

# ACACIA, CATTLE AND MIGRATORY BIRDS IN SOUTHEASTERN MEXICO

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(Accepted 11 July 1996)

## Abstract

*Acacia pennatula* groves in mid-elevation valleys of southern Mexico supported both the highest density and diversity of migratory birds compared to other habitats in the region. In addition, we found the highest numbers for over half of the common migratory species. Despite the high degree of leaf loss during the late winter, acacia groves do not experience greater declines in insectivorous migratory bird populations than other local habitats. Color-marked individuals of canopy species had a strong tendency to remain resident within a single acacia grove throughout the winter. Management of native acacias on subtropical rangelands for wood products, fodder, and soil improvement would probably directly and indirectly benefit migratory song bird populations. Neotropical acacia woodland is primarily associated with grazing land for livestock which might discourage some from considering acacia management a viable option for migratory bird conservation. However, acacias were probably widespread in recent geologic time under drier conditions with heavy browsing and seed dispersal by a now extinct megafauna. Two observations suggest a foraging advantage for acacia use: the higher density of migratory birds in acacia is a result of higher numbers of canopy insectivores; and acacias are selected by migrants when they occur in mixed habitat. We hypothesize that plant investment in mechanical defenses (thorns) reduces energy available for chemical defenses effective against insect herbivores.  
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**Keywords:** silvopastoral systems, paleoecology, tropical bird communities, Huizachales and agroforestry.

## INTRODUCTION

Cattle pasture is the most rapidly expanding habitat in the lowlands and mid-elevation areas of Mesoamerica (Gomez-Pompa *et al.*, 1993). If projected patterns of land use continue, we can expect that most of the Caribbean slope of Mesoamerica will be in active or regenerating cattle pasture by the turn of the century. The rapid conversion from forest to anthropogenic savanna has been implicated in the decline of a number

of forest-dependent migratory birds (Askins *et al.*, 1990). However, the new tropical landscape is usually a mosaic of grassland, savanna, ribbons of riparian vegetation and small patches of woods. The wooded habitats, in particular, can support an abundance of migratory birds (Powell *et al.*, 1992; Warkentin *et al.*, 1995). One possible strategy for increasing habitat for migratory birds is the promotion of silvopastoral systems which integrate tree management with cattle production on grazing lands.

During several years of censusing birds on the Caribbean slope of Chiapas, we discovered that managed patches of *Acacia pennatula* (Schlecht & Cham.) Benth support particularly high densities of migratory birds. In this paper we provide quantitative data on bird abundance in acacia woodlots. We then examine factors that account for their heavy use by migratory birds, and evaluate their distribution and abundance in the current landscape and during recent geological history.

## THE CURRENT DISTRIBUTION OF ACACIA GROVES

*Acacia pennatula* is common in disturbed sites from 500–2500 m throughout Mexico, Central America, and Northern South America (Siegler & Ebinger, 1988). It can grow to 12 m in height with a typical savanna tree physiognomy, i.e. spreading, flat-topped crown. Large (2–4 cm), red thorns are found among the foliage on shrubs and along the lowest 3 m of the trunks of trees, with small thorns distributed sparsely on the branches of most trees. Foliage becomes increasingly sparse during the dry season (January–April) and flushes out again in May. Trees flower in May and fruit ripens in the following dry season (February–April). Pods are 50–160 mm long by 30 mm wide and 7–12 mm thick. Immature fruits (August–February) are green and filled with a moist pulp, drying to the consistency of a dog biscuit and changing to a purplish brown hue upon ripening. The pods are indehiscent and the 6–10 hard seeds remain imbedded unless released through mastication by large animals. The seeds are commonly attacked by bruchid beetles.

*Acacia pennatula* grows commonly in single-species stands known throughout much of Mexico (Rzedowski,

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1962) as "Huizachales" and locally in Chiapas as "Quebrachales" (Spanish) or "K'an chichales" (Tzeltal). Huizachales are a typical successional habitat in dry tropical forest and pine-oak woodlands below 1500 m elevation (Rzedowski, 1962; Chazaro, 1977). In general, acacias are spreading in the New World in association with grazing (Chazaro, 1977; Janzen, 1986). Acacias and the ecologically similar mesquites are often considered pests, requiring control because their thorny vegetation harms cattle (Chazaro, 1977). However, both acacias and mesquites provide valuable products as well, including wood, fodder for livestock, fragrance for perfumes, gums and tanning agents (Gomez *et al.*, 1970), and these legumes are sometimes integrated in agroforestry or silvopastoral systems (mostly in Africa; Gray, 1970; National Research Council, 1979; Nair, 1990).

Acacia woods are managed in the Ocosingo Valley study area as part of the overall intensive management of pastures. The increase in productivity of cattle ranching on the rich valley soils has resulted primarily from shifting to more productive breeds of cattle, increasing production of cutting grass, increasing the rotation of pastures, and switching (partially) to dairy cattle. These changes, along with increasing the stock density, are characteristic of tropical areas with better soils and higher human population densities (Jarvis, 1986). As is common in other regions of Latin America, increase in the value of beef and milk products leads to the tendency to enclose pastures, and the traditional living fences used to demark property lines are replaced by dead wood and barbed wire (Sauer, 1979). The wood for this large number of fence posts (approximately 2 per m) must be replaced every 3–4 years and requires access to timber. Ranches in Ocosingo Valley use acacia woodlots to supply these materials.

In addition, ranchers move cattle into woodlots during the period of fruit drop and use the pods as a dry-season feed. Acacia pods contain significantly more protein than feed corn on a dry weight basis (Chazaro, 1977). Furthermore, based on information from the Escuela Agropecuaria de Ocosingo, we estimate production at approximately 4–6 metric tons per ha. This is similar to the mass of feed corn produced per ha on the same ranches. However, acacia seed pods are used primarily in a *de facto* manner and there is little evidence of wide-scale marketing or storage for use during other seasons.

With no input, pastures in the Ocosingo Valley regenerate into a mixed scrub with a high proportion of spiny acacias. Cattle avoid eating young acacia with their conspicuous red spines and concentrate on other, less noxious plants, thus encouraging the dominance of spiny acacias in arid or semiarid parts of southern Mexico (Chazaro, 1977; Greenberg, 1992; I. Olmsted & A. Lopez-Ornat, pers. comm.). In both Africa and the New World, mature plants of certain species of acacia (including *A. pennatula*) deposit large numbers of seed pods under their canopy which are only removed in significant numbers by livestock (Gutierrez and

Armesto, 1981). Normally, laborers remove acacia seedlings from pastures to promote the growth of grass for grazing. The silvopastoral system found in the Ocosingo Valley has been practiced for at least 15–20 years, and appears to have been developed by local farmers in conjunction with complete loss of mature forest cover, as well as an increase in transportation contact with the rest of Chiapas and Mexico resulting in more accessible markets and intensification of livestock production. However, such a system was probably derived from local indigenous practices. Leguminous trees traditionally have been selected for by Mayans (Gomez-Pompa *et al.*, 1993)—including the Tzeltal Maya (Nigh, 1976) of eastern Chiapas for centuries, and the system of selective weeding is widespread for other types of mimosoid legumes in Mexico (Wilken, 1987).

