Quantitative Diet Analysis of Selected Breeding Birds along the Colorado River in Grand Canyon National Park

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Principle Investigators:	Terry May, Graduate Studies and Research, Northern Arizona University, Flagstaff, AZ 86011 and Charles van Riper III, U.S.G.S. Biological Resources Division, Colorado Plateau Research Station, Northern Arizona University, Flagstaff, AZ 86011
Government Technical Representative:	John Ray, Resources Management, Grand Canyon National Park
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Prepared By:	Helen K. Yard, Colorado Plateau Research Station, Nothern Arizona University

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INTRODUCTION

Riparian zones in the southwest are extremely important for resident and migratory species of birds. Over 60% of neotropical migratory birds use riparian habitat in the West for stopover areas during migration or for breeding (Ehrlich *et al.* 1988). Of 166 species of nesting birds in the southwest, 77% were dependent on water associated habitats and 51% were completely dependent upon riparian habitat (Johnson *et al.* 1977). The thick, multi-storied vegetation found in riparian areas provides more nest sites and greater arthropod production for birds than adjacent xeric habitat (Gori 1992). Steven's *et al.*(1977) reported that western riparian areas contained up to 10 times the number of neotropical migrant birds per hectare than adjacent non-riparian habitats. Knowing how important riparian areas are to birds, it is of growing concern that estimates have placed riparian habitat loss at greater than 95% in the western United States (Krueper 1992). Recent studies suggest that neotropical migrant songbird populations are declining and that these decreases have accelerated in recent years possibly due to loss of this type of available habitat (Finch 1991).

Breeding bird densities along the Colorado River corridor have increased in the last 20 years due to the increased amount of new riparian habitat (Carothers and Johnson 1975, Brown and Johnson 1985). Before Glen Canyon Dam was built to control the water flows through Grand Canyon, vegetation adjacent to the river was sparse due to annual flooding (Turner and Karpiscak 1980). The pre-dam vegetation (termed old high water zone [OHWZ]) that still exists, is comprised of a band of vegetation characterized predominately by native honey mesquite (*Prosopis glandulosa*) and catclaw acacia (*Acacia greggii*) (Carothers and Brown 1991). A new zone of riparian habitat has become established along the Colorado River after the completion of

Glen Canyon Dam in 1963. The new riparian habitat zone or, new high water zone (NHWZ) established after the completion of the dam immediately adjacent to the river and composed predominately of introduced tamarisk (*Tamarix chinensis*), native coyote willow (*Salix exigua*) and several species of seep willow (*Baccharis*). More than 500 hectares (1,235 acres) of new riparian habitat has been established along the river from Lee's Ferry to Diamond Creek in the last 20 years (Brown and Trosset 1989). Lower Grand Canyon, below river mile 170, has experienced a more dramatic increase in vegetation. The canyon is wider there due to the geomorphology (Pucherelli 1988)

Another consideration of regulated water flows through Grand Canyon since the establishment of Glen Canyon Dam is the change in temperature and sediment load in the water of the Colorado River that affects the aquatic arthropod productivity. Pre-dam water temperatures were warmer and changed seasonally as with any natural river system (Blinn and Cole 1991) . High sediment loads were sporadic being associated with heavy rainfall and spring snow melt. Historically, there was an abundant and diverse assemblage of aquatic insects in the Colorado River (Ward 1976). Water presently released from the dam is clear and colder (8 to 10 degrees C) than in pre-dam times and varies very little in temperature seasonally, supporting a low diversity yet high abundance of aquatic insects (Valdez and Ryel 1995). Above the Little Colorado River (LCR) at River Mile (RM) 61.5, there is an abundance of aquatic insects emerging from the river, predominately Chironomide midges adapted to the clear, cold water of the Colorado river relased from the dam. Below the LCR, which has a high sediment load varying throughout the year, aquatic insect abundance drops in a stairstep fashion an order of magnitude as you continue downtstream from the LCR to Diamond Creek (Shannon 1993).

Past studies on breeding bird communities along the Colorado River corridor in the Grand Canyon have concentrated on species present, nesting habits and the effects of fluctuating flows on densities of birds in the riparian areas (Carothers and Sharber 1976, Brown 1987, Brown and Johnson 1988). Very little was known about the diet of birds that use the riparian vegetation along the river. Direct examination of avian diet is essential in gaining an understanding of avian habitat use and yet the diet of many neotropical bird species in general is poorly known (Karr 1976, Loiselle and Blake 1990). Diet studies are seldom undertaken in avian ecology due to difficulties in identifying fragmented arthropods found in diet samples of birds, but is a very effective method that can show direct habitat use and food selection by avian insectivores (Sherry 1984, Rosenberg and Cooper 1990, Johnson 1991). How several insectivorous bird species with similar foraging tactics coexist in fairly monotypic stands of exotic and native vegetation in riparian areas is poorly understood. Studies of resource partitioning among potential avian competitors are numerous, but studies that complement data on resource partitioning with dietary data are few (Rotenberry 1980, Robinson and Holmes 1982, Rosenberg et al. 1982).

Within the Grand Canyon, it is important to study avian diet for the purpose of : (1) understanding what several common songbirds are feeding upon within the riparian vegetation along the Colorado River and (2) determine if there is a link to the feeding ecology of these terrestrial bird species to aquatic resources (ie. insects emerging from the river) (Shannon 1993) and (3) to determine if the birds are feeding in the relatively recent NHWZ vegetation dominated by introduced saltcedar .

Stevens (1976, 1985) inventoried arthropods found in the NHWZ and OHWZ riparian vegetation at selected sites along the Colorado River in Grand Canyon. Information and results from these collections were invaluable for the identification of insects collected in this present study. This study is among the first to relate arthropod relative availability to actual composition of arthropods in bird diets along the Colorado River.

The specific objectives of this project were to:

1) Determine the similarities and/or differences in diet between six common insectivores in the riparian area along the Colorado River in Grand Canyon.

(2) Quantify proportions of the birds diets that are insects of aquatic origin (ie. insects emerging from the Colorado River) versus terrestrial origin in order to determine if these birds rely on aquatic based food resources

(3) Calculate the proportion of aquatic insects that emerged from the Colorado River found in the upper Grand Canyon (sites above the LCR at RM 61.5) versus sites in the lower Grand Canyon (below the LCR) related to differences in aquatic insect productivity in the upper canyon versus the lower canyon.

(4) Determine if the prey items found in avian diet samples overlap more closely with the relative (observable) prey availability in NHWZ or OHWZ (Vegetation zone of foraging preference)

Study area:

The four study sites were chosen along the Colorado River in Grand Canyon National Park were: Paria Creek (RM 1.0); Saddle Canyon (RM 46.7); Stairway Canyon (RM 171.0); Parashant Canyon (RM 198.0). Partway through 1994, Spring Canyon (RM 204.5) was substituted for the Stairway Canyon site due to low capture rate of birds at the latter. Stairway Canyon was sampled for birds March and April of 1994, then Spring Canyon was sampled in May, June and July (Fig. 1). Two study sites were chosen above the LCR and two below the LCR in order to compare upper and lower canyon differences in emerged aquatic insect composition at the sites and in the diets of the six species of birds.

Bird Species:

Six common insectivorous bird species were selected for dietary analysis: Lucy's Warbler (*Vermivora luciae*), Bell's Vireo (*Vireo bellii*), Yellow Warbler (*Dendroica petechia)* and the Yellow-breasted Chat (*Icteria virens*), all neotropical migratory birds associated with riparian vegetation, primarily forage by gleaning insects from foliage. The Ash-throated Flycatcher (*Myiarchus cinerascens*), also a neotropical migrant, is primarily an aerial forager, but gleans insects from stems and trunks of trees as well. Bewick's Wren (*Thryomanes bewickii*), a permanent resident of Grand Canyon, forages in foliage, on the ground and in dead wood. (Ehrlich *et. al* 1988).

METHODS

Bird Capture

Birds were captured live in 8 to 10 mist nets two days per month at each study site during the breeding season (March through June) of 1994 (Sogge *et al.* 1994). Measurements taken on each bird caught in mist nets included beak length in millimeters (mm) and body weight in grams (g). These measurements were averaged for each bird species. Nets were placed in the same general locations within each study site during each month to maintain sampling consistency. The netting efforts were already underway as part of the overall Avian Community Monitoring Study in Grand Canyon in effort to band birds with US Fish and Wildlife and color bands (Sogge et al. 1995).

Lavage

Stomach contents from the birds were obtained by flushing the digestive tract with a fixed amount of warm water (lavage) as described by Moody (1970). This technique involves using a syringe filled with water with a 5 cm tube attached to the end. The tube is gently placed into the beak and down the esophagus of the bird. The water is then slowed pushed out of the syringe into the stomach. Lavage has a low mortality rate compared to using chemical emetics for forced regurgitation (Laursen 1978, Robinson and Holmes 1982, Gavett and Wakeley 1986). In past studies, the efficiency rate of the flushing technique (prey particles remaining in the stomach after flushing) was 52% ± 29% (Laursen 1978). Diet samples were taken from birds caught between dawn and noon, a period when high feeding rates usually guaranteed full stomachs for sampling (Sherry 1984). Ten or fewer bird stomachs have been considered adequate for assessing species-specific diets during a sampling period (Rosenberg and Cooper 1990). The stomach content samples were labeled with the date, location of sample, and species of bird then stored in vials with 70% alcohol and identified later in the lab.

Prey Identification and Diet Comparisons

Each prey item was identified to taxonomic order and when possible, family and genus using a variable power dissecting scope (Borror *et al.* 1982). Individual arthropods, usually fragmented, were pieced together until I accounted for all identifiable prey fragments. One prey item (arthropod) was counted for each head capsule, pair of mandibles, four wings (two for Diptera), or two elytra found in each diet sample (Anthony and Kunz 1977). For example, if I found one elytra, two Hemipteran head capsules and a Dipteran wing, I counted one Coleopteran, two Hemipterans and one Diptera. In order to make dietary comparisons between the six species of birds, arthropods found in stomach samples were grouped into eight ordinal categories: Araneae (spiders); Hemiptera (true bugs); Homoptera (mainly leafhoppers); Coleoptera (beetles); Diptera (flies and midges); Hymenoptera (wasps, bees and ants); Lepidoptera (mainly moth and butterfly larvae) and "Other" (Thysanoptera, Neuroptera, Acari and unknown). Aquatic or terrestrial origin of the arthropod was also specified when arthropods could be identified to family. Proportions (or percent) of prey orders and aquatic verses terrestrial emerging insects were calculated for each stomach sample depending on the statistical test employed to analyze the data.

