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DIETS OF INSECTIVOROUS BIRDS ALONG THE COLORADO RIVER IN GRAND CANYON, ARIZONA

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Abstract. We examined diets of six insectivorous bird species (n = 202 individuals) from two vegetation zones along the Colorado River in Grand Canyon National Park, Arizona, 1994. All bird species consumed similar quantities of caterpillars and beetles, but use of other prey taxa varied. Non-native leafhoppers (*Opsius stactagolus*) specific to non-native tamarisk (*Tamarix chinensis*) substantially augmented Lucy's Warbler (*Vermivora luciae*) diets (49%), while ants comprised 82% of Yellow-breasted Chat (*Icteria virens*) diets. Yellow Warbler (*Dendroica petechia*) diets were composed of 45% aquatic midges. All bird species consumed the non-native leafhopper specific to tamarisk. Comparison of bird diets with availability of arthropod prey from aquatic and terrestrial origins showed terrestrial insects comprised 91% of all avian diets compared to 9% of prey from aquatic origin. Seasonal shifts in arthropod prey occurred in diets of three bird species, although no seasonal shifts were detected in arthropods sampled in vegetation indicating that at least three bird species were not selecting prey in proportion to its abundance. All bird species had higher prey overlap with arthropods collected in the native, mesquite-acacia vegetation zone which contained higher arthropod diversity and better prey items (i.e., Lepidoptera). Lucy's Warbler and Yellow Warbler consumed high proportions of prey items found in greatest abundance in the tamarisk-dominated vegetation zone that has been established since the construction of Glen Canyon Dam. These species appeared to exhibit ecological plasticity in response to an anthropogenic increase in prey resources.

Key words: anthropogenic, arthropods, avian diets, Colorado River, Grand Canyon National Park, insectivorous birds, Neotropical migrants.

Dieta de Aves Insectívoras a lo largo del Río Colorado en el Gran Cañon, Arizona

Resumen. Examinamos la dieta de seis especies de aves insectívoras (n = 202 individuos) de dos zonas de vegetación a lo largo del Río Colorado en el Parque Nacional del Gran Cañon, Arizona, en 1994. Todas las especies de aves consumieron cantidades similares de orugas y escarabajos, pero el uso de otras presas fue variable. Los Cicadellidae (Homóptera) exóticos (*Opsius stactagolus*) específicos del tamarisco exótico (*Tamarix chinensis*) comprendieron una parte sustancial de la dieta de *Vermivora luciae* (49%), mientras que las hormigas representaron el 82% de la dieta de *Icteria virens*. La dieta de *Dendroica petechia* incluyó un 45% de dípteros acuáticos de la familia Cecidomyiidae. Todas las especies de aves consumieron el cicadellide exótico específico del tamarisco. La comparación de las dietas de aves con la disponibilidad de presas de artrópodos de origen acuático y terrestre mostró que los insectos terrestres comprendieron el 91% de todas las dietas de aves, comparado con un 9% de presas de origen acuático. Se registraron cambios estacionales en los artrópodos de la dieta de tres especies de aves, aunque no se detectaron cambios estacionales en los artrópodos muestreados en la vegetación, indicando que al menos tres especies de aves no estuvieron seleccionando las presas en proporción a su abundancia. Todas las especies de aves presentaron mayor superposición de presas con los artrópodos colectados en la zona de vegetación nativa de mesquite (*Prosopis*) y *Acacia*, la cual contuvo mayor diversidad de artrópodos y presas de mejor calidad (i.e., Lepidoptera). *V. luciae* y *D. petechia* consumieron altas proporciones de presas encontradas en mayor abundancia en la zona de vegetación dominada por el tamarisco, que ha sido establecida desde la construcción de la Presa Glen Canyon. Estas especies parecieron exhibir plasticidad ecológica en respuesta a un incremento antropogénico en las presas como recuso alimenticio.

