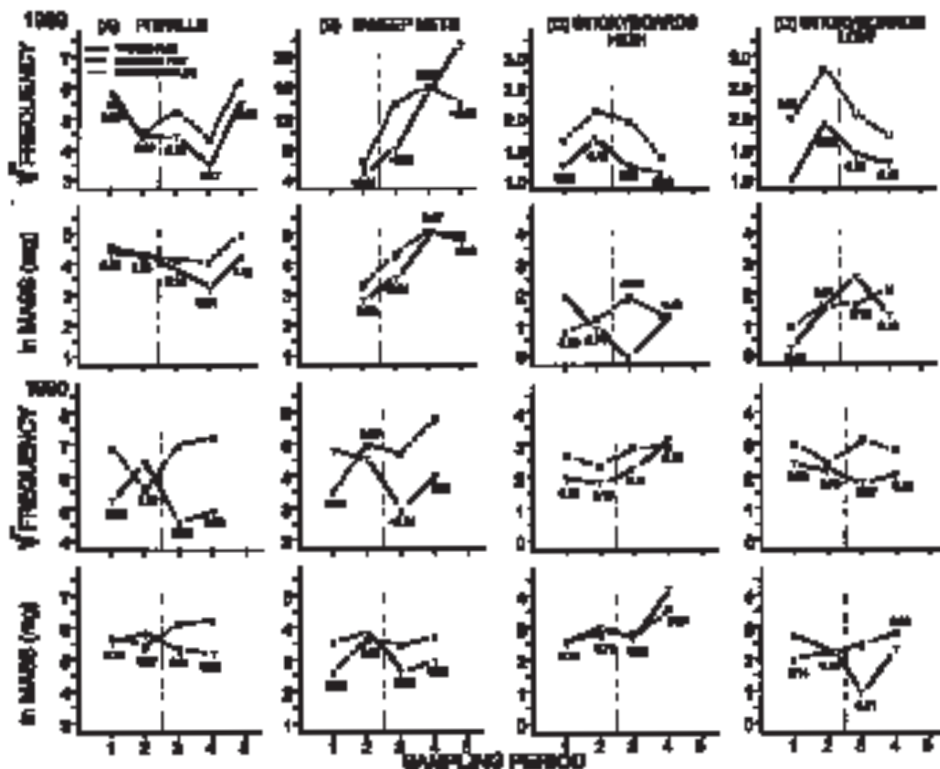
Fig. 2. *Oreoscoptes montanus* food abundance (frequency and mass of arthropods) before and after insecticide treatment in 1989 and 1990. Arthropod families were combined and represent only those taxa actually consumed by nestlings. Within figures, letters (T = treated, U = untreated) indicate means and numbers indicate probability (ANOVA) of between-plot differences occurring by chance. In 1989 sampling periods 1 and 2 were 13 and 2 d pretreatment, respectively; periods 3, 4, and 5 were 7, 21, and 35 d posttreatment, respectively. In 1990 sampling periods 1 and 2 were 14 and 2 d pretreatment; periods 3, 4, and 5 were 11, 17, and 27 d posttreatment.

Homoptera (frequency in sweep nets), and other (both variables in sweep nets and frequency in stickyboards) showed significantly greater values on the treated plot.

After treatment in 1990 Coleoptera (frequency in pitfalls and stickyboards), Orthoptera (both variables in pitfalls and stickyboards), Homoptera (frequency in sweep nets), and other (both variables in sweep nets) were lower on the treated plot. Before treatment all taxa except Coleoptera (frequency in pitfalls) showed either no difference or greater treatment plot values (Appendix B).

Food Delivery

Food reduction was expected to cause birds on the treated plot to forage longer for prey and thus have greater intervals between food deliveries to nestlings. Figure 3 illustrates differences in food delivery intervals for *S. brew-* *eri* in 1989. Because there were significant differences between delivery intervals for early and late nests, they were analyzed separately. We found no between-plot differences in food delivery intervals during any posttreatment periods for the 1- to 3-d-old (early) nestlings. However, a significant increase was detected in the food delivery interval between the 1st (1–10 d) and 3rd (>20 d) posttreatment periods on the treated ($P = 0.02$) but not untreated ($P = 0.57$) plot. No other between-period differences for the early age group were found.