In the event of rare accidental mortality, the entire stomach was removed and dissected after flushing, to determine what, if any, prey remained in the stomach after lavage.

Arthropod Samples

Arthropod sampling was conducted at each site one day per month from March through July during the same time period that birds were captured in mist nets and lavaged for diet samples. Three invertebrate sampling methods were used to obtain a better representative collection of what prey items were present at the sites during the time of diet sampling (Cooper and Whitmore 1990). In order to collect vegetation dwelling arthropods, I made 25 sweeps with a standard sweep net (37 cm in diameter) through the vegetation and 25 beats on the vegetation (collected onto a beating canvas). A passive Malaise trap was used to collect flying insects. All three sampling methods described above were used in both the NHWZ and OHWZ to compare arthropod availability between zones. Relative prey availability is very difficult to quantify because each sampling method has its own inherent biases, therefore I used the three methods described above to determine what arthropods were in *observable* abundance or availability. Arthropods were stored in 70% alcohol and later identified to order and family level, and in some cases genus using a variable power dissecting scope. They were then grouped into the same eight categories as the prey fragments found in the diet samples from the birds. At a later date, arthropods representing every family found in the bird diet samples were measured and grouped into three categories: >3 mm, 3 - 5 mm and < 5 mm. The origin (aquatic or terrestrial) of each arthropod was also recorded to determine proportion of aquatic insects collected during sampling at each site.

Statistical Analysis and Calculations

Diet Analysis. A multivariate analysis of variance (Manova) comparing the mean proportion of prey orders between the six species of birds was used to determine if the diets were significantly different between species (Sokal and Rohlf 1995). All mean proportions were arc sine transformed to correct for non-normality. Only stomach samples containing four or more prey items were used for statistical analysis to reduce the bias of finding, for example, 100% spiders in a diet sample when only one spider was found in the entire sample. A one-way analysis of variance (Anova) was used to detect if there were significant differences in the proportion of prey orders present in each species (showing what bird species had a higher proportion of what prey order) (Sokal and Rohlf 1995).

Descriptive Calculations. Descriptive calculations such as dietary overlap between bird species and dietary or prey diversity for each bird species were used to help determine similarities and differences between the diets of the six species of birds. Diet overlap between species of birds was calculated as: $O_a = \sum (P_{ia}P_{ij})/\sqrt{(\sum P^2_{ia})(\sum P^2_{ja})}$, where P_{ia} and P_{ij} are the proportions of prey category and "a" in the diets of species "I" and "j" respectively (Pianka 1974). A value of zero would represent zero dietary overlap and a value of 1.0 would represent 100% overlap. Prey-type diversity was calculated of each bird species using $B = (\sum p_i^2)/1$, where p_I is the proportion of taxon "I" in the diet samples of the bird species (Levins 1968). This index value is an indicator of whether the bird species has a sterotypic diet (specialization consuming a narrow range of prey taxa) or is opportunistic in their diet (a generalist consuming a wide variety of prey items)(Sherry 1990). A value of 8.0 is considered opportunistic or a generalist, a value of 1.0 is a specialist. Proportions of arthropod orders were used for both of these equations.

Aquatic insects in diet. A Kruskal-Wallis one-way analysis of variance (Anova) was used to determine if there was a significant difference in the percent of arthropods with aquatic origin versus terrestrial origins in the diets of the six species (Sokal and Rohlf 1995). A Mann-Whitney U (post hoc analysis) was used to detect significant differences in the percent of aquatic insects in the diets between species (Sokal and Rohlf 1995). A Kruskal-Wallis Anova was used to determine if the birds were consuming a higher percent of insects of aquatic origins at the two upper study sites versus the two lower sites.

Aquatic Insect availability. A G-statistic (Goodness of fit) was calculated to determine if there was a significant difference in the number of insects from aquatic origins in *observable* availability at the sites above the LCR (ie. Paria and Saddle) versus the sites below the LCR (ie. Parashant and Spring) (Sokal and Rohlf 1995).

Avian Diet and Zone of Vegetation Overlap (foraging preference). Pianka's index (Pianka 1974) for overlap was used as an indicator of foraging location (OHWZ or NHWZ) used by the six species of birds. Indices of overlap have been proven to be useful to ecologist in comparative studies of diet and habitat preference as well as a descriptor of dietary similarity between bird species (Horn 1966). This formula was described in detail in the *Descriptive Calculations* sections.

Additionally, a Manova was used to determine if there were significant differences between mean proportions of arthropod orders collected in the NHWZ and the OHWZ.

RESULTS

Diet samples were successfully obtained from 202 (92%) of 220 birds having received lavage in 1994 (Table 1). The average body weight, beak length and sample size for each bird species caught for diet sampling is shown in Table 2. To avoid sampling biases for the statistical analysis, I used 161 (73%) of the diet samples all of which contained four or more prey items.

Dietary analysis. Manova results showed that the diets of the six species of birds evaluated (fig. 2) were significantly different from each other (Wilk's Lambda approx. $F_{5,155} = 5.22$, $p < 0.001$). The "other" category of the arthropod fragments found in the diets of the six bird species represented only 2% of their overall total diet and was therefore omitted from the statistical analysis. Anova results showed that each bird species had consumed a higher proportion of one particular prey order. Lucy's Warbler had consumed a significantly higher proportion of Homopterans ($p < 0.005$) (Fig.3) averaging < 3 mm in size; Bell's Vireo had eaten a significantly higher proportion of Hemipterans ($p < 0.005$) and an higher proportion of Lepidopterans ($p < 0.01$) (Fig.4a and 4b), both prey types averaged 3 - 5 mm in size; Bewick's Wren had a higher proportion of spiders ($p < 0.01$) (Fig. 5) sizes averaging 3 - 5 mm; Yellow Warbler had a significantly higher proportion of Dipterans ($p < 0.005$) (Fig. 6) size range of 3 - 5 mm; Yellow-breasted Chat had a significantly higher proportion of Hymenopterans ($p < 0.005$) (Fig. 7) average size of < 5 mm. The diet of Ash-throated Flycatcher contained a higher proportion of Hymenopterans than four of the other bird species, having the second highest proportion compared to the Yellow-breasted Chat ($p < 0.01$) (Fig. 7) average size of < 5 mm. When I examined the Hymenopterans in the diet of the Yellow-breasted Chat, 98% consisted of wingless ants (family Formicidae) while the Hymenopterans in the diet of the Ash-throated

Flycatcher were equally divided between wingless ants and flying wasps. There was no significant difference in the proportion of Coleopterans found in the diets of the birds (Fig. 8).

Approximately 69% of the arthropod fragments found in the diets of the birds were identified to family. In the order Homoptera, I was able to identify one family of Cicadellidae to genus and species. All six bird species were consuming a species of leaf hopper (*Opsius stactagolus*) that is linked exclusively to tamarisk and no other vegetation (Stevens 1985). The highest proportion of use was by Lucy's Warbler's whose diet contained 40.3% of this species (Fig. 9).

Descriptive Calculations for Dietary Similarities and Differences. Dietary overlap was highest between the Yellow-breasted Chat and the Ash-throated Flycatcher (0.93), two species that are very close in body weight and bill length. The lowest overlap occurred between the Yellow-breasted Chat and Lucy's Warbler (0.49), one of the largest species and one of the smallest species of birds I examined. With the exception of the value for overlap between the Yellow-breasted Chat and Lucy's Warbler, all other overlap values between birds species were greater than 60% (Table 3a).

Prey type diversity (showing the specialization or generalization of bird diet) is shown in Table 3b. Bewick's Wren had the highest prey-type diversity value (6.32) being a opportunist or generalist and the Yellow-breasted Chat had the lowest value (2.33) indicating specialization in their diet. The other four species of birds had similar values between 4.04 and 5.9, indicating they are opportunistic or general in their diet .

Aquatic insects in diet. I was able to classify the source of 95.2% of the arthropods identified in diet samples as aquatic or terrestrial in origin. Arthropods of unknown origin comprised 4.8% of the diets in the six bird species analyzed. Overall diet composition of arthropods having aquatic origins in all six bird species combined was 8.7%, while arthropods of terrestrial origin comprised 91.3%.

There was a significant difference in the percent of arthropods having an aquatic origin versus terrestrial origin found in the diet of the six species of birds (Kruskal-Wallis Anova, n = 161, DF = 5, P = 0.001). The percent of arthropods having aquatic origins found in each species of bird were variable (Fig. 10), with the Yellow Warbler consuming the highest percent of aquatic insects (10%), and the Yellow-breasted Chat consuming the lowest percent (2%). Post hoc multiple analysis (Mann-Whitney U) revealed the Yellow Warbler had a significantly higher percent of aquatic origin arthropods in their diet when compared with the other five species ($P < 0.05$). No other significant differences in percent of aquatic origin arthropods were found in the diets between bird species.

Aquatic Insect availability. Arthropods of aquatic origins composed 46.5% of the those collected in sampling at the upper sites above the LCR. Only 13.4% of the arthropods collected at the lower sites were of aquatic origin. There was a significant difference in the number of aquatic insects found at the sites above the LCR versus the sites below the LCR ($X^2 = 228.38$, DF = 1, $P < 0.001$). This clearly shows that aquatic insects were in higher observable availability at the upper sites. There was no significant difference in the percent of aquatic insects consumed by the birds (n = 68) at the upper sites versus aquatic insects consumed by birds (n = 93) at the lower sites (Kruskal-Wallis Anova: $X^2 = 0.835$, DF = 1, P = 0.359).