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INTRODUCTION

Food exploitation strategies are central to our knowledge of habitat use by birds, yet direct examination of Neotropical migratory bird diets is generally underrepresented in avian ecology studies. This is especially true of riparian areas throughout the southwestern United States where arthropods on vegetation adjacent to rivers and streams are important food resources for insectivorous birds (Rosenberg et al. 1991, Gray 1993). Previous studies have found that arthropods from aquatic origins play a key role as prey for insectivorous birds in riparian habitats (Jackson and Fisher 1986, Gray 1993). Aquatic midges (Chironomidae), for example, have been demonstrated to be an important prey item for some riparian bird species (Busby and Sealy 1978).

Riparian habitat in the southwestern United States supports a disproportionately high density and diversity of birds (Johnson et al. 1977, Rosenberg et al. 1982). Szaro and Jakle (1985) have shown that southwestern riparian woodlands may support up to 10 times the number of birds ha^{-1} when compared to adjacent upland habitats due primarily to greater availability of food and cover. Before the completion of Glen Canyon Dam, riparian habitat along the Colorado River in Grand Canyon, Arizona, was sparse (Turner and Karpiscak 1980). Riparian breeding bird abundance in the last 40 years has increased commensurate with vegetation changes along the Colorado River through Grand Canyon (Carothers and Brown 1991). Following dam construction, more than 500 ha of new riparian vegetation has been distributed linearly along the shores of the Colorado River from the dam to Lake Mead (478 km, Brown and Trosset 1989).

Two changes in arthropod availability have resulted from the completion of Glen Canyon Dam. Prior to dam construction, an abundant and diverse assemblage of aquatic arthropods was found in the river (Ward and Stanford 1979). Presently, midges are the most abundant arthropod of aquatic origin emerging from the river (Shannon 1993). Aquatic diversity in and emerging from the river is presently low when compared to unregulated rivers (Blinn and Cole 1991). Postdam regulated water flows have all but eliminated seasonal variability in water temperature and restricted sediment loads affecting aquatic arthropod productivity. Another factor influencing arthropod composition along the Colorado River after the completion of the dam was the invasion of non-native tamarisk (*Tamarix chinensis*), now the most common shrub found in the vegetation zone established along the river's edge. Tamarisk supports a high abundance of a host-specific, non-native leafhopper (*Opsius stactogalus*; Stevens 1985; Yard and Cobb, unpubl. data), yet it is unknown if these changes to the arthropod community have affected the way birds forage as no previous studies have examined diets of insectivorous birds along the Colorado River in Grand Canyon.

The goals of our study were to quantify diets of six insectivorous, Neotropical migrant passerines, to determine if seasonal dietary shifts occurred between spring (March–May) and summer (June–July), and to examine arthropod availability between vegetation zones and seasons. We compared proportions of prey taxa found in stomach samples among six bird species, determined the origin of the prey (aquatic versus terrestrial) consumed by each bird species, and qualitatively related prey items to arthropod availability in the tamarisk-dominated versus the mesquite-acacia zone. This information may provide insight into the influence of anthropogenic change on avian ecology in dam-controlled river systems and highlight management options which could affect birds.

METHODS

STUDY AREA

The Colorado River flows 478 km through Grand Canyon National Park, Arizona, starting in the northeast corner of the park near Glen Canyon Dam on the Arizona-Utah border and stretching to Lake Mead in northwestern Arizona. The postdam vegetation zone adjacent to the river is composed predominantly of non-native tamarisk (the tamarisk zone). The predam vegetation zone adjacent to and upslope from the tamarisk zone is predominantly native honey mesquite (*Prosopis glandulosa*) and catclaw acacia (*Acacia greggii*; Carothers and Brown 1991; the mesquite-acacia zone).

We selected four representative study sites at intervals along the river to document bird diets and to estimate arthropod prey availability: River km (rk) 1.6 (Paria Creek) was entirely dominated by tamarisk (2.3 ha, mesquite-acacia = 0 ha). The other three sites contained both vegetation zones: rk 75.1 (Saddle Camp; tamarisk = 3.4 ha, mesquite-acacia = 0.8 ha), rk 318.6 (Parashant Camp; tamarisk = 1.5 ha, mesquite-acacia = 1.4 ha), and rk 329.0 (Spring Canyon; tamarisk = 1.8 ha, mesquite-acacia = 2.5 ha). Eight to 10 mist nets (36-mm mesh, 12 m) were erected at each site for 2 days per month from late March–July 1994 in each vegetation zone. The two vegetation zones were immediately adjacent to each other with no discernible space or barrier between them. Logistical constraints limited us to 10 days of bird netting and insect collections at each site.