## STUDY SITES

Located at the confluence of the Jatate and Virgen Rivers, the Ocosingo Valley (900–1000 m above mean sea level) is one of the largest in the eastern highlands of Chiapas, Mexico. The valley floor consists primarily of cattle pastures held in large (100–400 ha) latifundios. Ejidos (community-managed lands) are situated in the surrounding hills which are covered by degraded pine-oak woodland and pine or oak savanna. The three major arboreal habitats on the valley floor are gallery woods, rustic coffee plantation under broad-leaved trees, and acacia woodlot (Fig. 1).

Coffee plantations are found primarily along arroyos, whereas acacia woodlots are often found on hilltops and other well-drained sites. Acacia woodlots range from 0.2 to 20 ha ( $\bar{x} = 3.9 \pm 0.9$ ,  $n = 30$ ), with average tree densities of  $174 \pm 8.7$  per ha. Canopy height ranged from 5 to 11 m with a median of 8. The understory (median = 1 m, 0.5–4 m) varies from a light herbaceous or grassy understory to a shrubby understory with vines growing into the canopy. Acacias also grow at lower densities ( $100 \pm 4.3$  per ha,  $n = 8$ ) with pasture grass as understory—a habitat we call acacia savanna. We usually found old relict pines or oaks growing among the acacias which suggests that the original vegetation was pine-oak woodland. Acacia is also found mixed among oaks, in a belt of woodland and savanna that occupies the bases of the hills surrounding the valley floor.

## METHODS

### Bird surveys

Birds were censused using two complementary techniques: fixed-radius point counts designed to provide broad coverage of numerous sites; and repeatedly censused, fixed-width transects (Greenberg, 1992) to determine seasonality of habitat use. Fixed distances were used to assure homogeneity of habitat surveyed

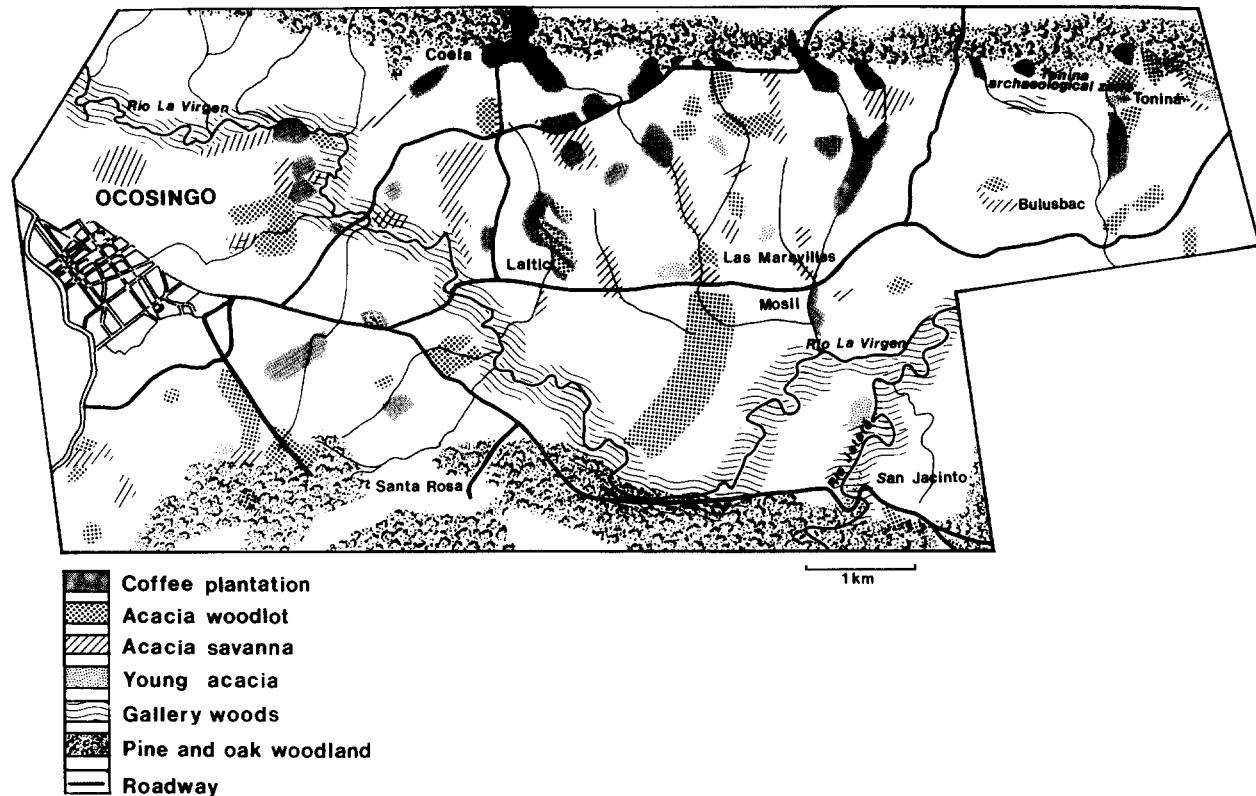


Fig. 1. Map of the Ocosingo Valley study area indicating the distribution of acacia groves and other managed forest patches.

(Hutto *et al.*, 1986; Petit *et al.*, 1995) since the surveys were conducted at characteristically patchy habitats. Point counts were conducted from January through March 1993 for 10 min each during the period 0645–1000 h. Points were at least 25 m from the edge of the woodlots and 200 m from the nearest point. All birds within 25 m were recorded. For points in acacia habitat, we also recorded the size of the patch in which the point was located (for 37 different patches), the distance from the edge, estimated canopy height, estimated understory height, and number of trees within the count circle.

Point counts were conducted from January through March 1991–1993 in the following major habitats (lowland sites < 500 m, mid-elevation 900–1500 m and high-elevation > 2000 m): lowland tropical forest, lowland tropical second growth, lowland tropical pasture, mid-elevation pine–oak woodland, mid-elevation pine–oak *Liquidambar*, montane forest, mid-elevation pine forest, mid-elevation farm and garden, mid-elevation second growth, mid-elevation coffee plantation (both under diverse forest canopy and under a monoculture of planted trees, i.e. *Inga*), high-elevation farm, high-elevation pine–oak woodland, high-elevation second growth, high-elevation pine forest.

Transects were 1 km long by 40 m wide and flagged each 50 m. Each 1 km transect was surveyed weekly during the winters of 1992–93 and 1993–94 from October to late March ( $n = 18$  weeks). Using these data we can examine seasonal changes in the detection and presumably the abundance of migrants in different

habitats. Data presented here were collected as a more general assessment of migratory bird distribution in Southern Mexico. The detailed descriptions of the transect habitats are presented in Greenberg, in prep.). The following is a brief description of the habitats surveyed: mid-elevation pine–oak woodland (two), mid-elevation riparian trees in pasture, mid-elevation coffee plantation (under forest trees), mid-elevation scrubby second growth, mid-elevation acacia woodland, mid-elevation broad-leaved forest, high-elevation pine, high-elevation pine–oak, high-elevation second growth, and high-elevation farms. During the dry season, foliage height profiles were taken at 10 m intervals along each transect. From these we computed an index of foliage volume (total foliage contacts per point) to determine the relationship of bird abundance to total foliage in a habitat (see Ulfstrand & Alerstam, 1971).