Avian Diet and Zone of Vegetation Overlap (foraging perference). All six bird species had a high index of overlap with the OHWZ, with no species having an overlap value less than

0.76 (Table 4). Lucy's Warbler, Bewick's Wren and Yellow Warbler had similar overlap indices for both zones, where Bell's Vireo, Yellow-breasted Chat and the Ash-throated Flycatcher clearly showed a preference for the OHWZ. Before calculating the overlap of the birds diet in relationship to the two habitat types (NHWZ and OHWZ), it was necessary to determine if the arthropods were statistically different between the two zones. Malaise trap samples were omitted from the observable availability data because it appeared to have over-sampled Diptera (flies) (Table 5). All the arthropod orders were represented in the beat and sweep samples and therefore were believed to reflect a better representative sample of what was availiable in the habitat. Mean proportions of arthropod orders collected in each vegetation zone are shown in Figure 11. A Manova showed there was a significant difference in arthropods collected in the two zones (Wilks Lambda $F_{1,64} = 11.658$, $P < 0.001$). Anova results showed there were significantly higher proportions of Dipterans (Wilks Lambda $F_{1,64} = 16.8$, $P < .001$) and Homopterans (Wilks Lambda = $F_{1,64} = 8.30$, $P < .005$) in the NHWZ and a significantly higher proportion of Coleopterans in the OHWZ (Wilks Lambda $F_{1,64} = 21.60$, $P < .001$). No other arthropod orders were found to be significantly different between the two zones.

Only three birds out of 220 (1.4%) died of apparent stress due to lavage in 1994 and 1995. All three were Lucy's Warblers that died after using the lavage method. The stomachs of all three warblers were removed and preserved immediately after mortality. Arthropod fragments were lavaged from the stomachs of two out of the three birds, while no prey items were obtained from the third. No prey items were detected in the preserved stomachs of the three accidental mortalities when they were examined in the lab. This suggests that lavage was effective in obtaining stomach contents from birds.

DISCUSSION

Diets of the six species of birds were significantly different, each species of bird showing a preference for a particular order of arthropod. The significant difference in prey order proportions in the diets of the six species of birds is a clear indication of resource partitioning that helps shape the bird community co-existing in the riparian vegetation along the Colorado River. These dietary differences can be attributed to many reasons.

Classic foraging theory states that different bird species will tend to specialize in a different prey types if resources are abundant (Recher 1990). According to Stevens (1985), the highest standing crop of herbivores on willow and tamarisk occurs from mid June through August. This time period coincides with part of the breeding season for the bird species in the diet study. The birds, therefore, are able to specialize on different prey types because of the high availability.

Bird body weight and bill length in relation to prey size is also a known reason for dietary differences between bird species (Cambell 1989). Lucy's warbler, the smallest bird sampled in this diet study having the lowest average body weight and bill length had consumed the highest proportion of Homopterans, specifically the exotic leaf hopper *Opsius stactogalus* (averaging 2 mm in length). The Bell's Vireo, Yellow Warbler and Bewicks Wren, the "mid-sized" birds similar in average body weight and bill length, consumed prey in the mid-sized category (3 - 5 mm). The main prey items found in higher proportions in the Yellow-breasted Chat and Ash-throated Flycatcher , the largest birds sampled for diet, averaged 5 mm or greater.

Foraging tactics also play a role in dietary differences. Lucy's Warbler, Bell's Vireo, Bewick's Wren, Yellow-breasted Chat and Yellow Warbler are all foliage gleaners. With the exception of the Yellow-breasted Chat and Lucy's Warbler, dietary overlap among these species is greater than 60%. The low dietary overlap value between Yellow-breasted Chat and Lucy's Warbler is most likely due to the size difference of the birds. The Ash-throated Flycatcher is primarily an aerial forager. The diet of the Ash-throated Flycatcher had a higher proportion of Hymenopterans, primarily flying insects as to be expected. The flycatcher and the Yellow-breasted Chat were found to be similar in the proportion of Hymenopterans with an overlap value of 93%. When the diets of the two species of birds were examined by family level, however, it was found that the chat had consumed a high proportion of non-flying Hymenopterans (ants), in contrast to the higher proportion of flying Hymenopterans found in the diet of the Ash-throated Flycatcher. The high overlap values in regards to these two species diets with the arthropods in the OHWZ for both species would indicate the difference in the diets of these two similar sized species could be explained by foraging tactics. The Yellow-breasted Chat was found to be more of a prey specialist in comparison to the other five species of birds, while the Ash-throated Flycatcher is somewhat of a generalist (refer to Table 3b).

Another consideration in prey selection is that migrant bird species will chose different prey than permanent residents. A diet study conducted on birds in Panama that showed permanent residents consumed larger proportions soft bodied arthropods having high nutritional value, such as spiders, in contrast to the migrant species found to co-exist in the same habitat. Migrants fed mostly on low quality invertebrates easy to prey upon and were found to be opportunist in regards to diet. Bewick's Wren, a permanent resident I collected diet samples from in this study, had consumed more spiders than the other five bird species, all neotropical migrants (Poulin and Lefebvre 1996). Bewick's Wren also has a slightly different foraging tactic than the other four foliage gleaners, foraging low in the canopy and on the ground. It's bill is longer and slightly down curved allowing for probing in bark and leaves (Ehrlich *et al.* 1988). This bird species is considered a broad generalist according to the prey diversity index. This is understandable considering the bird stays in the same general area all year, being able to prey on changing insect fauna throughout the year.

Birds similar in size with similar foraging tactics have been documented to forage at different heights in forest canopies and therefore consume different prey (Morse 1989). The Yellow Warbler and Bell's Vireo have similar average body weight and bill size, and yet their diets are significantly different. These two bird species exhibit similar foraging tactics, though the Yellow Warbler is known to hawk insects as well as glean (Ehrlich *et al.* 1988). The prey type diversity in the Yellow Warbler (refer to Table 3b) was lower than the Bell's Vireo, having the highest proportion of Diptera (primarily Chironomide midges) in it's diet than any other species. The Bell's Vireo had a higher proportion of two prey taxa, Hemipterans (true bugs) and Lepidptera larvae (caterpillars) and therefore could be considered more generalized in diet.

My findings that the Yellow Warblers had consumed a high proportion of Chironomide midges is consistent with dietary data from a study conducted in Canada (Busby and Sealy 1978). The Yellow Warblers observed there showed that overall, the birds were consuming a high proportion of midges and foraging high in the canopy. From personal observations, I have repeatedly seen Yellow Warblers foraging high in the tamarisks hawking midges that swarm above the trees.

Bell's Vireo has historically been associated with mesquite, though more current data indicates they are utilizing the tamarisk as well (Brown 1985). This vireo can be difficult to see because of their affinity to dense shrub (Ehrlich *et al.* 1988). There is very little prior information available on the diet and foraging of Bell's Vireo. I conclude that one reason for the high proportion of Lepidoptera larvae and Hemipterans present in their diet was due to their foraging height in the vegetation. However, this is a speculation without data on arthropod availability throughout the vertical structure within the vegetation. A consideration for future diet studies would be to include observational data on foraging behavior and location.

Identification of arthropod prey remains in the diets of the six bird species revealed the main food resources selected were arthropods of terrestrial origin, comprising approximately 90% of their diet. Insects from aquatic origins only comprised approximately 8.0% of the total diet of the six species of birds analyzed. In arthropod sampling, five times as many terrestrial-origin arthropods were found in the riparian habitat as opposed to those arthropods with aquatic origin. The Colorado River has been shown to support a limited diversity of emerging arthropods because of cold water temperatures (Shannon 1993). This was supported by our finding low proportions of aquatic arthropods in invertebrate collections from the riparian vegetation. The riparian vegetation along the Colorado River supports an abundance of terrestrial-origin arthropods providing a rich food resource for riparian birds. Although, while the river is clearly important in that it supports the riparian vegetation which in turn supports arthropod food resources, it's role as a direct source of arthropod prey for these species of birds is minor.

Arthropods collected at the two sites sampled above the LCR (Paria and Saddle Canyon) contained a higher percent of those from aquatic origins (46.5%) than the samples taken at sites below the LCR (Parashant and Spring Canyon with 13.4%). The six species of birds were not relying heavily on aquatic insects for a food resource, therefore, the fact that aquatic insects were in higher abundance at the upper sites as opposed to the lower sites had no bearing on their diet. There was no significant difference in the proportion of aquatic insects in the diets of the six species of birds at the upper sites above the LCR than in the diets of the birds at the lower sites (below the LCR). This indicates the six species of birds are not interested in preying on aquatic insects during the sampling period in 1994 regardless of the observable abundance.

The arthropods identified in the diets of the six bird species showed higher overlap indices with the arthropods collected in the OHWZ vegetation as opposed to the arthropods collected in the NHWZ (refer to Table 4). I speculate that the higher overlap between the birds diets with the OHWZ is probably due to the fact this band of vegetation existed for centuries prior to the dam. The birds present in the Grand Canyon historically used this vegetation for nesting and as a food source. The predominate vegetation in the OHWZ (mesquite and acacia) has less dense foliage than tamarisk possibly allowing the birds to find prey more easily in these types of vegetation than in the dense foliage of tamarisk. In addition, tamarisk may contain biochemicals that discourage most plant herbivores (Carothers and Brown 1991).

Management considerations and recommendations:

There is strong evidence supporting that neotropical migrant birds are adjusting to the relatively recent expansion of exotic tamarisk not only for higher availability of nest sites (Brown and Trosset 1989, Hunter *et al.* 1988) but for opportunistic utilization of an abundant food resource as well. All six bird species I collected diet samples from were consuming the tamarisk specific leafhopper. Future decisions in regard to the avifauna along the Colorado River in the Grand Canyon should bear in mind that birds rely heavily on the recent band of vegetation established along the river in the last 30 years for their food resources as well as for nesting sites (Brown and Trosset 1989). Returning flows in the Colorado River through Grand Canyon to pre-dam conditions would eliminate much of the vegetation that has been established in the river corridor and therefore would decrease avian populations along the river. Extermination of exotic tamarisk would have the same repercussions.

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Table 1. Number of individuals caught, by species, for avian diet analysis during the breeding season in 1994 at five sites along the Colorado River in Grand Canyon National Park.

SITE	Lucy Warbler	Bell's Vireo	Bewick's Wren	Yellow Warbler	Yellow-breasted Chat	Ash-throated Flycatcher	TOTAL
Paria Beach RM 1.0	4	0	11	0	3	4	22
Saddle Canyon RM 46.5	27	0	15	6	3	10	61
Stairway Canyon RM 172.0	2	2	0	0	0	0	4
Parashant RM 198.0	23	22	5	1	8	2	61
Spring Canyon RM 204.5	21	15	2	11	4	1	54
TOTAL	77	39	33	18	18	17	202

Table 2. The average body weight (grams), bill length (millimeters) and the sample size for the six bird species sampled for diet along the Colorado River in Grand Canyon during the breeding season, 1994. Measurements used were taken from adult birds.

