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THE COMPOSITION OF AVIAN COMMUNITIES IN REMANESCENT WOODLOTS IN SOUTHERN BRAZIL

EDWIN O. WILLIS

ABSTRACT

Censuses of birds in remanescent woodlots of 1400, 250, and 21 ha on the subtropical São Paulo plateau in southeastern Brazil showed 202, 146, and 93 species of birds still present. Presumably all areas originally had about 230 species before forest cutting became widespread. Few species present in a small woodlots were absent from a larger one, so that the small woodlots added to bird preservation mainly by repeating species in a different area. The large and medium woodlots had much the same numbers of individuals per 100 h of observation, but the small woodlot had few individuals and hence did not show density compensation. Certain groups of birds and mammals were especially prone to extirpation in small woodlots: large frugivores of the canopy (parrots, cotingids, monkeys, etc.), birds eating large insects on or near the ground (antbirds, woodcreepers), and small insectivores of forest bamboo thickets and other tangles. Frugivores were to some extent replaced by edge-living omnivores, ground-living doves, and by ground-living mammals (apparently leading to increases in owls) in small woodlots. Small birds eating small insects. on or near the ground became more abundant, although not more diverse. in small woodlots. Migrants, which here were mostly birds of the forest canopy and edges, were common in the medium-sized woodlot but not in the small one. Edge-living species became more abundant or relatively more abundant in small woodlots. These changes cause small woodlots to become more like temperate zone forests in emphases on oscine birds of canopy and edge and on migrants, and in loss of fruit-eating birds.

Losses of large hawks and of birds of the forest understory may be due to low population numbers and occasional extinctions in small areas. Losses of canopy frugivores and of hummingbirds, which fly easily between woodlots, are more likely due to loss of specific flowering or fruiting trees used at certain times of the year.

The conservation of ecosystems has received less attention over the years than has the preservation of conspicuous species. The hope has rather been that, when by diligent effort one sets aside and protects a patch of habitat that is the home of one or several species

Department of Biology, Princeton University, Princeton, N.J. 08540.

of particular interest, other species of that community will also survive. In a world increasingly preempted by agricultural and other human uses, the remaining patches of habitat have become smaller and smaller.

Preston (1962) was first to point out the danger of leaving only small patches of habitat, using data from biogeographical studies of islands. It had long been known that small islands support fewer species than do large ones; as a general rule, dividing area by 10 causes loss of half the species (Darlington, 1957). Preston noted that, since this is true for any isolated area, species must disappear from remanescent patches of habitat even if humans do not interfere inside the patches. This implies that communities will rearrange themselves internally, becoming impoverished with time, if restricted in area.

MacArthur & Wilson (1967) extended these ideas to suggest that immigration and extinction rates set equilibria that are lower on small and isolated islands than on close and large ones. Diamond (1972) suggested that species have been disappearing from islands off New Guinea since these islands were connected to it in the last glacial period of low sea level; and he suggested that species have disappeared fastest on the smallest islands.

Censuses of birds of the protected forest reserve of Barro Colorado Island, a hilltop isolated by Gatun Lake during construction of the Panama Canal about 1914, showed that some species have disappeared over the years (Chapman, 1938; Eisenmann, 1952; Willis, 1974; Willis & Eisenmann, *in press*). Preston's suggestion was thus proved correct in one fairly well-documented case. Decreases were often losses of birds of secondary woodland, but there were some losses of large forest hawks and of large and small ground birds. The Barro Colorado evidence stimulated suggestions that habitat reserves be left as large and interconnected as possible to slow down changes due to "ecological truncation" of guilds of species (Wilson & Willis, 1975; Terborgh, 1974).

Changes in the structure of communities as an ecosystem is diminished in size can perhaps indicate possible reasons for loss of species. Simberloff & Abele (1976) looked at insects on a mangrove islet that they subdivided; species numbers did not decrease, at least in the short term. However, they did not report on internal structures of the insect communities thus created nor on changes over the course of several years. Others have looked at present conditions on naturally created islands of differing sizes. Diamond (1975) found that some "forbidden" combinations of bird species never occur together on islands of different sizes off New Guinea, and that some bird species persist only on small and depauperate islands. These "supertramp" species generally are good at moving about and can persist in small areas of habitat, but do not stay when many species move in on large islands. Johnson (1975) looked at birds of forested mountains in the deserts of the Great Basin in the western United States. More species were present when more macrohabitats were present, even when habitat areas were limited. Like the mangrove insects of Simberloff & Abele and the supertramp birds of Diamond, these birds seem able to survive in even small patches of habitat. In a sense, nontramp species were already gone before man arrived.

To look directly at changes within communities due to decrease in area of habitat in places where the natural faunas are still relatively rich, human tendencies to leave only scattered patches of habitat of different sizes in settled regions can be used as natural experiments. Each such patch often represents many years of coevolution of a flora and fauna, unlike such short-term experiments as those of Simberloff & Abele; and it is often recent enough that the original fauna is fairly well known, unlike the original avifaunas of islands off New Guinea or of mountaintops in the Great Basin. Ideally, such patches should be followed from the natural state on; but not even Barro Colorado Island was censused before it became an island. Currently, there are some studies of such habitat patches in the United States (Whitcomb *et al.*, 1976) and elsewhere in temperate zones. Here I report on a study of the avifaunas in three such woodlots of the subtropical São Paulo plateau in southeastern Brazil.

STUDY AREAS

The São Paulo plateau is a rolling tableland, which slopes irregularly westward from elevations of some 800 to 1200 m on the wet ranges of the Serras da Mantiqueira, do Mar, and de Paranapiacaba to about 200 m elevation in the wide interior valley of the Paraná River. The Tropic of Capricorn passes across the plateau. Rainfall is generally near 1500 mm per year, mostly in the hot summers; winters can be dry, with occasional frosts. Most of the plateau, except for patches of savannas ("cerrado" vegetation) or dense woodlands ("cerradão") was originally covered by subtropical broad-leaved forest 20-35 m in height (Chiarini & Coelho, 1969). The spread of sugar cane and, after 1840, coffee cultures led to widespread deforestation, since shade trees were not retained (Hueck, 1966:178). Coffee became difficult to raise without fertilizers in many areas, and current uses favor cotton and pasturelands. Scattered woodlots of small size remain; only a few large farms had owners interested enough in hunting or conservation to preserve large tracts on their lands.