We found no between-plot differences in the 1st posttreatment period for the late (4- to 6-d-old) nestling group in 1989. However, during the 2nd posttreatment period (11–20 d), feeding intervals on the treated plot were over 3 min longer ($P = 0.07$) than on the untreated plot. This was followed by a significant decline ($P = 0.04$) in the food delivery
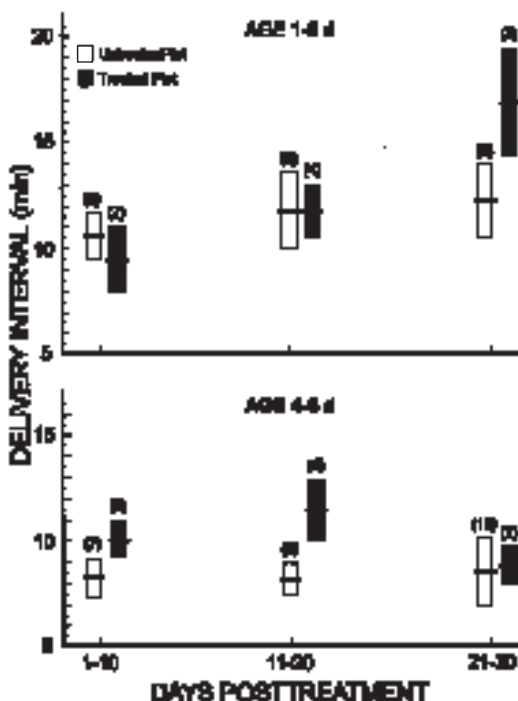
Fig. 3. Food delivery intervals for 1- to 3-d-old and 4- to 6-d-old *Spizella breweri* from an untreated and insecticide-treated site in 1989. Delivery intervals for each nest were averaged over a 2-h observation; horizontal lines represent mean of all nests observed $\pm s_{\overline{x}}$ (vertical bars); number of nests is in parentheses.

interval on the treated plot from the 2nd to 3rd posttreatment periods, with no between-plot difference during the 3rd period. No other significant differences were detected (Fig. 3). Power to detect a 5-min difference in delivery intervals between plots and between periods was good for all tests in 1989.

Because we detected no differences between early and late nests in 1990, these data were pooled for analysis. Before treatment, intervals on the untreated site were longer ($P = 0.01$) than on the treated plot. Feeding interval length on the untreated plot declined ($P = 0.04$) between the pretreatment and 1st posttreatment period. We detected no between-plot differences during either posttreatment period (1–10 d and >10 d).

On the treated plot *S. breweri* adults took more than 5 min longer per trip to feed their young during the 2nd posttreatment period than before malathion application ($P = 0.03$); however, this was within the range of feeding intervals measured on the untreated plot (Fig. 4). Power for all tests was moderate.

Arthropod Use and Prey Switching

Diets of nestling *S. breweri* were more diverse than those of nestling *O. montanus*, though Araneida, Coleoptera, Homoptera, Lepidoptera, and Orthoptera occurred in nestling diets of both species (Tables 1, 2). We found no significant between-plot differences in frequency (number hr^{-1}) of birdfood arthropods from *S. breweri* nestling diets following the treatment application in either study year. Pretreatment comparisons were not made for *S. breweri*.

The mass (mg hr^{-1}) of ligature samples from nestling *S. breweri* did not differ significantly between untreated and treated plots. In 1989 mass was almost identical ($P = 0.49$, $N = 32$) on untreated ($\overline{x} \pm s_{\overline{x}} = 42.95 \pm 1.2$ mg hr^{-1}) and treated (43.38 ± 1.3) plots; in 1990 mass on the treated plot (45.15 ± 1.3) was marginally smaller ($P = 0.07$) than on the untreated plot (83.93 ± 1.2), but sample size was low ($N = 10$).

