

## Neotropical Stopover Sites and Middle American Migrations: The View from Southern Mexico

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### ABSTRACT

The movements of birds in Middle America are probably the poorest known aspect of the biogeography of North American vertebrates. Neotropical migrants are composed of intratropical, nearctic-neotropical, altitudinal, and neaustral-neotropical migrants. Individuals of the first three categories are common at stopover sites in southern Mexico. The Isthmus of Tehuantepec is the northernmost narrowing of the North American continental landmass, causing a funneling and concentration of nearctic-neotropical landbird migrants. This paper focuses on woodland birds in this region in autumn, examining abundance (using mist nets), patterns of movement, community composition, and mass gains. This avian community is dominated by nearctic-neotropical migrants during October. The presence of these migrants might affect the resident community. Resident species are in many cases not sedentary. From the perspective of habitat use, woodland migrants in Los Tuxtlas constitute a heterogeneous assemblage, requiring a wide array of habitat types. Many species seem to deposit fat in migration at this site. In two species, mass deposition is correlated with stopover behavior. It is suggested that migratory route selection is rather poorly known, and the autumn route of the Red-eyed Vireo (*Vireo olivaceus*) is updated and discussed based on data from this study and the literature. Without knowledge of distributions, movements, and habitat selection in neotropical migrants, conservation plans focusing on this broad group are not likely to achieve a high degree of success. This knowledge is not likely to be obtained under current research agendas.

### RESUMEN

Los movimientos de aves en Mesoamérica son probablemente el aspecto menos conocido de la biogeografía de los vertebrados de Norteamérica. Las especies migratorias neotropicales están compuestas de aves migratorias intratropicales, neárticas-neotrópicas, altitudinales, y neaustrales-neotropicales. Es común que algunas de las tres primeras categorías hagan escala en sitios del sur de México. El Istmo de Tehuantepec es la masa continental más angosta de la porción sureña de Norteamérica, provocando un embudo y una concentración de las aves terrestres migratorias neárticas-neotropicales. Este estudio enfoca el análisis de los pájaros migratorios de las tierras boscosas de esta región en el otoño, examinando la abundancia (usando redes de neblina), patrones de movimiento, la composición de la comunidad y el aumento de masa. Esta comunidad de aves está dominada por los migrantes neárticos-neotropicales durante el mes de octubre. La presencia de estos migrantes puede afectar a la comunidad de aves residentes. Las especies residentes, en muchos casos, no son sedentarias. Desde la perspectiva del uso del hábitat, los migratorios de las tierras boscosas en Los Tuxtlas constituyen un conjunto heterogéneo, necesitando un amplio despliegue de tipos de hábitats. Muchas especies parecen depositar grasa en migración en este sitio. En dos especies, la acumulación de masa está correlacionada con la conducta en las escalas. Se sugiere que la selección de la ruta migratoria es en general poco conocida; y la ruta otoñal del *Vireo olivaceus* se encuentra actualizada y se discute, basada en información del presente estudio y del material publicado. Sin el conocimiento de la distribución, los movimientos, y la selección de hábitats en las aves migratorias neotropicales los planes de conservación que se enfocan en este amplio grupo no pueden lograr un alto grado de éxito. Este conocimiento no es fácil de obtener en los temas actuales de investigación.

The main obstacle to progress is not ignorance, but the illusion of knowledge.

Daniel J. Boorstin, Librarian of Congress Emeritus

### INTRODUCTION

The movements of birds in Middle America are probably the poorest known aspect of the biogeography of North American vertebrates. Following the remarkable efforts of the Division and Bureau of Biological Survey to determine the nonbreeding movements and wintering ranges of nearctic-neotropical migrants (summarized largely by Wells W. Cooke, e.g., Cooke 1888, 1904, 1905), and the

systematic work of Robert Ridgway (1901–1919), which necessarily included discernment of nonbreeding movements and distributions, comparatively little has been done to advance this body of knowledge. Some important recent exceptions have appeared in the works of Wetmore (e.g., 1965, 1968, 1972), Rappole et al. (1979), Ramos (1983, 1988), Wetmore et al. (1984), Phillips (1986, 1991), Isler and Isler (1987), Hilty and Brown (1986), Pashley and Martin (1988), Binford (1989), and Ridgely and Tudor (1989). Nevertheless, the opening statement remains painfully true.

Although Cooke began his studies of migration before the Division of Biological Survey was estab-

lished (see Cooke 1888; Bean 1986), the work was broadened and continued because it served two important functions of the Biological Survey: the study of the economic relations of birds, and the formulation of "proper legislation for bird protection" (Cooke 1915:2). These reasons for studying avian movement and distribution are largely outdated. Legislation for bird protection has succeeded where it could (e.g., control of waterbird hunting, elimination of wild plumage in the millinery trade). Recent declines in migrant songbirds detected in the nearctic (e.g., Robbins et al. 1989) suggest that we need new directions in avian conservation. To be successful, conservation efforts must be based on a sound scientific knowledge of the biology of the organisms to be protected. Efforts to conserve neotropical migrants will of necessity entail renewed research on Middle American migrations. This knowledge is also necessary if we are ever to understand the dynamics and evolution of the nearctic-neotropical migration system.

Although past efforts laid a foundation in this broad and difficult area, the mantle of ignorance cloaking the nonbreeding movements of birds is such that we still face broad and simple questions: "Who is where? When are they there? What are they doing?" The breadth of the topic ensures that no single research program will answer the pertinent questions in a researcher's lifetime. So little has been done, however, that single, well-designed studies can contribute a comparative wealth of data to address these questions. This paper reports on a study taking the site-specific approach, examining from several perspectives the spectrum of woodland-associated migrants susceptible to mist net capture on the Isthmus of Tehuantepec in southern Mexico. The results have implications beyond this region, however.

### Categorizing Types of Migration

It will help to define the general types of migrants expected in Middle America. Migration is used here as a descriptor of round trip, "go-and-return" movements, largely biannual, and largely (though not necessarily) between breeding and wintering areas. Nearctic-neotropical migrants are birds of the western hemisphere breeding north and wintering south of the Tropic of Cancer (see Rappole et al. 1983). Intra-tropical migrants are birds whose biannual movements occur entirely between the Tropics of Cancer (23° 27' N) and Capricorn (23° 27' S). Although these descriptors are suitable at individual and population levels, some species may not fit conveniently into any category, including neaustral-neotropical migrant

(the southern equivalent of the nearctic-neotropical migrant). Further, individuals may show altitudinal movements constituting altitudinal migration.