The transect data from our focal acacia grove allow us to examine the spatial pattern of bird distribution from shrubby edge vegetation to the grove interior. We categorize each of the 20 units as outer shrubbery, edge (within 50 m of edge), or interior, and compare the mean number of sightings per unit of migratory and resident species.

#### Banding and resighting of individual migrants

To determine their persistence through the winter, we banded 223 individuals with unique combinations of two plastic color bands. These birds were captured in mist nets during two 5-day banding periods (23–28

October, 21–26 December) on a 5 ha grid in our focal woodlot. The grid was surveyed on a regular basis and the location of each color-marked bird was recorded the first time it was sighted in a given survey. In addition, areas of gallery forest within 1 km of the gallery woods were flagged and searched for marked birds. Resighting continued during the period 15 February–15 April. We examined persistence in two ways. Firstly, we calculated the number of color-marked birds resighted in the late February–April period (Period II) divided by the total number color banded of that species. Secondly, we divided the total number resighted in period II by the number of birds for which we had at least one resight or recapture. The latter measure was employed because the banding took place early enough in the winter that the presence of transients was likely.

#### Use of acacia and oak in mixed woodlands

During the period 26–30 December, one of us (R.S.G.) conducted surveys to determine relative use of acacias and oaks in mixed oak–acacia woodlands. The observer walked approximately 5 km of transects through the

mixed woodland and recorded the type of tree in which each bird was first observed, for all individuals detected within 20 m of the transect. At the same time, the observer kept a tally of the number of individual oaks and acacias greater than 5 cm dbh within the 40 m wide transect. The proportion of sightings in acacia was compared to the relative abundance of acacia with a chi-squared test. (An estimate of crown area or volume might have been the more appropriate comparison. However, the outbreak of civil unrest in the region on 1 January 1994 prevented us from further refining the sampling.)

## RESULTS

#### Composition and abundance of acacia grove bird assemblage

The most common species of birds in acacia groves were migratory species (9/10 and 15/20 most commonly detected species, Table 1). Points in acacia patches had an average of 9.0 ( $\pm 0.5$  SE) migrants within 25 m, and

Table 1. The mean number of individuals per point of common species<sup>a</sup> acacia woodland and savanna ( $n=97$  counts)

	Species	Status <sup>b</sup>	Mean no./pt
Magnolia warbler	<i>Dendroica magnolia</i>	M	1.6
Black-throated green warbler	<i>Dendroica virens</i>	M	1.01
Least flycatcher	<i>Empidonax minimus</i>	M	0.77
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	M	0.69
MacGillivray's warbler	<i>Orporornis tolmiei</i>	M	0.51
American redstart	<i>Setophaga ruticilla</i>	M	0.41
Ovenbird	<i>Seiurus aurocapillus</i>	M	0.35
Gray catbird	<i>Dumetella carolenensis</i>	M	0.29
Yellow-breasted chat	<i>Icteria virens</i>	M	0.23
Plain wren	<i>Thryothorus modestus</i>	R	0.22
Yellow warbler	<i>Dendroica petechia</i>	M	0.22
Wilson's warbler	<i>Wilsonia pusilla</i>	M	0.19
Common yellowthroat	<i>Geothlypis trichas</i>	M	0.19
Yellow-throated euphonia	<i>Euphonia hirundinacea</i>	R	0.19
Grayish saltator	<i>Saltator coerulescens</i>	R	0.19
White-eyed vireo	<i>Vireo griseus</i>	M	0.16
Lesser goldfinch	<i>Carduelis psaltria</i>	R	0.14
Indigo bunting	<i>Passerina cyanea</i>	M	0.14
Rufous-tailed hummingbird	<i>Amazilia tzacatl</i>	R	0.14
Red-throated ant tanager	<i>Habia fuscicauda</i>	R	0.14
Solitary vireo	<i>Vireo solitarius</i>	M <sup>c</sup>	0.14
Yellow-olive flycatcher	<i>Tolmomyias sulphureus</i>	R	0.11
Nashville warbler	<i>Vermivora ruficapilla</i>	M	0.11
Summer tanager	<i>Piranga rubra</i>	M	0.11
Social flycatcher	<i>Myiozetetes similis</i>	R	0.09
Brown-crested flycatcher	<i>Myiarchus tyrannulus</i>	R	0.09
Rufous-breasted spinetail	<i>Synallaxis erythrorhox</i>	R	0.09
Brown jay	<i>Cyanocorax morio</i>	R	0.07
Melodius blackbird	<i>Dives dives</i>	R	0.07
Fork-tailed emerald	<i>Chlorostilbon canivetii</i>	R	0.06
Common ground dove	<i>Columbina passerina</i>	R	0.06
Boat-billed flycatcher	<i>Megarhynchus pitangua</i>	R	0.06
Gray-crowned yellowthroat	<i>Geothlypis poliocephala</i>	R	0.05
Barred antshrike	<i>Thamnophilus doliatus</i>	R	0.05
Rusty sparrow	<i>Aimophila rufescens</i>	R	0.05
Rose-throated becard	<i>Pachyrhamphus aglaiae</i>	R	0.05

<sup>a</sup>Frequency > 0.05 individuals per point.

<sup>b</sup>M, migratory; R, resident.

<sup>c</sup>Species breed and winter in Chiapas. Based on absence of summer surveys we classify them as migrants.

**Table 2.** The number of individual and species of migrants per point and overall species richness in acacia groves and other habitats in Chiapas based on point counts

Habitat	<i>n</i> <sup>a</sup>	Common Migrant Species <sup>b</sup>	Migrant individuals/ point	Total individuals/ point
Acacia woodlot	73	18	9.0	11.8
Acacia savanna	21	11	6.0	8.2
Low elevation pasture	70	3	0.7	4.1
Low elevation, 2nd growth	100	6	1.3	6.2
Low elevation gallery	187	13	4.7	12.1
Low elevation forest	102	5	1.2	10.0
Mid-elevation pasture	70	5	0.7	3.2
Mid-elevation 2nd growth	100	4	2.1	3.6
Mid-elevation milpa	70	8	1.2	4.4
Shade coffee <sup>c</sup>	212	14	4.9	12.3
Mid-elevation gallery	52	13	5.1	7.7
Mid-elevation pine-oak liquidambar	100	3	1.3	2.6
Mid-elevation pine-oak	82	7	3.2	13.2
Mid-elevation pine	70	3	1.1	3.0
High elevation milpa	70	3	1.1	2.6
High elevation, 2nd growth	100	2	1.3	2.5
High elevation pine	70	4	1.8	4.1
High elevation pine-oak	50	4	1.3	2.4

<sup>a</sup>*n* is the number of points.

