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Nearctic avian migrants in coffee plantations and forest fragments of south-western Guatemala

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Summary

Habitats at intermediate and upper elevations of the volcanic cordillera of south-western Guatemala harbour a diverse terrestrial vertebrate fauna that includes at least 423 avian species, 108 of which are known to be Nearctic migrants, and 43 of which are known or suspected to have both resident and long-distance migrant populations. During the course of floral and faunal inventories in a proposed Multiple Use Area in this region from 1987 through 1991, FIIT researchers collected or observed 254 avian species, of which 44 are regarded as Nearctic migrants and 26 are known or suspected to have both resident and long-distance migrant populations. Study sites included climax and selectively logged lower montane forest fragments, as well as subtropical agroecosystems. Data are presented to support the conclusion that a significantly higher percentage of resident avian species reported from this region in the literature continue to occupy these habitats than do species known to undertake cyclical long-distance migrations. Non-quantitative, historical reports of relative abundance of all Nearctic avian migrants in the region during the early and mid-twentieth century are compared with current status of these species. Threats to Nearctic avian migrants in the western Guatemalan highlands are discussed, and areas of future research for ornithologists working with this community in the region are proposed. Recommendations are made to preserve or improve habitats on wintering grounds and along migration routes considered to be of critical importance for the long-term survival of a number of threatened and vulnerable Nearctic avian migrants in Guatemala.

Los hábitats localizados en elevaciones intermedias y altas de la cordillera volcánica del suroccidente de Guatemala poseen una diversa fauna de vertebrados que incluye por lo menos 423 especies de aves, de las cuales 108 son migrantes neárticos y 43 se sabe, o sospecha, que tienen poblaciones residentes y migratorias. Durante la realización de inventarios de flora y fauna en un Area de Uso Múltiple en esta región entre 1987 y 1991, investigadores de la FIIT colectaron u observaron 154 especies de aves, de las cuales 44 son conocidas como migratorias y 26 se sabe, o sospecha, tienen poblaciones residentes y migratorias. Las áreas de estudio incluyeron fragmentos de bosque climax, bosque montano bajo sujeto a tala selectiva y agroecosistemas subtropicales. Se presentan datos que apoyan la conclusión de que un porcentaje significativamente más alto de especies de aves residentes citadas en la región siguen ocupando estos hábitats, en comparación con aquellas especies que ciclicamente efectúan migraciones a grán distancia. Informes históricos, no cuantitativos, sobre la abundancia relativa de las aves migratorias neárticas en la región que datan desde inicios y mediados del siglo veinte, son comparados con el estado actual de estas especies. Un resumen final discute las amenazas a las aves migratorias neárticas en el altiplano guatemalteco y sugiere áreas de investigación para ornitólogos que trabajen con esta comunidad de aves en la región. Se presentan recomendaciones para preservar o mejorar los hábitats en zonas utilizadas durante su paso o estancia en el país y a lo largo de las rutas migratorias consideradas de importancia crítica para la supervivencia a largo plazo de las aves migratorias neárticas consideradas amenazadas o vulnerables en Guatemala.

Introduction

The past decade has witnessed a dramatic increase in public concern over dwindling numbers of migrant songbirds that winter in the Neotropics (Terborgh 1989). While ornithologists have predicted for some time that populations of many "Nearctic" avian species that effect seasonal movements to tropical America would inevitably suffer from accelerating habitat loss, fragmentation and modification (Rappole *et al.* 1983), few studies have been made in the region that have quantified the declines of individual migrant species, or to determine the underlying causes behind them.

It has been known for some time that migrant birds originating in both the eastern and western U.S.A. occur in mixed flocks in the western Guatemalan highlands during the fall (Wetmore 1941). A review of the literature indicates that there have been few recent studies on the status of Nearctic avian migrants in Guatemala. Although some accessible areas of the country have been reasonably well sampled by ornithologists (e.g. Tikal National Park, Sierra de las Minas), published information suggests that migrant birds have not received a great deal of attention from researchers.

The flora and fauna of western Guatemala were inventoried by a number of biologists during the past century. Noteworthy collections of the region's vertebrates were assembled by the Salvin and Godman expeditions (1879–1904), the U.S. Biological Survey (Goldman 1951), by A. W. Anthony (Griscom 1932), and by the University of Texas-FIIT (Campbell and Vannini 1988, Vannini 1989a). Apart from these general surveys, collections and observations of the region's avifauna have been accounted for by Wetmore (1941), Baepler (1962) and Skutch (1967), and summarized in Land (1970). The ability to identify many of the localities visited by earlier researchers and studying these same sites permits comparison of the actual relative abundance of a number of bird species with that reported in the literature.

The present study documents the status of 70 species of Nearctic avian migrants in a proposed Multiple Use Area located in south-western Guatemala, and examines some potential causes behind the apparent population declines evident in a significant percentage of this community.

The region

In this paper, the western portion of the volcanic cordillera at elevations above 1,000 m, the central plateau, and the Sierra de los Cuchumatanes are considered a single biotic province, the Western Highlands Region. This region once included the largest block of cloud-forest in Central America (de la Cruz 1982). The cordillera proper runs along a north-west–south-east axis from the Chiapan frontier as far east as 90°30′W, and consists of an uninterrupted chain of strato-volcanoes and massifs that dominate the Pacific coastal plain. The lower slopes of these volcanoes are dissected by ravines and watercourses, most of which feed the major river systems that flow into the Pacific.

The proposed Tres Volcanes Multiple Use Area is located near the geographic centre of the Western Highlands Region. It encompasses 192.5 km^2 of subtropical, lower montane and montane habitats between 1,000 and 3,771 m elevation. The Santiaguito crater, an active volcanic cone that arose after the catastrophic eruption of Volcán Santa María in 1902, has had considerable, continual impact on forests and plantations located adjacent to the proposed reserve's western boundary. Apart from the volcanoes and the Zunil Ridge, the dominant physiographic feature in the area is the Río Samalá basin, which divides the reserve on a roughly north–south axis.

Analysis of current land use in the area, compiled from aerial photographs and ground reconnaissance, shows that the proposed reserve retains 57.2% native forest cover, composed of 35.3% tropical broadleaf and 21.9% conifer or mixed associations. In spite of a deceptively high percentage of closed-canopy forest within the proposed reserve's boundaries, Tres Volcanes is best viewed as a mosaic of forest fragments of 500 ha or less with no natural corridor linking these to adjacent volcanic ecosystems. Most accessible broadleaf forests continue to be logged for commercially valuable members of the Rubiaceae, Meliaceae and Lauraceae families.

The remaining non-forest area, consisting of 82.4 km^2, has undergone extensive conversion over the past century, primarily into coffee, corn and vegetable production. Land-use analysis shows that c. 18.1% of total land mass of the proposed reserve is dedicated to the production of annual or perennial fruit, nut and vegetable crops, c. 12.2% is under coffee cultivation (shaded and unshaded), c. 11.5% has been affected by forest fires or ongoing volcanism, while the remaining 1% is urban.