COLLECTION TECHNIQUES FOR DIET AND ARTHROPODS

We selected six insectivorous passerine bird species for dietary analysis: Ash-throated Flycatcher (*Myiarchus cinerascens*), Bewick's Wren (*Thryomanes bewickii*), Bell's Vireo (*Vireo bellii*), Lucy's Warbler (*Vermivora luciae*), Yellow Warbler (*Dendroica petechia*), and Yellow-breasted Chat (*Icteria virens*). These six species are among the most abundant breeding riparian birds along the Colorado River in Grand Canyon (Brown et al. 1987) and elsewhere in the Southwest. Immediately upon capture, stomach contents were obtained by lavage (Moody 1970, Laursen 1978, Rosenberg and Cooper 1990). A 6-cm-long plastic tubing was slowly inserted into the bird's beak and then guided gently down the esophagus. A syringe attached to the tubing released saline solution into the bird's stomach, causing the bird to regurgitate its stomach contents. Stomach contents were collected in a plastic dish, then transferred into a glass vial and preserved with 70% ethyl alcohol.

Arthropods were collected from the tamarisk and mesquite-acacia vegetation zones one day each month, concurrent with bird diet-sample collections. We used sweep-net and beat-sheet sampling to obtain representative collections of arthropods present in each vegetation zone (Cooper and Whitmore 1990). Collections were made by taking 25 sweeps in the vegetation branches with a standard 37-cm-diameter net, at 1–3 m above ground. On undisturbed adjacent vegetation, we beat 25 branches to dislodge arthropods onto a beating canvas. Arthropods collected were preserved in 70% ethyl alcohol.

Prey items from stomach contents and vegetation sampling were all identified to order, then to the lowest taxonomic level possible using a variable-power dissecting microscope (Borror et al. 1989). Only stomach samples containing ≥5 items were used for analyses. A possible bias may have been that birds with one or a few large prey items were omitted from the analysis. Minimum numbers of prey individuals in each stomach sample were determined from diagnostic fragments (e.g., head capsules, caterpillar mandibles, elytra, wings) and compared with our reference collection (Chapman and Rosenberg 1991, Sillett 1994). Proportions of the number of prey items found in stomach contents of each bird species pooled were calculated for the following nine taxa categories: Araneae (spiders); Hemiptera (bugs); Homoptera (primarily leafhoppers); Coleoptera (beetles); Diptera (flies and aquatic midges); Hymenoptera (subclassified as either wasps or ants); Lepidoptera (primarily caterpillars) and other (Thysanoptera, Neuroptera, Acari, and unknown). To determine if dietary shifts occurred within the breeding season, we compared diet information collected from the six bird species in spring (March, April, and May) with that collected in summer (June and July).

STATISTICAL ANALYSES

We used multivariate analysis of variance (MANOVA) to test for overall difference in mean arthropod proportions between the two vegetation zones. Arthropods collected were pooled by vegetation zone for all sites, and proportions were arcsine transformed to meet normality assumptions (Sokal and Rohlf 1995, SPSS Inc. 2000). The Paria site was excluded from between-zone analysis because it had no mesquite-acacia vegetation zone. One-way analysis of variance (ANOVA) was used to test for differences in mean proportions of prey categories present between vegetation zones (Sokal and Rohlf 1995, SPSS Inc. 2000). We also used an analysis of similarity (ANOSIM; Clarke 1993) to compare arthropod prey items in each zone between seasons. This nonparametric, permutation-based procedure compares mean ranks of dissimilarities of samples within and between groups. When groups of samples are distinct from each other, the compositional dissimilarities between samples within a group are smaller than dissimilarities between samples from different groups. The ANOSIM test statistic, R, varies between -1 and 1, reaching its maximum value when all between-group dissimilarities are greater than all within-group dissimilarities. Statistical significance is determined by comparing the sample *R* with those produced by randomly assigning samples to groups. The proportion of random arrangements with *R*-values higher than the sample value is the significance level of the test (Clarke and Gorley 2001). The two-way layout is described in Clarke and Warwick (2001).