Three of the last large tracts of forest remaining on the plateau are in the pastures of Fazenda Barreiro Rico, at 500 to 600 m elevation between the arms of the Barra Bonita Reservoir at the junction of the Tietê and Piracicaba Rivers. One of the three tracts still measures about 1400 ha, despite occasional conversion of segments to pastures as late as 1971-75 (when 176 ha were cut). I censused birds of this tract (centered about 22°45'S and 48°09'W, according to the 1974 Carta do Brasil 1:50000 contour map, Santa Maria da Serra quadrangle, of the Instituto Brasileiro de Geografia e Estatística) on three-day visits nearly every month from March, 1975, to August, 1977. I looked at birds on the other smaller forest tracts (a formerly connected one of 500 ha only 200 m west, and one of 325 ha off southeast a few km) now and then. Extensive collections of birds, made by Emílio Dente and others in 1957-64, were available in the Museu de Zoologia. Universidade de São Paulo, and give some idea of the avifauna before reservoir construction flooded nearby lowland and swamp forests about 1961. Wesley E. Lanyon and David Ewert kindly provided information from a visit in 1970.

Two smaller tracts of forest at 620 m elevation, on Fazenda Santa Genebra just north of the city of Campinas and 110 km airline from Barreiro Rico, were censused for birds from February 1975 to March 1978. One, the "Santa Genebra" tract, is 250 ha of forest (centered about 22°49' S and 47°07' W on the Campinas quadrangle of the Carta do Brasil 1:50000) in cotton fields. In 1969, this area was reduced to its present size by cutting of about 145 ha. Another, the "Unicamp" tract, is 21 ha set in pastures and cotton fields near the Universidade Estadual de Campinas, at 3.75 km east (just northwest of 22°50' S and 47°04' W) of the Santa Genebra tract. Small cattail (*Typha angustifolia*) marshes and swamps next to both tracts were not censused.

Both the Santa Genebra and Unicamp woodlots are on red and fertile "terra roxa" latosols rather than the sandy soils of Barreiro Rico, and both include swampy areas with small creeks. The Barreiro Rico tract has two small creeks affsing at its north edge, but is mainly a dry hilltop woodland. The Santa Genebra and Unicamp forests should therefore be taller and better developed than the forest at Barreiro Rico, which lies on an ecotone near areas of cerrado and cerradão.

The Santa Genebra and especially Unicamp woodlots are indeed taller and more imposing at their centers, with 35 m emergent jequitibá trees (*Cariniana legalis*, Lecithydaceae) towering over 20-25 m guarantã (*Esenbeckia leiocarpa*, Rutaceae) and others. However, the edges and trail margins of both the Unicamp and Santa Genebra tracts are highly disturbed by wood cutting and therefore tend to a vine-tangled appearance not greatly different from the irregular canopy at Barreiro Rico. Some trees have been removed over the years at Barreiro Rico, and removal of valuable species by colonists and even Indians must be assumed for all areas. Parts of the Santa Genebra tract seem old second growth.

Scattered coffee plants and even rows occur in both the Unicamp and Santa Genebra tracts. The rows are remains of small nurseries in use to 35 years ago, but other plants probably do not indicate former cultivation; bird dispersion of coffee seeds occurs in many woodlots and state parks in eastern São Paulo.

Occasional windfalls have created tangled zones or low woodlands in all three forests, and occasional fires (notably extensive ones at the edges of the Santa Genebra tract in 1964) have also left tangled patches. Layers of charcoal are in the soil of sandy areas at Barreiro Rico. Freezes, such as one in July 1975, temporarily defoliated *Cecropia* sp. but do not seem to cause lasting changes. Drought periods, such as the winter of 1975 and the summer of 1978, cause much loss of canopy foliage.

Barreiro Rico has an included patch of 5 ha of cerrado vegetation (censused separately), and a few ha of sandy bordering woodlands add some diversity of habitat lacking in the Santa Genebra and Unicamp tracts. However, the swampy creeks of the last two areas, with palms (mostly Arecastrum romanzoffianum), add a diversity lacking at Barreiro Rico, as do the jequitibás and nectariferous scattered paineira trees (Chorisia speciosa, Bombacaceae). Trees common in all the censused areas include guarantã, peroba (Aspidosperma polyneuron, Apocynaceae), guaraiuva (Segurinega guaraiuva, Euphorbiaceae), canxim (Pachystroma illicifolium, Euphorbiaceae), tapixingui (Croton sp., Euphorbiaceae), guaritá (Astroneum graveolens, Anacardiaceae), pau d'óleo (Copaifera langsdorffi, Leguminosae), jatobá (Hymenaea courbaril stilbocarpa, Leguminosae), pau-jacaré (Piptadenia gonoacantha, Leguminosae), and canjarana (Cabralea canjarana, Meliaceae). A common understory shrub is carrapateiro (Metreodorea sp., Rutaceae). There are scattered patches of slender bamboos, and lianas are dense enough to clutter the forest understory and form tangles in the frequent treefall and other clearings.

METHODS

Two types of censuses were used: one-hour censuses and general censuses. In one-hour censuses, I recorded every bird seen or heard while walking slowly along standard routes in each woodlot between 07:00 and 09:00. Some censuses at Barreiro Rico were run at less favorable hours (10:00-17:00) but along alternate routes. General censuses were run by walking slowly through the woodlots, attempting to reach all parts of the areas. Usually general censuses at Unicamp and Santa Genebra were run in the favorable morning hours, but at Barreiro Rico I worked in the afternoons as well. Birds at Barreiro Rico tended to be more active all day long than in the two smaller woodlots, so that census totals at Barreiro Rico did not seem low. The Unicamp woodlot was often visited with students at noncensus hours; seven vagrant species encountered only at such times are not included in analyses. General censuses at Barreiro Rico totaled 550.4 hours, at Santa Genebra 444.3 hours, and at Unicamp 205.0 hours.

Birds were identified with 10×50 binoculars, and study skins of the Museu de Zoologia of the Universidade de São Paulo were checked to confirm identifications.

SPECIES NUMBERS

These forest tracts must originally have had similar total numbers of bird species, but I found (Table 1) 202 species in the tract at Barreiro Rico (B), 146 at Santa Genebra (S), and 93 at Unicamp (U). Not counted are a few birds of open areas that occasionally visit the edges of woodlots (notably *Guira guira*; 5 species at B, 6 at S, and 5 at U) nor some water or marsh birds that occasionally perch atop trees (*Cairina moschata* at B, *Donacobius atricapillus* at S, and *Syrigma sibilatrix* at U).

