Determinants of tree species preference of birds in oak–acacia woodlands of Central America

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Abstract: In mid-elevation areas of Mesoamerica, *Acacia pennatula* commonly occurs in mixed woods with various species of oak. During a 1-y study in Nicaragua, we found the abundance of birds in acacia was far higher than the representation of this species in the mix of trees, whether this is estimated by number of individual trees, canopy cover or foliage cover. This higher abundance was probably related to the fact that acacias supported approximately three to four times the abundance of arthropods that were found in oaks and twice the biomass. Although oak foliage supported fewer arthropods, relatively more of them were large (> 1 cm). The greater preponderance of small arthropods in acacias versus oaks was probably related to the small leaflet size of acacias. However, it is likely that the higher abundance of arthropods in acacias, particularly herbivorous species, was related to the higher nutritional content of the acacia foliage (crude protein, minerals, non-structural carbohydrates) and lower content of digestion-inhibiting compounds (structural carbohydrates, total phenolics, condensed tannins). The major defensive mechanisms of acacia are mechanical (thorns) or qualitative-defence chemicals (cyanogenic glucosides) that are apparently more effective against vertebrate than invertebrate herbivores. These observations support the hypothesis that the anti-herbivore defences of acacia are primarily directed against large mammalian herbivores, rendering the foliage highly palatable to arthropods.

Key Words: ant-herbivory defences, breeding currency hypothesis, foliage palatability hypothesis, insectivorous birds, migratory birds, tree preference, tropical savannas

INTRODUCTION

Different tree species often support distinct foliage structures and arthropod populations that lead to marked foraging preferences of insectivorous birds. If a forest or woodland is composed of a few species of trees, then the characteristics of the dominant species will play a large role in what types of birds occur in that habitat. The existence of such tree specializations has long been recognized in temperate forests (Abbott & Van Heurck 1985, Balda 1969, Franzreb 1976, Holmes & Robinson 1981, Holmes & Schultz 1988, Morse 1976, Parrish 1995, Peek 1989, Warburton *et al.* 1992). However, less attention has been paid to differences in insectivorous bird use of different tree species in tropical habitats. Tropical habitats often support a greater diversity of trees than is found in temperate habitats, and a single tree species may play a less decisive role in the composition of the avian insectivore guild. But in some tropical communities only a few species dominate, and the presence and absence of certain dominant tree species can be critical in determining bird use. One such habitat is the oak–acacia woodlands of Mexico and northern Central America where relatively dry mid-elevation areas have been subject to disturbance of fire and grazing (Greenberg 1994, Greenberg *et al.* 1997). We focus on this relatively simple tropical system to examine the pattern of avian preference for dominant tree species and the underlying causes of these patterns.

Although a number of studies have documented preferences of birds for particular tree species, far fewer studies have attempted to determine the factors that account for these preferences (Whelan 1989, 2001). The preference of a particular insectivorous bird species for a particular tree can be determined by the interaction between foraging style and foliage structure and architecture, as well as by the abundance of preferred prey (Holmes & Robinson 1981, Holmes & Schultz 1988). In contrast, the overall greater abundance of insectivorous birds may

be attributed to a greater abundance of arthropods or to foliage structure in which it is universally easier to locate arthropods. Differences in the abundance of foliage arthropods are thought to be related to the nutritional content and associated secondary compounds in the foliage. However, few studies have investigated the relationship between the use of trees by birds and the chemical content of the tree's foliage (but see Murakami 1998, Sipura 1999).

Acacia pennatula grows in association with livestock grazing, either in monospecific woodlots or in mixed woods and savannas with oaks and other broad-leaved trees (Greenberg *et al.* 1997). Greenberg *et al.* (1997) postulated that the oak–acacia vegetation may have been more widespread during cool dry periods of the late Tertiary and Quaternary. Changes in climate have led to the reduction in the extent of natural savannas in Mexico and Central America (Webb 1978). Also, the diminution of grazing that resulted from the loss of large ungulates and other herbivores during the Pleistocene extinctions (Janzen & Martin 1982) may have also reduced the presence of acacia (Greenberg *et al.* 1997). The recent introduction of livestock favours the spread of acacia through the consumption of the seedpods (Chazaro 1977) and the differential removal of competing plants.

In previous work in acacia savannas and woodlots in Chiapas, Mexico (Greenberg *et al.* 1997), we found that acacias supported a high abundance of insectivorous birds, particularly migratory species. Therefore, in this study we will examine two hypotheses regarding the relative use of acacia and oaks by insectivorous and migratory birds: the foliage palatability hypothesis and the breeding currency hypothesis.

