Stopover Ecology of Nearctic-Neotropical Migrant Songbirds in Hardwood Hammocks of the Florida Keys

FINAL REPORT

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Abstract: This report provides the first systematic quantification of Nearctic-Neotropical songbird migration in the Florida Keys and the first investigation of the stopover biology of migrants within the Florida-Caribbean flyway. We studied migrants during 5 different migration seasons on 2 properties within the Florida Keys Wildlife and Environmental Area. We sampled migrants during spring 2002, fall 2002, and spring 2003 on Key Largo in the Upper Keys and during fall 2003 and spring 2004 on Wahoo Key in the Lower Keys. We used daily mist-netting to collect data on migrant relative abundance, physiology, and diet. We collected observations of foraging behavior and biweekly samples of arthropod abundance within live foliage and leaf litter to assess food availability for migrants. We captured 2,753 individual migrants of 57 different species. Fifteen species made up 83.6% of the migrant sample. The 7 most abundant species, which comprised 62.7% of all migrants captured, were ovenbird (*Seiurus aurocapillus*), western palm warbler (*Dendroica palmarum*), American redstart (*Setophaga ruticilla*), common yellowthroat (*Geothlypis trichas*), prairie warbler (*Dendroica discolor*), worm-eating warbler (*Helmitheros vermivora*), and black-throated blue warbler (*Dendroica caerulescens*). Most Florida Keys migrant songbirds have core wintering areas within the Caribbean. Breeding origins of migrants range widely throughout eastern North America, from Canadian boreal forests to the southeastern coastal plain. Both the total number of species captured and capture rates were higher during fall migration than spring. We documented 51 Swainson's warblers (*Limnothlypis swainsonii*) during a single fall migration in the Upper Keys, suggesting that this species is much more common at stopover sites in the Keys than previously thought. We captured 2 Bicknell's thrushes (*Cathurus bicknelli*), an endangered species. Previously, there have been no accepted records of Bicknell's thrushes south of South Carolina during migration. Most species gained mass and accumulated fat (the primary fuel for migratory flight) during stopover, suggesting that hardwood hammocks in the Florida Keys provide adequate stopover habitat during both seasons. Three groups of arthropods made up the majority of both migrant diet and arthropod abundance samples: spiders, beetles, and ants. Diet and foraging data suggested considerable partitioning of resources and little interspecific competition within the migrant community for food. Both arthropod availability and rates of mass gain were higher during fall migration than spring and higher in the Upper Keys than the Lower Keys. The correspondence of high arthropod abundance with increased rates of mass gain suggests that local food availability exerts an influence on migrant physiology during stopover.

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INTRODUCTION

Many species of Nearctic-Neotropical migratory landbirds are experiencing population declines (Robbins et al. 1989, Askins et al. 1990, DeGraaf and Rappole 1995, Ballard et al. 2003, Rich et al. 2004). Habitat loss or degradation in both breeding areas and wintering areas has been implicated as a major factor contributing to these declines (Rappole and MacDonald 1994, Robinson and Wilcove 1994, Wunderle and Waide 1994). However, many migrant species spend a large proportion of each year at stopover sites during migration, and this period of the annual cycle has received relatively little attention for most species and populations of migratory birds (Moore and Simons 1992, Hutto 2000). Population regulation can occur during any period of a migratory bird's annual cycle (Sherry and Holmes 1994, Newton 2004), and the migration period may contribute disproportionately to the annual mortality of both juvenile and adult birds (Sillett and Holmes 2002). In addition to affecting survival, events during migration may strongly influence reproductive performance. Both body condition at the time of arrival at breeding areas and the timing of arrival at breeding areas can strongly influence reproductive success (Marra et al. 1998, Smith and Moore 2003). Reproductive performance of North American warblers that winter in the Caribbean has been linked to winter habitat quality and food availability (Norris et al. 2004). Understanding the factors that influence migration timing, body condition, and survival (including food availability during stopover) may be particularly important for the conservation of migratory birds.