Bird Species	Body Weight	Bill Length	Sample Size
Lucy's Warbler	6.5	8.9	62
Bell's Vireo	8.9	9.7	29
Bewick's Wren	9.3	12.8	27
Yellow Warbler	8.9	9.3	14
Yellow-breasted Chat	25.9	13.9	15
Ash-throated Flycatcher	26.4	16.8	14

Table 3a. Dietary overlap among the six species of birds sampled along the Colorado River during the breeding season 1994. A value of zero would be no overlap, a value of 1.0 would be complete overlap.

	Luwa	Bevi	Bewr	Yewa	Ybch	Atfl
Luwa		0.76	0.87	0.64	0.49	0.64
Bevi	0.76		0.85	0.71	0.69	0.76
Bewr	0.87	0.85		0.83	0.75	0.9
Yewa	0.64	0.71	0.83		0.8	0.88
Ybch	0.49	0.69	0.75	0.8		0.94
Atfl	0.64	0.76	0.9	0.88	0.94	

Table 3b. Prey-type diversity index values (B) for the six species of birds. A value of 8.0 is least specialized (a generalist), a value of 1.0 is most specialized (a narrow range of prey).

Bird Species	Luwa	Bevi	Bewr	Yewa	Ybch	Atfl
Diversity index	4.57	5.9	6.32	4.04	2.33	4.35

Luwa - Lucy's Warbler, Bevi - Bell's Vireo, Bewr - Bewick's Wren, Ybch - Yellow-breasted Chat, Atfl - Ash-throated Flycatcher

Table 4. Overlap of arthropods found in the diet of the six species of birds with the arthropods found in the New High Water Zone (NHWZ) and the Old High Water Zone (OHWZ). A value of 1.0 represents a 100% overlap.

Bird Species	NHWZ	OHWZ
Lucy's Warbler	0.63	0.76
Bell's Vireo	0.51	0.88
Bewick's Wren	0.76	0.93
Yellow Warbler	0.86	0.90
Yellow-breasted Chat	0.44	0.83
Ash-throated Flycatcher	0.65	0.93

Table 5. Frequency and percent (%) of arthropod orders collected in three sampling methods at Paria, Saddle Canyon, Parashant and Spring Canyon combined.

	Method of Arthropod Sampling					
	Beat		Sweep		Malaise	
Order	Frequency	%	Frequency	%	Frequency	%
Araneae	83	10.6	38	4.9	1	0.0
Hemiptera	45	5.8	63	8.2	3	0.1
Homoptera	123	15.7	144	18.7	25	0.9
Coleoptera	37	4.7	56	7.3	2	0.1
Diptera	194	24.8	328	42.5	2617	92.0
Hymenoptera	160	20.5	131	17.0	198	7.0
Lepidoptera	139	17.8	11	1.4	0	0

Figure 1. Location of study sites where samples were taken along the Colorado River in the Grand Canyon, 1994-1995.

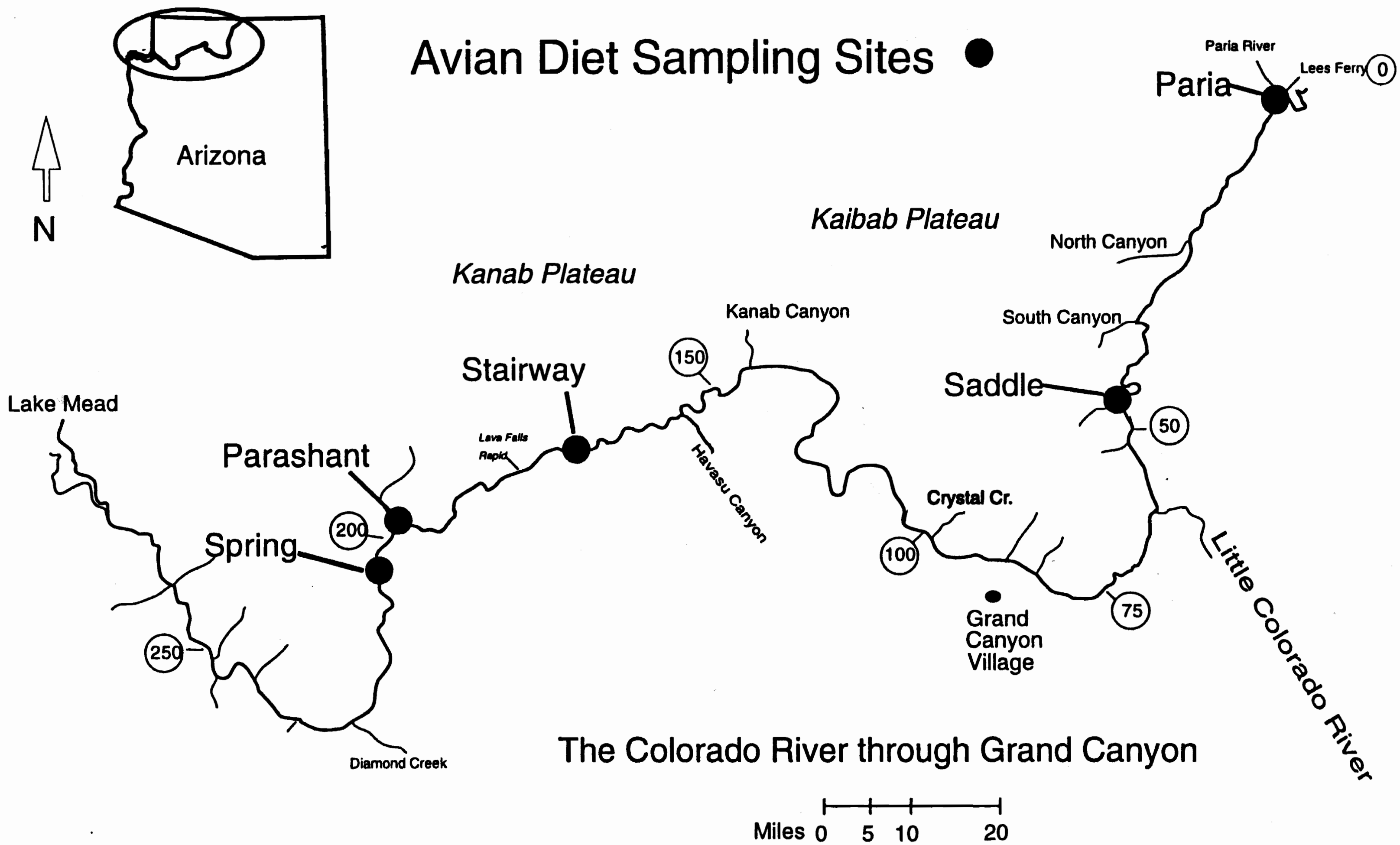


Figure 2. Mean proportion of arthropod orders found in the diets of the six species of birds.

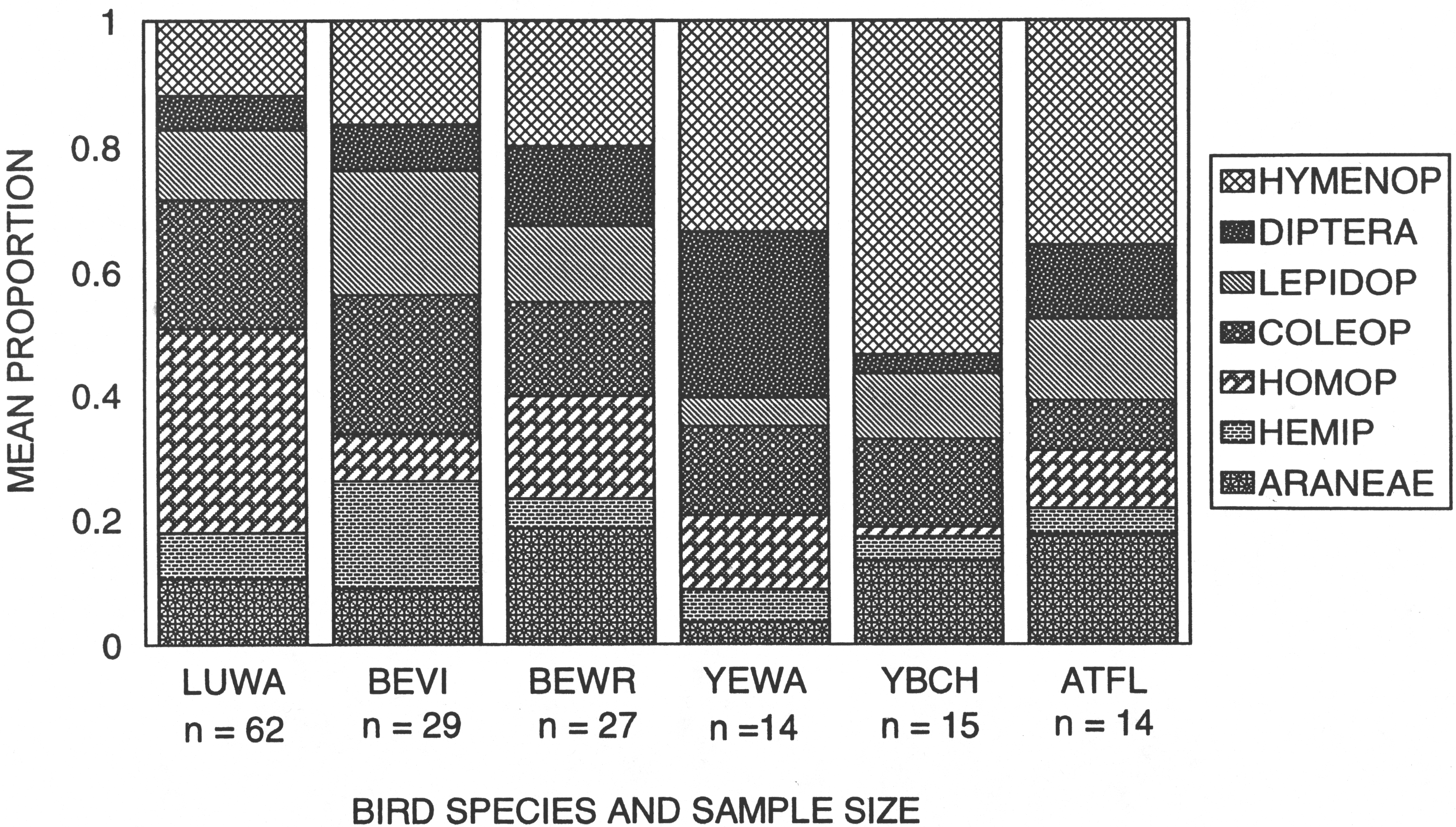


Figure 3. Mean proportion of Homopterans consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