MANOVA was used to compare proportions of prey taxa found in the diet samples among bird species (stomach samples were pooled for each species) and to compare proportions of arthropods between vegetation zones. All proportions were arcsine transformed to meet normality assumptions. We used ANOVA to test for differences in mean proportions of prey categories present within each bird species and between vegetation zones (Sokal and Rohlf 1995). A nonparametric Kruskal-Wallis test was used to compare mean ranks of percentages of aquatic arthropods found in diets of the six bird species (Sokal and Rohlf 1995, SPSS Inc. 2000).

We used an ANOSIM to compare arthropod prey items in diet samples between seasons to identify possible seasonal shifts in the diets of three bird species with adequate sample sizes. Diet composition data were divided between spring and summer. Dissimilarities between samples were calculated using the Bray-Curtis distance because it handles compositional information well (Faith et al. 1987). We performed an ANOSIM with periods as treatments for Bewick's Wren, Bell's Vireo, and Lucy's Warbler. The three remaining species were excluded from analyses because few or no diet samples were obtained during spring (Clarke and Gorley 2001.)

To determine whether individual prey taxa were differentiated in the spring and summer diets of each bird species, we used indicator species analysis (Dufrêne and Legendre 1997). The method combines information on the specificity and fidelity of prey taxa to one time period or another to calculate the test statistic, *IndVal*, which ranges from 0 to 100. Specificity is defined as the average abundance of a prey taxon per sample in a group compared to that in other groups. The fidelity of a taxon is defined as the proportion of samples within a group which contain the taxon. Values for *IndVal* from sample data are compared to those calculated from randomly assigning samples to groups (Monte Carlo test of significance, 999 trials). The probability of a Type I error is the proportion of runs from random data with higher *IndVal* scores than were found in the actual data set. Dufrêne and Legendre (1997) set a cutoff of greater than 25, which we followed, with the additional constraint that the probability of the indicator value be less than 0.10. Diet samples for each species pooled were divided into two groups based on period (spring and summer). Statistical significance was accepted at $P \leq 0.10$.

DIET AND ARTHROPOD AVAILABILITY OVERLAP

Foraging observations were not conducted; therefore we could not determine foraging locations for birds. Indices of overlap were used as an indicator of foraging location or zone of foraging preference (tamarisk or mesquite-acacia) used by the six bird species. These qualitative indices have proven useful to ecologists in comparative studies of diet and habitat preference as well as in descriptions of dietary similarity between bird species (Horn 1966). We assessed foraging preference using Pianka's (1974) index for overlap:

$$Oa = \sum (P_{ia}P_{ja}) \Big/ \sqrt{\left(\sum P_{ia}{}^2\right)\left(\sum P_{ja}{}^2\right)},$$

where P_{ia} and P_{ja} are the proportions of prey category *a* in the diets of each bird species *i* and the habitat *j* respectively. We made the assumption that birds were foraging in relation to the availability of prey in each habitat.

RESULTS

ARTHROPOD ABUNDANCE

We found a significant difference in mean proportions of arthropods collected in tamarisk versus mesquite-acacia zones (MANOVA: Wilks' lambda $F_{1.64} = 11.7$, $P < 0.01$; Fig. 1). Flies and midges were collected in overall highest frequency followed by leafhoppers, ants, caterpillars, spiders, hemipterans, beetles, and wasps. ANOVA results showed higher proportions of flies and midges ($F_{1,64} = 16.8$, $P < 0.01$) and leafhoppers ($F_{1,64} = 8.3$, $P < 0.01$) in the tamarisk vegetation zone. Higher proportions of beetles occurred in the mesquite-acacia zone ($F_{1,64} = 21.6$, $P < 0.01$). Mean proportions of caterpillars, hemipterans, ants, spiders, and wasps were not significantly different between vegetation zones. No seasonal difference was detected between arthropods in each zone be-