<sup>b</sup>Includes only those species with mean > 0.10 per point.

<sup>c</sup>Rustic and planted-canopy plantations are pooled.

migrants comprised 83% of the total birds recorded—a higher percentage than in any other habitat in the region. Migrant abundance was far greater than most other habitats we censused in Chiapas (Table 2), including other: good habitats for migratory birds shade coffee plantation ( $4.9 \pm 0.3$ ) and gallery woods ( $5.1 \pm 0.3$ ). Even acacia savanna, which has well-spaced trees and grassy pasture understory, had 6.0 ( $\pm 0.4$ ) migrants per point. In contrast, resident birds were rare in acacia woodland, averaging only 2.8 per point, which was among the lowest for all habitats surveyed (derived from Table 2).

### Migrant diversity

We focused on migrant species that were present in moderate to high numbers. Comparing the number of migrants that were found at densities higher than 0.10/point, acacia had the highest number of species (18) for all habitats sampled (Table 2). This value is only approached by shade coffee (14) and gallery forest (13).

### Key species

The common birds of acacia woodlots are migratory species, mainly wood-warblers (including *Dendroica*, *Setophaga*, *Orporornis*, *Seiurus*, *Wilsonia*, *Geothlypis*, see Table 1). Resident species are uncommon and include, primarily, sparrows and finches, as well as tyrant flycatchers. A number of migrant species achieved their highest abundances in the acacia habitat of all habitats we surveyed in Chiapas. These include magnolia warbler *Dendroica magnolia*, ovenbird *Seiurus aurocapillus*, black-and-white warbler *Mniotilta varia*, least flycatcher *Empidonax minimus*, black-throated green

warbler *Dendroica virens*, summer tanager *Piranga rubra*, Nashville warbler *Vermivora ruficapilla*, blue-gray gnatcatcher *Poliophtila caerulea*, yellow-breasted chat *Icteria virens*, white-eyed vireo *Vireo griseus*, solitary vireo *V. solitarius*, and MacGillivray's warbler *Oporornis' tolmiei* (Table 3). These 12 species comprise over half of the 23 species of common migrants in the region (those that occurred at abundances of > 0.10 individuals per point in at least one habitat). The magnolia warbler occurs in strikingly high numbers. Using the simplifying assumption that bird movement into and out of point circles is small over the 10-min count, we estimate a density of 8.7/ha. The strip transect results, which are affected less by bird movement, provide a density estimate of approximately 7/ha.

To test to see if the abundance is significantly higher in acacia for the above-listed species than in other habitats, we have taken the statistical approach of comparing the difference in abundance of migratory bird species in the habitat with the highest abundance with the habitats that had the second and third highest mean abundance, using orthogonal contrasts to protect the 0.05 alpha level (Wilkinson, 1990). In eight of 12 cases, acacia had higher numbers of individuals per point than the next runner-up habitat. Only for Nashville warbler, solitary vireo and summer tanager was the acacia abundance not significantly greater than the third ranked habitat.

### Foraging guild

Canopy insectivores, primarily foliage-gleaners, comprise the largest increment of increased migrant abundance in acacia over other mid-elevation forest habitats

**Table 3.** Mean number of individuals per point for the three habitats in eastern Chiapas (of the 18 surveyed) with highest values for selected migratory bird species that are particularly common in acacia woodlots

Species	First	Habitat <sup>a</sup> rank second	Third
Least flycatcher	ACA, 0.80	LEG, 0.36 <sup>b</sup>	MEG, 0.32 <sup>b</sup>
Blue-gray gnatcatcher	ACA, 0.85	COF, 0.52 <sup>b</sup>	MEG, 0.33 <sup>b</sup>
Solitary vireo	ACA, 0.18	COF, 0.18	MEPI, 0.07
White-eyed vireo	ACA, 0.16	LES, 0.11	LEG, 0.08
Black-and-white warbler	ACA, 0.78	COF, 0.24 <sup>b</sup>	MEG, 0.24 <sup>b</sup>
Nashville warbler	ACA, 0.12	MEP, 0.10	COF, 0.09
Black-throated green warbler	ACA, 1.05	COF, 0.99	MEG, 0.47
Magnolia warbler	ACA, 1.76	MEG, 0.88 <sup>b</sup>	COF, 0.69 <sup>b</sup>
MacGillivray's warbler	ACA, 0.60	MES, 0.28 <sup>b</sup>	MEA, 0.19 <sup>b</sup>
American redstart	LEG, 0.79	MEG, 0.45 <sup>b</sup>	ACA, 0.44 <sup>b</sup>
Ovenbird	ACA, 0.43	COF, 0.12 <sup>b</sup>	MEG, 0.06 <sup>b</sup>
Yellow-breasted chat	ACA, 0.32	LEG, 0.19 <sup>b</sup>	LES, 0.09 <sup>b</sup>
Summer tanager	ACA, 0.15	LEG, 0.12	COF, 0.08

<sup>a</sup>See Methods for complete listing of habitats: ACA, Acacia grove; LEG, Low-elevation gallery; LES, Low-elevation scrub; MEG, Mid-elevation gallery; MES, Mid-elevation scrub; MEA, Mid-elevation agriculture; MEPO, Mid-elevation pine-oak; MEP, Mid-elevation pine.

<sup>b</sup>Indicates habitat where mean number of individuals is significantly less ( $p < 0.05$ ) than acacia based on an *a posteriori* orthogonal contrast.

(Fig. 2). Canopy insectivores comprise 75 and 86% of the migrants in acacia grove and acacia savanna, and approximately 60% of the migrants in other habitats.

#### Sex biases

Two dimorphic species showed sex ratios in acacia that deviated strongly from 50:50. Seventy-six percent of the

yellow warblers *Dendroica petechia*,  $n = 23$ ,  $p < 0.05$  Binomial test) and 73% of the American redstarts ( $n = 27$ ,  $p < 0.05$ ) were females. When compared to other more mesic habitats (Table 4), five species showed significantly higher proportions of females (Chi-square Contingency Test). Only black-and-white warblers failed to show significant inter-habitat heterogeneity in sex ratio.