The foliage palatability hypothesis holds that acacias are more attractive to insectivorous birds because they have relatively nutritious and palatable foliage with low levels of chemical defence. These foliage characteristics would lead to a greater abundance of arthropods in oak versus acacia foliage. To examine this hypothesis, we compared the abundance of insectivorous birds and arthropods in acacia and oak throughout the year. Furthermore, we examined the protein and condensed tannin content of acacia and oak foliage to see if the more spinescent acacia has higher values for the difference between the two classes of chemicals (Cooper *et al.* 1988). We also measured other aspects of the nutritional quality and tested for other classes of defensive compounds.

The breeding currency hypothesis posits that the abundance of migratory birds in the non-breeding season is determined by the surplus of arthropods that results because resident populations are limited by the abundance of large soft-bodied arthropods (breeding currency) during the breeding seasons. Based on this, we predicted that the relative abundance of migrants using a habitat (acacia versus oak) should correspond to the habitat with an arthropod fauna dominated by smaller individuals. Specifically, we examined the ratio of the abundance and biomass of large arthropods found in breeding season collections versus the overall abundance of arthropods in the non-breeding season.

STUDY SITES

The study was conducted in the cattle lands adjacent to the villages of Estanzuela, Despoblado and Amazaguero approximately 5 km south-west of the city of Esteli in north-western Nicaragua (13°04′N, 86°20′W) between 1100 and 1400 m asl. The region is xeric (averaging 873 mm rainfall y^{-1}, Instituto Nicaraguense de Estudios Territorios) and hot (mean annual temperature = 21 °C) with a long and intense dry season and subjected to high winds through most of the year. The vegetation consists of secondary oak woodlands dominated at lower and drier sites by a large-leaved, deciduous species, *Quercus sapotifolia* Liebm., and at higher and more mesic sites by an evergreen species with smaller, narrow leaves, *Quercus peduncularis* Née (Fagaceae) and by *Pinus* sp. Bordering the oak woods, usually at slightly lower elevations is a zone of savanna consisting of a mixture of *Acacia pennatula* Schlecht. & Cham. (Fabaceae) and *Quercus sapotifolia* with smaller numbers of *Lysiloma auritum* (Schltdl.) Benth. (Fabaceae), *Guazuma ulmifolia* Lam. (Sterculiaceae), *Bursera simaruba* (L.) Sarg. (Burseraceae), *Spondias mombin* L. (Anacardiaceae), *Ficus* spp. and *Trema micrantha* Blume (Ulmaceae).

Acacias sometimes support vines, notably *Cayaponia racemosa* Mill. (Cucurbitaceae), which produces crops of orange berries in the late dry season. Both oaks and acacia are mostly deciduous. From foliage surveys (see below), we found that the density of oak foliage was 58% lower in March than June (after leaf-out) and the reduction was 88% for acacia. During the March sampling period, when foliage density was at its lowest, both acacia and oaks were in flower.

METHODS

Sampling periods

We sampled bird distribution and arthropod abundance during four sampling periods: 5–15 December 1999 (early dry season), March 2000 (dry season), 15–25 June 2000 (early rainy season), and 15–25 October 2000 (late rainy season).

Bird surveys

We established 10 survey routes of 2 km each in areas of mixed oak–acacia savanna, small patches of

oak woodland and small patches of acacia woodland. Transects were surveyed one time during each of the four sampling periods. Each transect was walked slowly (approximately 0.5–$0.7\,\mathrm{km\,h^{-1}}$) and all birds located within $25\,\mathrm{m}$ were recorded. In addition, we recorded the activity and the tree species in which the birds were first located. We also noted if the bird was foraging in a vine supported by the tree or in the tree itself. All but four transects were surveyed four times; four transects were not surveyed during the late rainy season sampling because of inaccessibility.

For analysis, we classified birds by their residency status (based on American Ornithologists' Union 1983; M = migrant from North America; R = tropical resident; and SR = summer resident, wintering in South America). We obtained body masses for species in the study from Dunning (1992). We also classified species as insectivores, omnivore–insectivores and non-insectivores, on the basis of 15 y of field experience in the region and Howell & Webb (1995). We follow the taxonomic treatment of the Central American avifauna presented in the AOU Checklist (American Ornithologists' Union 1983).

Relative tree abundance

We walked each 2-km transect and recorded the number, height and maximum crown diameter of each tree within $50\,\mathrm{m}$ on either side. Although we found 24 species of trees along the 20 km of transects, 90% of the individuals were either oaks or acacias, and no other tree species comprised more than 3% of the total. Because of this, we focus our analysis of selectivity on oaks and acacias; for most calculations of availability and use, we ignore other tree species. During the December, March and June sampling periods we estimated foliage height profiles for a sample of 50 acacias and 50 large-leaved oaks (*Quercus sapotifolia*). We paced along the four cardinal directions from the trunk and at 1-m intervals counted the number of foliage intersections and estimated the height of each intersection along a line determined by sighting through a narrow straw aimed perpendicular to the ground. Using these measurements, we examined the regression between tree height and the average number of foliage intersections per point per tree. We multiplied the resulting number of foliage intersections per point by the canopy area ($\pi[\text{crown radius}]^2$) of the trees counted on the surveys to obtain an estimate of total foliage cover. From these data we can estimate relative availability of acacias and oaks based on (1) relative abundance, (2) relative crown cover and (3) relative foliage cover.