No between-plot differences in birdfood frequency or mass were detected in *O. montanus* diet samples in 1989. Also, arthropod frequency and mass did not decrease on the treated plot after the 1989 treatment as predicted. Furthermore, the plot × period interaction was not significant. In 1990 we detected a significant plot × period interaction in frequency of arthropods from *O. montanus* nestling diets ($P = 0.05$). However, the number of arthropods in *O. montanus* diets was significantly higher on the treated than untreated plot before ($P = 0.03$) malathion was applied. Frequency declined marginally ($P = 0.08$) on the treated site and rose slightly on the untreated site between periods and was not different between plots ($P = 0.29$) after pesticide application.

Prey switching was evident for *O. montanus* in 1990 (Fig. 5). *Oreoscoptes montanus* fed their young primarily Orthoptera (mostly crickets; family Gryllidae) on both untreated and treated plots before the treatment. After treatment, *O. montanus* switched to Homoptera (primarily Cicadas) on the treated plot but continued to feed Orthoptera on the untreated plot. Cicadas made up only a small fraction of *O. montanus* nestling diets on either plot before treatment. Despite the change in primary
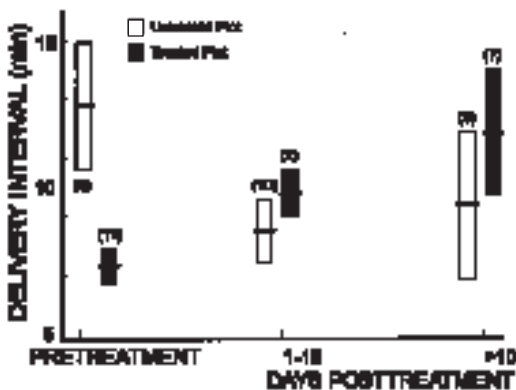
Fig. 4. Food delivery intervals for 1- to 6-d-old *Spizella breweri* from an untreated and insecticide-treated site in 1990. Delivery intervals for each nest were averaged over a 2-h observation; horizontal lines represent mean of all nests observed $\pm s_{\overline{x}}$ (vertical bars); number of nests is in parentheses.

prey taxa on the treated plot, mass of arthropods in posttreatment diet samples ($\overline{x} \pm s_{\overline{x}}$, 357.13 ± 1.36 mg hr^{-1}, $N = 5$) did not appear to change significantly ($P = 0.28$) from pretreatment samples (448.05 ± 1.25, $N = 9$), although sample size was small.

Prey switching in *O. montanus* in 1989 appeared to occur but was not as evident as in 1990. The proportion of Orthoptera in nestling *O. montanus* diets began and remained low on the treated plot, but began low and increased marginally between periods on the untreated plot (plot × period interaction, $P = 0.08$). After treatment there were more Orthoptera in nestling diets on the untreated than treated site ($P = 0.02$). Homopteran proportions on the treated site increased from 25% to >50% of the diet between periods, but neither this increase ($P = 0.38$) nor any between-plot comparisons were significant (Fig. 5).

Spizella breweri were not feeding nestlings before treatment applications, so we were not able to determine if they switched their diets in response to the treatment. However, posttreatment between-plot comparisons of nestling *S. breweri* diets could be made. In 1989 a greater proportion (by frequency) of Homoptera were fed to nestlings on the treated than untreated plot ($P = 0.03$). This does not appear to be a treatment effect since Homoptera abundance was lowered by the treatment. There were no significant between-plot differences in frequency or mass of any other prey

taxa measured. Additionally, none of the dietary proportions of arthropod taxa were significantly different between plots in 1990 (Fig. 6).

DISCUSSION

Food is usually "superabundant" during the breeding season in shrubsteppe ecosystems (Wiens 1984). However, in some years food abundance may be unusually low, leading to changes in avian productivity. This has been referred to as an ecological crunch (Wiens 1974, 1977, Wiens and Rotenberry 1980). In this scenario the food limitation threshold, i.e., the level of abundance below which food scarcity begins to influence productivity (Rodenhouse and Holmes 1992), is met or exceeded only rarely.