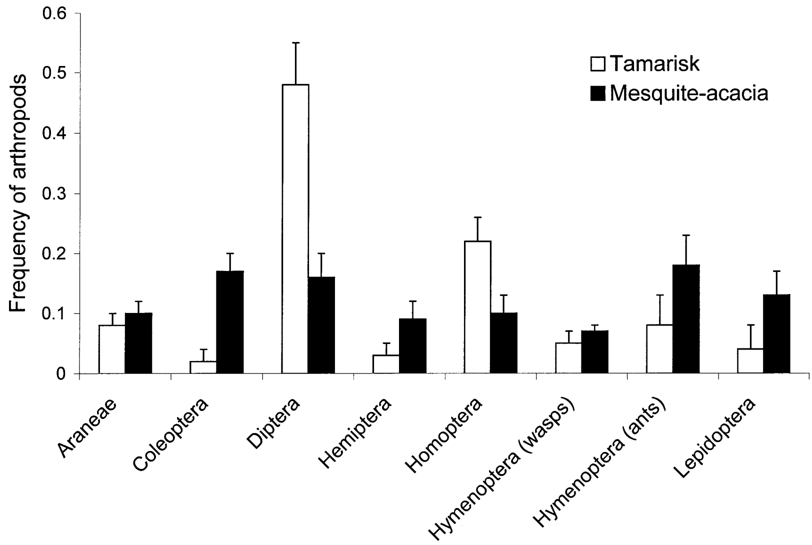

FIGURE 1. Proportion ± SE of arthropod taxa collected in the tamarisk and mesquite-acacia vegetation zones along the Colorado River, Grand Canyon, Arizona, spring and summer 1994.

tween spring and summer (ANOSIM, $R = 0.1$, $P = 0.20$).

BIRD DIET

Arthropod prey items were identified from 202 bird diet samples, with 98% identified to order. The ''other'' category was excluded as it represented only 2% of prey items. A significant difference in prey items was found among diets of the six bird species (MANOVA: Wilks' lambda $F_{5,195} = 5.0$, $P < 0.01$). ANOVA showed that Ash-throated Flycatchers consumed an overall higher proportion of wasps when compared to the other five species ($F_{5,195} = 8.0$, $P < 0.01$); Bewick's Wren a higher mean proportion of spiders ($F_{5,195} = 2.6$, $P = 0.01$), Bell's Vireo more hemipterans ($F_{5,195} = 5.3$, $P < 0.01$), Lucy's Warbler more leafhoppers ($F_{5,195} = 5.9$, $P < 0.01$), Yellow Warbler more diptera (flies and midges, $F_{5,195} = 2.9$, $P = 0.01$), and Yellow-breasted Chat more ants ($F_{5,195} = 20.8$, $P < 0.01$, Table 1). All six bird species consumed similar proportions of beetles ($F_{5,195} = 2.2$, $P = 0.06$) and caterpillars ($F_{5,195} = 2.2$, $P = 0.06$). All six bird species consumed non-native leafhoppers.

We classified 95% of arthropods from stomach samples as aquatic or terrestrial in origin. When diets of all six bird species were pooled,

TABLE 1. Bird species, sample size, number of prey items, and mean percent ± SE of prey items (in parentheses) in diet samples of six insectivores ($n = 202$ individuals) along the Colorado River in Grand Canyon, Arizona, spring and summer 1994.