Insect sampling

We used a foliage clipping procedure to determine arthropod abundance (Johnson 2000, Morse 1976). In each sampling period we sampled arthropods of the two oak species and acacia by clipping samples of foliage from terminal branches into a collecting bag and fumigating the sample with insecticides (Baygon™ or Pyrethrin aerosol spray) (Johnson 2000). Samples were collected from two sites (Almazaguera and Desplobabo), and for the large-leaved oak and acacia we collected five low samples (eye level) and five high samples (using a pole cutter and a deep canvas basket). A high sample was $8\,\mathrm{m}$ for oak and $4\,\mathrm{m}$ for acacia. We therefore collected 20 samples per species per period totalling 160 samples. The low sample was clipped directly into a bag, thus minimizing insect escapes; we carefully observed the collection of high baskets through binoculars to monitor escapes. For each arthropod we recorded the order, colour and length. We used published length–weight regressions to estimate total arthropod biomass (Zug & Zug 1979). We used this source because it is based on live weight rather than dry weight as in a number of other published regressions.

Foliage chemistry

Foliage samples were collected from terminal foliage on lower branches of oaks and acacias in December and June. Foliage samples were oven dried and cleaned (twigs and stems removed); the samples were split and half were sent to the Dairy One Forage Laboratory, Ithaca, New York, for nutritional analysis and the second half were analysed for tannins and total phenolics at the University of Utah.

Based on reports for other New World acacias (Clement *et al.* 1998) we tested *Acacia pennatula* foliage for the presence of alkaloids and related quaternary nitrogen compounds using a spot test of Dragendorff's Spray Reagent (potassium iodide and bismuth subnitrate in acetic acid) dropped on Whatman's #1 filter paper (Schall & Ressel 1991). A colour change from white to orange indicates presence of alkaloid or related amines. We used tobacco as a positive control substance. Rehr *et al.* (1974) reported significant concentrations of cyanogenic compounds in non-ant acacias from Costa Rica. We tested for cyanogenic compounds using a spot test of picric acid-soaked filter-paper strips (Williams 1979). Oak and acacia foliage was collected in the field and transported in a sealable plastic bag to a laboratory where the fresh plant material was crushed and sealed in small vials. The picric acid-soaked strips were dipped in 10% Na_2CO_3 solution and the excess solution was blotted off. We placed the strips in the vials which were then sealed. We recorded any change in colour in the paper within 30 min and after 12 h. A change in colour from yellow to brown indicates the presence of cyanide gas, which indicates cyanogenic compounds. We conducted six replicate tests for each species, including three on old and three on newly flushed leaves.

We quantified tannin content by analysing both total phenolics and condensed tannins. The condensed tannins are of particular interest because previous studies of subtropical savanna plants found that tannin content was a factor in the palatability to generalist herbivores (Cooper *et al.* 1988, Owen-Smith & Cooper 1987; see below). For the analysis of condensed tannins and total phenolics, 'self-standards' were made from acacia and oak samples to generate standard curves. Standards were made according to the methods of Appel *et al.* (2001). Briefly, *c.* 30-g samples of each species were extracted in 75% MeOH. Extraction was facilitated by homogenization with a polytron (Brinkman Kinematica PT 3100) (Torti *et al.* 1995). Phenolics were purified through a Sephadex LH20 column following the protocol of Appel *et al.* (2001).

Plant samples for phenolic and tannin quantification were extracted by homogenizing 0.1–0.6 g of plant material (dw) in 85% MeOH (Torti *et al.* 1995). Extracts were kept at $-20\,°C$ until quantification. Total phenolics were measured using the Folin Ciocalteu method (1927). Condensed tannins were measured using the proanthocyanidin method of Porter *et al.* (1986). Separate standard curves were generated for acacia and oak samples using the corresponding purified tannin. Results are given in mg of phenolics and tannins per g dry weight for each species.

RESULTS

Bird use of acacias and oaks

During the course of 36 transect surveys conducted over the four sampling periods, we recorded the tree location of 1977 foraging birds. We found 58.7% of the birds in acacias. Migrants were found 69% of the time in acacias (n = 880) and residents were found in acacias significantly less often – 50.1% of the time (n = 1097, $\chi^2 = 64.9$, P < 0.00001). Focusing on the preference for acacias over oaks (acacia/acacia + oak), we found that 76.9% of the migrants and only 60.1% of the residents were found in acacias. These figures are based on data pooled for all of the transects and periods. Analysing by individual transect, we found the mean percentage use of acacia (Figure 1) ranges between 60.9% and 75.5% for migrants and between 42.7% and 73.3% for residents (and summer residents).