Food reductions may not affect productivity if birds are able to compensate for lost resources through changes in behavior. Thus, indirect effects of food reductions might be reflected in behavioral changes, e.g., diet switching or increased foraging time, even when reductions in productivity are not evident.

Overall Prey Reductions

We expected applications of malathion to significantly reduce both frequency and mass of birdfood arthropods (see Jepson 1989). And, results from our pitfall, stickyboard, and sweep net samples indicate that abundance of ground-dwelling, aerial, and cover-dwelling birdfood arthropods was generally reduced by insecticide treatment. However, effects of the treatment varied among families of arthropods such that some prey taxa were more abundant than others after treatment.

Malathion is a nonpersistent, broad-spectrum, contact insecticide (Smith 1987) that does not affect all arthropod families equally (Pfadt et al. 1985, Swain 1986). Those arthropod taxa whose behavior or life history characteristics (Pascual 1994) allowed them to avoid contacting malathion would have been less susceptible to our treatments. Cicadas (order Homoptera, family Cicadidae), for example, did not emerge before the treatment in either year of study and were thus not affected by it. In contrast, crickets (order Orthoptera, family Gryllidae) emerged before the treatment and spent much of their time on the ground in relatively open areas that received greater insecticide coverage. The order Orthoptera, including
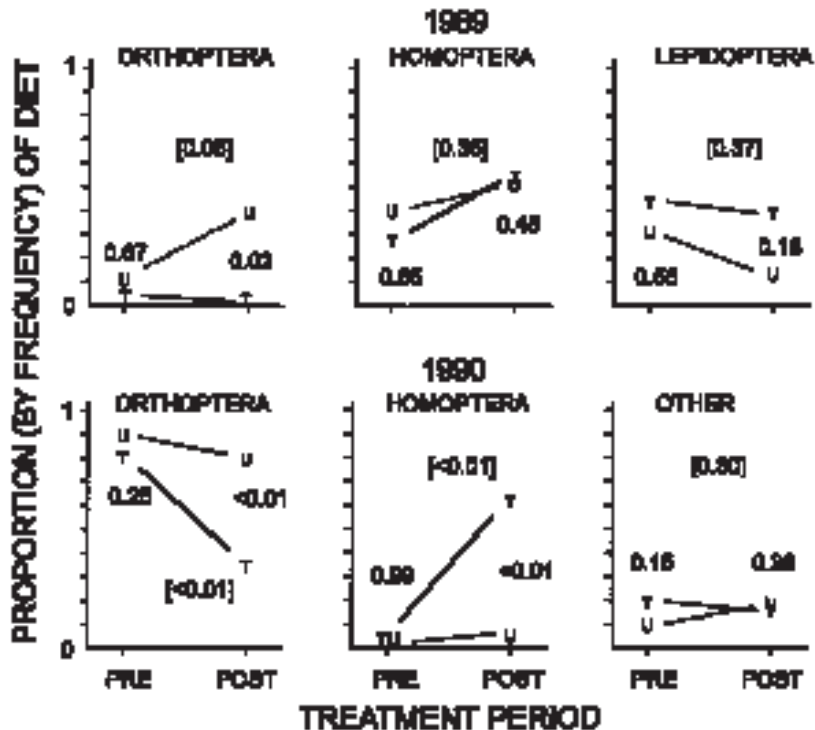
Fig. 5. Proportion of arthropods (by frequency) in nestling *Oreoscoptes montanus* diets before and after an insecticide treatment in 1989 (*N* = 20 samples) and 1990 (*N* = 32 samples). Items collected from different nestlings in the same nest were combined for each sample; nests may have been sampled more than once, and so samples may represent the same nest on different dates. Letters (T = treated, U = untreated) indicate means, bracketed [] numbers are ANOVA plot × period interactions, and unbracketed numbers are ANOVA between-plot test results.

crickets, was significantly reduced on the treated but not untreated site after the 1990 malathion application. Also, crickets, more than any other arthropod, were found dead after the 1990 treatment.