The avifauna of the Western Highlands Region

At least 423 species of birds, including residents, migrants and transients, have been reported from the Western Highlands Region, making it the second richest avian province in northern Nuclear Central America (Vannini unpublished ms). Cluster analysis of 758 avian species distributed in nine biotic regions of Guatemala and Belize demonstrates that its closest affinities are with the Mesetan and Central Atlantic Highlands Regions, both contiguous along the eastern boundary of the Western Highlands Region. Across political frontiers, the region's avifauna is similar to that encountered in upland habitats in Chiapas, Mexico (Alvarez del Toro 1971).

Characteristic resident birds of the region originally included the Atitlán Grebe *Podilymbus gigas*, White-breasted Hawk *Accipiter striatus chionogaster*, Horned Guan *Oreophasis derbianus*, Bearded Screech-owl *Otus barbarus*, Rufous Sabrewing *Campylopterus rufus*, Mountain Trogon *Trogon mexicanus*, Blue-throated Motmot *Aspatha gularis*, Belted Flycatcher *Xenotriccus callizonus*, Unicolored Jay *Aphelocoma unicolor*, Blue-and-white Mockingbird *Melanotis hypoleucus*, Rufous-collared Robin *Turdus rufitorques*, Golden-browed Warbler *Basileuterus belli*, Pink-headed Warbler *Ergaticus versicolor*, Azure-rumped Tanager *Tangara cabanisi* and the Guatemalan Junco *Junco phaeonotus alticola* (Vannini unpublished ms).

With the recent extinction of the Atitlán Grebe, Guatemala has no known endemic avian species, although many of those listed above have distributions limited to the highlands of Chiapas, Guatemala, Honduras and El Salvador (Monroe 1968, Land 1970, Alvarez del Toro 1971, Thurber *et al.* 1987). Of the 12 species classified as threatened in Guatemala by ICBP/BirdLife (Collar and Andrew 1988), eight are known to occur in the Western Highlands Region. Of these, only the Golden-cheeked Warbler *Dendroica chrysoparia* is a Nearctic migrant.

A total of 412 species of birds have been reported from or are presumed to occur within the boundaries of the proposed Tres Volcanes Multiple Use Area (Vannini unpublished ms), and of these, 261 are residents or local migrants, 108 are Nearctic migrants, and 43 are known or suspected to have both resident and migrant populations (see Appendix 1). The importance of the region within the context of a conservation strategy for Nearctic avian migrants in Guatemala is highlighted by the fact that of 240 long-distance migrant species reported for the country (Rappole *et al.* 1983, Vannini unpublished ms), 151 (c. 63%) have been collected or observed in this area during recent years.

Research sites

Five forest and plantation sites were surveyed with mist-nets across both "wet" (May–October) and "dry" (November–April) seasons by FIIT researchers between 1987 and 1991. Together, these include representative types of all major habitats (including agroecosystems) in the region, with two exceptions: montane "zacatón' *Muehlenbergia* spp. meadows and Guatemalan fir *Abies guatemalensis* forests. In addition to investigation at the study sites, point counts and casual observations were also made throughout much of the region during the same period. Results from both visual and mist-net surveys were utilized for the purpose of estimating relative abundance. Profiles of vegetational plots at four of the five formal sites are provided in Appendix 3.

Two sites are located on private subtropical plantations, two in municipal forest reserves, and one on a private forest reserve. Riparian or gallery forest tracts were present at all sites except the Chicavioc forest reserve.

The primary site was Finca "El Faro", a coffee, cardamom and macadamia plantation located on the south-western boundary of Tres Volcanes (Volcán de Santa María in Griscom 1932). The diurnal raptor fauna of this farm has been described (Vannini 1989b), and a check-list of the avifauna has been published (Vannini 1989a). Plantation conditions on "El Faro" include coffee under man-

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aged shade, unshaded coffee, cardamom under managed shade, and a mature macadamia orchard. Until it was incinerated by a volcanic eruption from the Santiaguito crater in May 1990, a significant tract of lower montane broadleaf forest existed on this farm above the 1,550 m contour.

Secondary sites include Finca "La Esperanza", a coffee plantation previously surveyed by Anthony in 1924–1925 (Finca "Ciprés" in Griscom 1932), and the Chicavioc forest reserve, both of which were surveyed during 1990–1991. The Esperanza site, essentially undisturbed except for understorey clearing, is adjacent to a large area of unshaded coffee on Finca "Las Nubes" (Sierra de las Nubes in Griscom 1932).

Sites surveyed for less than two months during the dry season include the Georginas forest reserve, and Finca "El Recreo" (Santa María in Griscom 1932), a small coffee farm in the Río Samalá valley. Collections and observations were made at both locations during 1991.

Conclusions drawn in the present study result from over 10,000 man-hours of observation in the region, and data from 309 individual Nearctic migrants taken in mist-nets at research plots from 1987 to 1991. Acoustical luring was not utilized during the course of the study, nor was the presence of any species confirmed on the basis of vocalizations alone.

For a summary of the materials and methods utilized during avian inventories in the region, see Vannini (1989b).

Results and discussion

A total of 184 species of resident or locally migrant birds, 44 species of Nearctic migrants, and 26 species of resident bird known or suspected also to have populations that conduct cyclical long-distance migrations were confirmed from Tres Volcanes during the period 1987–1991. These figures represent 70.8%, 40.4% and 61.1% of their respective categories. In all, 61.6% of the total number of avian species historically reported from the region were captured or observed during this same period.

During the course this study, it became apparent that a significant number of species of Nearctic migrants that had been classified by previous authors as "not uncommon", "fairly common", "common", or "abundant" in this region (Griscom 1932, Wetmore 1941, Land 1970) had suffered marked declines in relative abundance. Of 65 migrant species formerly considered to be "abundant" (see Appendix 2), only 22 (33.8%) appear to have populations that remained stable. Of the remainder, 18 species (27.7%) seem to be markedly less common than was reported earlier this century, and 25 (38.5%) have apparently either disappeared entirely from the region or are now rare visitors.

The possibility exists that these figures could be artefacts of collection and observation. A similar, non-quantitative evaluation of the status of the resident avifauna utilizing the same criteria suggests that this has not been the case. In contrast with the above figures for Nearctic migrant species, only 16 (6.2%) of resident species formerly classified as "common" (none "abundant") were not observed in Tres Volcanes during the period 1987–1991. Eleven of these tend to be restricted to conifer forests or mixed associations above 2,500 m elevation, the region sampled least intensively by FIIT researchers. Only a small number of these "missing" Nearctic migrant species appear to favour these habitats on northern Central American wintering grounds (Land 1970, Alvarez del Toro 1971, Rappole *et al.* 1983, Stiles and Skutch 1989). Additional evidence against observational bias being the principal factor behind these figures is that our fieldwork produced 12 records of avian species previously unreported for the Western Highlands Region (three Nearctic migrants), seven species new for the Pacific versant (two Nearctic migrants), and two species previously unreported for Guatemala (one Nearctic migrant) (Vannini 1989a).

In summary, two-thirds of the avian migrant species expected to be observed at least once daily in suitable habitat during the dry season in the region are now apparently uncommon, rare or locally extinct. This conclusion is concordant with the widespread belief that populations of many Nearctic avian migrants have suffered significant declines over the past two decades (Terborgh 1989).