In the above analysis, data from all species within a category were pooled. We also conducted the analysis for individual species found eight or more times in either acacia or oak. The average use of acacia (versus oak) of the 45 species was 63.5% (3.6% SE). The 12 migratory species (Table 1) were found an average of 76% (5.7% SE) of the time in acacias and the average for the 33 resident species was 59% (4.2%). A t-test based on pooled
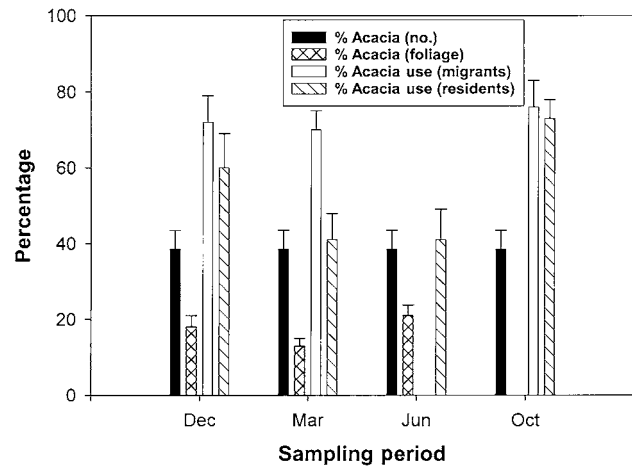

Figure 1. The percentage of individual acacia trees, estimated acacia foliage, and relative abundance of migrant and resident birds in acacia trees along 20 km of survey transects during four survey periods. The tree totals exclude all trees but oaks and acacias. Per cent acacia foliage is based on the estimated crown area weighted by the average number of foliage layers within the canopy area. Both trees and birds were included if within 25 m of the transects.

variances and arcsine-transformed ratios indicated a significant difference between the two classes of species (t = 2.24, P = 0.036). Because the analysis is focused on the relationship between bird use and arthropod abundance, we also analysed only those species that were classified as insectivorous, with similar results: eight species of migrants averaged 80% acacia use (5.6% SE) and 14 species of residents averaged 63% acacia use (4.5% SE) (t = 2.25, P = 0.03).

Migratory birds are smaller on average than residents. In this case we found the average migrant species to weigh 14 g and the average resident 51 g. In order to determine if migratory status was an important variable, given the difference in size distributions, we conducted an ANCOVA with migratory status as the grouping variable and body mass as the covariate. We restricted this analysis to insectivorous species, which are indicated in Table 2. We found no significant interaction (slope difference) between migratory status and mass, so we present the results of the ANCOVA without interactions (intercepts). Migratory status was significantly related to relative acacia use ($F_{1,19} = 4.39$, P < 0.05), whereas there was no significant effect of the mass covariate (P = 0.90).

Relative abundance, canopy cover and foliage cover of acacia and oaks compared with use by birds

When just oak and acacia were considered, acacia comprised an average of 38.8% of the individual trees along the 10 transects (SE = 4.7%). Individual trees varied greatly in size, so we used the estimates of canopy

Table 1. The number of individual birds using acacia, oak, scrub or other tree species for 45 species of birds with a minimum of eight individuals observed in oak and acacia combined, with mass and migratory status of each species.