Table 1.	Bird	species	in	three	São	Paulo	woodlots
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	Number of	Species in Giver	ı Locality
	\mathbf{B}^{a}	S	U
Total recorded	202	146	93
Breeding species	175	119	76
Summer only	13	12	8
Wintering species	5	5	2
Vagrants	22	22	15

^a B is Barreiro Rico, S is Santa Genebra, and U is Unicamp.

Figures 1 to 4 show cumulative species-individual and species-time curves for the three woodlots and two types of censuses. The cumulative curves suggest that general totals are reasonably complete. At 200 hours of observation in each woodlot, species recorded were about 90 for U, 130 for S, and 180 for B.



I failed to find 10 of the 136 forest species collected at Barreiro Rico in 1957-64. Tinamus solitarius is still present, according to local workers, but is a shy and rare bird. Aphantochroa cirrhochloris is a hummingbird that may still come to flowering trees occasionally. The other eight species should have been seen if still present. Cissonis leveriana, Cacicus haemorrhous, and Procnias nudicollis were probably in forest near the river, although the frugivorous bellbird called well away from the river as late as 1970 (D. Ewert, pers. comm.). [The frugivorous Columba plumbea also once called along the river, and frugivorous Pipile jacutinga was last shot in 1926, according to J. C. Magalhães.] One parrot (Triclaria malachitacea) and two toucans (Baillonius bailloni and Selenidera maculirostris) add to the list of vanished large frugivores, while Notharchus macrorhynchus once ate large insects in the treetops. Dysithamnus stictothorax, a small insectivorous antbird of the understory, is commonest in wet coastal forests.

In the early 1930's, wood-quail (*Odontophorus capueira*) and reintroduced *Tinamus solitarius* were still in the Santa Genebra woodlot, according to Jandyra Pamplona de Oliveira.



Fig. 2. Cumulative numbers of species recorded for given numbers of of individuals in general censuses.

Originally these and yet another 50 species should have been in all the forests of the region. Some 20 now present, mainly forest-edge species, would have been lacking; totals should have been near 230 species. Lacking today are most macaws (Ara sp.), large parrots (Amazona spp. other than forest-edge A. aestiva), araçaris (Pteroglossus aracari; see Haffer, 1974:229), eagles (Spizaetus spp., etc.), and several brightly colored treetop tanagers (Tangara spp., etc.).



Fig. 3. Cumulative numbers of species recorded by given times for one-hour censuses.



Fig. 4. Cumulative number of species recorded for given numbers of individuals in one-hour censuses.

COMPOSITIONS OF AVIFAUNAS

Appendices 1-20 present the species recorded and the numbers of individuals seen or heard per 100 h of field observation in the three woodlots. Only in a few cases were breeding birds recorded at Santa Genebra or Unicamp and not at Barreiro Rico; therefore, birds of Unicamp were in general a subset of those at Santa Genebra and birds of Santa Genebra a subset of those of Barreiro Rico. Woodrails (Aramides cajanea), streamcreeper (Lochmias nematura), and a dove (Leptotila rufaxilla) were absent in Barreiro Rico primarily because their creekside woodlands are absent. Large owls favored the smaller woodlots (Appendix 6), perhaps for reasons cited below. A single Great Antshrike (Batara cinerea) appeared for several months in the Santa Genebra woodlot, which lacked forest-edge Barred Antshrikes (Thamnophilus doliatus) for unknown reasons. The only other exception was the seeming absence of a small tyrannulet of scrub (Serpophaga subcristata) at the edge of Barreiro Rico. Some other species, such as the becard *Platypsaris rufus*, were very rare at Barreiro Rico. The piculet there was Picumnus minutissimus, that of Santa Genebra and Unicamp P. cirrhatus; but P. cirrhatus was in a 325-ha woodlot at Barreiro Rico. Veniliornis passerinus nearly replaced V. spilogaster in the main woodlot at Barreiro Rico, but was less common than it in the 500-ha woodlot.

1. Large Canopy Frugivores and Omnivores

Large fruit-eating birds, especially ones that eat large insects as well, were unusually poorly represented in both small woodlots (Appendix 1). One parrot (*Pionus maximiliani*) was more common in the medium-sized woodlot and to some extent took the place of other species there. Fruit-eating monkeys were commonest in the large woodlot (see Discussion).

2. Small Canopy Omnivores

Small treetop omnivores were generally present in all woodlots (Appendix 2), although less numerous in the smallest one. Only one species at Unicamp was a local vagrant. Several treetop omnivores, notably small tanagers (*Euphonia pectoralis, Tangara* spp.), were unaccountably lacking from all three woodlots.

3. Small Understory Omnivores

Most small omnivores of the understory were in all three woodlots, but became less common in the smaller ones (Appendix 3). None were migratory, except possibly *Laniisoma elegans*.

4. Edge Omnivores

Omnivorous medium to small flycatchers, thrushes, and nineprimaried oscines of forest edges were somewhat more common in smaller woodlots (Appendix 4). They eat some large fruits and insects that in the largest woodlot would have gone to large birds of Appendix 1. However, only *Saltator similis*, an uncommon bird of forest edge at Barreiro Rico, really became common inside the smaller woodlots rather than staying at woodlot edges or in the canopy. Species diversity did not increase in small woodlots. Many were vagrants: 8 or 9 species in each area. Some were migrants.

5. Ground Frugivores

If few large fruits are eaten in the trees, more must fall to the ground. Ground frugivores were more diverse in large woodlots but were about equally numerous in the three areas (Appendix 5). *Leptotila verreauxi*, which in most of the neotropics is a dove of forest edge, was common in all these woodlots. *Claravis pretiosa*, which was noted only August to May, may be a summer resident. Ground-foraging squirrels (*Sciurus guerlinguetus*) and large lizards (*Tupinambis* sp.) were more common in small woodlots.

6-8. Carnivores

Perhaps more large owls were in small woodlots (Appendix 6) because more nocturnal mammals ate fruits that fell to the ground. Diurnal carnivores were less diverse in the smaller woodlots, though not always less abundant (Appendix 7). Many eagles that once were in plateau forests were unrecorded even at Barreiro Rico. Carrion eaters (Appendix 8) were more diverse over the large woodlot, though huge numbers of nonfeeding *Coragyps atratus* soared over both Santa Genebra and Unicamp from nearby settlements.