Because these terms can overlap in their applicability, I suggest that individuals, populations, and species be categorized hierarchically, using first whichever migratory descriptor best fits the biannual movements, and then whichever other descriptor(s) apply. Thus, the species *Myiarchus tuberculifer* (Dusky-capped Flycatcher) is composed of populations of nearctic-neotropical, intratropical, neaustral-neotropical, and sedentary individuals (I have not seen descriptions of altitudinal migration in this species). The Wood Thrush (*Hylocichla mustelina*), on the other hand, is a nearctic-neotropical migrant which shows altitudinal movements on its wintering grounds in Los Tuxtlas, Mexico. These altitudinal movements seem to be "facultative migrations" (*sensu* Terrill and Ohmart 1984), caused by "nortes" (Ramos 1983). Although the distinction between altitudinal migration and altitudinal movement is an important one, it may in some cases be difficult to make. Lack (1944) also commented on the difficulty of separating true migration from hard weather movements.

Recognizing the many different types of migration is a first and important step in gathering, reporting, and assimilating information on migrants. The vague and currently popular phrase "neotropical migrant" is too broad to be useful. The lists of neotropical migrant species I have seen usually exclude the majority of species with migratory movements in the Neotropics.

Intra-tropical, nearctic-neotropical, and altitudinal migrants can all be found in large numbers from August through May in southern Mexico. These types of neotropical migrants use available habitats for various aspects of their annual cycles. I focus here on transient birds: birds en route to somewhere else (no matter what their speed or distance remaining to be traveled). Recaptures are ignored throughout this paper.

### STUDY SITE AND METHODS

The Isthmus of Tehuantepec is the northernmost narrowing of the North American continent, and thus causes a concentration of nearctic-neotropical landbird migrants. Little has been done to evaluate habitat use and avian abundance during migration in this area. This study focused on woodland migrants, quantitatively examining abundance (using mist nets), temporal patterns of movement, community structure, and daily

mass gain. Habitat selection was also addressed (see Winker 1995).

The study site was located just south of the Estacion de Biologia Tropical "Los Tuxtlas" of the Instituto de Biologia of the Universidad Nacional Autonoma de Mexico (UNAM), in the Sierra de los Tuxtlas, southern Veracruz, Mexico (18° 34' 30" N, 95° 04' 20" W). Los Tuxtlas occupy the northwestern region of the Isthmus of Tehuantepec and include the northernmost neotropical rain forest (Pennington and Sarukhan 1968). The site was located 5 km south and 3 km west of the Gulf of Mexico.

Thirty-six standard nylon mist nets (12 × 2.6 m) were placed 30 m apart on a grid system in an area of mature and second growth wooded habitats. Nets were oriented in an east-west direction. The site was composed of primary forest ("selva") bordered by second growth woodland ("acahual") changing gradually into old pasture (pasture was not sampled). Nets were set in the woodlands, with half in primary forest and half in second growth. The average canopy heights in these two macrohabitats were 21.5 m and 9.7 m, respectively. These woodlands were not homogeneous, and the structural differences quantified at the microhabitat level were important for discerning differences in capture distributions at the species level (see Winker 1995). Nets were opened whenever weather permitted during daylight hours between 5 September and 15 November 1992, and 12,608 net-h were accumulated. When removing birds from nets, the time, the net, and the side (north or south) of capture were recorded for every individual. Captured birds were weighed to the nearest 0.1 g on a spring scale (Pesola), and wing (chord) and tail lengths were measured to the nearest 0.1 mm using vernier calipers. The fat level of captured individuals was scored following Helms and Drury (1960). Additional measurements were made in some species, but will not be considered here.

### Mass Gain Analysis

Birds feeding in a favorable environment should show an increase in mass during the day and a decrease at night due to loss of undigestible material (defecation or regurgitation) and nocturnal metabolism (see Baldwin and Kendeigh 1938; Mueller and Berger 1966; Kendeigh et al. 1969). Birds not feeding, or birds in an unfavorable environment, should show a decrease in mass during the day due to metabolism. The method of mass gain analysis used here examines univariate and multivariate characteristics of

captured individuals in relation to time of capture, seeking evidence for significant trends among the entire captured sample. Body mass is the most important of these variables. Although mass varies due to several factors, in migrants the amount of fat carried is the most important variable (Connell et al. 1960; Odum 1960). Body size also affects mass, and removing some of the variation in mass caused by size improves estimates of fat content (Connell et al. 1960). Data from fat extractions in a variety of migrant songbird species (e.g., Connell et al. 1960; Odum 1960; Rogers and Odum 1964; Child 1969) suggest that rather accurate estimates of an individual's fat content can be made using body mass adjusted for individual size (wing length). Based on these findings, I calculate a "condition index" ( $[\text{mass/size variable}] \times \text{constant}$ ) for captured individuals; it is assumed that this condition value is correlated with the amount of fat carried by the individual, but no attempt is made to estimate the fat content of individuals. These values are examined in relation to the time of capture using simple linear regression, and estimates of daily gain are made for an average bird in the sampled population. Further details on these methods are given in Winker (in press b).

Fat-free mass data were not available for "Traill's" Flycatcher (*Empidonax traillii*). An estimate of 10.69 g is used here, based on the linear model of  $Y = 0.8357X + 0.1878$ , where  $Y$  is fat-free mass and  $X$  is the mean autumn mass of captured individuals. This model was based on the high correlation ( $r^2 = 0.997$ ) found between fat-free mass and mean autumn mass among ten nearctic-neotropical migrant species by Winker et al. (1992c).

## RESULTS

### Magnitude and Nature of Autumn Migration in this Area

During autumn 1992, 2,872 individuals of 137 species were captured (Appendix). The temporal distribution of these captures (Figure 1; recaptures not included) shows that avian abundance at this site reaches its peak during October (days 275–305). Segregation of initial captures into two groups, nearctic-neotropical migrants and tropical "residents," allows some revealing comparisons (Figure 1). I have not seen these comparisons made for neotropical data.