Species	Mass (g)	Diet[1]	Status[2]	Acacia	Oak[3]	Scrub[4]	Tree
white-winged dove *Zenaida asiatica*	153	N	R	14	16	1	0
groove-billed ani *Crotophaga sulcirostris*	105	I	R	10	2	13	1
squirrel cuckoo *Piaya cayana*	108	I	R	7	6	0	2
cinnamon hummingbird *Amazilia rutila*	5	N	R	10	0	6	3
azure-crowned hummingbird *Amazilia cyanocephala*	4	N	R	6	4	3	3
elegant trogon *Trogon elegans*	67	O	R	6	1	0	0
acorn woodpecker *Melanerpes formicivorus*	80	O	R	2	8	0	12
golden-fronted woodpecker *Melanerpes aurifrons*	80	O	R	6	1	0	4
yellow-olive flycatcher *Tolmomyias sulphurescens*	14	I	R	10	1	1	3
least flycatcher *Empidonax minimus*	10	I	M	105	6	10	7
tropical pewee *Contopus cinereus*	12	I	R	4	4	2	0
greater pewee *Contopus pertinax*	27	I	R	7	16	0	7
dusky-capped flycatcher *Myiarchus tuberculifer*	20	I	R	30	17	2	2
sulphur-bellied flycatcher *Myiodynastes luteiventris*	40	O	SR	11	3	2	0
boat-billed flycatcher *Megarynchus pitangua*	73	O	R	4	16	0	7
western kingbird *Tyrannus verticalis*	40	O	R	34	23	0	8
masked tityra *Tityra semifasciata*	80	N	R	0	14	0	4
bushy-crested jay *Cyanocorax melanocyaneus*	110	O	R	39	38	1	2
white-throated magpie jay *Calocitta formosa*	210	O	R	4	4	0	4
white-lored gnatcatcher *Polioptila albiloris*	6	I	R	5	3	1	0
rufous-naped wren *Campylorhynchus rufinucha*	30	I	R	89	10	55	21
banded wren *Thryothorus pleurostictus*	18	I	R	13	2	4	1
eastern bluebird *Sialia sialis*	32	I	R	6	9	0	5
clay-colored robin *Turdus grayi*	74	O	R	30	21	8	14
plumbeous vireo *Vireo pinicolus*	17	I	R	27	24	0	2
yellow-throated vireo *Vireo flavifrons*	18	I	M	9	8	0	1
Philadelphia vireo *Vireo philadelphicus*	12	I	M	7	2	1	4
yellow-green vireo *Vireo flavoviridis*	18	O	SR	9	8	0	1
rufous-browed peppershrike *Cychlaris gujanensis*	12	I	M	24	15	1	1
Tennessee warbler *Vermivora peregrina*	10	O	M	142	42	7	42
tropical parula *Parula pitayumi*	7	I	R	14	11	0	6
yellow warbler *Dendroica petechia*	9	I	M	14	1	0	5
magnolia warbler *Dendroica magnolia*	9	I	M	26	0	0	1
black-throated green warbler *Dendroica virens*	9	I	M	111	58	1	10
black-and-white warbler *Mniotilta varia*	10	I	M	46	10	0	9
Wilson's warbler *Wilsonia pusilla*	7	I	M	56	18	45	8
chestnut-capped warbler *Basileuteris delattrii*	11	I	R	12	6	63	4
hepatic tanager *Piranga flava*	38	I	R	6	13	1	6
summer tanager *Piranga rubra*	28	O	M	5	5	0	1
lesser goldfinch *Carduelis psaltria*	9	N	R	25	9	0	12
blue grosbeak *Guiraca caerulea*	28	N	R	7	7	3	3
indigo bunting *Passerina cyanea*	15	N	M	12	0	48	3
Baltimore oriole *Icterus galbula*	34	O	M	5	7	0	0
melodious blackbird *Dives dives*	96	O	R	3	6	0	0

[1] I = insectivore; O = omnivore; N = non-insectivore (frugivore, granivore, or nectarivore).

[2] R = resident; M = temperate–tropical migrant; SR = summer resident (temperate–tropical migrant).

[3] Scrub refers to observations of birds in understorey shrubs, grasses, or forbs.

[4] Tree refers to observations of birds in tree species other than oak or acacia.

cover and foliage abundance to establish the relative availability of acacias and oaks.

Foliage profiles of both acacias and oaks indicated that there was generally no correlation, between tree height and the number of foliage intercepts, or the relationship was very weak. The correlations (broken down by sampling period) for acacia ranged from an r^2 of 0.0002 to an r^2 of 0.02 and those for oak ranged from 0.005 to 0.11. We therefore used the mean number of foliage intercepts as a constant weight factor for a species in a given season.

Foliage intercepts differed significantly by species (two-way ANOVA, $F_{2,270} = 324$, $P < 0.00001$) and period variation ($F_{1,270} = 183$, $P < 0.00001$), with a significant interaction between these variables ($F_{2,270} = 19.0$, $P < 0.001$). The number of foliage intercepts of acacia ranged from 0.32 (March), to 1.9 (December) and 2.7 (June). These values for oaks were 1.06, 3.9 and 3.7.

Table 2. Nutritional content and chemical content of the foliage of *Acacia pennatula* and *Quercus sapotifolia*[1].

Component	Sample size (acacia, oak)	Acacia	Oak
Protein (% dry wt)	16, 11	23.4 ± 0.7	12.39 ± 0.4**
Neutral detergent fibre (% dry wt)	16, 11	25.2 ± 0.6	45.6 ± 0.9**
Non-structural carbohydrates (% dry wt)	16, 11	39.1 ± 0.7	33.6 ± 0.1*
Fat (% dry wt)	16, 11	5.2 ± 0.28	3.3 ± 0.2*
Ash (% dry wt)	16, 11	5.9 ± 0.35	5.1 ± 0.4
Total phenolics (mg g^{-1})			
(Dec)	4, 5	182.9 ± 92.0	220.7 ± 8.4**
(June)	7, 7	63.2 ± 4.8	108.7 ± 15.2*
Condensed tannins (mg g^{-1})			
(Dec)	4, 5	55.5 ± 3.9	152.9 ± 12.8*
(June)	7, 7	80.8 ± 9.2	58.1 ± 24.1
Alkaloids	5, 5	−	−
Cyanogenic glycosides	5, 5	++	−
Calcium (% dry wt)	5, 5	0.94 ± 0.06	0.64 ± 0.06*
Phosphorus (% dry wt)	5, 5	0.18 ± 0.02	0.13 ± 0.01*
Magnesium (% dry wt)	5, 5	0.20 ± 0.01	0.21 ± 0.02
Potassium (% dry wt)	5, 5	1.21 ± 0.09	0.89 ± 0.06
Sodium (% dry wt)	5, 5	0.01 ± 0.00	0.003 ± 0.02*
Molybdenum (ppm)	5, 5	1.0 ± 0.00	1.0 ± 0.00
Iron (ppm)	5, 5	113.6 ± 23.7	67.8 ± 12.9
Zinc (ppm)	5, 5	16.0 ± 0.9	14.4 ± 1.6
Copper (ppm)	5, 5	5.0 ± 0.4	7.4 ± 0.6*
Manganese (ppm)	5, 5	31.6 ± 3.5	186.4 ± 14.7*