Food Reduction Effects on Birds

Pesticide-induced reduction of food has been shown to affect a variety of physical and behavioral factors in birds. Food reductions decreased passerine renesting (Rodenhouse and Holmes 1992), lowered fat reserves (Whitmore et al. 1993), increased foraging area (Cooper et al. 1990), and led to diet shifts (Sample et al. 1993) in eastern deciduous forest studies. Food reductions lessened nestling size in a western shrubsteppe study (Howe et al. 1996). Such effects appear to be evident even when reductions in factors such as density (Howe et al. 1996) and productivity (Rodenhouse and Holmes 1992, Howe et al. 1996) are small or undetectable.

Bird densities were not significantly reduced on our treatment plots after the malathion-induced food reduction in either year (T.L. George, Humboldt State University, unpublished data). Similarly, George et al. (1992) found no declines in density of 10 common grassland birds in plots where a carbaryl bran bait treatment reduced birdfood arthropods. George et al. (1995) also found no effects on avian density, richness, diversity, or evenness from malathion, sevin-4 oil, carbaryl bait, and *Nosema locustae* applications in 5 western states.

Rodenhouse and Holmes (1992) lowered Lepidoptera abundance with 2 annual applications of a bacterial larvicide (*Bacillus thuringiensis*) and found a reduction of renests, but not overall productivity, of Black-throated Blue Warblers (*Dendroica caerulescens*). However, they also found significant reductions in fledging, nestling growth, nestling survival, and number of nest attempts during natural

declines in food abundance. They concluded that during most years in their eastern U.S. temperate forest study areas, food was probably a limiting factor for *D. caerulescens* productivity.

In another study of eastern deciduous forests, researchers found that a gypsy moth insecticide (diflubenzuron) reduced Lepidoptera and nontarget insects (Martinat et al. 1988). This food reduction did not affect abundance of 21 bird species but resulted in decreased Lepidoptera larvae consumption (Cooper et al. 1990) and diet shifting (Sample et al. 1993) in 5 bird species as well as lower fat reserves in 7 species (Whitmore et al. 1993) on treated plots. Foraging areas of male Red-eyed Vireos (*Vireo olivaceus*) were also found to be larger on these treated sites (Cooper et al. 1990). Only adult birds were sampled during these studies, and reproductive variables were not measured.

Pascual (1994) found a greater than 4-fold decline in density of Lepidoptera larvae after spraying a plot with malathion. Despite this decline, Lepidoptera densities were not lower on the treated than untreated plot during any of 3 posttreatment sample periods. This was because while 1 Lepidoptera species was nearly depleted, another species with different emergence characteristics was relatively unaffected. Also, Lepidoptera densities were significantly higher on the treatment plot before malathion application. The author did not measure bird abundance, behavior, or foraging, but found no detectable differences between untreated and treated plots in nestling mass, hatching success, number fledged per nest, daily survival rate, or nestling mass of Blue Tits (*Parus caeruleus*), whose primary food source is Lepidoptera larvae.

Diet switching allows individuals to cope with unpredictable food supplies and alleviate the effects of selective food reductions. In response to a reduction in crickets, *Oreoscoptes montanus* on the 1990 treated site switched from feeding primarily crickets to primarily cicadas. On the untreated site, however, they fed crickets almost exclusively to their young during both the pre- and posttreatment periods. The switch in *O. montanus* diets was not accompanied by a detectable reduction in mass of food items delivered to nestlings. So, if food quality of cicadas was comparable to that of crickets, *O. montanus* were able to compensate
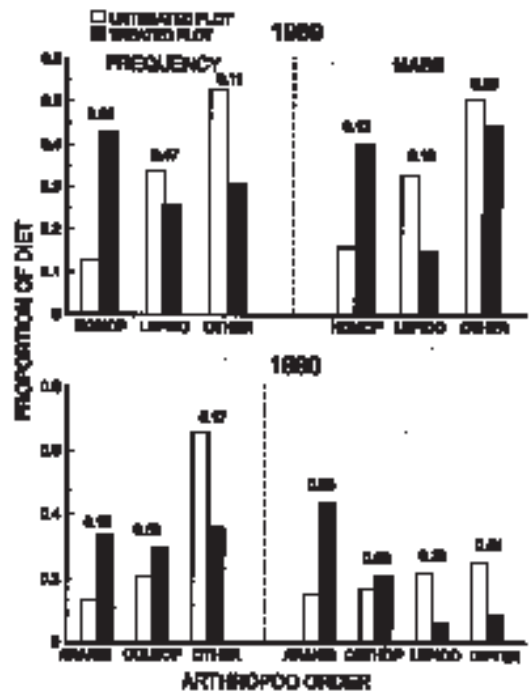
Fig. 6. Proportion of arthropods (by frequency and mass) in nestling *Spizella breweri* diets after an insecticide treatment in 1989 (*N* = 32, 1-h samples) and 1990 (*N* = 10). Items collected from different nestlings in the same nest were combined for each sample; each nest was sampled only once. Between-plot ANOVA probability values appear above histograms.