The Nearctic migrants of the proposed Tres Volcanes Multiple Use Area

For purposes of discussion, the Tres Volcanes region is divided into three elevational groups: lower (1,000–1,500 m), intermediate (1,500–2,500 m) and montane (2,500–3,771 m).

The long-distance migrant avifauna of lower elevations is dominated by seven ubiquitous passerines that together represent more than half of all captures during the period 1987–1991, and a similar percentage of observations. In descending order of abundance they are: Swainson's Thrush *Catharus ustulatus*, Wilson's Warbler *Wilsonia pusilla*, Tennessee Warbler *Vermivora peregrina*, Western Tanager *Piranga ludoviciana*, Orange-crowned Warbler *V. celata*, Rose-breasted Grosbeak *Pheucticus ludovicianus* and Western Kingbird *Tyrannus verticalis*.

All seven of these species are known to be both transients and winter residents of western Guatemala (Land 1970; pers. obs.). Six of the seven have been collected in both forest and agroecosystems throughout the region, but the data available seem to indicate an affinity for mature plantation habitats. Most of these species may be observed in the region from mid-October through late April. The latest date when all seven species were observed together at one site is 17 April.

The long-distance migrant community of intermediate elevations in the area is typical of the open, highly disturbed habitats predominating in the Samalá valley. The most commonly observed migrants are: Barn Swallow *Hirundo rustica*, Rough-winged Swallow *Stelgidopteryx serripennis* and Eastern Bluebird *Sialia sialis*. These three species are most often observed adjacent to corn and vegetable plots near the 2,000 m contour.

Montane conifer and broadleaf associations are generally lower in species diversity than the preceding two habitats in this region, and no single migratory species appears to be as abundant as several that occur in subtropical and lower montane ecosystems.

Three transients were observed in considerable numbers for brief periods during the fall, winter and spring at elevations below 3,000 m. Large flocks of Swainson's Hawks *Buteo swainsoni* were noted during October and early November; Cedar Waxwings *Bombycilla cedrorum* were extremely abundant in the region for brief periods during late December to early January; and flocks of Northern Orioles *Icterus galbula* assembled during April. Both Cedar Waxwings and Northern Orioles are winter residents elsewhere in Guatemala (Land 1970).

Several species of wader, duck and shorebird are occasionally noted along the Río Samalá and Río Nimá. The lack of wetlands in the region explains the paucity of records for these groups.

Factors relating to the decline of certain populations of Nearctic avian migrants at Tres Volcanes

A number of causal factors have been implicated in the population declines of Nearctic avian migrants. These were summarized in Rappole *et al.* (1983) into broad categories that include habitat loss, modification and fragmentation; environmental contamination; and direct exploitation. A subsequent study that defined threats to avian migrants on a world-wide basis reached similar conclusions (Biber and Salathé 1991).

Attempts to correlate habitat loss or degradation with population declines in 43 species of Nearctic migrants in Tres Volcanes produced no clear trend. Conventional wisdom dictates that expansion of the agricultural frontier should benefit groups such as buteonine hawks, doves, tyrant flycatchers, swallows and many emberizid finches, while at the same time have negative impact on populations of brush- or timber-dependent thrushes, wood-warblers and tanagers. An examination of Appendix 2 suggests that this has not been the case: species usually associated with open or disturbed habitats have apparently declined alongside those dependent on forest.

The human and natural pressures exerted on the Tres Volcanes ecosystems, in combination with those present outside the region that also affect the status of avian migrants, suggest that the causes behind population declines in this community are probably difficult to redress. Fieldwork in the region indicates that, aside from habitat loss and fragmentation, several other events may have played important roles resulting in apparent local extinction or significant declines in relative abundance since the early 1960s.

Selective or wholesale removal of floral components and disruption of floral cycles

The widespread conversion of subtropical wet forest to plantation has had an obvious negative impact on vegetational diversity in the region between 1,000 and 1,600 m. Parallel to the development of extensive coffee, cardamom and macadamia plantings on the Pacific versant, the fertile central sector of the Samalá valley has been almost completely denuded of native arborescent flora in order to establish market vegetable plots. The loss of critical floral components is a factor that has been linked in the past to declines in Nearctic avian migrant populations elsewhere (Rappole *et al.* 1983).

Fortunately, a fairly complete picture of the original floral community is available, owing to the Field Museum's work in the region earlier this century (Standley and Steyermark 1958–1979). We also have a reasonable idea of what the region originally looked like from photographers and geographers who worked in the region from the latter part of the nineteenth century through to 1941 (McBryde 1945, Burns 1986), and from the agricultural practices that were prevalent at that time.

FIIT researchers are still conducting baseline inventories of the region's flora, but based on preliminary data and observation it appears likely that three relatively recent activities are shaping the faunal community in general and the Nearctic avian migrant community in particular.

Much of Tres Volcanes has been selectively logged in the past, beginning in the early part of this century, and accelerating during the past decade. While a few of the targeted softwood species remain common in the region (e.g. *Cupressus lusitanica, Pinus pseudostrobus*), several are now largely restricted to inaccessible areas (*Abies guatemalensis, P. hartwegii, P. ayacahuite*). The effects on Nearctic migrants resulting from a reduction of their numbers, and the subsequent recolonization or establishment of monocultures of more adaptable or faster-growing species (especially *C. lusitanica*) needs to be evaluated.

The logging of hardwoods has had a great impact on the structure of subtropical and lower montane ecosystems in this region. Species of economic value that have been largely eliminated from the forest matrix in most areas include several that are known to be dispersed by frugivorous birds (*Litsea glaucescens, Nectandra sinuata, Ocotea* spp., *Phoebe* spp., *Prunus capuli*), as well as a number that provide food and cover for the native avifauna (*Quercus* spp., *Cedrela pacayana, Guarea* spp., *Arbutus xalapensis, Alnus* spp., *Genipa* spp.) (pers. obs.). Large light-gaps and sheet erosion resulting from extraction of these species on slopes that frequently exceed 30° are visible throughout the region, and appear to regenerate slowly. The removal of these and other arborescent species from the Tres Volcanes ecosystems may be exerting significant influence on the avian community's composition and overall numbers.

Through the late 1960s, coffee was primarily cultivated under native shade (thinned forest) in Guatemala. Personal experience and comments in the literature (Griscom 1932) indicate that traditional low-traffic/low-input coffee cultivation has had a relatively minor impact on avian communities in the country. During the 1970s, the trend shifted towards coffee under managed shade, typically trees of the genus *Inga* (Mimosaceae), in order to establish high-density plantings of precocious, dwarfed coffee varieties. This conversion, combined with other intensive management practices implemented thereafter, has rapidly reduced the amount of suitable habitat for resident and migrant avifauna.

Several species of *Inga* are utilized as canopy for shade-dependent crops in Guatemala. In the Tres Volcanes region, the most commonly cultivated is "chalum" (*I. spuria*). Two additional species are frequently observed as natural components of moist forests through 2,000 m elevation (*I. micheliana* and *I. paterno,*), while a third indigenous species (*I. punctata*), is restricted to the piedmont at elevations below 1,200 m.