Most small passerines migrate at night with bouts of foraging at stopover sites during the day (Alerstam 1990). Nocturnal migrants increase their body mass seasonally to carry high loads of body fat during migration (Bairlein 2002), and fat is the primary light-weight, high-energy fuel for long-distance migration (Alerstam and Lindström 1990). During fall migration many migrants are observed stopping over in coastal habitats where they put on fat to fuel flights across geographic barriers such as the Gulf of Mexico (Moore and Simmons 1992, Russell et al. 1994). In spring migration, many migrants stop in gulf-coastal forests to refuel for continued migration after an energy-depleting non-stop flight across the Gulf (Moore and Kerlinger 1987). The relative value of stopover habitats in coastal areas may be related to the availability of high-quality food resources that allow migrants to quickly deposit fat to prepare for or recover from energy-intensive flights and to maximize their speed of migration towards breeding or wintering areas (Alerstam and Lindström 1990, Moore and Simons 1992).

During fall migration, many species that are insectivorous during the breeding season switch to diets that include a higher proportion of fruit

(Bairlein 1990). In both field and laboratory studies, species that switched to a mixed diet of insects and fruit during migration were able to gain mass (in fat) more quickly than insectivorous species; however, purely insectivorous species gained significant amounts of mass as well (Parrish 1997, Suthers et al. 2000, Bairlein 2002). Thus, the relative abundance of arthropods and fruit intake at stopover sites should be related to rates of mass and fat gain by migrants during stopover. Although many studies have suggested that differences in food availability may explain differences in mass gain observed among sites, seasons, and years, very few studies have investigated the relationship between food availability and rates of mass gain during stopover (but see Bibby et al. 1976, Kelly et al. 2000).

The upland tropical hardwood hammock forests of the Florida Keys have been extensively cleared or fragmented by development (Strong and Bancroft 1994*a*). Habitat loss and fragmentation in the Keys has contributed to the extirpation of at least 1 snail species (Forys et al. 2001), extensive loss of breeding habitat for birds (Bancroft et al. 1995), and decreased availability of critical post-fledging dispersal habitat for white-crowned pigeons (Strong and Bancroft 1994*b*) (see Appendix A for scientific names of all bird species captured during this study). In addition to physical habitat loss and degradation due to fragmentation, Monroe County has a long history of spraying aerial adulticides for mosquito control, which has contributed directly to population declines of several different species of butterflies and which may have reduced overall arthropod abundance and diversity in the Florida Keys (Emmel 1988). A number of mid-sized tropical hardwood hammocks are managed by the Florida Fish and Wildlife Conservation Commission as part of the Florida Keys Wildlife and Environmental Area. These properties are protected from development and do not currently allow the direct spraying of aerial adulticides or larvicides, with the exception of health emergencies (e.g., a nearby West Nile Virus case). Since most "protected" properties in the Keys are surrounded by development, insecticide drift from both plane- and truck-mounted aerial sprayers into these properties is probably a regular occurrence.

In the southern United States there are 3 primary routes of transit for migrants between temperate breeding areas in eastern and central North America and tropical wintering areas in Mexico, the Caribbean, central America, and South America: (1) the circum-Gulf route, which follows land around the Gulf of Mexico to the west; (2) the trans-Gulf route, which requires long-distance flights directly across the Gulf of Mexico; and (3) the Florida-Caribbean route, where birds travel down the Florida peninsula into the Caribbean (Stevenson 1957; Lowery and Newman 1966; Moore et al. 1993, Figure 4). Of these 3 migration routes, the Florida-Caribbean route has received proportionately little research attention. At the most basic level of distribution and abundance, there have been very few studies to inventory or quantify the relative abundance of migrants among sites, seasons, or habitats along this route. We know of no investigations of the aspects of stopover biology such as stopover length, mass gain, diet, or food availability that may be related to migrant survival along this route.