for the food reduction in our experiment by shifting their diets.

Sample et al. (1993) also found diet shifts in response to an insecticide-induced food reduction of Lepidoptera larvae. They found that adults of 5 eastern deciduous forest birds shifted diets from Lepidoptera larvae to a variety of other prey taxa.

One would expect that a reduction in food would cause an increase in time taken by adults to deliver food to their young. This could, however, be compensated for by adults delivering a greater amount or mass of food to nestlings. Few studies have directly monitored feeding rates after food reduction, though several studies have noted effects of brood manipulation on feeding rates (review by Martin 1987).

Results from our experiment indicated a slight effect of food reduction on delivery times (we could not measure feeding rates per se) of adult *S. breweri* in both years of the

study. However, delivery intervals on the treated plot posttreatment were not greater than intervals measured on the untreated plot, and no effective between-plot difference in food mass delivered to nestlings was detected.

In a related study Howe et al. (1996) found that food reduction on the treated plot resulted in smaller nestling sizes for *O. montanus* in 1989 (but not 1990) and *S. breweri* in 1990 (but not in 1989). They also found that fewer *O. montanus* fledged per nest attempt in 1989 (but not 1990). The number of *S. breweri* fledged was not affected, and neither species showed lower Mayfield nest survivorship in either year. Stochastic factors, such as weather (Howe 1991, Rotenberry and Wiens 1991) and ectoparasitism (Howe 1991), may act to confound effects of prey reduction on behavior and productivity of shrubsteppe birds. Such factors may partially account for the inconsistent results between years in Howe et al. (1996) and this study.

Thus, it appears that food reduction did, under the conditions of this study and Howe et al. (1996), affect physical and behavioral responses in shrubsteppe birds without greatly affecting adult density or productivity. Since treatment did not significantly affect all measured factors in both years, it appears that both *S. breweri* and *O. montanus* were able to at least partially compensate for the malathion-induced reduction in birdfood arthropods in this study.

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APPENDIX A. Power to detect a 50% change or difference in arthropod abundance to *Spizella breweri* and *Oreoscoptes montanus* based on pitfall, sweep net, and stickyboard samples.

| | Pitfall | | | | Sweep net | | | | Stickyboard high[d] | | | | Stickyboard low[e] | | | |
| | Frequency[b] | | Mass[c] | | Frequency | | Mass | | Frequency | | Mass | | Frequency | | Mass | |
Pd[a]	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990
Spizella breweri																
1	0.81	0.69	0.78	0.94	—	0.52	—	0.76	*	1.00	0.187	0.38	0.44	0.81	0.21	0.26
2	0.67	0.59	0.78	0.94	*	0.71	*	0.76	*	0.91	*	0.38	0.78+	0.61	0.23	0.26
3	0.88	*	0.86	0.97+	*	0.74	*	0.84	*	*	*	0.50	*	*	*	0.37
4	0.77+	0.87+	*	*	0.96	0.89	0.90	0.84	0.76	*	*	0.50	0.63	*	0.34	0.37
5	0.97+	—	*	—	0.90	—	*	—	—	—	—	—	—	—	—	—
Oreoscoptes montanus																
1	0.85	0.54	0.71	0.84	—	0.44	—	*	0.56	0.48	0.18	0.38	0.34	0.30	0.28	0.27
2	0.72	0.39	0.71	0.84	*	0.66	*	0.47	0.90	0.41	0.26	0.37	0.47	0.21	0.33	0.27
3	0.89+	*	0.81	*	*	*	*	*	*	0.75	*	0.52	0.40	0.41+	0.94	*
4	0.76	*	*	*	0.95	*	0.85	*	0.59+	0.74	0.29	0.53	0.29+	0.39	0.34+	0.38
5	0.97+	—	*	—	0.89	—	0.85	—	—	—	—	—	—	—	—	—