At lower elevations within the Tres Volcanes region, chalum flowers from January through March. This species, like most of its congeners, produces a large number of compound inflorescences and large, leguminous seed-pods attractive to many vertebrates (including man). The floral parts secrete copious amounts of nectar, which attracts a number of invertebrates, chiropterans and birds. In addition, members of this genus possess extrafloral nectaries on newly expanded leaves, which appear to promote ant associations at low and intermediate elevations (Koptur 1983).

Observations made in mature, unpruned chalum stands grown over coffee and cardamom in western Guatemala suggest that these trees constitute an extremely valuable resource for resident and migrant birds. Recent reports by other researchers working with migrant songbird communities in shaded coffee and cocoa plantations in southern Mexico appear to support these findings (Greenberg in press). A number of species have been observed to consume floral parts, tap nectaries and glean the limbs, leaves and inflorescences of chalum for invertebrates.

There has been a recent trend towards severe pruning of chalum prior to flowering in order to reduce the amount of human traffic by collectors of its edible seed-pods, which results in collateral damage to coffee trees. The vast majority of chalum cultivated in the region now has primary limbs removed early in the year, resulting in physical conditions unsuitable for most native birds. This also eliminates a valuable food source once available at the height of the dry season, when Nearctic migrant diversity and densities are high in this region (pers. obs.).

Of more concern is the increasing area that has been transformed to unshaded or "sun-hedge" coffee plantations either as the result of conversion of native forest or of existing low-input plantations. This system of management, first proposed by Cowgill (1958) based on experience in Guatemala, was reintroduced from Costa Rica and El Salvador in the early 1980s, and has had a catastrophic impact on native flora and fauna at low and intermediate elevations. Coupled with the total elimination of arborescent cover, these so-called "full sun" plantings also require significantly greater inputs in the form of herbicides, insecticides, nematicides and fertilizer, with the attendant proportionate increase in human traffic. Preliminary data derived from investigation in the Tres Volcanes region indicate that almost all vertebrate populations collapse during the initial conversion, and do not recover as long as these intensive management practices continue.

Unregulated use of agrochemicals

As discussed earlier, changes in plantation management regimes in coffee have resulted in the increase of both frequency of application and volumes used of a wide range of pesticides (comprising acaricides, larvacides, insecticides, ovicides and nematicides) and fungicides. Interviews with local dealers of agrochemicals familiar with use patterns in the Tres Volcanes region revealed that a number of highly toxic pesticides are routinely applied to both coffee and vegetable crops (J. Pontazza pers. comm.).

An evaluation of the 10 most commonly utilized pesticides in coffee and market vegetable plantations showed that two target lepidopteran larvae (Permethrin, Dipel), three are combination insecticide-nematicides (Methomyl, Oxamyl and Terbufos), and five are broad-spectrum, non-selective insecticides (Carbaryl, Malathion, Methamidophos, Aldrin and Endosulfan). Known toxicity to birds varies from extremely high (Methamidophos, an organic phosphate insecticide) to nil (Dipel, a bacterial larvacide) (Thomson 1989). Frequency of use appears to range from seven to 14 days in vegetable crops to single, annual applications in coffee. The commonest method of application is by backpack sprayer.

In addition to pesticide use by the private sector, USDA-APHIS has announced the implementation of an aerial Malathion bait and spray programme in Guatemala to eradicate of the Mediterranean fruit fly *Ceratitis capita* in Guatemala. Targeted areas include the low and intermediate elevations along the Pacific versant of the Tres Volcanes region. Although an environmental impact assessment of the programme has been published (USDA 1991), its findings have been widely criticized on a local level.

Mortality linked to pesticide use in Palearctic birds wintering in the western Sahel has recently been documented (Mullié *et al.* 1991). Based on these findings and observations made during the course of this study, the direct effects that agrochemicals are having on resident and migrant avifauna are probably significant, but remain difficult to quantify at this time. Nevertheless, the threat posed by pesticides to native and migrant avifauna deserves immediate research in order to determine the impact that these chemicals have on direct mortality (fatal intoxication), indirect mortality (non-lethal intoxication that may result in increased mortality through predation), and reproductive failure on breeding grounds.

Direct exploitation

A number of Nearctic avian migrant species are subject to direct mortality from humans in the Tres Volcanes region. The heaviest pressure is on wintering populations of pigeons, doves and songbirds. Owing to the scarcity of lakes and marshes in the area, the few ducks that wander through are not traditional targets.

Both Mourning Doves *Zenaida macroura* and White-winged Doves *Z. asiatica* are sporadically trapped and shot by subsistence and sport hunters at several sites on the Pacific versant (pers. obs.). Although the cagebird trade in the area is largely concentrated on showy representatives of the resident avifauna (cracids, psittacines and toucans), some trapping of Nearctic migrant passerines occurs there as well as elsewhere in the Western Highlands Region and on the Pacific coastal plain. Favoured species include all thrushes, most tanagers, Painted Bunting *Passerina ciris*, Indigo Bunting *P. cyanea* and several oriole species (pers. obs.).

Elsewhere in the Western Highlands, Baepler (1962) reported that the Kanjobal Maya in the Soloma region of Huehuetenango attract large flocks of Nearctic avian migrants (including waders, shorebirds, cuckoos, flycatchers and wood-warblers) to bonfires built on ridges at c. 3,000 m elevation in the Sierra de los Cuchumatanes during the fall. These birds are then clubbed and consumed or sold. This method of capture, known as "chival", is still widely practised in the area (J. E. López pers. comm.). These observations underline the dangers posed by brightly lit industrial projects located at high altitudes in the region. Other trapping techniques utilized in Guatemala include the use of bird lime, fish nets, and wire traps baited with decoys.

Of greatest concern are the numbers of slingshots evident in Guatemala in general and this region in particular. Traditional bird-hunting methods practised by the highland Maya historically included the use of wooden blowguns and fired clay pellet projectiles. The spread of rubber-propelled slings is of relatively recent origin, probably dating from the early twentieth century. Proliferation has been rapid. Today, it is common to see youths or agricultural labourers carrying carved wooden slingshots and dead songbirds throughout western Guatemala (pers. obs.). It would be difficult to overestimate the impact that thousands of slingshot-armed rural inhabitants have on avian communities.

Environmental degradation outside the Tres Volcanes region

The loss, modification or fragmentation of ecosystems is not a problem restricted to the Western Highlands Region of Guatemala. Deforestation, conversion of grasslands and aquatic habitats to agriculture, and urban development on migration routes and breeding grounds may, in some cases, play important roles in contributing to the apparent population declines of the long-distance migrant avifauna observed at Tres Volcanes and elsewhere in the Neotropics (Thurber *et al.* 1987, Stiles and Skutch 1989, Rappole 1991).

A noteworthy example involves the Golden-cheeked Warbler. Historically, this endangered wood-warbler was known to winter in subtropical or lower montane moist forests from southern Chiapas to central Nicaragua (Monroe 1968, Land 1970, Rappole *et al.* 1983), primarily in conifer and pine–oak woodlands. Recently it has also been observed in broadleaf associations in lower montane and tropical wet forests of central and eastern Guatemala (Howell and Webb 1992; pers. obs.). While conifer forests and mixed associations remain common throughout upland areas of northern Central America, the Ashe juniper–cedar–oak woodlands inhabited by the species on the breeding grounds of the Edwards Plateau and Dallas County in Texas have been reported to be under considerable pressure from development (Anon. 1991). It is tempting to speculate that this species is more threatened by urban sprawl within its geographically and ecologically restricted breeding range than it is across a wide variety of habitats that it occupies in northern Central America during fall and winter.