Arthropod orders	Ash-throated Flycatcher ($n = 17$)	Bewick's Wren ($n = 33$)	Bell's Vireo ($n = 39$)	Lucy's Warbler ($n = 77$)	Yellow Warbler ($n = 18$)	Yellow-breasted Chat ($n = 18$)
Araneae	15 (21 ± 3)	54 (28 ± 5)	28 (12 ± 2)	76 (18 ± 2)	12 (8 ± 3)	16 (14 ± 3)
Hemiptera	3 (3 ± 2)	14 (6 ± 2)	98 (17 ± 3)	61 (7 ± 2)	27 (4 ± 2)	7 (4 ± 2)
Homoptera	9 (11 ± 5)	76 (16 ± 3)	20 (7 ± 5)	555 (27 ± 3)	32 (12 ± 4)	2 (1 ± 1)
Coleoptera	7 (9 ± 3)	41 (13 ± 2)	82 (23 ± 3)	202 (20 ± 2)	40 (15 ± 4)	18 (14 ± 3)
Diptera	8 (10 ± 4)	43 (10 ± 3)	23 (12 ± 4)	56 (6 ± 1)	173 (24 ± 6)	4 (3 ± 1)
Hymenoptera						
Wasps	22 (26 ± 7)	18 (4 ± 1)	40 (8 ± 2)	70 (6 ± 1)	73 (25 ± 5)	18 (13 ± 4)
Ants	6 (7 ± 3)	57 (13 ± 3)	15 (4 ± 1)	33 (7 ± 2)	10 (5 ± 2)	343 (42 ± 7)
Lepidoptera	10 (13 ± 4)	36 (10 ± 2)	80 (17 ± 2)	75 (9 ± 1)	18 (7 ± 4)	12 (9 ± 2)

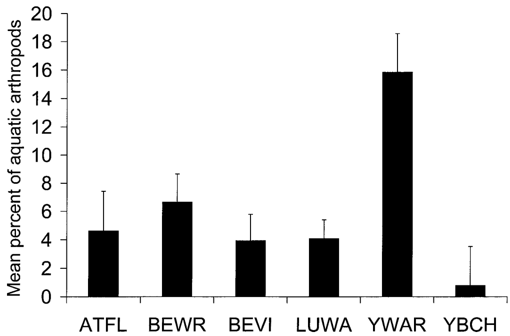

FIGURE 2. Mean ± SE percent of aquatic arthropods in bird diets (n = 202) along the Colorado River, Grand Canyon, Arizona, in spring and summer 1994. ATFL = Ash-throated Flycatcher; BEWR = Bewick's Wren; BEVI = Bell's Vireo; LUWA = Lucy's Warbler; YWAR = Yellow Warbler; YBCH = Yellow-breasted Chat.

the resulting combination exhibited 91% terrestrial and 9% aquatic arthropods. The mean percentage of arthropods from aquatic origins differed among bird diets (Kruskal-Wallis, χ^2_5 = 18.5, $P < 0.01$; Fig. 2). Yellow Warblers had a higher mean percent of arthropods from aquatic origin (16% Chironomidae [midges]) than the other five bird species. Midges comprised 45% of their total diet.

The diet similarity analyses revealed significant seasonal shifts in diets of the three species most adequately sampled. Bewick's Wren diets differed between spring and summer (R = 0.18, P = 0.02), as did Bell's Vireo (R = 0.11, P = 0.03), and Lucy's Warbler (R = 0.22, P = 0.01).

Indicator species analysis revealed Bewick's Wren diets were not characterized by any one particular prey item in either spring (n = 10) or summer (n = 23). Bell's Vireo averaged approximately five times more hemipterans in their diet during spring than in summer (n = 12, *IndVal* = 63, P = 0.001) but twice as many ants during summer (n = 27, IndVal = 29, P = 0.09). Lucy's Warbler diets contained a significantly higher number of caterpillars in the spring than in summer (n = 22, *IndVal* = 22, P = 0.001), with twice as many ants (n = 55, *IndVal* = 33, P = 0.02), and five times as many leafhoppers (*IndVal* = 71, P = 0.01) in their diets during the summer period, leafhoppers being the most abundant prey item in their diet.

TABLE 2. Overlap values (Pianka 1974) between arthropods found in diets of six bird species and arthropods sampled from foliage in two vegetation zones along the Colorado River, Grand Canyon, Arizona, spring and summer 1994. A value of 1.0 represents 100% overlap between diets and available arthropods.