First, the relative abundance of nearctic-neotropical migrants in relation to the resident component is clarified: migrants are numerically



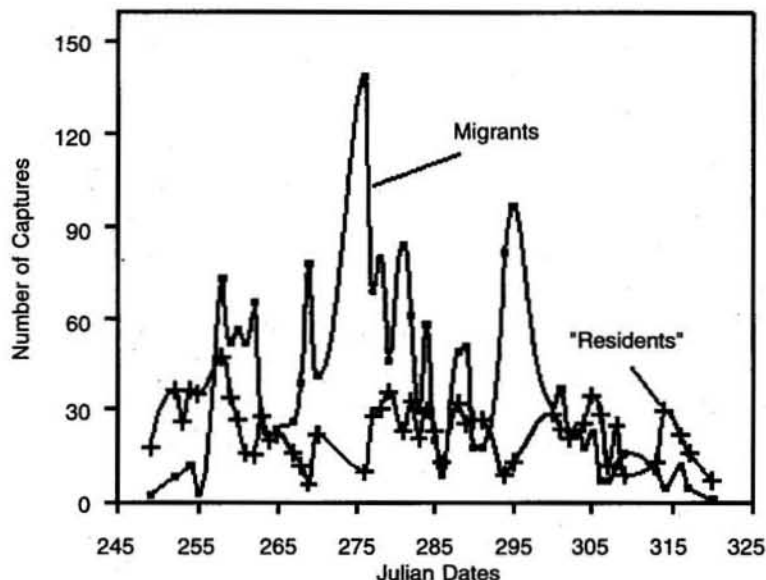


Figure 1. The temporal distribution of an artificial segregation of "migrants" versus residents illustrates three things: (1) the tremendous temporal concentration of nearctic-neotropical migrants in this neotropical community during autumn migration; (2) the artificiality of the groups (residents clearly demonstrate substantial seasonal movements); and (3) (possibly related to 2) heretofore undescribed relationships between the relative abundances of nearctic-neotropical migrants and neotropical residents. See text.

dominant during the migratory period at this site, and are furthermore temporally rather concentrated, with the bulk of captures occurring between 14 September (Day 258) and about 28 October (Day 302). The initial peak of resident captures from 5 September (Day 249) through ca. 17 September (Day 261) is caused by the gradual capture and marking of the local birds, most of which are truly resident (unpubl. data). Subsequent increases in resident captures (e.g., post-Day 276, and post-Day 294; 2 October and 20 October, respectively) are caused by influxes of transient individuals of species usually considered sedentary. These species include (but are not limited to) Long-tailed Sabrewing (*Campylopterus excellens*) (see Winker in press a), Little Hermit (*Phaethornis longuemareus*), Yellowish Flycatcher (*Empidonax flavescens*), Ochre-bellied Flycatcher (*Mionectes oleagineus*), White-throated Robin (*Turdus assimilis*), Clay-colored Robin (*Turdus grayi*), and Common Bush-Tanager (*Chlorospingus ophthalmicus*). Few of these birds appear in early-season captures and most are largely restricted to higher elevations during the breeding season. (The movements of residents will be discussed later in this paper.)

Finally, in Figure 1 it can be seen that the numbers of migrants and residents often change in a negative relationship: when migrant numbers

increase, residents tend to decrease, and vice-versa. What might this tendency indicate? Abundances in two groups can change between sample periods in two ways: captures can show either similar (increase-increase, or decrease-decrease), or dissimilar relationships (increase-decrease, or decrease-increase) with captures from the previous period. After the first 15 days of the netting period I assume that new captures are largely transients. Following this period there were 35 chances for captures of residents and migrants to be compared with captures on the previously sampled day. On 21 of those days, the two groups showed changes in opposite directions (when one increased, the other decreased, and vice-versa); on 14 days they changed in the same directions. While this trend does not differ from random ( $0.5 > P > 0.1$ ; *G*-test with Williams' correction), the sample size is too small to consider the question adequately addressed. A simple model showed that it would take four years of similar results, or a single year (similar sample) imbalance of 2.5:1 to show a significant difference. Further examinations of this are warranted.

### Habitat Selection

We know rather little about the distribution of passerine migrants among available habitats at stopover sites (but see Bairlein 1981; Hutto 1985; Berthold 1988; Winker et al. 1992a, 1992b). Given

that migrating individuals may not depend on resources at all of the sites where they occur, selectivity might be low, with broad overlap among species. Although captures at this site were broadly distributed among the sampled habitats (and microhabitats), all 17 of the most common nearctic-neotropical migrants showed significant nonrandom distributions among the available nets, and exhibited a rather high level of species-specific distribution patterns (Winker 1995).

### Behavior and Daily Mass Changes in Two Flycatchers

Migrants are able to store energy and can be highly mobile, making it probable that individuals do not depend on food being available at all stopover sites visited. Even if they are feeding, the amount taken (per individual, on average) could range from very little to a large amount. The degree to which stopover sites are used for fat deposition can vary among the most common migrant species occurring at a site (e.g., Winker et al. 1992a, 1992c; Winker 1995). As an example of the differences that often seem to occur among woodland migrants, I present data on Great Crested Flycatcher (*Myiarchus crinitus*), the Willow Flycatcher, and the Alder Flycatcher (*Empidonax alnorum*) at this site. The latter two species are very difficult to separate in the field, and are treated here together as "Traill's" Flycatcher. It is clear from field and museum studies that the Alder Flycatcher is the more common of the two during autumn migration in Los Tuxtlas (A. R. Phillips, pers. comm.; pers. obs.). Of the 148 total captures of "Traill's" Flycatcher, 33 were ascribed with certainty to Alder Flycatcher and 12 to "Traill's" Flycatcher; the rest were designated as unknown or (many) as "probably Alder Flycatchers." The Great Crested Flycatcher and "Traill's" Flycatcher are common in migration at this site; Table 1 gives sample sizes and mensural characteristics of captured individuals.

Table 1. Characteristics of captured Great Crested and "Traill's" flycatchers (*Myiarchus crinitus* and *Empidonax traillii*). Means (and standard deviations) are given for mensural characters.

	<i>Myiarchus crinitus</i>	<i>Empidonax traillii</i>
N	46	148
Mass (g)	31.18 (2.87)	12.57 (1.33)
Wing (mm)	96.25 (3.26)	68.71 (2.49)
Tail (mm)	84.22 (3.91)	55.13 (2.11)

Before examining daily mass changes in Great Crested Flycatchers and "Traill's" Flycatchers, it is interesting to know something about the strikingly different behaviors shown by the two at this site. Individuals of both "species" are usually found feeding. Both are primarily insectivorous, although some fruits are taken, as evidenced by observations of fruit consumption and seed regurgitation in Great Crested Flycatchers and of occasional fruit in the feces of captured "Traill's" Flycatchers. Individuals of both groups call regularly: Great Crested Flycatchers give their typical "weep" call, and "Traill's" Flycatchers usually give a soft "pik" or "pit" (although other calls, including full or partial songs in Alder Flycatchers and a "wheew" call, are given with less frequency). Calls are given more frequently by "Traill's" Flycatchers than by Great Crested Flycatchers, not simply because they are more common. "Traill's" Flycatcher individuals are highly territorial, and their calling is an important part of this behavior, acting, it seems, as an advertisement of presence. Calls are not always given, however. I have observed silent individuals feeding during high-density situations, and at lower densities individuals commonly call in bouts, with an increase in local calling frequency being stimulated by a local battle or nearby song. During peak passage of adult "Traill's" Flycatchers, I have encountered birds at densities of up to eight individuals in a circle approximately 20 m in diameter. Battles between individuals are conspicuous and brief, generally involving chase; contact is often made. Under these conditions, battles occurred at a rate of about 10 per hour. Calls were given at a rate of approximately 55 per minute, and were audible over a range of about 40 m. Territorial behavior in this "species" was also present at very low densities, but was of course less frequently exhibited.