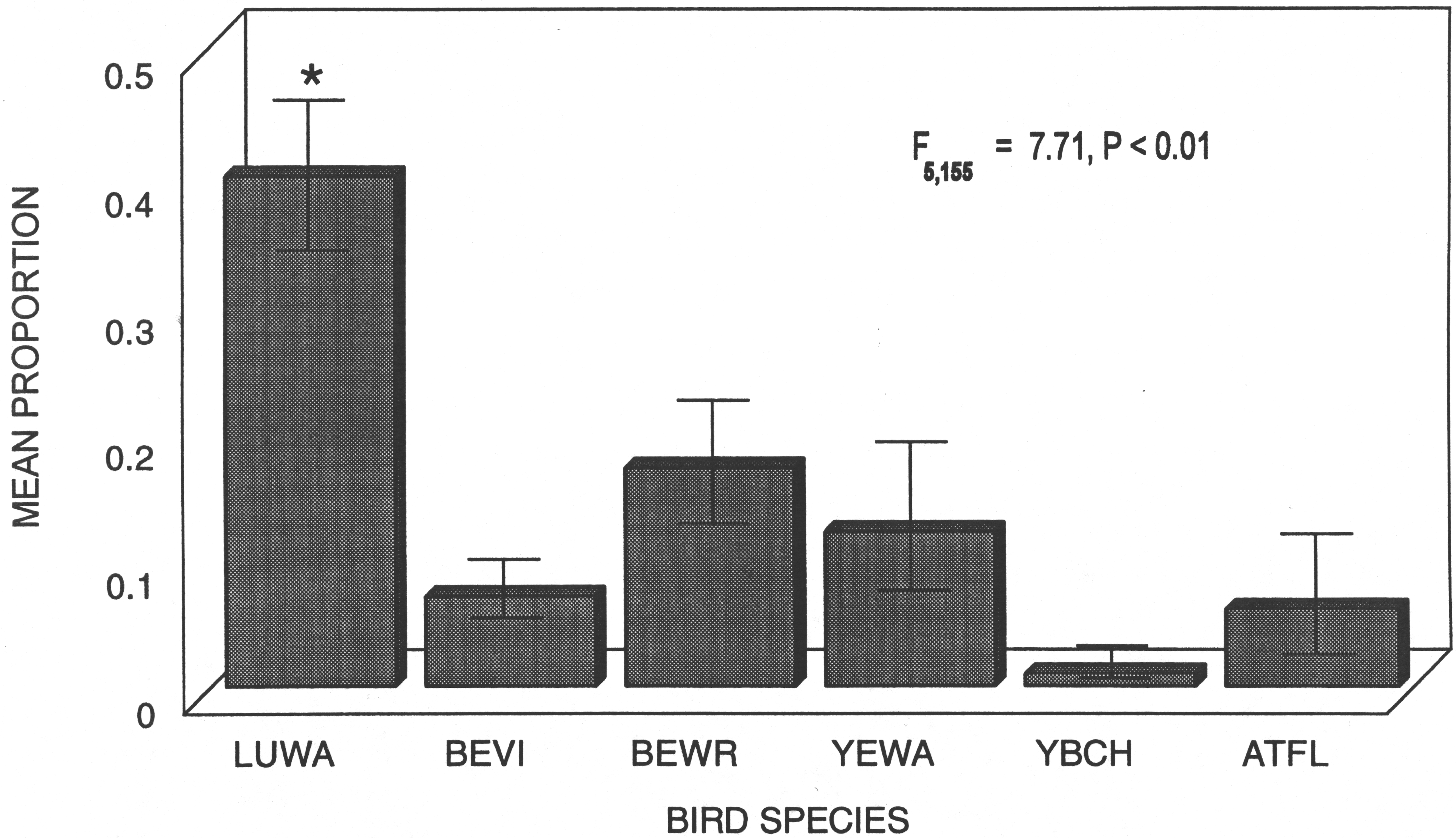


Figure 4a. Mean proportion of Hemiptera consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

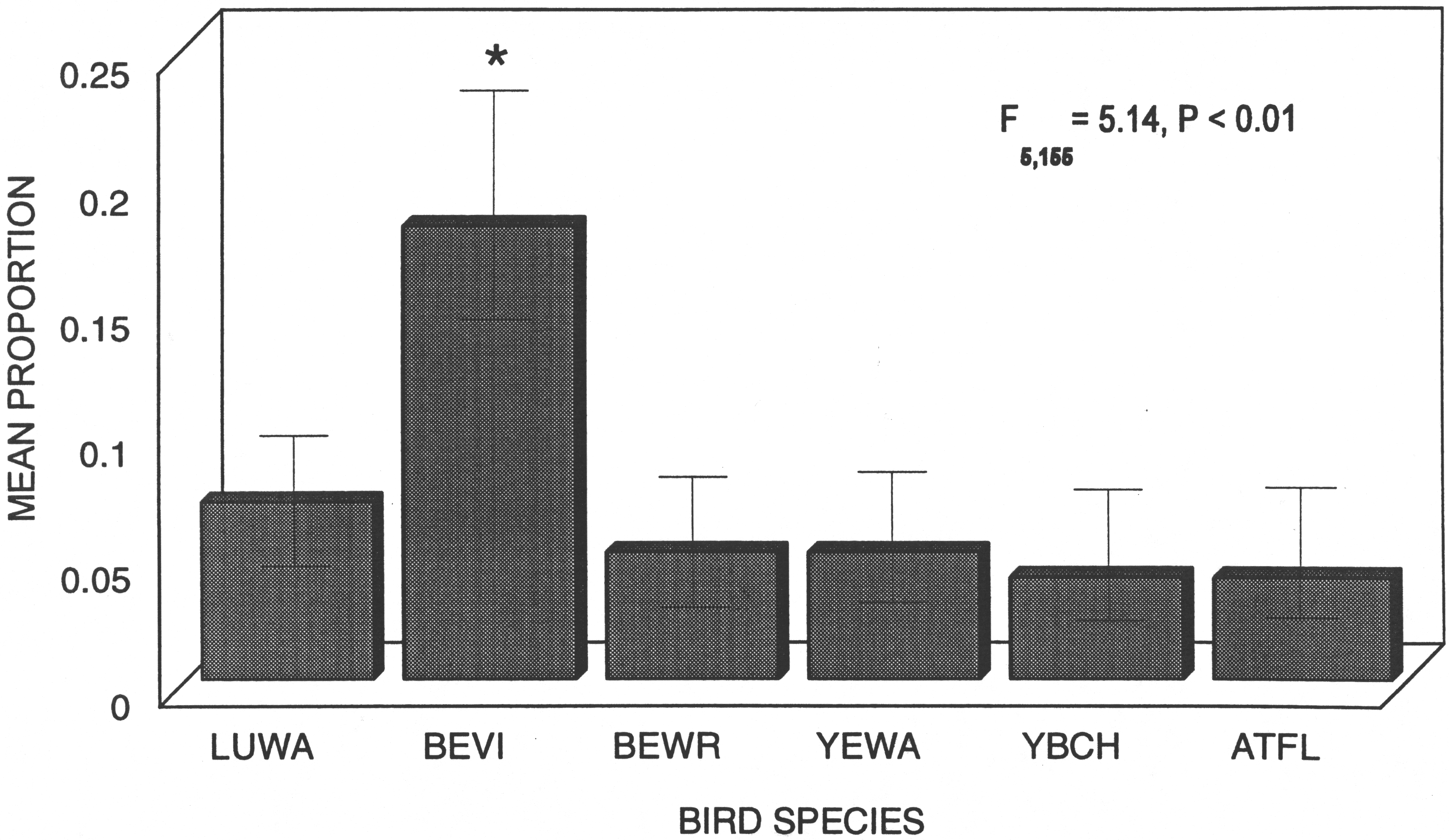


Figure 4b. Mean proportion of Lepidoptera larvae consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