A parallel case for population declines that may be the product of human activities in the Nearctic include observations of poisoning in Townsend's Warblers *Dendroica townsendi* by drifting pesticide spray in commercial conifer plantations in the Pacific north-western U.S.A. (D. Whitacre pers. comm.). This species, along with American Redstarts *Setophaga ruticilla* and wood-pewees *Contopus* spp. share the behaviourial trait of hunting flying insects from exposed perches in aerial sallies. Perhaps coincidentally, both these species of wood-warblers and all migrant wood-pewees appear to have suffered population declines at Tres Volcanes.

Nest predation and nest-parasitism in fragmented breeding habitat has been cited as a factor involved in the declines of Nearctic avian migrants (Wilcove 1985). Several species reported to be suffering extremely high rates of nest-parasitism by Brown-headed Cowbirds *Molothrus ater* in the U.S.A. are now rare or unreported for Tres Volcanes (e.g. Wood Thrush *Hylocichla mustelina*).

I explored the possibility that a differential rate of loss exists between those avian species whose breeding grounds are concentrated in the western and those of the eastern U.S.A. Of the 65 species listed in Appendix 2, 38 have breeding populations on both versants, 19 breed in the western U.S.A., and eight breed in the eastern U.S.A. (Rappole *et al.* 1983). A statistical analysis showed no discernible relationship linking population declines at Tres Volcanes to habitat loss on either versant of Mexico or the U.S.

The impact that habitat disturbance on migration corridors or adjacent lowland ecosystems has on the Nearctic migrant avifauna of Tres Volcanes remains poorly understood. The expansion of the agricultural frontier on both coasts of Mexico and Guatemala has been rapid over the past two decades (Rappole 1991; pers. obs.). It is possible that populations of many species whose migration routes cross regions most affected by man's activities in the U.S.A., Mexico and Guatemala, as well as species that effect seasonal elevational migrations from Guatemalan tropical life zones into the subtropics or highlands, are more vulnerable to local extinction than populations of species that travel less disturbed migration corridors directly into the Western Highlands Region. Further study may demonstrate that populations of trans-Gulf migrants (originating in the eastern U.S.A.) are less at risk than those utilizing overland routes.

Thurber *et al.* (1987) proposed habitat loss outside of El Salvador as a possible cause for decline in the population of Black-throated Green Warblers *Dendroica virens* evident this century. This species has apparently also decreased in numbers at Tres Volcanes (see Appendix 2).

Interspecific competition within the Nearctic avian migrant community or between members of resident and migrant communities

It has been known for some time that many Nearctic avian migrant species defend territories on Neotropical wintering grounds (Thurber and Villeda 1980, Rappole *et al.* 1983, Stiles and Skutch 1989, Winkler *et al.* 1990), while others appear to exhibit little or no site-fidelity.

A study in Veracruz, Mexico (Rappole and Morton 1985), documented that modification of a forested plot there resulted in significant changes in the composition of the forest-dwelling avian community and passerine guild structures. Declines were reported in both species diversity and relative abundance following disturbance and fragmentation. These declines were coupled with an apparent increase in the size of territories required by winter resident Hooded Warblers *Wilsonia citrina*.

Few studies on site-fidelity in wintering Nearctic migrants and the size of territories they defend have been effected to date in Guatemala (Whitacre *et al.* 1992). The results of the Rappole and Morton (1985) study suggest the possibility that interspecific competition between Nearctic avian migrant species, or with the resident avifauna, or both, may result in the displacement of less adaptable members of the avian community from modified or fragmented ecosystems. A more recent paper, discussing observations made in southern Mexico (Greenberg in press), documents defence of feeding territories against both conspecifics and other avian migrants by wintering Yellow Warblers *Dendroica petechia*.

Rappole and Morton speculated that wandering individuals, forced from forest habitats as a result of their alteration or loss, may result in a floating population of normally territorial Nearctic migrant species. These individuals are believed to be unable to establish territories in previously occupied preferred habitat, and are presumably obliged to tenant marginal habitats where they are subject to a greater risk of predation and an unstable resource base. Winkler *et al.* (1990), referring to a radio-tracking study conducted in Veracruz, reported significantly higher mortality rates in nomadic Wood Thrushes than in territorial individuals.

In the same region Rappole and Morton (1985) documented several instances of agonistic interaction between resident and long-distance avian migrant species, but concluded that interspecific aggression between these two groups was rare and had negligible impact on either group.

It is puzzling that many families of Nearctic avian migrants historically known from the Tres Volcanes region contain both species that have apparently increased in numerical density and species that appear to have suffered local extinction or have declined significantly in numbers since the 1960s. Many of these families, such as wood-warblers and tyrant-flycatchers, have species that share broadly similar ecological requirements in the Neotropics but originate in separate regions or habitat types (Rappole *et al.* 1983). Discrete populations presumably face varying levels of pressure on their breeding grounds and/or migration routes, resulting in differing population trends on their wintering grounds. Alternatively, specific floral or faunal components indigenous to ecosystems on which a given species is dependent may have been directly removed by man, or have themselves been unable to adapt to habitat modification and declined owing to indirect intervention. This may also be a factor contributing to conflicting trends in populations observed in this region. It is also likely that a number of resident and Nearctic avian migrant species are considerably more adaptable to alteration or fragmentation of habitat than others (Rappole 1991). Likewise, these "deforestation tolerant" species may successfully exploit man-altered ecosystems to the degree that related species with similar ecological requirements, but more susceptible to decline owing to habitat modification, may be displaced or locally extirpated.

An additional possibility is that species which do not normally defend fixed territories are more likely to adapt to increasingly adverse conditions on Neotropical wintering grounds than those that do. In theory, these nomadic individuals should be less susceptible to changes in habitat size and structure at specific localities. Analysis of the behaviour of 14 of the 17 species of wood-warblers listed in Appendix 2 shows that eight of the 11 species that are known or suspected to maintain winter territories elsewhere in Central America and southern Mexico have suffered apparent population declines at Tres Volcanes. Significantly, three species appear to have retained stable populations: two species not known to defend territories remain common or abundant, and the single species (*Wilsonia pusilla*) believed to exhibit either behaviour is also abundant in the region. Classifications in this analysis are derived from Thurber and Villeda (1980), Rappole *et al.* (1983), Rappole and Morton (1985), Stiles and Skutch (1989), and personal observation.

The evidence available indicates that increased interspecific competition, resulting from a shrinking resource base, may result in higher rates of displacement and/or direct mortality in Nearctic avian migrants. If so, this could be an increasingly important factor affecting Nearctic migrant diversity in regions subject to indiscriminate exploitation of forest resources.

Conclusions and recommendations

A combination of several human activities, including habitat modification in overwintering areas, along migration routes, and on northern breeding grounds, in addition to unregulated agrochemical use and direct persecution, appear to have reduced or extirpated populations of a number of Nearctic avian migrant species in the proposed Tres Volcanes Multiple Use Area of Guatemala during the past few decades. Several other secondary pressures resulting from these human activities may also be important factors causing population declines in this community (i.e. interspecific competition, chemical and microbiological contamination).