Although only careful study of marked birds will illuminate the exact nature of the territoriality exhibited by these birds, I think it is a defense of individual space (a space that moves with the individual), rather than a fixed area. The purpose of calling in Great Crested Flycatchers is unknown; I have seen no aggressive behavior toward conspecifics at this site. Although they do not reach the densities of "Traill's" Flycatchers, Great Crested Flycatchers are often very common, and the lack of territoriality is not simply a result of low abundance (pers. obs.).

Because flycatching is the primary feeding method of both "species," it is odd that one defends a feeding area while the other does not. Territoriality is generally considered to occur when a

Table 2. Relationships between captured individuals and time of capture in Great Crested and "Traill's" flycatchers (*Myiarchus crinitus* and *Empidonax traillii*). Results from linear regressions. "+" indicates positive relationship; "n.s." indicates  $P > 0.05$ .

	<i>Myiarchus crinitus</i>	<i>Empidonax "traillii"</i>
Mass (g)	n.s.	+
Wing	n.s.	n.s.
Tail	n.s.	n.s.
Fat	n.s.	n.s.
WingCOND <sup>a</sup>	n.s.	+
TailCOND <sup>b</sup>	n.s.	+

<sup>a</sup> Condition index calculated as  $(\text{mass}/\text{wing}) \times 100$ .

<sup>b</sup> Condition index calculated as  $(\text{mass}/\text{tail}) \times 100$ .

resource is both in short supply (not enough available for all individuals) and economically defendable (Brown 1964). The comparatively even distribution of the flying insect food base is similar for both species, so the behavioral differences that occur must be due to the relative abundance of the resource in relation to the number of potential or actual consumers. For Great Crested Flycatchers, there is either a surfeit of available food or the resource base is of such poor quality that it is not worth expending energy to defend a portion of it. Mass gain analyses of captured individuals enable us to determine which of these hypotheses is more probable.

Regressions of mass, mensural characters, fat levels, and two condition indices in the two spe-

cies reveal differences as striking as the behavioral differences described above (Table 2). Great Crested Flycatcher do not appear to be gaining mass during the day at this site, while "Traill's" Flycatcher do. "Traill's" Flycatchers show positive trends in mass and condition indices (Table 2; see also Figure 2). Although Great Crested Flycatchers are usually found feeding when encountered, it appears that, as a species, they are not gaining very much mass at this site (the sample size is such that very small mass gains might not be detectable). In contrast, "Traill's" Flycatchers show substantial mass gains. The linear regressions of the two condition indices in this "species" were highly significant, with rather steep slopes (for condition index using tail length:  $Y = 0.00290897 X + 19.51$ ;  $R = 0.32$ ,  $F = 16.50$ ,  $P = 0.0001$ ; for the condition index using wing chord:  $Y = 0.00223879 X + 15.73$ ;  $R = 0.33$ ,  $F = 18.08$ ,  $P < 0.00005$ ). When converted to grams, average gross daily gains for the captured sample were 1.83 g and 1.76 g for condition indices calculated using tail and wing lengths, respectively. These figures are very similar, suggesting that wing chord and tail lengths work equally well in removing some of the variability in body mass caused by individual size differences. This is not the case for all species (see Winker 1995). These average gross daily gain estimates are useful values based on field data. Beyond this, estimates of net daily gain are made using various formulae, estimates, and values from the literature. Subtraction of two estimates of nocturnal loss (4.5% of body mass [0.567 g], and this value *plus* mass lost in noctur-

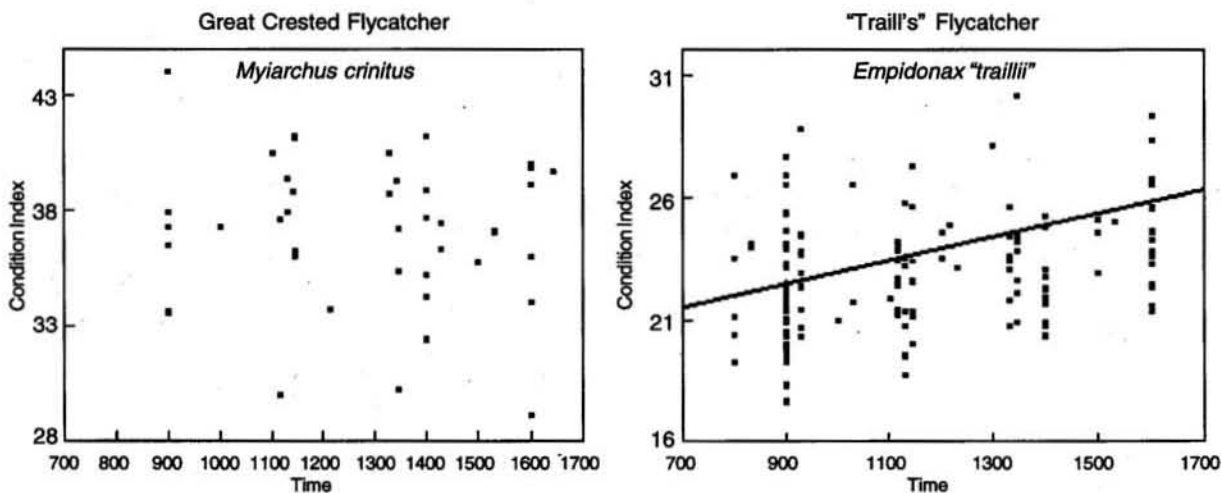


Figure 2. Condition index ( $(\text{mass}/\text{tail}) \times 100$ ) plotted against time of capture for initial captures of Great Crested Flycatcher (*Myiarchus crinitus*) and "Traill's" Flycatcher (*Empidonax traillii*).

nal metabolism [+0.417 g]) gives estimates of net 24 h mass gains of 0.77–1.27 g. These are substantial gains, representing 6.2%–10.1% of the average mass of captured individuals. Gains of this magnitude, if they are made up of fat, would allow 7.6–12.3 h of flight. The lack of a significant relationship between fat level and time of capture is puzzling, however, and perhaps all of this gain is not fat.