South Florida, and the Florida Keys in particular, have long been known to be a major concentration point for migrant landbirds (Howell 1932, Stevenson and Anderson 1994, Pranty 1996). Most of what is known about species composition and relative abundance of migrant landbirds in South Florida comes from 3 sources: (1) summarized observations of birdwatchers; (2) a single mist-netting study near Homestead, Florida; and (3) published summaries of birds killed in collisions with communications towers, lighthouses, or tall buildings. The first published mention of heavy songbird migration in South Florida was of migrant collisions with the Sombrero Key lighthouse, just offshore of the Middle Florida Keys (Merriam 1885). As early as the late-nineteenth century, Scott (1890) observed large numbers of spring migrants stopping over in the Dry Tortugas, a small group of islands 90 km to the west of Key West. Observations of migrant landbirds in the Dry Tortugas have been reported regularly in the seasonal birding summaries of *Audubon's North American Birds* and major fallouts have been described several times in Audubon journals such as *Bird Lore* (Bennett 1909) or the *Florida Naturalist* (Abrahamson 1960; Sprunt 1962*a,b*). Aside from observations from the Dry Tortugas, the only published descriptions of the relative abundance of migrants in the Florida Keys are summarized observations of birdwatchers (Hundley and Hames 1960, 1961, 1962; Pranty 1996). Fisk (1979*a,b*) used mist-nets to capture birds during both spring and fall migration at a suburban/agricultural site near Homestead, Florida, between 1967 and 1973. Although this study documented large numbers of gray catbirds, indigo buntings, and painted buntings, few other forest migrants, a major component of the Florida-Caribbean migrant landbird community, were documented because no forest habitat was available near the study site. These references, additional gray literature, and observations of thousands of birdwatchers have been summarized in Stevenson and Anderson's (1994) *Birdlife of Florida* and Pranty's (1996) *Birder's Guide to Florida* to produce a fair understanding of the relative abundance and seasonal timing of migration through South Florida.

The goal of this project was to improve our understanding of the seasonal distribution and stopover biology of migrant landbirds in hardwood hammocks of the Florida Keys. To this end, this project had 4 specific objectives:

1. provide the first systematic quantification of the relative abundance of migrants in hardwood hammocks in the Florida Keys;

2. evaluate the basic stopover biology of individual migrants including stopover length, energetic condition, and changes in mass during stopover;

3. describe foraging and dietary relationships among migrant species during stopover in the Florida Keys; and

4. investigate seasonal or site-specific variation in food availability for migrants.

A detailed investigation of these inter-related factors should provide an excellent starting point for understanding the importance of hardwood hammock habitats in the Florida Keys to migratory landbirds.

METHODS

Study Sites

The Florida Keys are a northeast-southwest trending island chain stretching nearly 210 km from the southern tip of Florida. The primary upland habitat of the Florida Key is tropical hardwood hammock (Strong and Bancroft 1994*a*). This study took place at 2 different hardwood hammock study sites within the Florida Keys Wildlife and Environmental Area, one in the Upper Keys, the other in the Lower Keys (Fig. 1). The Upper Keys study site was located between Casa Court and Meridian Street on the northwest side of US Highway 1 on lower Key Largo at 25.06°N, 80.26°W. The Lower Keys study site was located on Wahoo Key, a small island just to the north of Summerland Key at 24.41°N, 81.27°W. The Lower Keys study site was approximately 90 km to the southwest of the Upper Keys site. The Upper Keys study site contained approximately 12.1 ha of tropical hardwood hammock and was surrounded by residential neighborhoods with mixed hardwood hammock/exotic vegetation. The Lower Keys study site was located on a small island with approximately 1.8 ha of tropical hardwood hammock surrounded by 3.3 ha of mostly buttonwood vegetation with some mangroves. The nearby vegetation of Summerland Key was mostly cleared residential neighborhoods with a mix of exotic, buttonwood, and mangrove vegetation. (Appendix B lists the scientific names of all plant species mentioned in this report.)

Fig. 1. South Florida and the Florida Keys with locations of Upper Keys and Lower Keys study sites (2002–2004) in relation to Cuba, the Bahamas, and the Dry Tortugas.