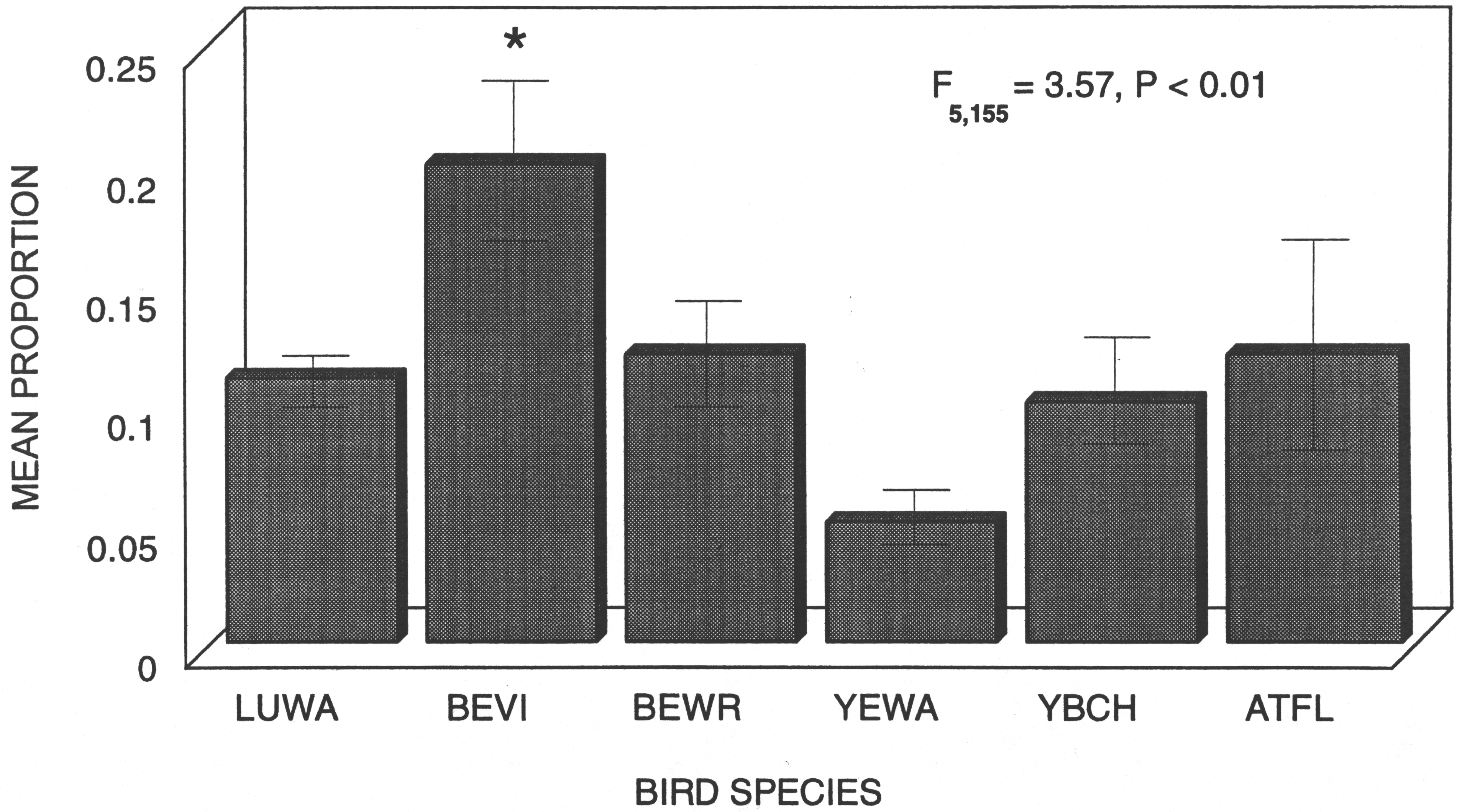


Figure 5. Mean proportion of Araneae consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

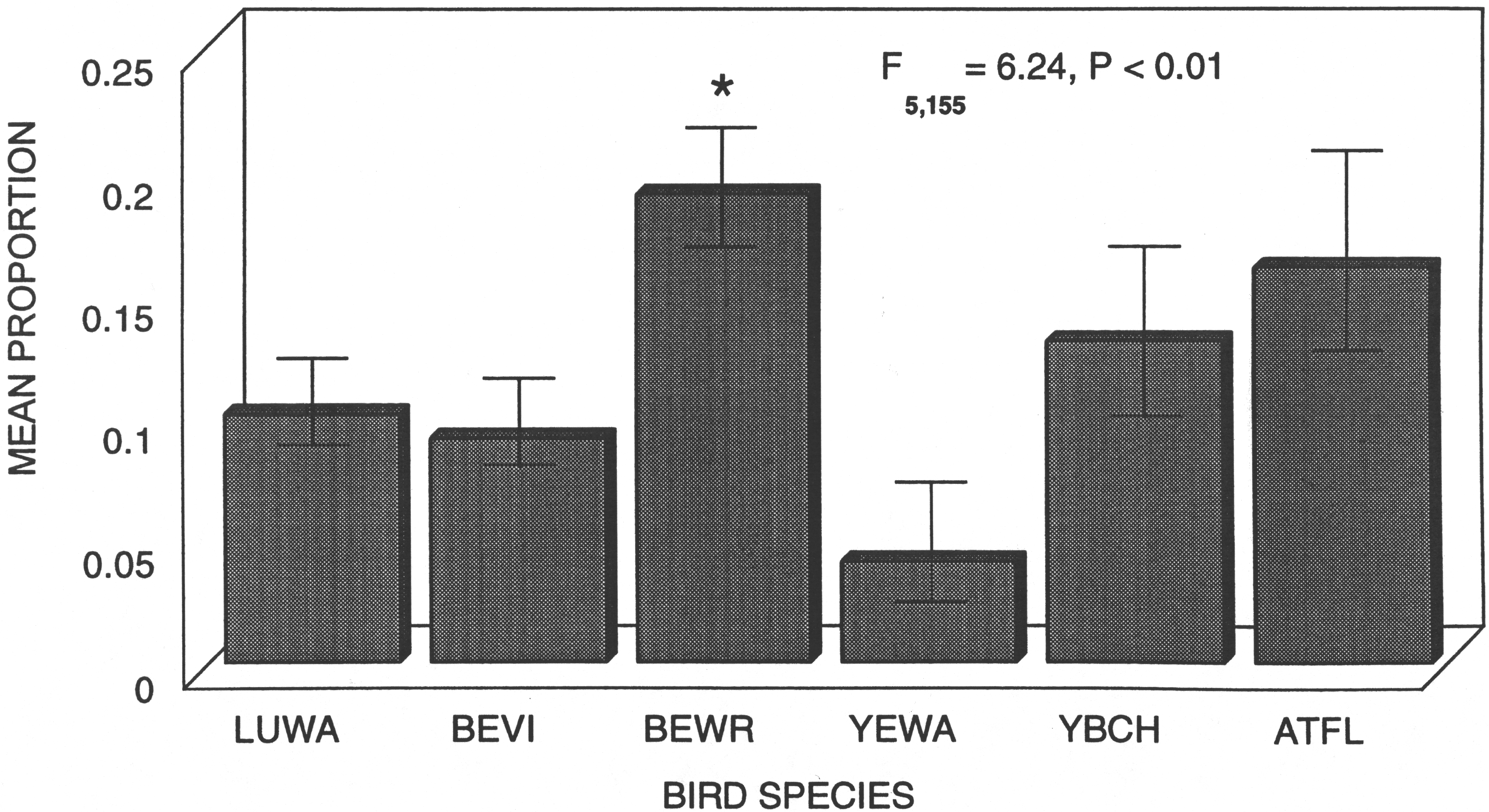


Figure 6. Mean proportion of Diptera consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

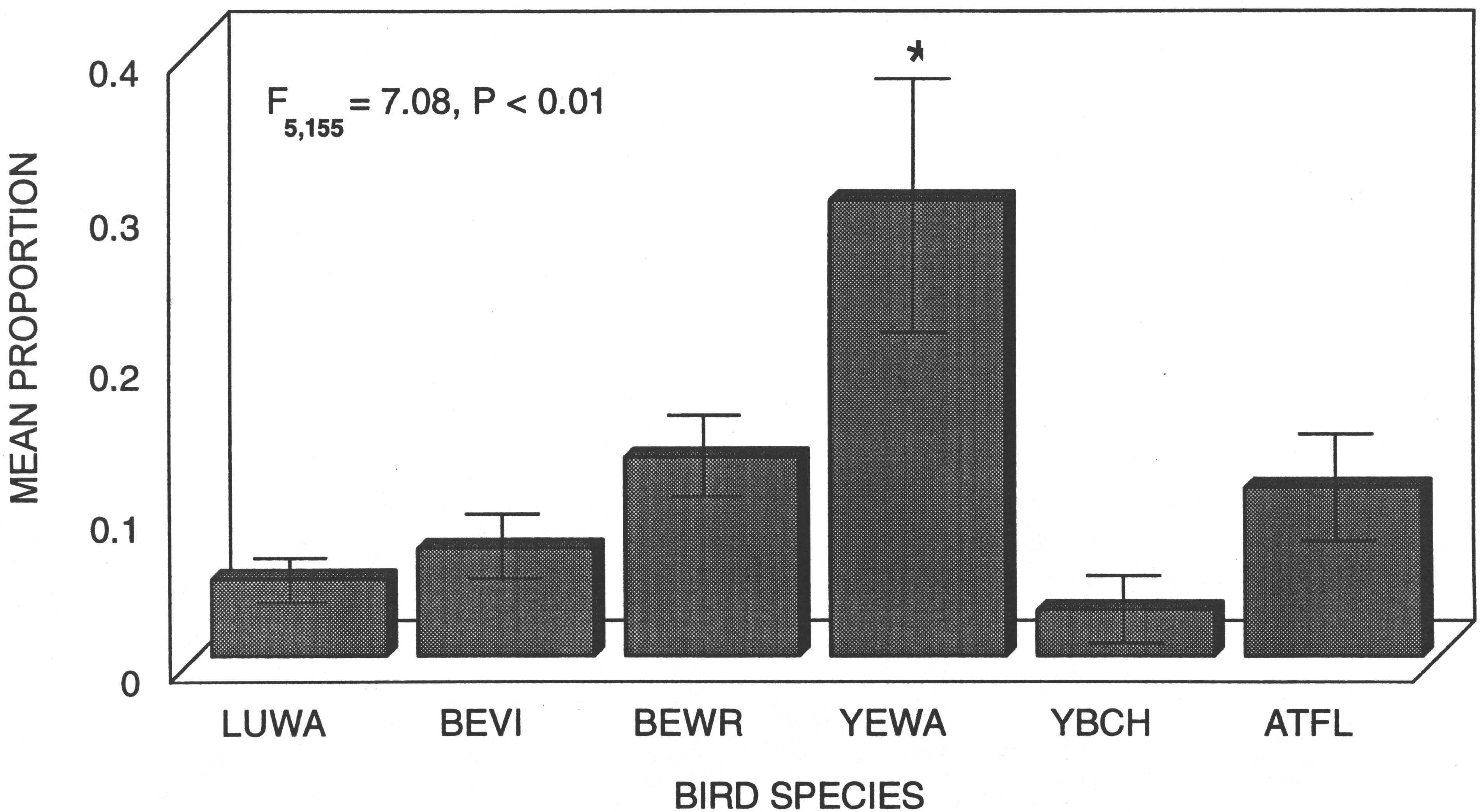


Figure 7. Mean proportion of Hymenopterans consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