The mass gains shown by "Traill's" Flycatcher at this site are remarkable. These gains are higher than any shown by seven other nearctic-neotropical migrants at this site (see Winker 1995). If "Traill's" Flycatchers have the opportunity to gain enough during the day for nearly a full night of migration, then resources are comparatively plentiful and obviously worth competing for. On the other hand, the lack of mass gain shown by Great Crested Flycatchers suggests they may not defend feeding territories here because there is too little available to make defense economical. I have observed a conspicuous lack of resource defense in several other tyrannids on migration. It would be interesting to learn how the incidence of territoriality in migration corresponds with apparent fat deposition across wider groups.

### Rounding Out the List of Neotropical Migrants

Several of the resident species captured in this study showed movements suggestive of genuine

migration (e.g., continued influxes of new captures after day 275, Figure 1). How to categorize these movements remains difficult, however. In several species (at least) these movements were not caused by nortes (unpubl. data), and so are not simply weather-related altitudinal movements. The magnitude and seasonality of the movements make it clear that several of these species are at least altitudinal migrants in this area. This is likely to be true of many other resident species in this and other regions in the neotropics. It will be difficult to determine the extent of these movements (i.e., which are simply altitudinal and which are broader, intratropical migrations), without research that is broader in scope. An example follows.

By accident, two groups worked on the same species in Los Tuxtlas: *Chlorospingus ophthalmicus wetmorei* (one of the endemic subspecies). Peterson et al. (1992) learned that the isolated Los Tuxtlas population is genetically distinct from populations in Hidalgo, Oaxaca, and Guerrero. In fact, there is a rather large degree of genetic distinctiveness between the Los Tuxtlas population and these other populations (mean Rogers' genetic distance to other populations of 0.225). Peterson et al. (1992) attributed the high inter-population genetic differentiation observed to the species' presumed sedentary status. In this study, I found that the Los Tuxtlas population (which does not breed in the lowlands, where my site was located) shows remarkably strong seasonal movements (Figure 3). The profundity of the move-

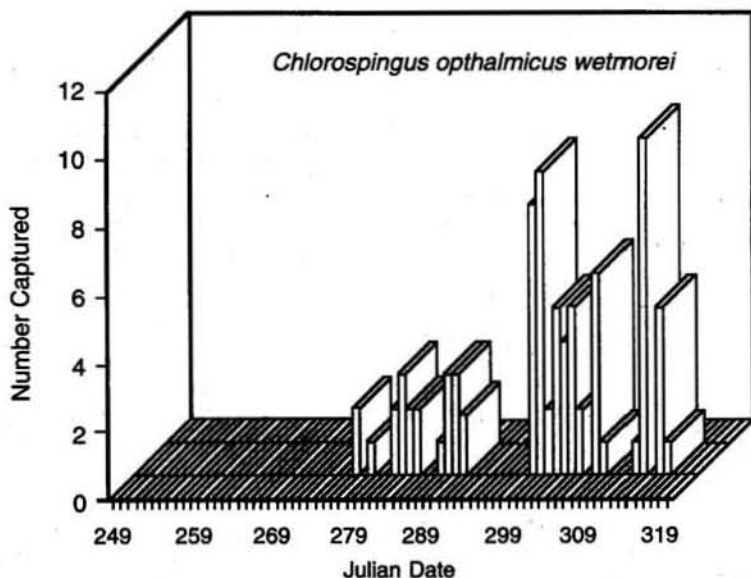


Figure 3. The temporal distribution of captures of *Chlorospingus ophthalmicus wetmorei* in the Sierra de los Tuxtlas, during 5 September–15 November (Julian Days 249–320). Although considered a resident species, these captures clearly demonstrate that it is at least an altitudinal migrant in the area.



ments and the seeming lack of residency among the lowland captures led me to wonder if they might be intratropical rather than simply altitudinal migrants. Neither result would have been predicted by the other, for mobility tends to obscure genetic differences between populations. Together, however, the two studies reveal an intriguing aspect of neotropical avian evolution. Either philopatry is extremely high in the Los Tuxtlas population (unlikely), or the individuals of Los Tuxtlas are altitudinal migrants whose nonbreeding wanderings (although apparently strong) do not take them within the ranges of other populations (the hypothesis I presently favor).

## DISCUSSION

It is a well known truism that theorizing becomes increasingly difficult as the number of known facts becomes larger (Friedmann 1929:v).

### Residents versus Migrants

The huge numbers of migrants descending upon the tropics each autumn and winter have often been commented upon (e.g., Moreau 1972). It has long been thought that broad-based competition between migrants and tropical residents must play an important role in tropical avian community ecology (e.g., Morse 1971; MacArthur 1972). As data have accumulated, this view has gradually been replaced with another: that migrants are an integral part of tropical ecosystems, and that generalities regarding migrant-resident interactions cannot be made (see discussion in Rappole et al. 1983; Rappole 1995). In examining the data in Figure 1, I have (reluctantly) decided to raise the issue of broad-based competition again. The presence of so many nearctic-neotropical migrants could (and probably does) have a strong impact on the standing crop of resources at stop-over sites. The presence of migrants could therefore result in exploitation, or indirect, competition with the resident community. Whether the possibility of such broad competition affects residents remains to be demonstrated.

Although numerous comparisons of species composition have been made in tropical avian communities (see Rappole 1995 for a neotropical review), comparisons of the relative abundances of migrants and residents during migration (e.g., Figure 1) do not seem to have been made. Investigations of migrant-resident interactions have tended to focus on wintering communities (perhaps because movements have become more stable by this time), despite the fact that migrant abundance tends to peak in autumn. Migrant effects

upon residents might be most readily observed at this time, particularly when it is considered that resident numbers are also at their peak due to breeding season recruitment. Examination of the effect(s) of migrants on residents during migration has the additional advantage that every day during migration brings a different avian community to the same site. The comparison of Figure 1 raises far more questions than it answers. More data will be needed to fully address this topic.

### Middle American Migratory Routes: Autumn Migration in the Red-eyed Vireo

In recent years we have made remarkably little progress in determining the nonbreeding ranges and movements of nearctic-neotropical migrants. We will never understand the evolution of the nearctic-neotropical migration system without a much more extensive knowledge of these ranges, including the timing and routes of migration. I suggest that one can choose almost any nearctic-neotropical migrant songbird and with some study not only significantly improve our knowledge of its nonbreeding distributions, but also address interesting evolutionary questions. As an example I discuss the widespread and common Red-eyed Vireo (*Vireo olivaceus*). The capture data in this study provide new insight into the autumn migratory route of this species.

Cooke (1915) provided the only graphical summary I have seen of the migratory route of the Red-eyed Vireo. His concept of the route was in error, however. For example, in his scenario the species did not occur in southern Veracruz. However, Cooke's map serves as a better beginning than route discussions in literature on distributions (e.g., A.O.U. 1983) because this literature tends to deal primarily with overall distribution, discussing the full range of a species within the zone of coverage, rather than delimiting the areas of densest occurrence. Our knowledge of the geographic densities of non-breeding nearctic-neotropical migrants is exceptionally crude. Nevertheless, even the little that exists has generally not been synthesized.