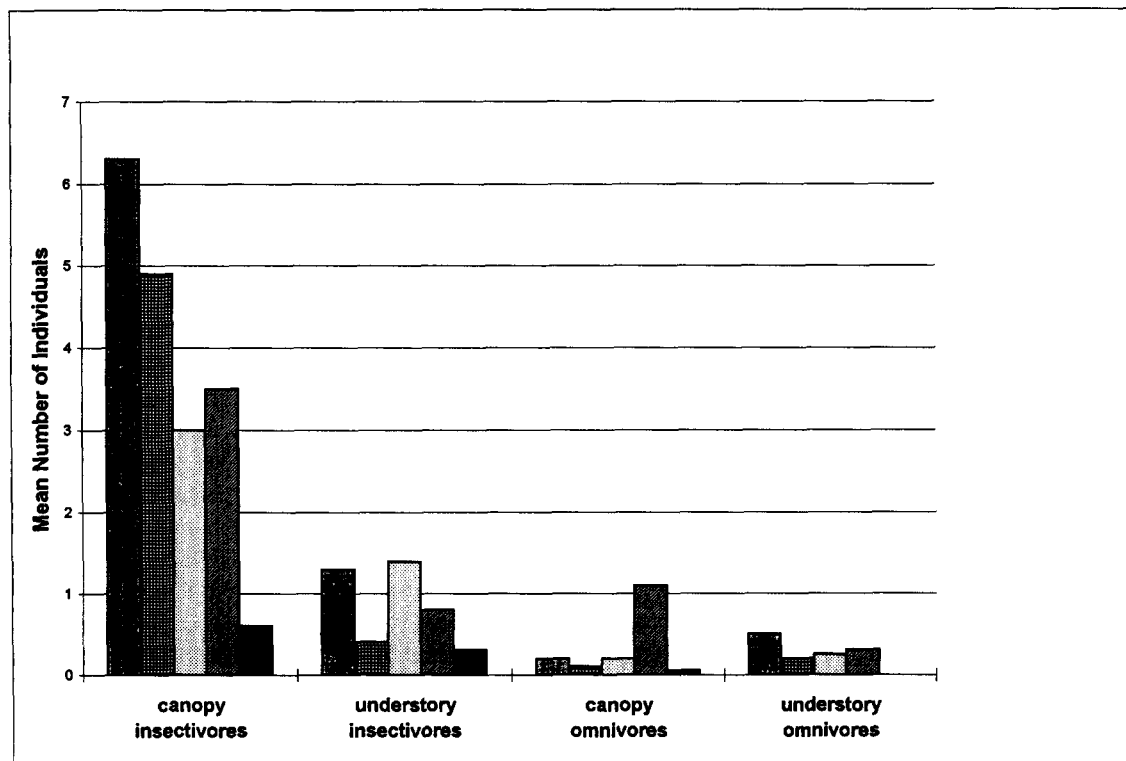
**Fig. 2.** The number of individual migratory birds per point in four major guilds in wooded habitats of the Ocosingo Valley, Mexico. ■, Acacia grove; ■, Acacia savanna; □, Gallery forest; ■, Shade coffee; ■, Pine-oak woodland.

Table 4. The sex ratio of dimorphic migratory wood warblers detected on point counts in Ocosingo Valley<sup>a</sup>

Species	Acacia woodlot	Gallery forest	Shade coffee
Magnolia warbler	46 (104)	60 (35)	75 (64)
Yellow warbler	8 (17)	83 (12)	—
Black-throated green warbler	46 (52)	66 (15)	78 (104)
Black-and-white warbler	69 (55)	50 (80)	60 (35)
American redstart	35 (23)	53 (15)	61 (23)

<sup>a</sup>Numbers are percentage males with total number of individuals observed per habitat in parentheses.

#### Microhabitat features and migrant abundance

Using a step-wise multiple regression of the five site variables (mean values were used for patches with multiple census points), we determined that migrants were more common in larger patches of acacia with higher tree density ( $R^2 = 0.28$ ,  $p < 0.001$ ). This relationship was largely determined by the habitat use of the common canopy species. The step-wise regression also revealed a significant relationship between canopy migrants and tree density ( $R^2 = 0.23$ ,  $p < 0.005$ ). However, understory migrant (ovenbird, MacGillivray's warbler, yellow-breasted chat, common yellowthroat) abundance was significantly related only to understory height ( $R^2 = 0.34$ ,  $p < 0.001$ ). Resident birds showed no significant relationships.

#### Seasonality of migratory birds

The habitats in the Ocosingo Region show strikingly different seasonal patterns in the number of migrants. We have restricted the analysis to insectivorous migrants, because acacia habitats are dominated by insectivorous species, and highly frugivorous or nectarivorous migrants (e.g. orioles, *Vermivora* warblers, *Catharus* thrushes, buntings, and grosbeaks) show considerably more regional movements and, therefore, a consistently different seasonal pattern of abundance (Greenberg, in prep.). Over the 18-week period from 25 October to 20 March, five habitats showed a strong decline in the number of migratory birds (Table 6). The more mesic, riparian habitats (gallery forest and coffee plantation) showed either increased bird numbers or no significant relationship between numbers of birds and week of census.

To test whether the population of insectivorous migrants showed a greater seasonal decline than other habitats, we conducted an analysis of covariance

(ANCOVA) to test for heterogeneity of slopes. For each year we tested the regression of migrant numbers and week of census between acacia, mesic habitats (gallery forest and shade coffee plantation pooled and upland habitats (pine-oak woodland, pine-oak savanna, and secondary scrub pooled). In year 1, acacia populations declined at a significantly greater rate than the mesic habitats ( $F_{1,28} = 10.34$ ,  $p < 0.005$ ), but at a rate that was not significantly different from the other upland habitats ( $F_{1,28} = 0.7$ ). During year 2, acacia populations declined at a rate that was not distinguishable from the mesic habitats ( $F_{1,32} = 2.7$ ), but was significantly lower than upland habitats ( $F_{1,32} = 6.4$ ,  $p < 0.005$ ).

#### Persistence of individuals

The two measures of site persistence (Table 7) were highly correlated ( $r = 0.97$ ). The overwinter persistence of individuals varied considerably between species (0–100%) regardless of which measure was used. Much of this variation can be explained by the vertical distribution of the migrant species. When canopy species are compared with understory species (for those species with greater than two captures) we find a significantly greater persistence (median = 77 vs 19.1%,  $U = 42$ ,  $p < 0.001$ ). Canopy species were either territorial (least flycatcher, magnolia warbler) or had broadly overlapping home-ranges (black-and-white warbler), but all showed a high probability of spending the winter in a single acacia woodlot. The low resighting rate of understory species (except MacGillivray's warbler) may be related to the low probability of sighting these species.

#### Micro-distribution of migrants and residents in acacia groves

Contrary to the typical pattern for tropical habitats, migratory birds are numerically more important in the

Table 5. The mean number of birds on fixed transects in the Ocosingo study area standardized by the foliage volume index

Habitat	Birds	Foliage volume index	Standardized bird total
Acacia	140	1.7	82.3
Second-growth shrub	78	1.5	52.0
Gallery forest	153	2.3	66.5
Rustic shade coffee	144	2.9	49.6
Planted shade coffee	186	2.3	80.8
Pine-oak I	88	2.3	38.2
Pine-oak savanna	45	1.9	23.6
Pine-oak II	80	3.9	20.7

**Table 6.** Mean number of migrants and correlation between insectivorous migrant numbers and week of census for transects in the Ocosingo Area (mean values two winter seasons)

Transect	Mean	<i>r</i>
Acacia	104.1 (8.1)	-0.438 <sup>a</sup>
Shade coffee	75.4 (6.0)	-0.375
Gallery	87.2 (7.2)	+0.261
Pine-oak I	50.4 (3.6)	-0.533 <sup>a</sup>
Pine-oak II	36.4 (2.3)	-0.396
Montane forest	15.5 (1.7)	-0.648 <sup>a</sup>
Milpa	20.7 (1.9)	-0.814
Shrub	39.5 (2.5)	-0.410 <sup>a</sup>
Pine-oak savanna	19.3 (1.3)	-0.342

<sup>a</sup>significant correlation,  $p < 0.05$ .

interior of acacia woods and residents are most common near the edge. Migrants were evenly distributed with respect to the shrubby edge of the acacia grove (mean of  $99 \pm 29$ ,  $97 \pm 16$ , and  $89 \pm 13$  bird observations per unit in edge, near edge ( $< 50$  m), and center of patch, respectively, Kruskal-Wallis = 2.4, d.f. = 2,  $p = 0.30$ ). However, residents were observed much more frequently in the edge ( $83 \pm 11$ ,  $41 \pm 9$ , and  $20 \pm 7$ , KW = 13.7, d.f. = 2,  $p < 0.001$ ).