9. Trunk and Twig Insectivores

Piculets (*Picumnus* sp.) and small *Veniliornis* woodpeckers were common in small woodlots, but larger trunk and twig foragers were more diverse and common in the larger woodlots (Appendix 9).

10. Large Ground Insectivores

Insectivores that get large insects from or near the ground were rare in small woodlots (Appendix 10). Absence of army ants (*Eciton burchelli* and *Labidus praedator*) from both small woodlots probably caused reduced numbers of ant-following *Dendrocincla turdina* and *Dendrocolaptes platyrostris* and absence of *Pyriglena leucoptera*. A fourth ant-following species, *Trichothraupis melanops*, eats fruits as well and remained in all three woodlots (Appendix 3).

11. Small Ground Insectivores

Small ground insectivores (under 25 g) did well in small woodlots (Appendix 11), probably because large ones did not. However, some small species were absent from small woodlots.

12. Small Understory Insectivores

Most small insectivores of the understory were in all woodlots (Appendix 12). None were migratory, except for a few wandering winter individuals.

13. Tangle Insectivores

Forest insectivores that inhabit bamboo and vine thickets or their edges (Appendix 13) tended to drop out in small woodlots.

14. Midlevel Insectivores

Some midlevel insectivores (notably *Piaya cayana, Hypoedaleus guttatus,* and *Herpsilochmus rufimarginatus*) also use tangles, but most species use more open foliage than members of the preceding group. Like them, they were less diverse in small woodlots (Appendix 14). High abundance of the three that also use tangled vegetation (and of a summer species that liked edges of such tangles) in Santa Genebra was not repeated in Unicamp, although vine-tangled midlevels are common in both areas.

15. Small Canopy Insectivores

Small insectivores of the treetops (Appendix 15) were much like small canopy omnivores (Appendix 2) and midlevel insectivores (Appendix 14) in being more common in the medium-sized woodlots but no more diverse there. They were uncommon but fairly diverse in the smallest woodlot.

16. Edge Insectivores

Edge insectivores, which vary in foraging between tangles and midlevels and treetops, were usually present in all three woodlots (Appendix 16). High densities of some tangle-foraging species (*Hylophilus poicilotis, Synallaxis* spp.) in Santa Genebra raised total numbers there. Presence of dead trees and cerrado-like vegetation in pastures at Barreiro Rico accounted for addition of *Myiarchus tyrannulus* and *Troglodytes aedon* at forest edges.

17. Aerial Insectivores

Aerial insectivores (Appendix 17) were generally present over all woodlots and over intervening open areas as well. Five species bred outside each woodlot and hence were local vagrants, totals surpassed only by edge omnivores of Appendix 4 and perhaps by birds of Appendices 19 and 20.

18. Nocturnal Insectivores

Nocturnal insectivores, in contrast to carnivores, were poorly represented in small woodlots (Appendix 18).

19. Nectarivores

Birds that use nectar and small insects (Appendix 19) were less diverse and numerous in the small woodlot. Since most of these birds find flowering trees or sugar-water feeders even in suburbs at Campinas (*Thalurania glaucopis* is the only forest-interior species that does not appear outside the forest), absence in the small woodlot probably reflects undependability of flowering there. *Phaethornis pretrei* and *Chlorostilbon aureoventris*, the least dominant and most vagrant of local hummingbirds, were common in the small woodlot.

20. Edge Granivores

Birds that eat seeds and small insects (Appendix 20) were mostly at forest edges. Only *Haplospiza unicolor* (a vagrant or winter visitor at Campinas, perhaps from the Serra do Mar) and *Tiaris fuliginosa* regularly wander through forests and find small trailside patches of grass seeds. Probably reduced diversity and abundance in small woodlots reflects reduced abundance in nearby cotton fields and intensively grazed pastures; Barreiro Rico seedeaters came mostly from weedy patches in nearby pastures. Also, many seedeaters are captured for cage birds near Campinas.

MIGRANT BIRDS

Summering birds reached all three woodlots, although the smallest woodlot unaccountably lacked a few species (notably *Myiopagis viridicata* and *Platypsaris rujus*, midlevel to treetop insectivores common at nearby Santa Genebra). Summering species were all edge, midlevel, canopy, or aerial species; most were insectivores, though some used fruits to some extent. None, except perhaps *Claravis pretiosa* if it really is absent in winter, used the forest trunks or lower levels. However, *Empidonax euleri* of the lower levels seemed less common in winter, and may emigrate to some extent at that season. The frugivorous *Tityra* spp. also were less common or absent in winter, and may migrate like their smaller relatives, the becards. One pair of *T. cayana* appeared in Santa Genebra on 21 August 1977, as if on spring migration. Two nocturnal species, *Caprimulgus rujus* and *Nyctibius griseus*, were unrecorded in winter; but they are not easily detected when not calling.

In the Campinas woodlots, many summering species disappeared by February and apparently failed to breed in the drought summer of 1978. In the drought winter of 1975, *Empidonax euleri* was nearly absent.

Summer migrants were most abundant in the medium-sized woodlot (Table 2). They thus frequented the area with more resident individuals in their foraging zones, rather than the area with many competing species (Barreiro Rico) or the area with few birds (Unicamp). Summering migrants represented 10% of 4007 birds per 100 hours in Santa Genebra, 6.9% of 3548 per 100 h in Barreiro Rico, and 5.6% of 1950 birds per 100 h at Unicamp.

Table 2. Summering inigrams of three Sao Faulo woodie	Table	2.	Summering	migrants	of	three	São	Paulo	woodl	ot
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Bird Species	Individuals/100 h			
	в	s	U	
Ictinea plumbea	14	24		
Lurocalis semitorquata	7	1	6	
Chaetura andrei	21	21	8	
Coccyzus euleri	0	1	0	
melacoryphus	1	3		
Platypsaris rufus	0	34		
Pachyramphus polychopterus	8	8	0	
Myiodynastes maculatus	7	11	7	
Empidonomus varius	3	19	4	
Legatus leucophaius	1			
Myiopagis viridicata	24	54		
Myiarchus swainsoni	43	64	32	
Vireo olivaceus	114	160	51	
Total	244	400	109	

The few passage migrants, in spring and fall, included several edge frugivores (*Elaenia mesoleuca* in all three woodlots and *E. albiceps* in the two larger ones; *Turdus amaurochalinus; Platycichla flavipes*). Several vagrants (*Pitangus sulphuratus, Myiozetetes simillis, Tersina viridis*) perhaps belong among passage migrants; Appendix 4 has many "vagrants." Probably the July-September fruiting peak in southeastern Brazil (Davis, 1945) exploits the many vagrants available at that time.