The Red-eyed Vireo is a mainland and trans-oceanic Middle American migrant. It is rare as a transient through the Bahamas and Cuba (Bond 1971). Wetmore and Swales (1931) and Wetmore and Lincoln (1933) did not record it from Haiti or the Dominican Republic. Raffaele (1983) noted it as an accidental migrant in Puerto Rico (see McCandless 1961) and as not recorded in the Virgin Islands. It is abundant in northwestern Florida (Crawford and Stevenson 1984) and common to abundant in southern Louisiana (Lowery 1974), but uncommon on the Texas Coastal Bend



(southern Texas) in autumn (Rappole and Blacklock 1985). Most individuals thus appear to depart the United States in autumn along the coast of the Gulf of Mexico between eastern Texas and northern Florida. Although a common autumn migrant on the northern slope of the Isthmus of Tehuantepec (this study), the high percentage of young birds in the total sample (82%; see Winker 1995) suggests this area may be at the edge of the main autumn route (see Ralph 1981; age ratios of this nature are often encountered in coastal areas). Additional data from further inland would be useful.

The status of the Red-eyed Vireo on the Yucatan Peninsula is not clear. Paynter (1953, 1955) noted its occurrence as a transient in Yucatan and Quintana Roo, and on the Campeche Banks, but did not give its abundance. Paynter (1955) noted only five specimens and two sightings (1953), and Rogers et al. (1986) recorded only two captured individuals in autumn (state of Yucatan), suggesting a status less than common. It is probably more common on this peninsula than these records indicate, however, and may simply overfly the dry northern zones. Russell (1964) found the species to be a "moderately common transient" in Belize. Records suggest it is uncommon in the highlands and Peten region of Guatemala (Griscom 1932; Land 1970). Russell's observations, coupled with the species' abundance on the Gulf slope of the Isthmus of Tehuantepec and regional topography, suggest that the southern Yucatan Peninsula and the Peten region of Guatemala will be found to be regions where considerable numbers pass in autumn.

Dickey and Van Rossem (1938:471) noted only a single specimen from El Salvador (San Salvador, 1 April 1912), and commented that "It is probable that the great majority of those passing through Central America migrate along the eastern coast." This view seems correct. The species is a common migrant in Honduras, particularly in the Caribbean lowlands (Monroe 1968). Monroe (1968:317) found that in Honduras they occur "in the interior on both slopes to 1100 meters, but there are no records for the Pacific lowlands below 750 meters." Further, he noted (1968:317) that most records occurred "in the Caribbean lowlands and in the islands off the north coast." He (1968) also noted that spring crossing of the Gulf of Honduras by nocturnal migrants is a regular phenomenon, and that autumn crossings also probably occur on a large scale. This overwater crossing has been largely neglected in considerations of Middle American migrations. It deserves more consideration and investigation. Rogers and Odum (1966) found some very thin Red-eyed Vireos at Almirante, Panama, again suggestive of an over-

water crossing (see also their data for Ovenbirds [*Seiurus aurocapillus*] and Gray Catbirds [*Dumetella carolinensis*]). Based on the evidence, it is likely that trans-Caribbean flights from the Yucatan Peninsula and Belize across the Gulf of Honduras to Honduras, and from the Costa de Miskitos (Mosquito Coast) of Nicaragua to Panama (and northwestern Colombia?) are probably regularly made by large numbers of landbird migrants in autumn.

The scarcity of the species in Oaxaca (Binford 1989), the highlands of Guatemala (Land 1970), in El Salvador (Dickey and Van Rossem 1938), and in the Pacific lowlands of Honduras (Monroe 1968) suggests that the main route in central Middle America is through the Caribbean and Gulf lowlands both in spring and autumn. Our understanding of migration in Nicaragua is decidedly poor. It is likely that an autumn and spring crossing to and from the Pacific slope of Central America occurs in this country, for Red-eyed Vireos are abundant migrants in Costa Rica on both slopes, primarily in the lowlands (Slud 1964; Stiles and Skutch 1989). Wetmore et al. (1984) and Ridgely and Gwynne (1989) noted that the species is common to very common in both spring and autumn migration nearly throughout Panama.

Given the winter distribution of the species (see Barlow 1980; A.O.U. 1983; Ridgely and Tudor 1989), a crossing of the eastern Pacific (Gulf of Panama and seaward environs) and the southwestern Caribbean is a likelihood, but I suggest that the Caribbean crossing from eastern Nicaragua to Panama and northwestern Colombia is likely to be much more extensive than portrayed by Cooke (1915). This could be ascertained through coastal observations and visits at the proper time to Isla de San Andres and Isla Providencia (east of Nicaragua). The winter range is primarily east of the Andes, however, (A.O.U. 1983:597; Ridgely and Tudor 1989; *contra* Barlow's Figure 10), and the trans-Andean movements of this and other songbird migrants appear to be unknown. Williams et al. (1977) found that the bulk of overwater migration occurred below 2 km altitude. It seems likely that this largely lowland species would use passes on nocturnal migration to cross the Andes, but it is possible that a broad front, high altitude migration is also made. Beebe (1947) recorded four individuals in spring at Paso Portachuelo in north-central Venezuela (easternmost Andes); Voous (1957) recorded only one specimen for the Netherlands Antilles. The method(s) used to cross the Andes probably affects the extent of overwater crossings in the southern Caribbean and eastern Pacific (Gulf of Panama region).