[1]*$P < 0.05$, **$P < 0.01$.

The resulting ratios of oak: acacia foliage intercepts range from 1.37:1 for June, to 2.05:1 for December and 3.31:1 for March. We use these values to obtain a weighting factor for the number of foliage intersections per point. Combining average weighting factor of 2.21 oak intercepts per acacia intercept with the estimate of canopy cover, we estimate the availability of acacia foliage to be an average of 17% ($2 \pm$ SE) of the combined acacia and oak foliage for the 10 transects. In order to determine whether species prefer acacia or oak, we compared the relative abundance of birds with the availability of oaks and acacia (Figure 1). Using relative foliage abundance as the most relevant measure, both resident and migrant birds were found in acacia five to six times more frequently than expected (Mann–Whitney U, $P < 0.001$).

Arthropod abundance

We collected 3800 arthropods in the 160 samples. The number of arthropods per 100 g of foliage was far greater for acacia than for oak. The overall means were 32.7 vs. 11.6, respectively (Figure 2a). When tested in a two-way ANOVA with time of day as a covariate, both species ($F_{1,150} = 87.4$) and sampling period ($F_{3,150} = 9.9$) were highly significant ($P < 0.0001$) and the interaction between these variables was significant as well ($F_{3,150} = 2, 97, P < 0.05$). Time of day was not a significant covariate. The number of large arthropods (> 1.0 cm) was significantly greater for acacia than oak (0.8 vs. 0.5 per 100 g, $F_{1,150} = 7.55$, $P = 0.006$; Figure 2b)

although the relative difference was much smaller than for total arthropods. Biomass was also much greater for acacia than oak (1.1 vs. 0.33 g; Figure 2c) although the difference was only significant at $P < 0.10$ based on an ANOVA. The significantly higher abundance of arthropods in acacia was found across the major taxonomic orders with the exception of Orthoptera (ANOVA tree type vs. season, Figure 3). In the latter group there were no significant differences between acacia and oak.

The breeding currency hypothesis predicts that migrants will favour habitats or tree species that support a smaller relative abundance of large arthropods in the breeding season to the abundance of total arthropods in the non-breeding season. For the total collection, the ratio of large (> 10 mm) to total arthropods was 0.011 for acacia and 0.026 for oak. We calculated the ratios assuming that June is during the breeding season for most insectivorous birds, but that the other sampling periods are not. The ratios are similar to the total ratios: 0.012 and 0.034. If we examine the ratio of biomass of large arthropods to biomass of total arthropods we find that for the breeding–non-breeding season comparison the ratio is 0.45 for acacia and 0.93 for oak. These data suggest that the ratio of large arthropods available for breeding efforts to the number of arthropods in the non-breeding season is substantially higher in oak than acacia.