Wintering birds were also low in numbers, except for flycatching *Contopus cinereus* of forest midlevels (Table 3). It seems to occupy a niche between the niches of summering *Myiarchus swainsoni* and *Myiopagis viridicata;* and its aerial sallying is presumably favored over the hover-gleaning tactics of the summer species because many midlevel and upper-level leaves are lost in the dry and cold months. Most wintering species summer at higher elevations to the southeast during the summer months. Perhaps numbers of these birds are now limited in summer by lack of wintering areas on the deforested plateau. Several other small wintering frugivores and insectivores move to open cerrado vegetation within and west of Barreiro Rico.

Species	Individuals/100 h				
	в	s	υ		
Phibalura flavirostris	0				
Pachyramphus castaneus	1				
Knipolegus cyanirostris	2	3			
Contopus cinereus	5	23	3		
Dendroica striata		0			
Pipraeidea melanonota	0	3	0		
Haplospiza unicolor		4			
Total	9	33	3		

Table 3. Wintering migrants of three São Paulo woodlots

Several rare birds, here considered vagrants (*Basileuterus culicivorus*, *Pyrrhocoma ruficeps*, *Cranioleuca pallida*, *Attila rufus*), probably come from the south and may represent individual wintering birds; they reached only the Campinas woodlots, which are closer to the wooded Serra do Mar than is Barreiro Rico.

A single *Dendroica striata* seen twice in Santa Genebra was the only migrant from North America.

WANDERING SPECIES

Counting only species known to be able to travel between woodlots ("T" species in the Appendices), 140 of 216 or about two thirds can wander. Only for the categories of ground and tangle insectivores (Appendices 10, 11, 13) are most species unlikely to cross open areas. Large fruit-eaters, small understory insectivores, and trunk birds average about half species that can cross open areas.

Diversity of nonwandering species was reduced in small woodlots: 74 species (37%) of the avifauna) at Barreiro Rico, 38 at Santa Genebra (26%) and 19 at Unicamp (20%). Many of the 19 at Unicamp are small and abundant species that are likely to be resistent to extinction; but many may wander better, especially as immatures, than is known at present. *Empidonax euleri* and *Turdus albicollis* are particularly likely to be transferred to the "travel-prone" category when more information is available, since both may be partially migratory.

DENSITY COMPENSATION

There were fewer birds per hour at Unicamp in general censuses than at Santa Genebra or Barreiro Rico (see above). In the one-hour censuses, there were 50.0, 87.5, and 79.9 birds per hour, respectively.

TAXONOMIC CHANGES

Passeriform birds and tyranniform birds, characteristic of forest edges and temperate-zone woodlands, both increase in small woodlots (Table 4). Most migrants are in these groups. Furnarioid tyranniform birds, nonmigratory insectivores of forests or of continuous vegetation, decrease in small woodlots. Other nonpasseriform birds also decrease, in part because such birds are often large (e. g., hawks) or are food specialists (parrots).

Table 4. Taxonomic composition of three São Paulo woodlot avifaunas

Taxon	Percentages of Avifauna			
	в	S	U	
Passeriformes	21	26	28	
Tyranniformes, Tyrannoidea	27	27	32	
Tyranniformes, Furnarioidea	15	14	10	
Others	37	33	30	

FOOD-USE CHANGES

Fruit eaters decreased from 9 to 6% of species in the two small woodlots, but omnivores were 23% in the two large woodlots compared to 27% in the smallest one. Insectivores were 51% in the largest woodlot, 54% in the two others. Carrion eaters and carnivores were 5-6% in all woodlots, nectarivores 5-8%, and granivores 2-5%. An increase in omnivory was expected in small woodlots, since omnivory would buffer against fluctuations in food supply (Willis, 1976); but the evidence instead suggests a shift toward insectivory in small woodlots.

DISCUSSION

Internal structures of these three woodlot avifaunas differed considerably, since decrease in area caused greater losses in some groups of species than in others. Two groups that seemed especially to decrease in small woodlots were large frugivores and large insectivores. Trunk and twig foragers and tangle-living insectivores also decreased considerably in small woodlots, as did diurnal carnivores, carrion eaters, and nocturnal insectivores. Aerial, edge, and treetop birds decreased little. Small ground and understory insectivores also decreased less than the average.

Reasons for high losses of large frugivores and large understory insectivores may be somewhat different. Most large frugivores fly well, and only about half the species in Appendix 1 are unlikely to fly between woodlots. Parrots and toucans could easily travel to the Campinas woodlots, and indeed a flock of *Aratinga leucophthalmus* has been seen to fly past Unicamp. Probably the large frugivores disappear from the small woodlots because they depend on scattered trees of different species at different seasons or years; and only large woodlots have enough tree diversity to keep populations from occasional famine. Hummingbirds, which also disappear from small

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woodlots even though most species travel easily between woodlots, probably face the same problem of finding food all year. Many hummingbirds may be nonbreeding vagrants in these woodlots, dependent on forests in the Serra do Mar for breeding and on scattered trees or bird feeders over the plateau at other times. Artificial feeding or plantings, or breeding in zoos, may be needed to preserve these species as forests are cut.

Large insects seem less likely to be absent in small woodlots, so that large ground insectivores should find food most of the year. Unlike frugivores other than the partially insectivorous trogons, most insectivores seem to stay on territories or wander little. Probably large insectivores and the trogons require large territories for their low-density foods, and hence few individuals occur per km2. Since most of these species do not move readily outside of forest, occasional years of unusual weather (leading to low food supplies) or predation can eliminate small populations in small woodlots. Perhaps, if a small woodlot had enough of a gradient in habitats to give a few pairs a wet place to live in dry years (and vice versa, or a cool place to live in hot years or vice versa), a small woodlot could preserve such species. Large carnivores and carrion eaters may have similar problems. Nocturnal insectivores are mostly ground-living species, and may also depend on environmental patchiness that is lacking in small woodlots. Increases in ground-living egg-eating opossums (Didelphis sp.) because of increased fruit fall in small woodlots could affect ground birds, too.