This pattern may result from the response of migratory birds to acacia, rather than their preference for the interior of the patch. Migrants as a group were more likely to occur in acacia trees than were members of resident species. We recorded type of plant in which we located a bird and found the ratio of migrants in acacia vs understory shrub was roughly 2:1 (861:408), whereas the same ratio for residents was only 1.2:1 (298:249,  $\chi^2 = 29.5$ , d.f. = 1,  $p < 0.001$ ).

#### Relative use of acacias and oaks in mixed woodlands

Overall, migrants were first detected in acacias in 127 of 183 observations (69%). Acacias made up only 36% ( $n = 483$ ) of the trees sampled along the transects. Migrants, therefore, occurred in acacia significantly more often than would be predicted by the relative abundance of the tree ( $\chi^2 = 48.6$ , d.f. = 1,  $p < 0.001$ ). Although we have a small number of observations of resident species, they were found significantly more often (71%,  $n = 21$ ) in oak than were migrants ( $\chi^2 = 14.9$ , d.f. = 1,  $p < 0.001$ ). There was significant variation among migrant species in the proportion of observations in acacia ( $\chi^2 = 21.3$ , d.f. = 1,  $p < 0.001$ , Fig. 3), with values ranging from 38% in black-and-white warbler to 100% in Nashville warbler.

#### Foliage volume

Acacia had relatively low foliage volume compared to most other wooded habitats, therefore the ratio of total birds to foliage volume was disproportionately high (Table 5).

## DISCUSSION

### Acacia and other mimosoid legumes as plants favored by migratory birds

The high abundance of migrants in acacia groves can be seen easily, not only through comparison to other habitats in eastern Chiapas (Table 2), but also with studies using similar point count methodologies in other areas. For example, Lynch (1989) found average values for unlimited radius counts (which result in higher values than fixed radius counts) of 1.9–3.4 migrants. Askins *et al.* (1992) and Wunderle and Waide (1993) reported lower values of 0.1–2 individuals per point for West Indian habitats (in both studies primarily forest). Hutto *et al.* (1986) and Hutto (1989) found 1.7–3.4 individuals within 25 m radius for the range of successional habitats near Chamela, and lower values for pine-oak woodland of Western Mexico. Data from unlimited radius counts from Costa Rica (Powell *et al.*, 1992; Blake and Loiselle, 1992) range from 0.1 (montane forest) to 3.3 (lowland second growth).

Observational artifact is a potential explanation for detecting more migrants in acacia groves than other habitats. Although the openness of acacia habitats, particularly in the dry season, might make detection of migrants easier, we do not believe it accounts for the degree of difference with all other habitats. Firstly, most detections in all habitats are made auditorily. Secondly, many acacia stands are quite dense and support thick understories. We found a positive correlation between number of migrants detected and tree density. Finally, the pattern of within-habitat preference for acacia trees in mixed woods is unlikely to occur due to openness of habitat structure.

Acacia and related mimosoid legumes are not only favored by migratory birds in Chiapas; the importance of acacias and mesquites to migratory birds has been noted by other observers, as well. *Acacia smalli* supports disproportionately large numbers of migratory birds in the coastal cheniers of southern Louisiana and Texas (Remsen *et al.*, 1996). Cheniers are patches of woods where energy-stressed birds forage just before or after completing the trans-gulf flight to Mexico. A similar situation has been reported for mesquite, *Prosopis juliflora*, naturalized in Puerto Rico (Staicer, 1992; J. Faaborg, pers. comm.), where the common foliage-gleaning warblers prefer this species. Mixed-acacia and mesquite habitats in Western Mexico have also been reported to support extraordinarily high densities of migratory birds (K. Rosenberg, pers. comm.).

That acacias have some specific quality that favors visitation by migratory birds is further suggested by observations from the Palearctic-African migration system. Several authors have shown that acacia woodlands support more migrants (and fewer resident species) than the broad-leaved forests in the same region (Ulfstrand and Alerstam, 1977; Morel, 1973). Riparian acacia woodlands are particularly important in the