Chemical composition of acacia and oak foliage

Acacia foliage generally contained higher levels of nutrients important to herbivorous animals than oak
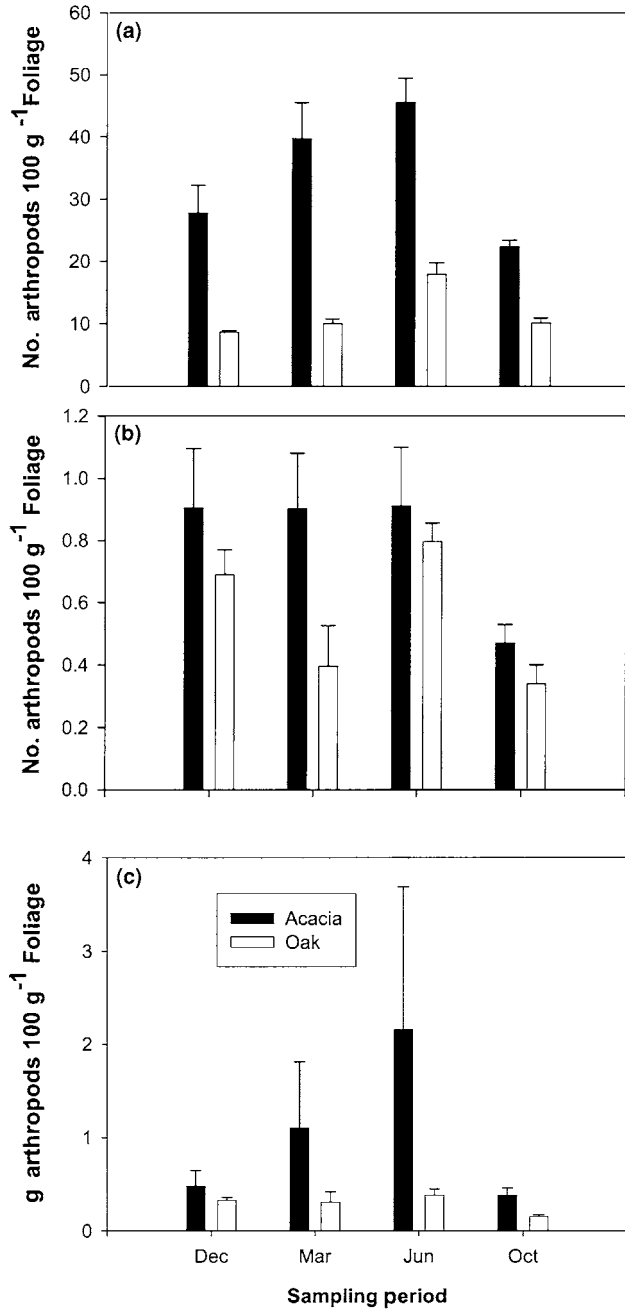
Figure 2. The abundance of arthropods (per 100 g foliage) in oak and acacia samples during the four sampling periods: (a) mean number of arthropods per sample; (b) mean number of large (> 1 cm) arthropods; and (c) mean estimated biomass. Error bars indicate 1 SE.
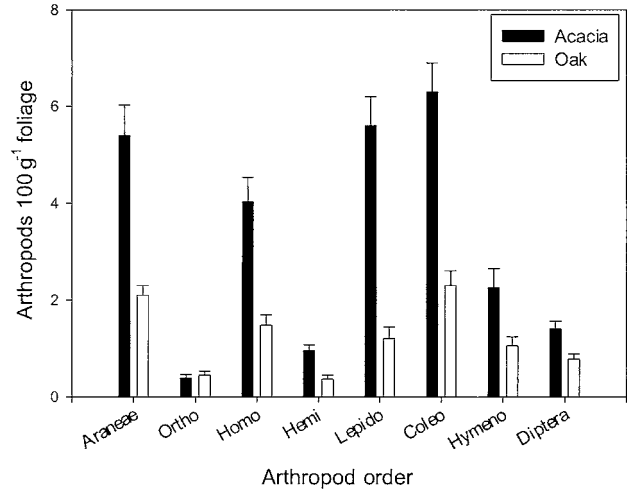

Figure 3. The mean number ($\pm$ SE) of arthropods in oak and acacia plotted by major orders. Abbreviations for taxa are: Ortho = Orthoptera; Homo = Homoptera; Hemi = Hemiptera; Lepido = Lepidoptera; Coleo = Coleoptera; and Hymeno = Hymenoptera.

Oak showed almost three times the level of condensed tannins as acacia in the old foliage collected in December, while displaying no difference in the recently flushed foliage collected in June (Table 2). In the June foliage, total phenolics were significantly higher in oak than in acacia, but the higher level of total phenolics in the December sample was not significant. However, the lack of significance is a result of a single, very high value in the small acacia sample. With this one value removed, the difference would be highly significant.

DISCUSSION

Foliage palatability hypothesis

As in the Chiapas study (Greenberg *et al.* 1997), birds are both absolutely more common in acacias and, more importantly, relatively more common when compared with the relative abundance of acacia in the mixed oak–acacia savanna. Almost all of the 44 species analysed occurred in acacia in greater relative abundance than acacia occurs. Most of the species (38) analysed in this study were insectivorous or insect-eating omnivores. Neither oaks nor acacias produce fruits and flowers used by birds, although some warblers were observed feeding in acacia flowers on small arthropods. Therefore, we have focused considerable attention on the relative abundance and estimated biomass of arthropods in the two trees. By all measures, arthropods are consistently more abundant in acacia.