Bird species	Mesquite-acacia zone	Tamarisk zone
Ash-throated Flycatcher	0.77	0.58
Bewick's Wren	0.86	0.63
Bell's Vireo	0.89	0.53
Lucy's Warbler	0.84	0.61
Yellow Warbler	0.81	0.77
Yellow-breasted Chat	0.78	0.33

DIET AND ARTHROPOD AVAILABILITY OVERLAP

Overlap index values for arthropods in the diets of the six bird species more closely matched arthropods collected in the mesquite-acacia zone than the tamarisk zone. Arthropods in all six species had overlap values of 0.77 or greater with the mesquite-acacia zone (Table 2). The Yellow Warbler had the highest overlap with arthropods in the tamarisk zone when compared with the other five species of birds (0.77).

DISCUSSION

The six bird species we studied consumed similar proportions of caterpillars and beetles but appeared to partition other prey, with each bird species consuming a higher proportion of one particular prey taxon. The similar proportions of caterpillars and beetles found in the diets of six insectivores are consistent with dietary data from birds on the Lower Colorado River (Rosenberg et al. 1991) and studies conducted on migrant species in the tropics (Sillett 1994, Poulin et al. 1994, Poulin and Lefebvre 1996). Caterpillars have been reported to be the single most important prey item for breeding birds, as caterpillars are markedly seasonal and most abundant in spring and summer (Thiollay 1988, Greenberg 1995). Productivity of breeding birds is a function of the abundance of large, soft-bodied arthropods (i.e., caterpillars) identified as ''breeding currency'' which are needed as food for growing nestlings (Greenberg 1995).

Dietary differences may partially be explained by different bill sizes and shapes among the six passerines since bill size was likely analogous to prey size (Newton 1972, Schoener 1974, Wiens and Rotenberry 1987). Other possible explanations for dietary differences may have included differences in foraging height, use of plant species, habitat selection, and competition (MacArthur 1958, Morse 1968, Perrins and Birkhead 1983). Foraging tactics must also be considered when examining dietary differences among species. Gleaners (Bell's Vireo, Bewick's Wren, Lucy's Warbler, and Yellow-breasted Chat) all preyed primarily on arthropods found on vegetation (spiders, beetles, leafhoppers, hemipterans, and ants). Yellow Warblers consumed a high proportion of aquatic midges and could have gleaned them from vegetation or captured them aerially by sallying from high perches. Ash-throated Flycatchers used aerial foraging tactics that would explain their higher consumption of wasps and bees. These findings are consistent with Ash-throated Flycatcher diets in California, where wasps and bees were the most prominent prey item (Cardiff and Dittmann 2002).

Arthropods of terrestrial origin provided the primary food base for five of the six riparian bird species, comprising 91% of their cumulative diets in contrast to only 9% of prey items of aquatic origin. The exception was the Yellow Warbler, whose total stomach samples were 45% aquatic midges (mean 16% per individual). Aquatic midges were the most abundant arthropod collected in the tamarisk during the breeding season. The finding that Yellow Warbler consumed a high percentage of midges is consistent with dietary information collected in Canada (Busby and Sealy 1978) and in Utah, where midges were among the most frequent prey items found in diet samples (Frydendall 1967).

A high percentage of ants (82% total, mean 42 $\pm$ 7% per individual) was found in Yellow-breasted Chat stomach samples, much greater than suggested in existing literature. Few quantitative data are available on chat diets; however ants occurred in 11 out of 14 stomachs collected from Yellow-breasted Chats at various locations throughout North America (although quantities were not reported; Eckerle and Thompson 2001). Chat stomach samples from the Lower Colorado River ($n = 4$) contained ants as one of four prey items, but again, proportions were not reported (Rosenberg et al. 1991).

Leafhoppers and ants were found in highest proportions in diets of two bird species during summer. Leafhoppers were the most common prey type in the tamarisk vegetation zone during the breeding season and are perhaps very important food for adults feeding fledglings and for fledglings learning to capture prey (Lucy's Warbler, Johnson et al. 1997). We found ants to be most abundant in the mesquite-acacia zone. Ants were reported in relatively high proportions in diets of migrant Neotropical species sampled in the tropics (Poulin and Lefebvre 1996) and may be an important year-round prey item for some migrant birds.