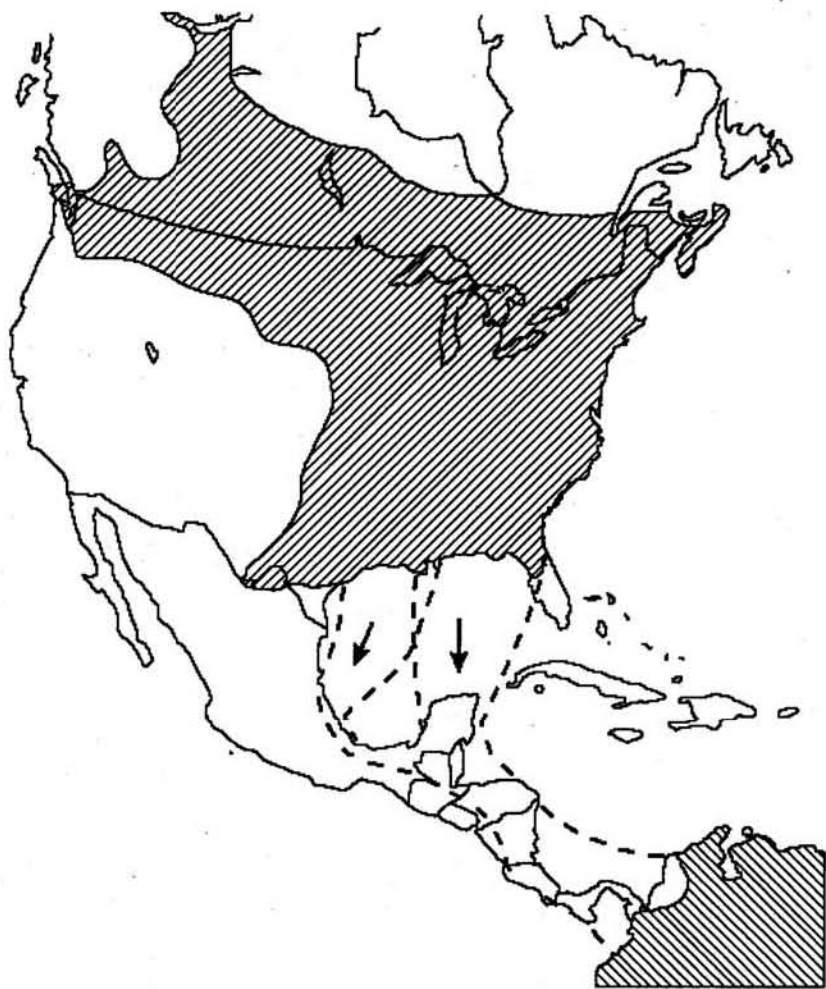


Figure 4. Autumn migration route of the Red-eyed Vireo in Middle America. Few birds seem to occur outside of the dashed lines.

The evidence and suppositions given above are portrayed in Figure 4, which is modified from Cooke (1915:40). The migratory hiatus shown in the southern Gulf of Mexico is based on observations at the Los Tuxtlas study site discussed in Winker (1995). This concept of the autumn route of the Red-eyed Vireo could be modified in several areas with the accumulation of more data.

How does the study of migratory routes address interesting evolutionary questions? Two factors are acting on migrants in determining the routes taken in their biannual journeys: historical constraints and present evolutionary pressures. It is often observed that migrants arrive and depart via the route by which their expansion into a present breeding range occurred, regard-

less of whether this route seems the best possible (see discussions in Cooke 1915; Lack 1968). These routes are subsequently modified by natural selection, and this is where we presume such modifications as trans-Gulf crossings and seasonal route differences arose. Attempting to disentangle likely causes for present routes becomes interesting when species occupying similar ranges arrive and depart using different routes.

Consider two species whose breeding ranges overlap extensively with that of the Red-eyed Vireo: Gray Catbird and Ovenbird. The wintering ranges of both lie primarily in Middle America (see Rappole et al. 1983; 1993), yet both occur very commonly in the Caribbean (surely not the route by which they arrived in the nearctic). It seems

odd, therefore, that the Red-eyed Vireo so completely avoids this area. Its winter range in South America would make trans-Caribbean movements energetically advantageous, but instead we find such crossings in species in which it would seem less likely, given ultimate destinations. Several other species whose breeding ranges overlap broadly with that of the Red-eyed Vireo, and whose wintering ranges are also in South America (e.g., Veery [*Catharus fuscescens*], Scarlet Tanager [*Piranga olivacea*], Bobolink [*Dolichonyx oryzivorus*]; see Rappole et al. 1983, 1993), do use an autumn trans-Caribbean migratory route. Unlike these five species, however, the Red-eyed Vireo has a very close congener in the Caribbean: the Black-whiskered Vireo (*Vireo altiloquus*). Perhaps this is why the migratory route of the Red-eyed Vireo so completely avoids this area?

The Red-eyed Vireo occurs sympatrically with at least 21 other vireo species (Barlow 1980). It probably arrived on its mainland nearctic breeding grounds through Middle America (Barlow 1980). Another close congener occurs across much of the migratory route the Yellow-green Vireo (*Vireo flavoviridis*), but these two species would theoretically have evolved in proximity to one another, making co-occurrence during migration no surprise. The Yellow-green Vireo, an intratropical migrant, is gone in autumn from Los Tuxtlas and much of the rest of Central America before large numbers of Red-eyed Vireos arrive from the north in autumn, and Ramos (1983) noted data showing that spring passage of Red-eyed Vireos seems to have no effect on the breeding of Yellow-green Vireos in Los Tuxtlas. Whether the presence of Black-whiskered Vireos in the Caribbean might have historically prevented Red-eyed Vireos from using this region on migration will remain unknown, but data on the nonbreeding movements, behaviors, and habitat use of the two species could be revealing. Black-whiskered Vireos and Red-eyed Vireos show a broad overlap in their wintering ranges (Barlow 1980; A.O.U. 1983), where they may coexist due to exploitation of different feeding niches (see Barlow 1980; cf. Hamilton 1962), and Black-whiskered Vireos may also be largely gone from the Greater Antilles by the time autumn Red-eyed Vireos would arrive if they used the Caribbean (Phillips 1991).

Many of our ideas of the forces affecting the distributions of nonbreeding birds remain speculative for lack of data. Wintering ground segregations of species and populations (or races) are often considered circumstantial evidence of competition-based forces (see Lack 1968; Ramos 1988). These forces

are more complex in migration (because overlaps of species and populations are more extensive then), but nevertheless should theoretically act to promote both spatial and temporal segregations. The timing of nonbreeding movements and the relative densities of nonbreeding birds throughout their ranges constitute data needed to begin to answer these questions. These data alone will not be sufficient, however.

## CONCLUSIONS

...the present records are given merely because they are the best now obtainable, and because they may furnish some material for the use of the future student. (Cooke 1888:13).

Without knowledge of distributions, movements, and habitat selection in neotropical migrants, conservation plans focusing on this broad group are not likely to achieve a high degree of success. While I think the results of this study (see also Winker 1995) demonstrate the value of constant effort, single site research efforts at neotropical stopover sites, there are clearly limitations to these endeavors. Questions regarding diet, sex, and geographic origin of migrants are begging to be addressed throughout the ranges of all neotropical migrants. Answers to these questions have been most successfully generated from the examination of museum specimens. Consider also the light that genetic analyses shed upon the probable extent of movements in Common Bush-Tanager, and that mass gains in "Traill's" Flycatcher at this site may contain a nonfat element, a possibility best addressed through whole-carcass fat extractions. Future investigations should include a significant collecting component; there are simply too many important data that specimens provide to forego this avenue of investigation. Happily, our knowledge of population biology and the considerable annual mortality that most bird populations experience assures us that the vast majority of avian populations can withstand a limited harvest. The collection of birds for scientific reasons has made tremendous contributions to our knowledge of nonbreeding birds (e.g., Phillips 1986, 1991; Ramos 1988), yet has had an infinitesimally small impact on bird populations (see Banks 1979; Winker et al. 1991).