Reversing this trend will require a major effort to preserve remaining native ecosystems, restore or otherwise improve degraded habitat, implement practical measures to reduce or rationalize direct exploitation and regulate the use of agrochemicals in the region. Outside of Tres Volcanes, cooperation on both a national and international level is required to safeguard key habitats occupied by Nearctic avian migrants on their breeding grounds, along migration corridors and in tropical lowland ecosystems. A country-wide educational campaign is also required from the National Council of Protected Areas (CONAP) and other local conservation groups to reduce the impact that slingshots are having on songbirds and other small vertebrates.

After Mexico, Guatemala is the country containing the highest species diversity of Nearctic avian migrants in the Neotropics (Rappole *et al.* 1983, Vannini unpublished ms). Effective conservation measures to protect the forested slopes of the volcanic cordillera in western Guatemala, the remaining Pacific coastal wetlands, the subtropical and lower montane ecosystems on the Caribbean versant, and the tropical forests of the Petén department, remain critical to ensure the long-term survival of populations of winter residents and other avian species whose migrations take them through the country.

Both the Sierra de las Minas and the northern Petén have recently been declared Biosphere Reserves. To date, there is no national park, reserve or equivalent management area in south-western Guatemala. International and local interest has long been focused on preservation of lowland habitats in northern Guatemala, despite the fact that intermediate and upland habitats of western Guatemala contain high biological diversity, a number of regional endemics, and a unique vegetational association not replicated outside of the highlands of eastern Chiapas, Mexico.

Parallel to implementing conservation programmes in the region, studies are urgently required to determine patterns of local elevational migration, to identify critical habitats threatened by development, and to document the existence of other "funnel points" where enormous numbers of Nearctic migrants gather for brief periods during the fall migration (e.g. the Sierra de los Cuchumatanes and the upper slopes of the central volcanic cordillera) (Baepler 1962; pers. obs.). Additional investigations into site-fidelity and behaviour on Guatemalan wintering grounds would also be useful in order to provide wildlife managers with better criteria for declaration and management of new protected areas. Responding to this need for more data, in early 1993 FIIT initiated a long-term study of the composition and behaviour of migrant wood-warbler communities in four twinned sites at Tres Volcanes in order to compare population dynamics and territoriality in both mature and disturbed subtropical habitats.

While land acquisition by foreign conservation organizations remains a politically sensitive issue throughout much of the Neotropics, a properly coordinated effort to purchase key properties in countries with flexible land tenure laws in Central America (Guatemala, Honduras and Costa Rica), and further managed by *private* conservation trusts within the context of a regional network of protected areas, may be the only viable short-term option to preserving critical habitats for Nearctic migrants. Five regions in western Guatemala high in Nearctic avian migrant diversity and where this option is feasible are: the estuary and marsh at the Manchón-Guamuchal adjacent to the Chiapan border; the Pacific versant of the Atitlán complex (Volcanes Atitlán, San Pedro and Tolimán); the Pacific versant, eastern and western slopes of the Acatenango-Fuego complex; the upper slopes and inland valleys of the Sierra de los Cuchumatanes; and the Tres Volcanes region.

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Appendix 1. List of Nearctic avian migrants reported historically or recently from the Tres Volcanes region of the western Guatemalan highlands and their probable elevational distribution in the area.

Species marked with an asterisk (*) are known to have both resident and migrant populations; species marked with a query (?) are suspected of having both resident and migrant populations. Elevational data is provided from the lower limit of the Western Highlands Region along the Pacific piedmont (1,000 m) through the crater rim of Volcán Santa María (c. 3,770 m). C, collected or observed by FIIT researchers during the period 1987–1991.

Family/species	Resident population	Elevational range (m)	
Podicipedidae			
1 *Podilymbus podiceps*	*	1,000–1,500	C
Ardeidae			
2 *Ardea herodias*	*	1,000–1,550	
3 *Botaurus lentiginosus*		1,000–1,350	
4 *Casmerodius albus*	*	1,000–1,350	

Appendix 1 – continued

Family/species	Resident population	Elevational range (m)	
5 *Butorides striatus*	*	1,000–2,050	
6 *Egretta caerulea*	*	1,000–1,350	
7 *Egretta thula*	*	1,000–1,550	
8 *Ixobrychus exilis*	*	1,000–1,500	C
Anatidae			
9 *Anas acuta*		1,000–1,550	
10 *A. americana*		1,000–1,500	
11 *A. clypeata*		1,000–1,500	
12 *A. discors*		1,000–1,550	C
13 *Aytha affinis*		1,000–1,550	
14 *A. americana*		1,000–1,500	
15 *A. collaris*		1,000–1,350	
Cathartidae			
16 *Cathartes aura*	*	1,000–3,770	C
Pandionidae			
17 *Pandion haliaetus*	*	1,000–1,550	C
Acciptridae			
18 *Accipiter cooperi*		1,000–1,850	C
19 *A. striatus*	*	1,000–2,600	C
20 *Buteo albonotatus*	*	1,000–3,000	C
21 *B. jamaicensis*	*	1,000–3,200	C
22 *B. platypterus*		1,000–1,600	C
23 *B. swainsoni*		1,000–3,770	C
24 *Circus cyaneus*		1,000–2,800	C
Falconidae			
25 *Falco peregrinus*		1,000–2,500	
26 *F. sparverius*	*	1,000–3,350	C
Rallidae			
27 *Fulica americana*	*	1,000–1,500	
28 *Gallinula chloropus*	*	1,000–1,350	C
29 *Laterallus jamaicensis*	*	1,000–1,350	
30 *Porzana carolina*		1,000–1,500	
31 *Rallus limicola*		1,350–1,550	
Charadriidae			
32 *Charadrius vociferus*		1,000–3,100	C
Scolopacidae			
33 *Actitis macularia*		1,000–2,200	
34 *Bartramia longicauda*		1,000–2,900	
35 *Calidris himantopus*		1,000–1,350	
36 *C. mauri*		1,000–1,350	
37 *C. melanotus*		1,000–1,350	
38 *C. minutilla*		1,000–1,350	
39 *Gallinago gallinago*		1,000–3,100	
40 *Limnodromus griseus*		1,000–1,350	
41 *L. scolopaceus*		1,000–1,350	
42 *Numenius americanus*		1,000–1,350	
43 *Tringa flavipes*		1,000–2,200	
44 *T. melanoleucas*		1,000–1,500	
45 *T. solitaria*		1,000–1,500	
Phalaropodidae			
46 *Phalaropus tricolor*		1,000–1,600	C