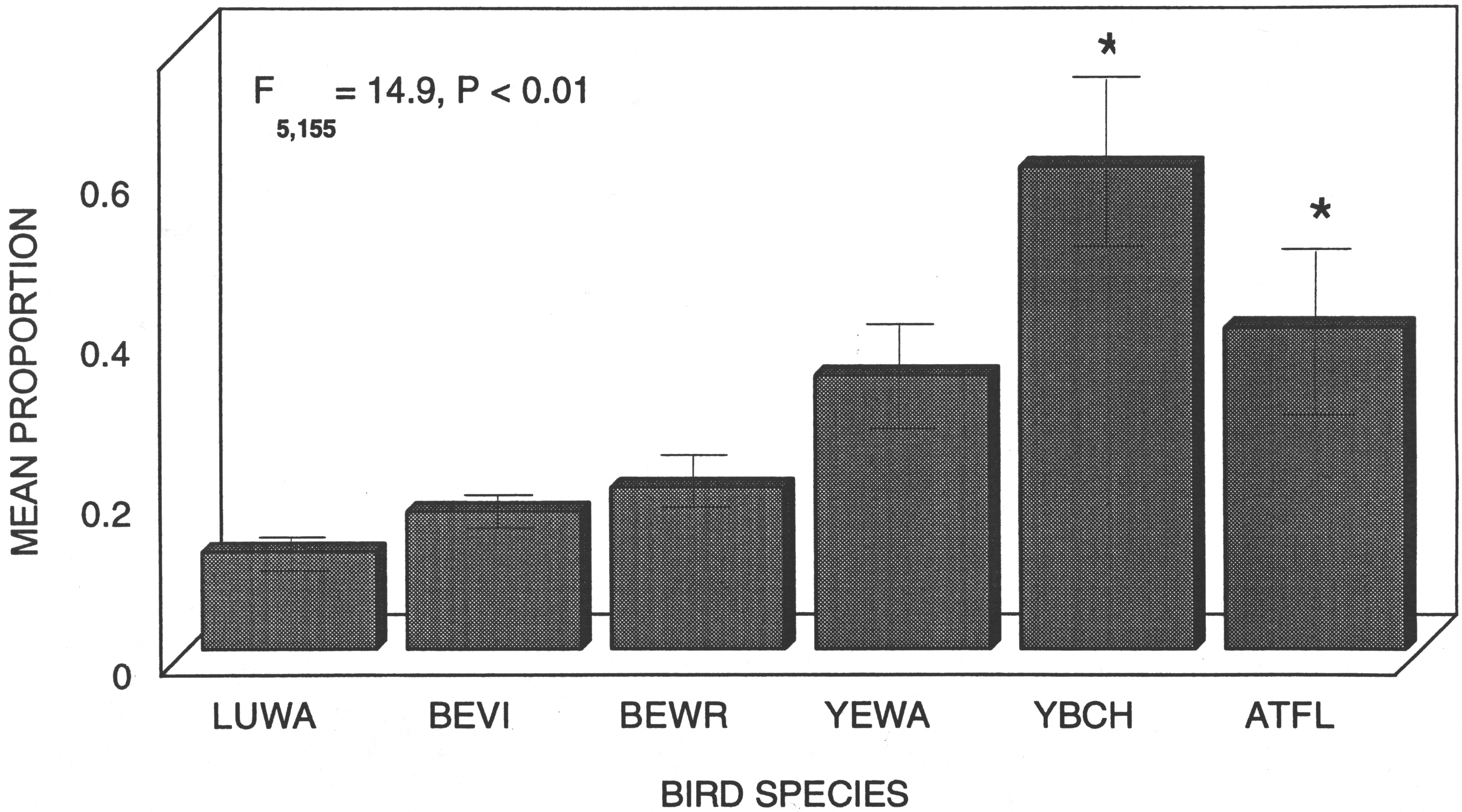


Figure 8. Mean proportion of Coleoptera consumed by the six species of birds. Standard error bars represent one standard deviation.

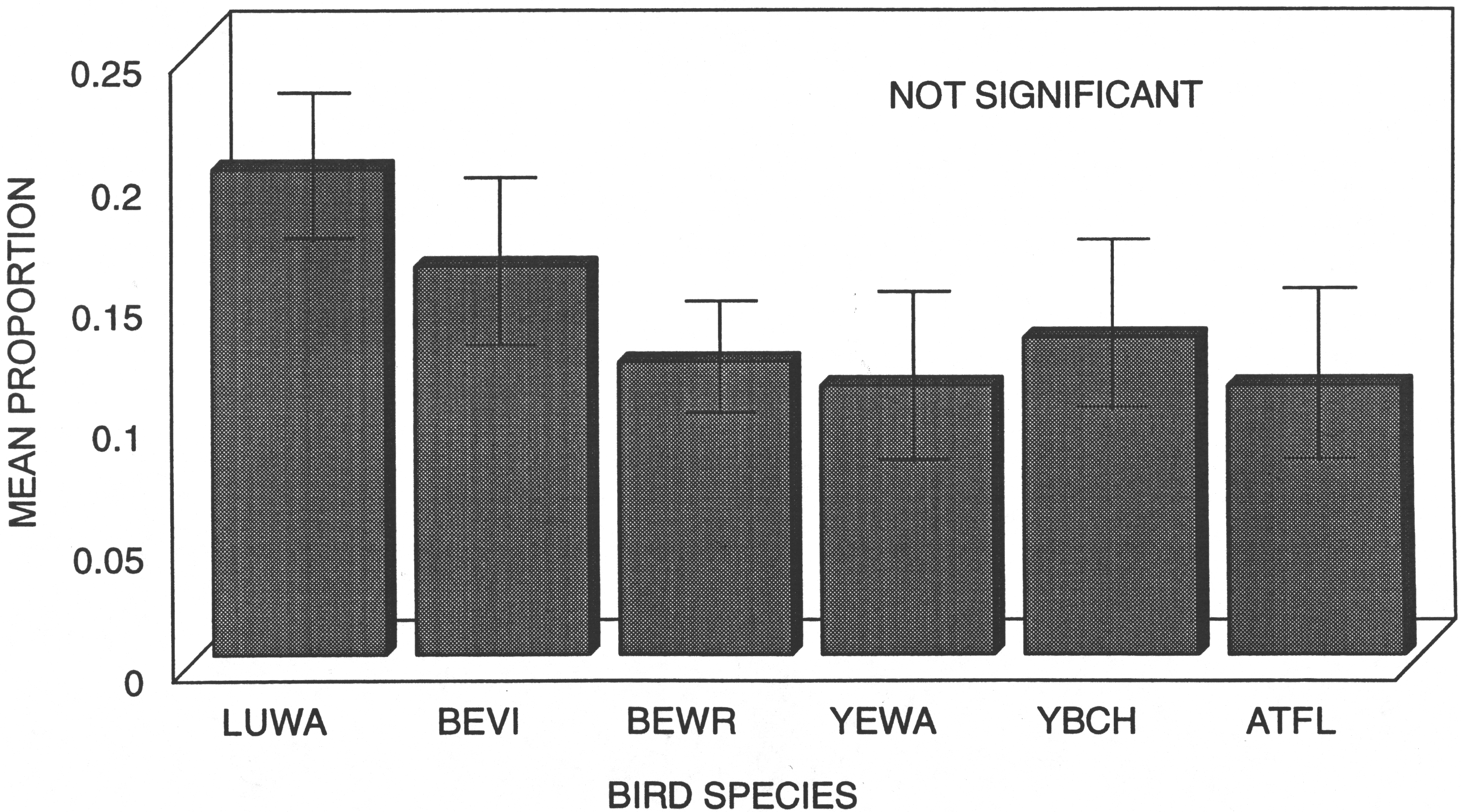


Figure 9. Proportion of leafhoppers (*Opsius stactogalus*) in the diet of the six species of birds.

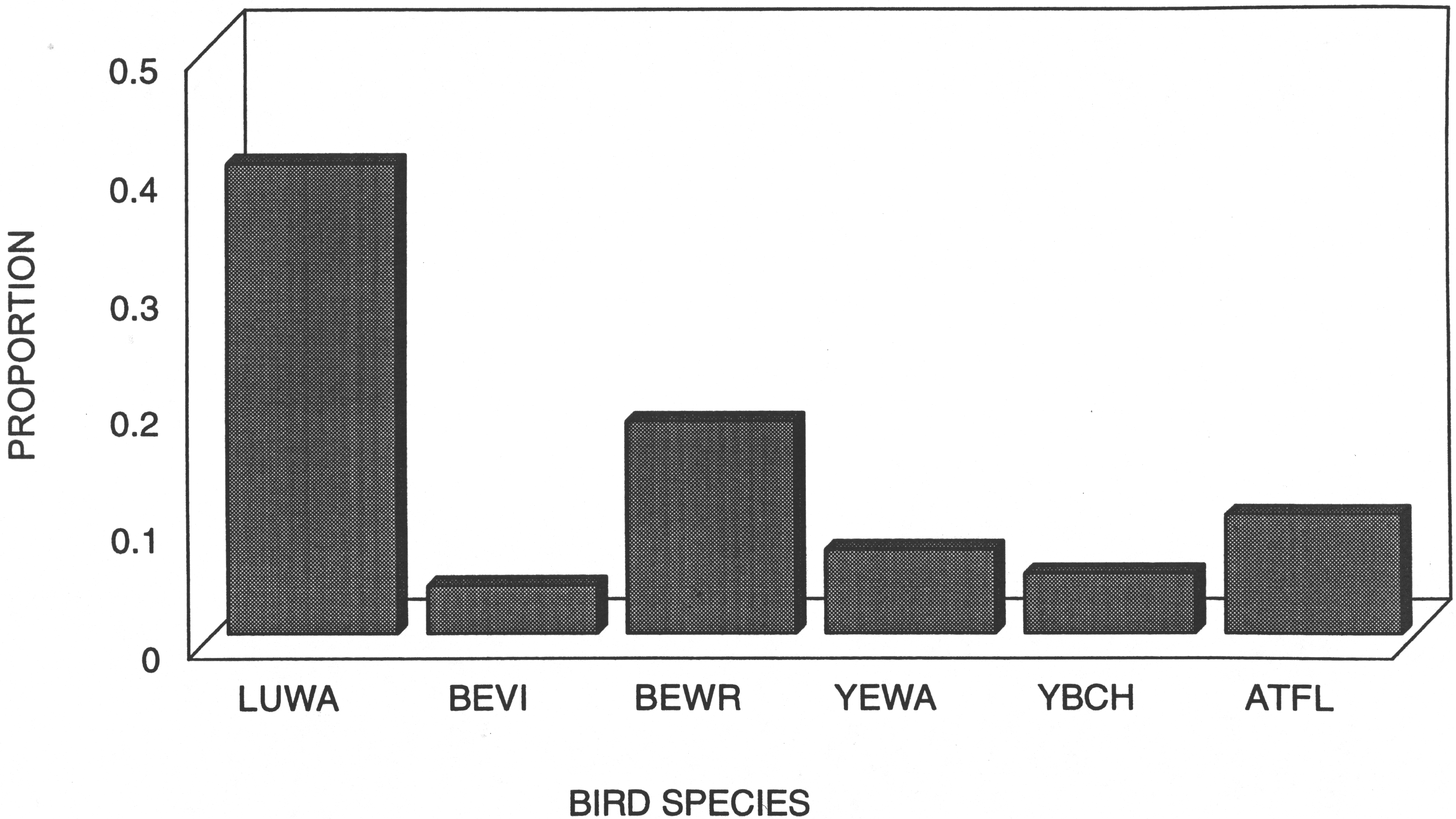


Figure 10. Percent of aquatic arthropods found in the diets of the six species of birds. Significance denoted by asterisk.