The loss of large insectivores near the ground in small woodlots is partly compensated by increased populations of small insectivores near the ground in such woodlots (Appendices 10, 11). It may be that partly insectivorous mammals also increase. However, the total energy flow through ground insects to birds, as well as species diversity of birds, does decrease in the smaller woodlots. Some of this change, perhaps most, is caused by loss of army ants and associated birds in the small woodlots.

The loss of upper-level frugivores in small woodlots is not compensated well at all. Frugivorous monkeys are also rare in the small woodlots. One *Cebus apella*, survivor of a group introduced in 1969 from cutover areas in Santa Genebra, still lives in the Unicamp woodlot. Both Cebus apella and Alouatta are still common in Santa Genebra and at Barreiro Rico, while the additional species Brachyteles sp., Callicebus personatus, and Saguinus sp., occur at Barreiro Rico. To a certain extent, edge omnivores like Pitangus sulphuratus and especially *Thraupis sayaca* and *Saltator similis* move into the small woodlots, but do not approach the fruit-use intensity of frugivores at Barreiro Rico. Fruits therefore either are less common in the small woodlots or fall to the ground there. Large ground frugivores of the Tinamidae and Phasianidae disappear from small woodlots, probably for reasons similar to losses of large ground insectivores. (Small tinamous, and the parrot Pionus maximiliani, did increase somewhat in the medium-sized woodlot and may be compensating for losses of other parrots there.) More mobile Columbidae increased to some extent in the lower levels of small woodlots, and probably use some fruit that falls to the ground. The addition of Leptotila rufaxilla in Santa Genebra may be related to the increase in density of Leptotila verreauxi there, making possible

a niche subdivision, as well as based on the presence of creekside woodlands. Increases in squirrel and lizard abundance in small woodlots are probably due to increased fruit on the forest floor.

Nocturnal ground mammals may also increase in small woodlots, causing the presence of nocturnal large owls in these woodlots and seemingly not at Barreiro Rico. This possible chain of effects needs investigation, for owls were not studied well. They could be responding to better soil conditions and forests of the Santa Genebra and Unicamp sites, or to other factors.

Small treetop and understory birds that eat fruit and insects (Appendices 2,3) persist in small woodlots better than do large birds, although in reduced numbers in the smallest woodlot. However, the absence of small treetop *Tangara* tanagers from all three woodlots is puzzling, as these birds occur in large forest tracts both eastward (Serra do Mar) and westward (Iguagu National Park).

Small understory, midlevel, and treetop insectivores (Appendices 12, 14, 15) persisted better in the small woodlots than did tangle insectivores (Appendix 13). Treefalls may be too few in number in very small woodlots, or edge species may outcompete tangle species for them. Edge insectivores (Appendix 16) persisted well in all woodlots, but were as high in numbers in the medium-sized woodlot as were midlevel insectivores. Perhaps the large woodlot had increased competition from large forest omnivores (Appendix 1), large ground insectivores (Appendix 10), and from trunk and twig insectivores (Appendix 9). The generally lower numbers of insectivores of all these types in the smallest woodlot are not readily explainable, unless very small woodlots do not provide enough habitat variation to support such small insectivores all year long by local movements. If small woodlots do support dependable insect populations, edge insectivores should move to such woodlots. Instead, edge omnivores (Appendix 4) moved into the smallest woodlot and replaced to some extent both fruit eaters and insect eaters. This suggests that generalist birds that can switch from fruit to insects or vice versa are favored in small woodlots, perhaps in cold waves or other environmental "disasters" that may be as important in small woodlots as at margins of tropical forests generally (Willis, 1976).

Roles of Migrants: Migrants were birds of the air, forest upper stories, and edge. No migrant species came from the categories of trunk or insectivorous understory birds. These forests lose leaves mainly in the canopy, perhaps accounting for lack of migrants from the understory. Migrants from the forest understory are a conspicuous part of the migratory avifauna in cold coniferous or deciduous forests of the northern hemisphere, which differs in at least that respect from the migratory avifauna in São Paulo. Migrants in São Paulo are mostly cotingas and tyrant-flycatchers rather than the nineprimaried oscines so common among North American migrants, too.

Migrants that eat seeds move into many northern woodlands in winter as well as to open areas and forest edges. This component of migration is very weak on the São Paulo plateau, where only *Haplospiza unicolor* winters in very small numbers. Many seed-eating birds of open areas or forest edges become rare or disappear in the winter: *Sporophila caerulescens*, for instance. These forests seem to produce fruit-eating birds rather than seed-eating species, except that ground-living tinamous and doves probably eat seeds as well as fruits.

Some summer migrants are known to eat fruits, at least in other regions (Morton, 1977 for Vireo and Legatus leucophaius). These migrants seem mostly insectivorous when on the São Paulo plateau, although detailed study is needed. Certain wintering and passage migrants of forest edge and cerrado zones are mainly frugivorous (*Elaenia* spp., *Turdus* spp.), and a few thrushes move into the local woodlots when certain trees are in fruit. *Pionus maximiliani* moves into the Unicamp woodlot mainly in the spring, but is thought not to breed there. Local movements of fruit-eating edge birds bring them into all woodlots (Appendix 4). The numbers of these birds in forest are rather low, even though they increase slightly in small woodlots as one might expect from the low numbers of resident frugivores in such woodlots.

Many hummingbirds appear in the local woodlots only when there are certain trees in flower, notably *Mabea fistulifera* (Euphorbiaceae) of the sandier parts of Barreiro Rico in April and May. The necessities and numbers of nectarivorous species should depend not on the size of local woodlots but on the presence of other woodlands in the Serra do Mar, close enough to permit altitudinal and local migrations that must be rather complex. However, the decrease in hummingbird numbers in small woodlots (with a small increase in *Coereba flaveola* populations in the medium-sized woodlot as a partial compensation) indicates that nectarivorous migrants must find food more easily in large woodlots. Perhaps, like fruit-eating species, they can stay longer in the larger woodlots, which are likely to have a greater seasonal spread of fruit and flower resources than are small woodlots.