Our data indicate that anthropogenic changes to the Colorado River ecosystem downstream of Glen Canyon Dam have resulted in an increased abundance of two arthropod prey taxa: tamarisk-specific leafhoppers and aquatic midges. Midges, a food source not abundant before the dam was built but which are the most common prey type in the tamarisk-dominated zone, comprised 45% of the total number of prey items consumed by the Yellow Warbler (mean 16 $\pm$ 3% per individual). An unexpected finding of our study was that all diet samples from the six bird species contained varying proportions of the non-native leafhopper, a prey item found exclusively on tamarisk (Carothers and Brown 1991). Leafhopper presence in bird stomachs was likely related to the increased availability of these abundant and easy to detect insects. Lucy's Warblers, whose total diet consisted of 49% leafhoppers (mean 27 $\pm$ 3% per individual), have recently increased during the breeding season along the Colorado River (Brown et al. 1987, Felley and Sogge 1997). This increase may be directly related to the increased abundance of this non-native leafhopper. Yellow Warbler and Lucy's Warbler diets directly reflected arthropod abundance in the tamarisk vegetation zone, while the other four bird species did not.

All six bird species showed higher overlap values of prey items with arthropods collected from the mesquite-acacia zone. Ongoing studies have found a higher diversity of arthropods and a higher proportion of profitable prey types, those considered to be better ''breeding currency'' (large soft-bodied arthropods, Greenberg 1995) in the native mesquite-acacia zone (Yard and Cobb, unpubl. data). In studies conducted on arthropods and bird abundance in acacia versus adjacent vegetation in the tropics, a higher abundance of foraging migrant birds was found in acacia presumably due to better quality prey availability (Greenberg et al. 1997, Greig-Smith 1978). South African acacia is reported to have high palatability to arthropods (Coe and Coe 1987, Cooper et al. 1988). In addition to foliage palatability for arthropods, Coe and Coe (1987) reported that leguminous seeds produced by acacia supported high numbers of beetles (Bruchidae). Similarly, we also found high proportions of Bruchidae in both mesquite and acacia (Yard and Cobb, unpubl. data) and in most bird diet samples (Table 1).

Examples of ecological plasticity or the tendency of bird species to exploit new, abundant food resources (Greenberg 1990), illustrate how dietary opportunism has the potential to enhance or maintain fitness in certain passerines. Increased abundance of breeding birds, specifically Lucy's and Yellow Warblers, along the Colorado River in Grand Canyon may be related to their ability to exploit new food resources established because of Glen Canyon Dam's alteration of the ecosystem. Our data show both vegetation zones have much to offer insectivorous birds in terms of arthropod prey. The tamarisk zone appears more useful than previously thought, but the mesquite-acacia zone is clearly more important when considering all bird species together.

Tamarisk, though low in arthropod diversity, offers two new and abundant prey resources as well as cover for nesting birds (Brown and Trosset 1989). The salty exudate from tamarisk leaves has been reported as a deterrent to arthropod diversity, while native vegetation has been suggested to exhibit a more diverse arthropod assemblage and better bird food (i.e., large, soft bodied insects) for foraging birds (Anderson and Ohmart 1977). Management decisions for riparian vegetation should consider the importance of both vegetation zones to foraging Neotropical birds. Present tamarisk eradication projects throughout the Southwest have the potential for negative effects on at least two species of Neotropical migrant birds, unless replacement by native woody vegetation is rapid.

Two bird species examined for seasonal dietary shifts showed significant differences in prey items found in stomach contents when compared between the spring and summer periods. In contrast, arthropods collected in the vegetation did not reflect seasonal shifts in abundance. This clearly demonstrates that two bird species were seeking different prey items seasonally and that their prey selection was not based on prey abundance. Future dietary studies of Southwestern riparian birds should consider (1) multiple years of data collection and (2) concurrent foraging studies to determine where prey are obtained. These recommendations would allow a more complete understanding of dietary patterns and seasonal differences.

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