[a] Power estimations were based on 2-tailed tests in pretreatment periods (Pd) 1 and 2 and 1-tailed tests in posttreatment periods 3–5.
[b] All frequency data were normalized with square-root transformations.
[c] All mass data were normalized with logarithmic transformations.
[d] Stickyboards placed at height of sagebrush canopy.
[e] Stickyboards placed near the ground.
* Test result significant at $P \leq 0.05$, power not calculated.
+ Test result significant at $0.05 < P \leq 0.10$, power calculated.
— Not tested

APPENDIX B. Probability values by sampling period resulting from ANOVA tests on the abundance (frequency and mass) of arthropod orders fed to nestling *Spizella breweri* and *Oreoscoptes montanus* in 1989 and 1990. Probability estimates were based on 2-tailed tests for periods 1 and 2 (pretreatment) and 1-tailed tests for periods 3–5 (posttreatment). Italicized values were significant differences in the direction opposite our predictions.

Spizella breweri

Pitfalls

| | Frequency[a] | | | | | | | | | Mass[b] | | | | | | | | |
| | 1989 | | | | | 1990 | | | | 1989 | | | | | 1990 | | | |
Taxa[c]	1	2	3	4	5	1	2	3	4	1	2	3	4	5	1	2	3	4
ARAN	0.07	0.46	0.18	0.04	0.17	0.74	<0.01	0.07	0.19	<0.01	0.19	0.15	0.02	0.20	0.72	0.03	0.12	0.33
COLE	*	*	*	*	*	0.56	0.07	<0.01	0.03	*	*	*	*	*	*	*	*	*
HOMO	—	—	0.03	0.24	*<0.01*	0.21	0.18	*<0.01*	*0.02*	—	—	*<0.01*	0.44	0.30	—	0.76	0.44	0.40
LEPI	0.72	0.71	0.08	0.20	0.29	0.45	0.32	0.31	0.06	0.32	0.76	0.44	*0.04*	0.10	0.32	0.56	0.40	0.04
ORTH	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0.30	0.48	—	0.03
OTHER	0.28	0.99	0.06	0.06	0.07	0.31	0.57	0.04	0.01	0.85	0.98	0.07	0.02	0.18	0.53	0.05	0.01	0.15

Sweep nets

| | Frequency | | | | | | | | Mass | | | | | | |
| | 1989 | | | | 1990 | | | | 1989 | | | 1990 | | | |
Taxa	2	3	4	5	1	2	3	4	3	4	5	1	2	3	4
ARAN	0.41	0.17	0.39	0.23	0.10	0.87	0.43	0.39	0.28	0.50	0.48	0.42	0.96	0.20	0.08
COLE	*	*	*	0.33	0.33	<0.01	0.09	0.39	*	*	*	*	*	*	*
HOMO	0.44	<0.01	0.24	<0.01	0.01	0.06	0.48	0.11	0.12	0.35	0.41	0.79	0.91	0.33	0.06
LEPI	0.74	0.14	0.08	0.29	0.31	0.33	0.12	0.23	0.12	0.12	0.23	0.20	0.81	0.41	0.02
ORTH	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
OTHER	<0.01	<0.01	<0.01	<0.01	0.97	0.82	<0.01	<0.01	<0.01	<0.01	0.05	0.03	0.11	<0.01	<0.01

APPENDIX B. Continued.