Foliage quality appears to play an important role in the higher abundance of arthropods in acacia. In all ways measured, acacia foliage contains more usable nutrients

foliage did (Table 2). Crude protein averaged 25% of dry weight, which was over twice as high as the protein content of oak foliage. Non-structural carbohydrates (sugars and starches) also occurred at higher levels, as did most major minerals. We tested both young and old leaves of each species and found little difference in the nutritional composition by age, and therefore we have pooled these data.

than oak leaves. In addition, acacia foliage is probably far more palatable than oak foliage. This was not measured directly, but inferred from chemical composition. Owen-Smith & Cooper (1987) and Cooper *et al.* (1988) reported that for woody plants of African savanna, the best predictor of palatability was the difference between the protein content and $1/2 \times$ (condensed tannins). This is roughly five times higher in acacia than oak. The difference between oaks and acacias was most marked in the early dry season sample, when oaks showed a significant seasonal increase in tannins – a phenomenon that has been established for temperate oaks as well (Murakami 1998). The higher structural carbohydrate content is indicative of higher leaf toughness in oaks – also an important aspect of defence against herbivory in mature foliage (Coley & Barone 1996). We found two modes of anti-herbivore defence in acacia not found in oaks: the presence (particularly in young foliage) of lignified thorns and the presence of cyanogenic compounds. Thorns are a specialized defence against herbivory and damage caused by vertebrates.

Why does acacia have more palatable foliage?

The greater nutrition is paired with general lower quantitative chemical defences, particularly the higher concentration of condensed tannins and structural carbohydrates (neutral detergent fibre). The presence of lower levels of quantitative chemical defences may fit well with the theory that fast-growing pioneer plants show reduced levels of these types of defences and higher levels of qualitative defences than slow-growing shade-tolerant species (Coley *et al.* 1985). The higher protein content itself is associated with faster growth rates in plants (Cooper *et al.* 1988). *Acacia pennatula* regenerates only under full sun conditions, whereas oaks regenerate in the shade. Although we do not have growth data for the local oak species, Stewart & Dunsdon (1994) found that *Acacia pennatula* has very high rates of biomass accumulation compared with a selection of 25 tropical dry-zone species of trees.

The resource availability hypothesis for variation in chemical defences (Coley *et al.* 1985), however, does not consider the potential trade-off between thorn-based versus chemical defences. The defence trade-off hypothesis (Greenberg *et al.* 1997) posits that acacia and certain other thorny plants are dependent upon growing in conditions of high grazer and browser densities. In order to do this with minimal animal-caused damage, a great investment is made in defences that discourage the activity of vertebrate herbivores (Cooper & Owen-Smith 1986) at the expense of defences that work specifically on arthropod herbivores. This results in a plant well defended against livestock, but poorly protected from

insect herbivory. In support of this general hypothesis, Cooper *et al.* (1988) found a strong relationship between the presence of thorns and foliage palatability in African savanna shrubs and trees.

In light of this hypothesis, it is interesting to note that cyanogenic compounds are also ineffective against many invertebrate herbivores (Jones 1988, Rehr *et al.* 1974). The presence of these defences in acacia supports the hypothesis that the anti-herbivory defences of acacia are focused more on vertebrates than invertebrates. However, Rehr *et al.* (1974) suggested that some unknown class of compound might be responsible for defence against caterpillar herbivory in the non-ant acacias that they studied.

Migrant use of acacia and the breeding currency hypothesis

Most insectivorous migratory species are small (Greenberg *et al.* 1997) and smaller birds tend to forage on smaller arthropods (Thiollay 1988). Furthermore, migratory species do not require large arthropods for reproduction during their stay in the tropics (Greenberg 1995). The size distribution of arthropods over the entire annual cycle in different habitats may be particularly important in determining the relative abundance of migrants and residents (Greenberg 1995, Johnson 2000) by influencing resident abundance. The arthropod assemblage of acacias, compared with that of oaks, is disproportionately represented by small arthropods; in particular, the ratio of large arthropod biomass during the breeding season to total arthropod biomass is much lower in acacia than in oak. These observations are consistent with the predictions of the breeding currency hypothesis.

Habitat complementation

The survey data were gathered in the morning hours, because we assume birds forage most actively at this time. Attempts to conduct similar surveys in the afternoon yielded too few data for us to continue. However, some observations suggest to us that birds may move from acacias to oaks during the hottest hours of the day. This would suggest that the two trees provide complementary resources (food and protection) (Dunning *et al.* 1992). Further work using radio tracking would provide insight into the overall pattern of use of the two types of trees.

CONCLUSIONS

We found that in a simple subtropical savanna system, insectivorous birds show marked preference for foraging

in acacias as opposed to oaks. This preference is a response to the higher biomass of arthropods and much higher abundance of small arthropods. This higher abundance is probably related to the higher nutritional value and lower levels of quantitative chemical defences. Acacias appear to be defended primarily by mechanical (spine) and qualitative chemical defence (cyanogenic compounds). The higher proportion of migratory birds using acacias is consistent with the breeding currency hypothesis, which holds that the carrying capacity of migrants in a habitat is a function of the ratio of large arthropods to total arthropod biomass present in the non-breeding season.

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