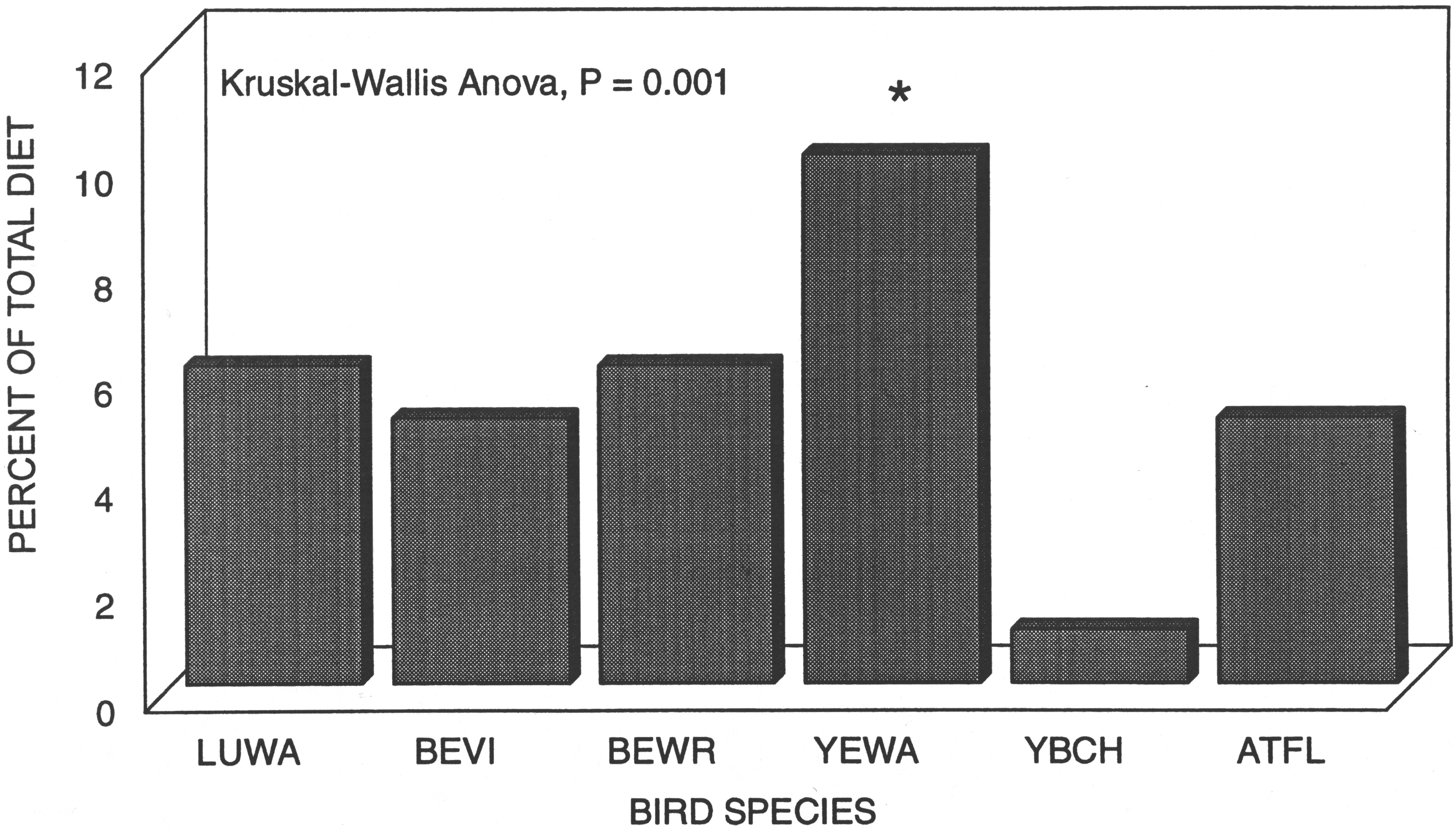
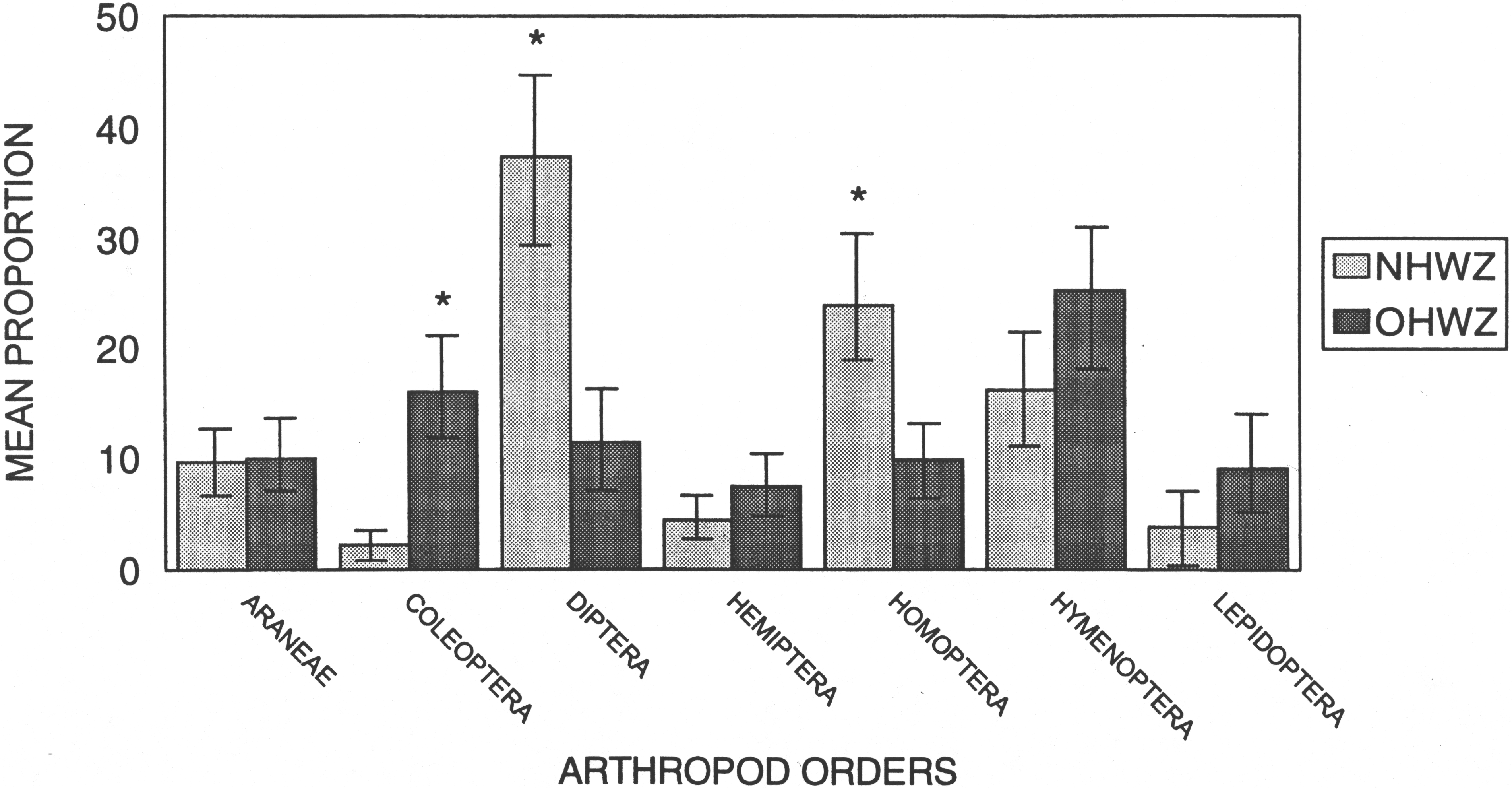


Figure 11. Mean proportion of arthropod orders collected in the old high water zone (OHWZ) and new high water zone (NHWZ). Error bars represent one standard error. Asterisks show significant differences.



United States Department of the Interior

USGS BIOLOGICAL RESOURCES DIVISION
Colorado Plateau Research Station
P.O. Box 5614
Northern Arizona University
Flagstaff, AZ 86011-5614
Phone: (520) 556-7466
FAX: (520) 556-7500

December 16, 1996

Memorandum

FINAL

To: GCES Program Manager

Through: Lawrence D. Garrett, Chief
Grand Canyon Monitoring and Research Center

From: Mark Sogge, Ecologist
Colorado Plateau Research Station

Subject: Grand Canyon Avian Diet Final Report

Enclosed are three copies of Helen Yard's final report entitled *Quantitative Diet Analysis of Selected Breeding Birds along the Colorado River in Grand Canyon National Park*, one of the required deliverables associated with our National Park Service Cooperative Agreement work order CA 8031-8-0002. This is the final version of the report, modified per Grand Canyon staff review of an earlier draft. The project, which began in 1994, was funded by the U.S. Bureau of Reclamation Glen Canyon Environmental Studies program in order to determine the potential effects of Glen Canyon Dam interim-flow operations on the diet of riparian birds of the Colorado River corridor in the Grand Canyon.

I have already distributed four copies of the report directly to the Grand Canyon Senior Scientist. Please feel free to call me (520/556-7311 ext 232) if you have any questions or comments.

cc:
C. van Riper, CPRS/NAU