Roles of Travel-prone Species: Local wanderers of many species visit all three woodlots in very small numbers. Some are probably wintering immatures or other birds that normally winter on the lower slopes of the nearby Serra do Mar: Basileuterus culicivorus certainly is at most accidental here, as the very similar B. hypoleucus replaces it about 50 km southeast of Campinas, inside the Serra do Mar near São Paulo. A snail-eating kite, Chondrohierax uncinatus, once soared past but did not enter the Unicamp woodlot. The ovenbird Cranioleuca pallida appeared and sang for several months in the Santa Genebra woodlot. These vagrants could colonize the local woodlots, and may occasionally do so. Some species counted as residents in the small woodlots (notably Chiroxiphia caudata in the Unicamp woodlot, where I have never seen an adult male) may be birds produced in larger woodlots nearby. There is enough movement that the small woodlots are probably enriched unduly by birds from larger tracts of forest, notably from the coastal mountains of São Paulo. Low species numbers in small woodlots may be due more to rapid extinction than to failure to immigrate.

Still, one must remember (with MacArthur and Wilson, 1967) that long distances of movement reduce chances of pairs reaching isolated woodlots. Also, not considered by MacArthur and Wilson, there is the possibility that source areas may be deforested. Gradual deforestation of the coastal ranges of São Paulo is to be expected, plus gradual loss of woodlots that now are scattered over the São Paulo plateau. When the Unicamp or Santa Genebra or Barreiro Rico woodlots (assuming that they survive) lose these outside sources of birds, they are likely to take up species configurations even more biased toward small and edge-living species than today. Large frugivores are likely to decrease even farther, and both they and specialized insectivores may be replaced by greater numbers (even if not greater diversity) of omnivores. Since oscine songbirds and tyrannoid tyranniforms are edge and omnivorous species *par excellence*, we may expect them to increase as the furnarioid tyranniforms and most other nonpasserines decrease. The avifaunas of these woodlots will take on a more "temperate-zone" aspect with these changes, except that understory insectivores will probably remain nonmigratory and seedeaters other than ground-living doves will never become common.

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Appendices

1. Forest birds eating large fruit and insects a

Penelone superciliaris-F	22	3	0 b
Columba cavennensis-FT	42	51	14
Pionus marimiliani-FT	71	100	7 °
Ara maracana-FT	11		
Aratinga leucophthalmus-FT	19		
Purrhura trontalis-F	43		
Amazona aestiva-FT	9		
Trogon rutus-0	11		
surrucura-O	52		
Ramphastos toco-FT	35		
dicolurus-FT	Ő		
Linguous lanioides O	1		
Titura cayana OT	Ē	0	
inquisitor.	10	•	
Puroderie scutatus-F	-0		
Cyanocorar chrysons O	23		
Pitulue fulicinosue	20		
rugus jungmosus-0	41		
Total	383	154	21
2. Small canopy omnivores d			
Phibalura flavirostris-OT	0		
Camptostoma obsoletum-OT	23	32	25
Oxuruncus cristatus-O	1		
* Vireo olivaceus-OT	114	160	51
Dacnis cauana-OT	32	10	0
Eunhonia chlorotica-OT	14	9	10
violacea-O	3	3	
Nemosia nileata-OT	3	5	
Hemithraunis ruticanillus-O	32	19	
Pipraeidea melanonota-OT	0	-3	0
Total	223	241	86
3. Small understory omnivores			
Chiroxiphia caudata-OT	142	1:)9	15
Manacus manacus-O	21	2	23
Schiffornis virescens-O	56	43	9
Antilophia galeata-OT	0	3	
Laniisoma elegans-O	0		
Pipromorpha ruțiventris-O	1		
Habia rubica-O	43	62	26
Trichothraupis melanops-O	68	61	5
Turdus albicollis-O	13	3	1
Total	344	283	79

4. Edge omnivores or frugivores Forpus xanthopterygius-FT Pitangus sulphuratus-OT Megarhynchus pitangua-OT Myiozetetes similis-OT * Myiodynastes maculatus-OT * Empidonomus varius-OT * Legatus leucophaius-OT Elaenia spp. 1, 2-OT flavogaster-OT Turdus leucomelas-OT amaurochalinus-OT rufiventris-OT Platycichla flavipes-OT Icterus cavanensis-OT Ramphocelus carbo-OT Tachyphonus coronatus-OT Tangara cayana-OT Thlypopsis sordida-OT Tersina viridis-OT Thraupis sayaca-OT Saltator similis-OT Total 5. Large ground frugivores Crupturellus tataupa-F obsoletus-F Odontophorus capueira-F Claravis pretiosa-FT Geotrygon montana-F violacea-FT Leptotila verreauxi-FT _ е *rufaxilla*-FT Total 6. Large nocturnal carnivores Tuto alba-T Pulsatrix sp. Total 7. Diurnal carnivores Leptodon cayanensis Heterospizias meridionalis-T Buteo brachyurus-T magnirostris-T Harpagus diodon-T Polyborus plancus-T Milvago chimachima-T Herpetotheres cachinnans-T Micrastur ruficollis Total

8. Carrion eaters			
Sarcoramphus papa-T	3		
Cathartes aura-T	14		
Coragyps atratus-T	76 f	247 f	70 f
Total	17		
9. Trunk and twig insectivores			
Picumnus cirrhatus-IT		88	62
minutissimus-IT	35		
Veniliornis passerinus-IT	11	~~	-
spilogaster-I'I'	3	29	20
Leuconerpes canaiaus-II	12	10	11
Camponhilus robustus	10	12	11
Colantes melanochloros.IT	10	4	
Piculus flaviaula-T	6		
Celeus flavescens-I	7		
Melanerpes flavitrons-I	ġ		
Xenops minutus-I	5		
rutilans-IT	13	1	3
Sittasomus griseicapillus-I	51	6	
Lepidocolaptes fuscus-I	4	1	
Campyloramphus falcularius-I	9	0	
Total	177	139	96
10. Understory birds eating large	ground arthro	opods	
Aramides cajanea-IT		1	12
Dromococcyx pavoninus-IT	2	0	
Baryphthengus ruficapillus-I	30		
Nonnula rubecula-I	1		
Malacoptila striata-I	11		
Dendrocincla turdina-I	5	2	
Dendrocolaptes platyrostris-I	10	2	
Xipnocolaptes albicollis-1	8		
Chamacaa campanicona I	126		
Solorwryg gogngor I	4		
Lochmias nematura T	-	0	
		0	10
Total	198	6	12
11. Understory birds eating small	ground arthro	pods	
Synallaxis ruficapillus-I	40	69	40
Myrmeciza squamosa-I	0		
Conopophaga lineata-1	48	115	154
melanops-1	9	11	1.**
Coryinopis aciaianai-1 Basiloutomus flavoolus I	14	11	15
busileulerus jiubeolus-1	40 21	14	10
ieucooiepiturus-1	91	14	
Total	165	283	279