Stickyboards

	Frequency								Mass							
	1989				1990				1989				1990			
Taxa	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
ARAN	0.99	0.91	0.03	0.15	0.42	0.27	0.20	0.27	0.41	0.99	0.03	0.23	0.72	0.73	<0.01	0.45
COLE	*	*	*	*	0.02	0.01	<0.01	<0.01	*	*	*	*	*	*	*	*
HOMO	0.08	<0.01	0.31	0.02	0.03	0.85	<0.01	<0.01	0.28	0.19	0.34	0.01	0.79	0.22	0.17	0.07
LEPI	0.08	0.79	<0.01	0.09	0.30	0.28	0.19	0.50	0.88	0.61	<0.01	0.12	0.10	0.48	0.10	0.03
ORTH	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
OTHER	0.07	<0.01	<0.01	0.13	0.15	0.23	<0.01	0.02	0.66	0.02	<0.01	0.17	0.61	0.45	<0.01	0.06

Oreoscoptes montanus

Pitfalls

	Frequency									Mass								
	1989					1990				1989					1990			
Taxa	1	2	3	4	5	1	2	3	4	1	2	3	4	5	1	2	3	4
COLE	0.11	0.27	0.28	0.32	0.07	0.26	0.02	0.03	0.49	*	*	*	*	*	*	*	*	*
HOMO	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
LEPI	0.71	0.40	0.07	0.20	0.20	0.38	0.58	<0.01	<0.01	0.50	0.39	0.47	0.04	0.04	*	*	*	*
ORTH	—	0.22	0.40	—	—	0.91	<0.01	0.12	0.26	—	0.39	0.29	—	—	0.61	0.88	<0.01	<0.01
OTHER	0.41	0.90	0.20	0.11	0.08	0.91	<0.01	0.12	0.26	<0.01	0.15	0.36	0.12	0.35	0.66	0.08	0.06	0.10

APPENDIX B. Continued.

Sweep nets

	Frequency								Mass							
	1989				1990				1989				1990			
Taxa	2	3	4	5	1	2	3	4	2	3	4	5	1	2	3	4
COLE	0.93	<0.01	<0.01	0.02	*	*	*	*	*	*	*	*	*	*	*	*
HOMO	0.44	<0.01	0.24	<0.01	0.31	0.11	<0.01	<0.01	0.16	0.12	0.30	0.41	0.97	0.61	0.03	0.07
LEPI	0.74	0.13	0.08	0.29	0.14	0.86	0.09	0.34	0.68	0.34	0.12	0.23	0.24	0.32	0.15	0.25
ORTH	—	—	0.17	0.17	0.63	0.84	0.48	0.04	—	—	0.26	0.23	0.20	0.81	0.41	0.02
OTHER	<0.01	<0.01	<0.01	<0.01	0.37	0.42	<0.01	0.03	<0.01	<0.01	<0.01	0.03	0.32	0.86	<0.01	0.02

Stickyboards

	Frequency							Mass							
	1989			1990				1989				1990			
Taxa	1	2	3	1	2	3	4	1	2	3	4	1	2	3	4
COLE	*	*	*	0.09	0.88	0.31	0.01	*	*	*	*	*	*	*	*
HOMO	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
LEPI	0.08	0.79	<0.01	0.38	0.62	0.17	—	0.86	0.61	<0.01	0.12	0.01	0.85	0.45	—
ORTH	*	*	*	0.09	0.39	0.03	0.01	*	*	*	*	0.09	0.32	0.11	0.01
OTHER	0.02	0.01	<0.01	0.36	0.91	0.39	0.22	0.74	0.43	0.06	0.31	0.37	0.42	0.13	0.02

[a]All frequency data were normalized with square-root transformations.
[b]All mass data were normalized with logarithmic transformations.
[c]Arthropod taxa: ARAN = Araneida, COLE = Coleoptera, HOMO = Homoptera, LEPI = Lepidoptera, ORTH = Orthoptera, OTHER = Diptera, Hemiptera, Hymenoptera, Neuroptera (*Spizella breweri* only).
*Sample not sufficient to analyze separately; included in OTHER.
—Sample not sufficient to analyze; not included in OTHER.