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Appendix 1 – continued

Family/species	Resident population	Elevational range (m)	
Columbidae			
47 *Columba fasciata*	*	1,000–2,900	C
48 *Zenaida asiatica*	*	1,000–2,750	C
49 *Z. macroura*	*	1,000–3,200	C
Cuculidae			
50 *Coccyzus americanus*		1,000–1,350	
51 *C. erythrophthalmus*		1,000–2,900	
Strigidae			
52 *Asio flammeus*		1,000–3,050	
53 *Athene cunicularia?*		1,000–2,500	
Caprimulgidae			
54 *Caprimulgus carolinensis*		1,000–2,000	
55 *C. vociferus*	*	1,000–2,350	C
56 *Chordeiles acutipennis*	*	1,000–2,500	C
57 *C. minor?*		1,000–1,200	C
Apodidae			
58 *Chaetura vauxi*	*	1,000–1,500	C
59 *Cypseloides rutilus*	*	1,000–2,050	C
Trochilidae			
60 *Archilochus colubris*		1,000–2,450	
Alcedinidae			
61 *Ceryle alcyon*		1,000–1,500	
Picidae			
62 *Sphyrapicus varius*		1,000–3,350	
Tyrannidae			
63 *Contopus borealis*		1,000–2,600	
64 *C. pertinax*	*	1,000–3,350	C
65 *C. sordidulus*	*	1,000–2,650	
66 *C. virens*		1,000–2,700	
67 *Empidonax affinis*		2,000–3,350	
68 *E. flaviventris*		1,000–2,900	C
69 *E. hammondi*		1,400–2,900	
70 *E. minimus*		1,000–2,900	
71 *E. oberholseri*		1,000–1,100	C
72 *E. trailli*		1,000–1,500	C
73 *Myiarchus cinerascens*		1,000–1,850	
74 *M. crinitus*		1,000–2,050	
75 *Myiodynastes luteiventris*	*	1,000–1,350	C
76 *Tyrannus forficatus*		1,000–1,500	C
77 *T. tyrannus*		1,000–1,500	C
78 *T. verticalis*		1,000–1,500	C
79 *T. vociferans*		1,000–1,750	
Hirundinidae			
80 *Hirundo lunifrons*		1,000–2,100	
81 *H. rustica*		1,000–2,450	C
82 *Progne chalybea?*		1,000–1,500	
83 *Stelgidopteryx serripennis*	*	1,000–2,500	C
84 *Tachycineta bicolor*		1,000–1,500	
85 *T. thalassina*		1,000–3,350	
Mimidae			
86 *Dumetella carolinensis*		1,000–2,050	C

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Appendix 1 – continued

Family/species	Resident population	Elevational range (m)	
Muscicapidae			
87 *Catharus fuscescens*		1,800–2,500	C
88 *C. guttatus*		1,200–3,650	
89 *C. minimus*		1,000–1,100	C
90 *C. ustulatus*		1,000–2,200	C
91 *Hylocichla mustelina*		1,000–2,200	
92 *Regulus calendula*		2,800–3,050	
93 *Sialia sialis*	*	1,200–3,250	C
94 *Turdus migratorius*		1,200–2,500	C
Sylviidae			
95 *Polioptila caerulea?*		1,000–3,750	C
Motacillidae			
96 *Anthus spinoletta*		1,000–1,350	
Bombycillidae			
97 *Bombycilla cedrorum*		1,000–2,450	C
Vireonidae			
98 *Vireo belli*		1,000–1,350	C
99 *V. flavifrons*		1,000–2,000	
100 *V. gilvus?*		1,000–2,100	C
101 *V. olivaceus*	*	1,000–1,500	C
102 *V. philadelphicus*		1,000–1,450	
103 *V. solitarius*	*	1,000–1,750	C
Parulidae			
104 *Cardellina rubrifrons?*		1,500–2,650	
105 *Dendroica aestiva*		1,000–1,700	
106 *D. caerulescens*		1,000–1,500	
107 *D. coronata*	*	1,000–3,650	
108 *D. chrysoparia*		1,000–2,550	
109 *D. dominica*		1,000–1,100	
110 *D. fusca*		1,000–2,750	C
111 *D. magnolia*		1,000–2,500	C
112 *D. occidentalis*		1,000–3,350	
113 *D. pensylvanica*		1,000–1,100	
114 *D. tigrina*		1,000–1,500	
115 *D. townsendi*		1,000–2,900	C
116 *D. virens*		1,000–2,400	C
117 *Geothlypis trichas*		1,000–1,500	
118 *Helmitheros vermivorus*		1,000–1,500	C
119 *Icteria virens*		1,000–1,500	C
120 *Mniotilta varia*		1,000–2,250	C
121 *Oporornis formosus*		1,000–2,900	
122 *O. philadelphia*		1,000–1,500	
123 *O. tolmei*		1,000–2,600	
124 *Protonaria citrea*		1,000–1,850	
125 *Seiurus auricapillus*		1,000–1,900	C
126 *S. motacilla*		1,000–1,850	C
127 *S. noveboracensis*		1,000–2,600	
128 *Setophaga ruticilla*		1,000–2,450	C
129 *Vermivora celata*		1,000–2,900	C
130 *V. peregrina*		1,000–2,400	C

Appendix 1 – continued

Family/species	Resident population	Elevational range (m)	
131 *V. pinus*		1,000–2,000	C
132 *V. ruficapilla*		1,000–2,000	C
133 *Wilsonia canadensis*		1,000–2,950	
134 *W. citrina*		1,000–2,200	C
135 *W. pusilla*		1,000–3,050	C
Thraupidae (Emberizidae: Thraupinae)			
136 *Piranga flava*	*	1,000–2,150	
137 *P. ludoviciana*		1,000–3,050	C
138 *P. rubra*		1,000–2,600	C
Emberizidae			
139 *Ammodramus savannarum*	*	1,000–2,150	
140 *Guiraca caerulea*	*	1,000–2,300	
141 *Melospiza lincolni*		1,000–2,600	
142 *Passerculus sandwichensis?*		1,000–3,350	
143 *Passerina ciris*		1,000–1,850	C
144 *P. cyanea*		1,000–2,300	C
145 *Pheucticus ludovicianus*		1,000–2,150	C
146 *Spiza americana*		1,000–1,500	
147 *Spizella pallida*		1,000–1,200	
Icteridae			
148 *Euphagus cyanocephalus*		1,000–3,350	C
149 *Icterus galbula*		1,000–2,600	C
150 *I. spurius*		1,000–1,500	
151 *Sturnella magna*	*	1,000–3,500	C

Appendix 2. List of Nearctic–Neotropical avian migrants reported by Griscom, Land and FIIT.
Relative abundance was reported by Griscom (1932) during the period 1924–1928 or by Land (1970) as being "fairly common", "common", or "abundant" in the Western Highlands region during the period 1958–1966, as compared with FIIT evaluation of their respective relative abundance in the proposed Tres Volcanes Multiple Use Area during the period 1987–1991 utilizing similar or the same criteria. Owing to habitat considerations, families excluded from this analysis are: Podicipedidae, Ardeidae, Anatidae, Pandionidae, Rallidae, Charadriidae, Scolopacidae and Phalaropodidae. An asterisk (*) indicates that a resident population is known from Guatemala.

Under the GRISCOM column, historical abundance in the region is derived from comments in Griscom (1932) where applicable to the region. Comments are quoted from text; ND, no data or relevant commentary.

Under the LAND column, historical abundance in the region is derived from Land (1970) and classified as: F, "fairly common" (should be recorded once or twice a week); C, "common" (should be seen at least once on almost any day in the field); and A, "abundant" (likely to be seen several times per day). Where U (to denote "uncommon") appears under this heading, it will be accompanied by another code listed herein and denotes variable relative abundance noted by Land for the region.