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Philudor atricanillus-T	4		
Automolus leucophthalmus-IT	24 94	50	10
Thamnonhilus caerulescens.IT	Q1	169	107
Dusithamnus mentalis.	111	126	62
Drumonhila ferruginea.T	57	16	02
Mujohius atricaudus-IT	51	10	
Platurinchus leucorunhus.T	0		
mustacous T	0	•	14
Idiontilon orbitation T	24	3	14
Interference amanungen halus I	98	7	40
Leptopogon unuurocepnatus-1	19	29	3
Enephuonax euleri-1	39	08	69
Busileulerus nypoleucus-11	126	261	146
Culletoorus-11 Barrahooomor muticomo III		0	
Pyrrnocoma ruficeps-11		0	
Total	591	751	457
13. Insectivores of bamboo or forest	tangles		
Mackenziana severa-I	8	7	
Batara cinerea-IT		3	
Psiloramphus guttatus-I	6		
Drymophila ochropyga-I	3		
Terenura maculata-I	14		
Myiornis auricularis-I	38		
Todirostrum plumbeiceps-IT	0		
poliocephalum-I	55	96	84
Hemitriccus diops-I	1	2	
Total	125	108	84
14. Midlevel insectivores			
Piaya cayana-IT	36	119	33
* Coccyzus euleri-IT	0	1	0
Philudor lichtensteini-I	12		
Cranioleuca, pallida-I		1	
Hunoedaleus auttatus-T	12	78	
Hernsilochmus rutimarainatus-	91	151	
Pinrites chloris-T	2	101	
Pachuramphus castaneus.IT	1		
Sirustee sibilator-IT	34	1	
* Muionagie miridicata.IT	24	54	
Contonue ginereus IT	5	23	3
Attila matters IT	0	20	1
Tolmomulas subhurescens-T	68	68	32
	205	406	60
10(4)	200	490	05
15. Small treetop insectivores g			
* Platypsaris rufus-IT	0	34	
* Pachyramphus polychopterus-IT	8	8	0
Colonia colonus-IT	46	91	10
* Myiarchus swainsoni-IT	43	64	32

12. Understory birds eating small foliage arthropods

Myiopagis caniceps-I	19	14	
Cyclarhis gujanensis-IT	58	70	30
Parula pitiayumi-IT	19	6	7
Dendroica striata-IT Conirostrum speciosum-IT	20	0 35	1
Controstrum speciosum-11	20	00	
Iotai	221	322	00
16. Edge insectivores			
Crotophaga ani-IT	27	25	7
Tapera naevia-IT	4	17	2
Supallarie eniri IT	1	э 11	0
frontalis-IT	12	44	20
Thamnophilus doliatus-IT	1		2
Pachyramphus viridis-IT	1		
Tyrannus melancholicus-IT	0	32	16
Myiarchus ferox-IT	18	20	21
tyrannulus-IT Kninglasus, susminostuis III	6	2	
Cansiemnis flaveola IT	21	ۍ 16	2
Mujanhobus tasciatus-IT	21 17	13	5
Cnemotriccus fuscatus-IT	19	26	5
Serpophaga subcristata-IT		2	0
Idioptilon nidipendulum-IT	13	13	0
Todirostrum cinereum-IT	1	7	6
Troglodytes aedon-IT	4	79	14
Hylophius poecuotis-II	3	13	14
Total	156	305	103
17. Aerial insectivores			
* Ictinea plumbea-IT	14	24	0
* Chaetura andrei-IT	21	21	8
Cypseloides fumigatus-IT	9	0	
Streptoprocne zonaris-IT	5	21	
Notiochelidon cyanoleuca-IT	19	6	32
Progne chalubeg.IT	13	15	1 5
matal		00	417
Total	88	90	47
18. Nocturnal insectivores			
Otus choliba-IT	0		
atricapillus-I	3	1	
Glaucidium brasilianum-IT	3	0	
Nyctiaromus aloicollis-11 * Lunocalia semitorquata IT	7	11	4
Chordeiles sp-IT	•	1	0
Nuctiphrunus ocellatus-I	12	4	
Caprimulgus rufus-IT	4		
Nyctibius griseus-IT	1		
Total	37	14	10

19. Nectar and insect eaters			
Phaethornis pretrei-T	7	5	9
Colibri serrirostris-T	0	0	
Chlorostilbon aureoventris-T	4	2	6
Thalurania glaucopis	15	5	0
Amazilia lactea-T	8	12	4
versicolor	13	3	
Leucochloris albicollis-T	7	1	
Melanotrochilus fuscus-T	3	2	
Anthracothorax nigricollis-T	0	2	
Eupetomena macroura-T	0	1	
Heliomaster squamosus-T	1		
Coereba flaveola-T	8	25	
Total	66	58	20
20. Edge seedeaters			
Columbina talpacoti-T	14	32	
Cyanocompsa cyanea-T	1		
Sicalis flaveola-T	3		
Coryphospingus cucullatus-T	9	0	
Haplospiza unicolor-T		4	
Oryzoborus angolensis-T	0		
Sporophila caerulescens-T	25	2	
Tiaris fuliginosa-T	0	2	1
Volatinia jacarina-T	9	3	
Zonotrichia capensis-T	22	5	6
Total	83	48	7

- ^a In these appendices, omnivores are marked "O", frugivores are marked "F", and insectivores "I." "T" is a travel-prone species, known or likely to fly over open areas between woodlots. Numbers are birds seen or heard per 100 h of field studies at Barreiro Rico (left column), Santa Genebra (center), and Unicamp (right).
- ^bLess than 0.5 bird per 100 h afield.
- ^c Nonbreeding birds are italicized. Some, such as *Pitangus sulphuratus*, probably get food within a woodlot while breeding outside
- d Asterisks mark summering birds.
- Dashes mark cases where a bird breeds in a small woodlot but is absent from a larger one.
- f Nonfeeding birds.
- g Many may eat fruit.