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## Appendix. Species and numbers of birds captured during study.

<i>Accipiter striatus</i>	1	<i>Geothlypis trichas</i>	12	<i>Pipra mentalis</i>	34
<i>Aimophila rufescens</i>	2	<i>Geotrygon montana</i>	1	<i>Piranga leucoptera</i>	1
<i>Amazilia candida</i>	25	<i>Glaucidium brasilianum</i>	3	<i>Piranga olivacea</i>	3
<i>Amazilia tzacatl</i>	1	<i>Guiraca caerulea</i>	11	<i>Piranga rubra</i>	8
<i>Amazilia yucatanensis</i>	2	<i>Habia fuscicauda</i>	26	<i>Pitangus sulphuratus</i>	2
<i>Amblycercus holosericeus</i>	5	<i>Habia rubica</i>	34	<i>Platyrinchus cancrorninus</i>	18
<i>Anabacerthia variegaticeps</i>	5	<i>Helmitheros vermivorus</i>	34	<i>Polioptila caerulea</i>	1
<i>Arremonops rufivirgatus</i>	5	<i>Henicorhina leucosticta</i>	19	<i>Protonotaria citrea</i>	1
<i>Atlapetes brunneinucha</i>	1	<i>Hylocichla mustelina</i>	60	<i>Pteroglossus torquatus</i>	2
<i>Attila spadiceus</i>	12	<i>Hylomanes momotula</i>	8	<i>Ramphocaenus melanurus</i>	5
<i>Automolus ochrolaemus</i>	4	<i>Hylophilus decurtatus</i>	9	<i>Ramphocelus sanguinolentus</i>	2
<i>Basileuterus culicivorus</i>	43	<i>Hylophilus ochraceiceps</i>	3	<i>Rhynchocyclus brevirostris</i>	24
<i>Basileuterus rufifrons</i>	3	<i>Icteria virens</i>	45	<i>Saltator maximus</i>	2
<i>Campylopterus excellens</i>	31	<i>Icterus galbula</i>	11	<i>Seiurus aurocapillus</i>	110
<i>Campylopterus hemileucurus</i>	48	<i>Lanio aurantius</i>	4	<i>Seiurus motacilla</i>	2
<i>Campylorhynchus zonatus</i>	3	<i>Lepidocolaptes souleyetii</i>	1	<i>Seiurus noveboracensis</i>	17
<i>Caryothraustes pollogaster</i>	6	<i>Leptopogon amaurocephalus</i>	7	<i>Setophaga ruticilla</i>	51
<i>Catharus fuscescens</i>	7	<i>Leptotila rufaxilla</i>	7	<i>Sittasomus griseicapillus</i>	5
<i>Catharus ustulatus</i>	29	<i>Leptotila verreauxi</i>	12	<i>Sporophila torqueola</i>	6
<i>Chlorospingus ophthalmicus</i>	80	<i>Limnithlypis swainsonii</i>	23	<i>Thamnophilus doliatus</i>	5
<i>Coereba flaveola</i>	2	<i>Megarynchus pitangua</i>	3	<i>Thryothorus maculipectus</i>	12
<i>Columbina passerina</i>	1	<i>Melanerpes aurifrons</i>	10	<i>Tiaris olivacea</i>	23
<i>Columbina talpacoti</i>	3	<i>Melanerpes pucherani</i>	1	<i>Tinamus major</i>	1
<i>Contopus virens</i>	8	<i>Mionectes oleagineus</i>	156	<i>Tityra semifasciata</i>	2
<i>Crotophaga sulcirostris</i>	5	<i>Mniotilta varia</i>	28	<i>Tolmomyias sulphurescens</i>	11
<i>Cyanerpes cyaneus</i>	6	<i>Momotus momota</i>	9	<i>Trogon collaris</i>	5
<i>Cyanocompsa cyanooides</i>	3	<i>Myiarchus crinitus</i>	46	<i>Trogon massena</i>	1
<i>Cyanocompsa parrellina</i>	13	<i>Myiarchus tuberculifer</i>	8	<i>Turdus assimilis</i>	8
<i>Cyanocorax yncas</i>	1	<i>Myiobius sulphureipygius</i>	3	<i>Turdus grayi</i>	32
<i>Dendrocincla anabatina</i>	6	<i>Myioborus miniatus</i>	2	<i>Tyrannus tyrannus</i>	2
<i>Dendrocolaptes certhia</i>	5	<i>Myiodynastes luteiventris</i>	1	<i>Veniliornis fumigatus</i>	1
<i>Dendroica magnolia</i>	83	<i>Myiopagis viridicata</i>	2	<i>Vermivora chrysoptera</i>	3
<i>Dendroica pensylvanica</i>	1	<i>Myiozetetes similis</i>	1	<i>Vermivora peregrina</i>	16
<i>Dendroica petechia</i>	5	<i>Oporomis formosus</i>	87	<i>Vermivora pinus</i>	14
<i>Dendroica virens</i>	11	<i>Oporomis philadelphia</i>	1	<i>Vireo flavifrons</i>	4
<i>Dumetella carolinensis</i>	107	<i>Ornithion semiflavum</i>	3	<i>Vireo griseus</i>	140
<i>Empidonax trillii</i>	103	<i>Pachyrhamphus aglaiae</i>	7	<i>Vireo olivaceus</i>	273
<i>Empidonax alnorum</i>	33	<i>Parula americana</i>	2	<i>Vireo philadelphicus</i>	19
<i>Empidonax flavescens</i>	12	<i>Parula pitayumi</i>	2	<i>Vireolanius pulchellus</i>	1
<i>Empidonax flaviventris</i>	17	<i>Passerina ciris</i>	15	<i>Volatinia jacarina</i>	13
<i>Empidonax minimus</i>	32	<i>Passerina cyanea</i>	69	<i>Wilsonia canadensis</i>	20
<i>Empidonax trillii</i>	12	<i>Phaethornis longuemareus</i>	6	<i>Wilsonia citrina</i>	97
<i>Empidonax virescens</i>	17	<i>Phaethornis superciliosus</i>	68	<i>Wilsonia pusilla</i>	31
<i>Euphonia gouldi</i>	17	<i>Pheucticus ludovicianus</i>	5	<i>Xenops minutus</i>	7
<i>Euphonia hirundinacea</i>	135	<i>Playa cayana</i>	2	<i>Xiphorhynchus flavigaster</i>	12
<i>Geothlypis poliocephala</i>	4	<i>Piculus rubiginosus</i>	3		