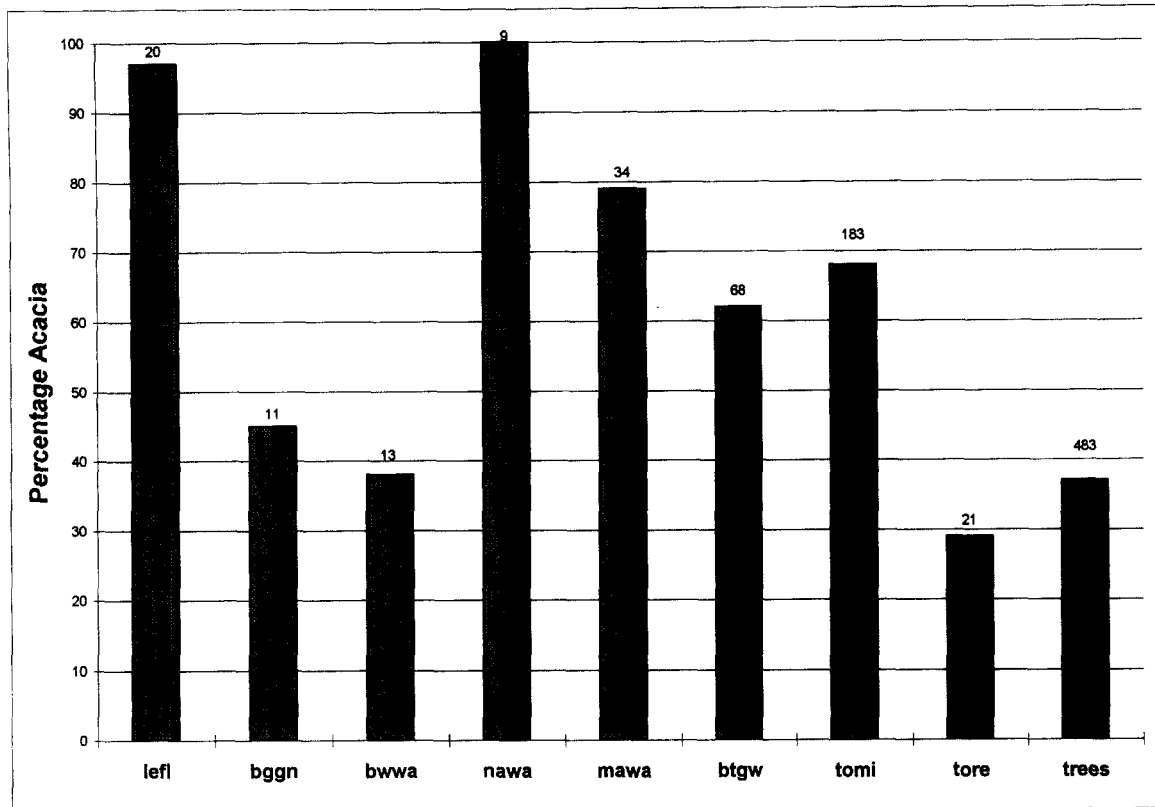


Fig. 3. The proportion of individuals observed in acacias along a transect through mixed acacia-oak woodland: Lefl, least flycatcher; Bggn, blue-gray gnatcatcher; Bwva, black-and-white warbler; Nawa, Nashville warbler; Mawa, magnolia warbler; Btgw, black-throated green warbler; Tomi, total migrants; Tore, total residents; Trees, total trees along transect.

Table 7. Number of birds captured in autumn and resighted in late winter (15 February–15 April) 1993–94 in a 5 ha acacia grove

Species	No. banded	No. resighted <sup>a</sup>	% Total resighted period II	Adjusted total <sup>b</sup>
Understory species				
Ovenbird	75	38	6.7	13.2
Yellow-breasted chat	35	22	5.7	9.1
MacGillivray's warbler	15	15	40.0	60.0
Common yellowthroat	9	4	11.1	25.0
Wilson's warbler	8	2	0	0
Northern waterthrush	6	4	16.7	25.0
Painted bunting	6	0	0	—
Median			6.7	19.1
Canopy species				
Magnolia warbler	29	26	75.9	84.6
Least flycatcher	16	12	56.3	75.0
Black-and-white warbler	12	12	100.0	100.0
Blue-gray gnatcatcher	3	3	66.7	66.7
White-eyed vireo	3	3	66.7	66.7
American redstart	5	5	80.0	80.0
Median			71.3	77.5

<sup>a</sup>Total number of individuals resighted in either Period I or Period II.

<sup>b</sup>Percentage of individuals resighted at least once in Period I or II that were resighted in Period II.

Sahel, supporting 18–20 migrants/ha. T. Price (pers. comm.) noted that passage migrants favor the use of acacias in dry forest in India.

We have located only one detailed study of the ecology of birds of acacia woodlands (Rabol, 1987). *Acacia xanthophloe* characteristically grows in monospecific

stands (Coe & Beentje, 1991). Rabol (1987) found that a single species of palearctic migrant, the willow warbler *Phylloscopus trochilus*, comprised up to 50% of the insectivorous birds. Willow warblers concentrated on the canopy and exterior foliage of acacia trees. Although only one species of Palearctic migrant was

represented, it achieved remarkably high densities (up to 25/ha). These densities are far higher than has been reported for migrants in other habitats in Africa (range <1–13/ha; Lack, 1990). This is similar to the numerical dominance of the magnolia warbler. However, other palearctic migrants were rare and Rabøl (1987) found 16 species of common resident foliage-gleaning birds. As in Chiapas, a single migratory species in Africa—the willow warbler—numerically dominates the canopy of the interior portion of acacia stands.

#### **Why acacias support high densities of migratory birds**

We consider the following four explanations why migratory birds might favor acacia woodlands.

##### *Foliage structure*

By this hypothesis, the simplicity and familiarity of the foliage structure of acacia may contribute to its use by insectivorous migrants. Acacias have foliage structure similar to that which some migratory birds experience on the breeding grounds, e.g. fir *Abies* and spruce *Picea*. Perhaps the boreal forest species (black-throated green and magnolia warblers) respond to this similarity with their natal foliage (Greenberg, 1992). In addition, the small leaflets presented in a planar arrangement provide a simple foraging surface for small-billed migrants to exploit. However, the phenomenon of migrants in Huizachales is far more general, and includes bark foraging and ground foraging species.

##### *Habitat fragmentation and degradation*

By this hypothesis, due to their fragmented nature acacia woodlots support few breeding birds and leave an ecological vacuum for migratory birds. However, acacia woodlots are not significantly smaller than coffee plantations or patches of gallery woods, yet they support almost twice as many migrant individuals. Habitat degradation may be an important factor. Acacia groves not only support the highest numbers of migrants, but also had the highest percentage of migrants in the overall avifauna. The low abundance of resident breeding birds means that the arthropods are free from avian predators during several months of the year. Perhaps this explains the heavy use of acacias during the autumn (both in Mexico and in Gulf Coast stopover sites). The lack of resident birds may be a result of the general lack of cover for nesting or disturbance by livestock.

##### *The direct and indirect action of cattle*

By this hypothesis, the activity of cattle directly favors the use of acacia woodlots by migratory birds. Arthropods are often attracted to the abundance of fresh fecal matter. In addition, on a number of occasions we observed flocks of migratory birds following cattle through the understory, apparently feeding on the arthropods flushed in the procession. However, cattle were generally only present during the latter part of the winter, when migrant abundances were at their nadir.

##### *Foliage palatability*

By this hypothesis, acacias support relatively high densities of small foliage arthropods and, thereby, provide a source of abundant food for migratory birds, which disproportionately use this food resource. This hypothesis is supported by the observation (Fig. 2) that the bulk of the added individuals and species are canopy insectivores. Magnolia warbler is by far the most common species and it is a foliage insectivore of the acacia canopy. Furthermore, as the results in Fig. 3 indicate, migratory birds selectively occur in acacias even when they occur in mixed woodlands—which would argue against the fragmentation hypothesis alone. The high abundance of migrants is even more remarkable when the general lightness and sparseness of the acacia foliage is considered (Ulfstrand and Alerstam, 1977). Acacia often has only a thin monolayer of leaflets and the overall foliage density is lower than other woodlands or coffee plantation.

We hypothesize that the herbivory on acacias by large browsing animals acts to increase arthropod numbers in acacia woodlands. The basis for this hypothesis is that there is an energetic trade-off between modes of defense used by plants where energy needs to be devoted to rapid growth (Coley *et al.*, 1985). Herbivory by large mammals selects for spinescence as the major mode of plant defense. For example, spines occur in African and New World acacias, but not in Australian acacias, where a much reduced megafauna occurred (Brown, 1960). Furthermore, mammals are forced to take small bites and reduce foraging efficiency on spiny vs non-spiny plants (Cooper & Owen-Smith, 1986). In addition, spinescence is a first-line defense against breakage and trampling, which explains their superiority over chemical defenses in the face of an abundance of large animals (Milton, 1991). Therefore, investment in mechanical defenses, which are specialized for ruminants, may necessitate a reduction in defenses more effective against insect herbivores, resulting in high arthropod densities and hence high densities of insectivorous birds. The high palatability of acacia foliage (Coe & Coe, 1987; Cooper *et al.*, 1988) and that of many other mimosoid legumes lends some credence to this suggestion. In African savannas, there is a strong tendency for spinous plants (mainly mimosoid legumes) to be highly palatable and non-spiny plants to be unpalatable (Owen-Smith & Cooper, 1987). Palatability appears to be related to the interaction between crude protein content and the amount of condensed tannins. Interestingly, Greig-Smith (1978) reported that mixed flocks of insectivorous birds tended to forage preferentially in acacias, a phenomenon he attributed to the high abundance of insects in these trees.