Under the FIIT column, recent relative abundance in the region is derived from collection and observation made during the past five years. FIIT classifications match those of Land, with the additional codes indicating: U, uncommon (one or two individuals observed weekly); R, rare (one or two individuals observed annually); Ac, one or two individuals observed during the past five years; and ND, no data (no individuals observed during the past five years). In addition, symbols are utilized to facilitate evaluation of the populations of these species in the region: >, stable population, or apparent recent increase in relative abundance; –, mild or moderate decline since the 1960s; and <, major decline in recent years.

Appendix 2 – continued

Family/species	GRISCOM	LAND	FIIT
Cathartidae			
1 *Cathartes aura**	ND	A	A
Acciptridae			
2 *A. striatus**	"common"	F,U	C>
3 *Buteo jamaicensis**	"not uncommon"	F	F>
4 *B. swainsoni*	"enormous flocks"	F	A>
Falconidae			
5 *Falco sparverius**	"abundant"	F	C>
Columbidae			
6 *Columba fasciata**	"not rare"		CU–
7 *Zenaida asiatica**	ND	C,F	U–
8 *Z. macroura**	"abundant"	A,C	U<
Strigidae			
9 *Athene cunicularia*	"not uncommon"	F	ND<
Caprimulgidae			
10 *Caprimulgus carolinensis*	ND	F	ND–
11 *C. vociferus**	ND	F	R<
12 *Chordeiles acutipennis**	"common"	F	U–
13 *C. minor*	"abundant"	F	U–
Apodidae			
14 *Chaetura vauxi**	"common"	C	C>
Trochilidae			
15 *Archilochus colubris*	"common"	F	ND<
Alcedinidae			
16 *Ceryle alcyon*	"abundant"	F	ND<
Picidae			
17 *Sphyrapicus varius*	"common"	F	ND<
Tyrannidae			
18 *Contopus pertinax**	"fairly common"	C	Ac<
19 *C. sordidulus**	ND	F	ND–
20 *Empidonax affinis*	"uncertain status"	F	ND–
21 *E. hammondii*	"abundant"	F	ND<
22 *E. minimus*	"abundant"	F	ND<
23 *E. traillii*	"common"	F	Ac<
24 *Myiarchus cinerascens*	ND	F	ND–
25 *Myiodynastes luteiventris**	"common to abundant"	C	U–
26 *Tyrannus forficatus*	"common"	F	C>
27 *T. verticalis*	ND	F	A>
Hirundinidae			
28 *Hirundo rustica*	"not uncommon"	F	A>
29 *Progne chalybea*	"not uncommon"	F	ND<
30 *Stelgidopteryx serripennis**	"common"	F	A>
31 *Tachycineta thalassina*	"regular . . . visitant"	C,U	ND<
Muscicapidae			
32 *Catharus guttatus*	"not uncommon"	F	ND<
33 *Catharus ustulatus*	"common"	F	A>
34 *Sialia sialis**	"common"	C	A>
Sylviidae			
35 *Polioptila caerulea*	"abundant"	F	R<
Bombycillidae			
36 *Bombycilla cedrorum*	"abundant"	F	A>

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Appendix 2 – continued

Family/species	GRISCOM	LAND	FIIT
Vireonidae			
37 *Vireo flavifrons*	"common"	F	ND<
38 *V. gilvus*	"quite common"	F	U–
Parulidae			
39 *Cardellina rubrifrons*	ND	F	ND–
40 *Dendroica coronata**	"common"	F	ND<
41 *D. magnolia*	"abundant"	C	Ac<
42 *D. occidentalis*	"common"	F	ND<
43 *D. townsendi*	"abundant"	A	R<
44 *D. virens*	"abundant"	A,C	U<
45 *Geothlypis trichas*	"common"	C,F	ND<
46 *Helmitheros vermivorus*	"uncommon"	F	C>
47 *Icteria virens*	"relatively uncommon"	F	F>
48 *Mniotilta varia*	"common"	A	U<
49 *Oporornis tolmei*	"abundant"	C	ND<
50 *Seiurus aurocapillus*	"common"	F	F>
51 *Setophaga ruticilla*	"common"	F	Ac<
52 *Vermivora peregrina*	"common . . . abundant"	C	A>
53 *V. ruficapilla*	"fairly common"	F	C>
54 *Wilsonia citrina*	"common"	F	U–
55 *W. pusilla*	"abundant"	C	A>
Thraupidae			
56 *Piranga flava**	ND	F	ND–
57 *P. ludoviciana*	"fairly common"	C	A>
Emberizidae			
58 *Guiraca caerulea**	"Probably . . . common"	F	ND<
59 *Melospiza lincolnii*	"not uncommon"	F	ND<
60 *Passerina ciris*	"common"	C	R<
61 *P. cyanea*	"abundant"	A	U<
62 *Pheucticus ludovicianus*	"common . . . abundant"	C	A>
63 *Spiza americana*	"common . . . abundant"	F,U	ND<
Icteridae			
64 *Icterus galbula*	"uncommon . . . abundant"	C	A>
65 *I. spurius*	"abundant"	C,F	ND<

Appendix 3. Summarized profiles of four 1 ha vegetational parcels in the proposed Tres Volcanes Multiple Use Area where resident and migrant avifauna were sampled during the period 1987–1991. Bitterlich method (Matteucci and Colma 1982); Life Zone classifications adapted from Holdridge (1967) and de la Cruz (1982).

Site: Finca "El Faro"
Location: 14°42′1″N, 91°35′45″W
Elevation: 1,120 m
Life Zone: Subtropical Wet Forest
Exposure: south-west
Dominant arborescent flora: *Inga spuria, Cecropia obtusifolia, Cyathea* sp.
Degree of intervention: moderate-high
Mean dbh: 24.5 cm
Mean canopy height: 9.6 m
Mean canopy diameter: 4.2 m

Site: Finca "La Esperanza"
Location: 14°39′18″N, 91°29′18″W
Elevation: 1,800 m

Life Zone: Lower Montane Wet Forest
Exposure: south-east
Dominant arborescent flora: *Pseudolmedia oxyphyllaria, Pleuranthodendron mexicana, Guarea excelsa*
Degree of intervention: low
Mean dbh: 67.6 cm
Mean canopy height: 16.8 m
Mean canopy diameter: 10.9 m
Site: Las Georginas Forest Reserve
Location: 14°45′6″N, 91°28′48″W
Elevation: 2,415 m
Life Zone: Lower Montane Rain Forest
Exposure: west
Dominant arborescent flora: *Morus celtidifolia, Quercus* sp., *Billia hippocastanum*
Degree of intervention: very low
Mean dbh: 49.7 cm
Mean canopy height: 14.2 m
Mean canopy diameter: 9.6 m
Site: Chicavioc Forest Reserve
Location: 14°45′42″N, 91°32′18″W
Elevation: 2,740 m
Life Zone: Montane Moist Forest
Exposure: north-east
Dominant arborescent flora: *Alnus firmifolia, Cupressus lusitanica, Pinus pseudostrobus*
Degree of intervention: moderate
Mean dbh: 97.5 cm
Mean canopy height: 21.7 m
Mean canopy diameter: 10.3 m

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