Our preliminary data suggest that *Acacia pennatula* foliage is high in crude protein and low in tannins compared with other pasture trees (unpublished data). Evidence that might contradict this hypothesis is presented in Rehr *et al.* (1974), which shows that non-ant acacias

have reduced foliage palatability compared to ant acacias, possibly resulting from the presence of cyanogenic compounds, as well as unidentified secondary compounds. However, the comparison was only among acacias and did not involve the species discussed in this paper.

Unfortunately, we do not have adequate comparative samples of arthropod abundance and foliage density in different habitats. However, the high bird abundance per unit foliage volume (Table 6) and the disproportionate representation of canopy insectivores in the acacia bird assemblage are in themselves suggestive pieces of evidence. In addition, acacia groves support exceedingly high populations of orb-web building spiders during the wet season.

### Seasonality and long-term habitat quality of acacia woodlands

Habitats that support high densities of migratory birds might not provide the most stable or safe home for long periods (Rappole *et al.*, 1989). The acacias themselves show a strongly seasonal phenology—with much of the foliage lost during the late dry season. The predominance of females (Table 4) has been associated with more seasonal habitats in other areas (Parrish & Sherry, 1994). However, the analysis of seasonal trends in insectivorous migrants did not support the idea that acacias have higher rates of seasonal decline than other habitats in the Ocosingo area. Furthermore, color-marked canopy migrants maintained territories and persisted in the acacia woodlot through the winter at a high rate. The high rate of overwinter persistence in canopy species is particularly surprising considering the degree of leaf loss in acacia groves.

### Implications for conservation

The management of native mimosoid trees on pasture or degraded lands offers a promising avenue for the conservation of both migratory and, indirectly, resident forest bird populations. The growing of acacias provides habitat for migratory birds on lands that would otherwise be unsuitable. In addition, the use of acacia reduces the need to harvest wood for pasture maintenance from oak woodland or tropical forest. Finally, the use of acacia seed pods for cattle fodder needs further investigation. Harvesting acacia seed pods may require higher labor inputs for harvesting, but the plants demand little by way of chemical input. As the perennial crop of a nitrogen-fixing plant, acacia and mesquite pods offer a nutritious potential food source for livestock, produced with less environmental damage than feed corn or sorghum (Felker & Bandurski, 1979; National Research Council, 1979). The key, however, is management. Although acacias already grow commonly in cattle pastures, they are often unproductive and underused. Management of woodlots should increase the efficiency of pod and wood production. In addition, the data on bird abundance show that woodlots with an

understory of shrubs, rather than trees over pasture, support the greatest populations of migratory birds. Such managed woodlots should be incorporated into existing ranches (as they are in Ocosingo) and not located on natural habitats cleared for this purpose.

### Prehistoric distribution of acacia woodlands in Middle America

*Acacia pennatula* is currently associated with human-managed grazing systems which may make acacia management an unattractive activity for conservationists to be involved in. However, we consider it possible that acacia-dominated habitats were prevalent during the recent geologic past. Favorable conditions for the widespread growth of acacia woodlands, including low rainfall and a high density of large ungulates, were probably prevalent during much of the later Tertiary and Pleistocene. It is likely that acacias are far more common now in Middle America than they were in pre-Columbian times, when there was considerable agricultural clearing, but no pasture for grazing large domesticated ungulates. Acacias probably had a much more local distribution than they do today.

Savanna was common over the Central American land bridge for much of the Cenozoic (Webb, 1978; Rich & Rich, 1983). Tropical rainforest did not become established in most of Central America and Mexico until late in the Pleistocene (Toledo, 1982). During much of the past 40 000 years vegetation along the Caribbean lowlands of Mexico was either pine-oak woodland or deciduous dry forest. Cool and dry climates also prevailed at sites studied in Guatemala (Leyden, 1984) and Panama (Piperno *et al.*, 1990) during the late Pleistocene. These sites supported oak woodland where tropical deciduous forest now grows. Leyden (1984) showed that there was an elevational shift in vegetation of about 1000 m in the Peten, which would mean that the vegetation over much of the Caribbean slope of Guatemala was similar to conditions around Ocosingo today.

Mesoamerica supported a high density of large mammals (Martin, 1977; Janzen & Martin, 1982; Miller & Carranza-Castaneda, 1984). Large grazers probably dispersed acacia and mesquite seeds and grazed the competitors of the resulting seedlings (Janzen, 1986). The large, hard, pulp-filled and indehiscent pods of *Acacia pennatula* and a few other New World species show the characteristics of the megafaunal dispersal syndrome in general (Janzen & Martin, 1982; Traveset, 1992) and the ungulate dispersal syndrome as defined operationally in contemporary Africa (Lamprey, 1967; Gwynne, 1969; Coe & Coe, 1987; Milton, 1987). Large grazing mammals would have the additional effect of reducing grass biomass and thereby reducing the frequency of fire—a threat to the regeneration of acacia scrub (Sinclair & Norton-Griffiths, 1979). Owen-Smith (1987) further argued that the largest herbivores (> 1 metric ton, primarily elephants and relatives)

suffered the most in the late Pleistocene of North and South America. These megaherbivores are a major source of habitat disturbance and favor coppicing species that are relatively browse-resistant—which would include spiny acacias and mesquites.

Because it produces an abundant crop of nutritious pods during the dry season, *A. tortilis* is probably a keystone species (Terborgh, 1986) for African savanna ecosystems. It is possible that certain species of New World acacias played the same role in ancient Neotropical savannas (Greenberg, 1994), and with the aid of livestock, acacias may be reoccupying areas where they were found before the advent of recent warm, wet periods with the concomitant loss of primary browsing and dispersal agents. This would provide ample opportunity for the migrant bird community to adapt to the use of acacia habitats.

## ACKNOWLEDGEMENTS

Field work in Ocosingo was assisted by Javier Salgado, Andrea Cruz, Robert Reitsma and Hector Flores. Support for field work in Ocosingo was provided by the National Geographic Society, Scholarly Studies Program of the Smithsonian Institution, and the Smithsonian Migratory Bird Center. Field work for comparative sites in Chiapas was supported by the above organizations as well as the National Fish and Wildlife Foundation and the Neotropical Fund of the Lincoln Park Zoo. We benefited from communications with J. Bryant, J. V. Remsen, N. Owen-Smith, T. Sherry and J. Wunderle. Drafts were reviewed by M. Marvin, E. S. Morton, L. Petit and J. V. Remsen.

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