Canopy height at the Upper Keys study site ranged from 8 to 12 m and the predominant, mature canopy tree species were wild tamarind, poisonwood, gumbo limbo, Jamaica dogwood, and pigeon plum. The major, well-shaded under story trees were white stopper, Spanish stopper, crabwood, and strongbark, with lesser numbers of small pigeon plum, torchwood, wild lime, and marlberry. Many of these tree species were seasonally deciduous and leaf litter was well developed.

In the Lower Keys, canopy height was much lower, ranging from 4 to 7 m. The canopy was also much more open in the Lower Keys than in the Upper Keys, and there was not a strong distinction between the canopy and under story at this site. The most common large hardwood hammock tree species were poisonwood, sea grape, Florida thatch palm, dilly, and buttonwood. Smaller hammock trees such as black bead, black torch, and Spanish stopper were also common. The hardwood hammock was surrounded by a grassy transition zone of buttonwood, with lesser numbers of shrubby joewood and saffron plum trees, which graded into a mix of white mangroves, black mangroves, and red mangroves at the island fringe. Because of the small size and low stature of the hardwood hammock in the Lower Keys, leaf litter was much less well developed than in the Upper Keys study site and more sunlight penetrated to the forest floor.

Capture and Recapture Data Collection

Twenty-four standard mist-nets (12 m x 2.6 m) with 30-mm mesh size were used to capture birds at each site during 5 different migration seasons: spring 2002, fall 2002, and spring 2003 in the Upper Keys and fall 2003 and spring 2004 in the Lower Keys. The same nets were operated in the Upper Keys (along with playbacks of calls) for a week in winter 2002-2003. The number of hours that each net was operated was recorded for each day. This allowed us to calculate total net-hours per field season as the total number of hours that all 24 nets combined were open. In the Upper Keys, nets were placed in pairs spaced 30 m apart on 4 transects that were spaced 40 m apart. All nets at the Upper Keys study site were surrounded by hardwood hammock habitat for at least 40 m in any direction. In the Lower Keys, due to the high density of vegetation and the presence of several endangered plants, this grid spacing of nets was not replicated. Instead, mist-nets were placed opportunistically on existing trails and in open areas that required little clearing of the vegetation. Half of the nets in the Lower Keys were placed in hardwood hammock, although most nets were within 20–40 m of the buttonwood transition zone. All remaining nets in the Lower Keys were placed within the buttonwood transition zone.

Nets were checked at 20- to 30-minute intervals depending on the temperature. Birds were extracted from nets and then transported to a central banding station for processing. With the exception of hummingbirds, each bird was banded with a single numbered aluminum leg band. During spring 2003 we stopped banding northern cardinals due to their ability to remove or damage aluminum bands. For each bird captured we measured body mass (±0.03 g using a Mettler electronic balance) and unflattened wing chord (±0.5 mm). Age and sex of migrants was determined from plumage and/or measurements using Pyle (1997). In spring 2002, we used the fat classification scale of Rogers (1991) to assess the fat loads carried by migrants. Observers frequently disagreed on boundaries between fat categories using this scale. Therefore, towards the end of this season we switched to the categorical fat scale proposed by Kaiser (1993) and found close agreement between fat scores assigned by different banders. We used this scale for fat scoring in all subsequent field seasons. Because fat scoring is subjective and can vary among individuals (Krementz and Pendleton 1990), field assistants were trained each season so that variation was minimal. In all seasons 95% of all fat scores were assigned by only 2 individuals who regularly checked their fat scores against each other. The same 2 banders did most fat scoring during fall 2002 and fall 2003, and 3 different banders did all fat scoring during spring 2003 and spring 2004.

For summaries of mist-net captures, all species were classified as either migrants or locally breeding birds (see Appendix A for the migratory status of all bird species captured during this study). Four different species occurred both as through migrants and locally breeding birds. We classified 3 of these species (prairie warblers, black-whiskered vireos, and yellow-billed cuckoos) as migrants because a large proportion of individuals had high fat stores typical of passage migrants. Individuals of these species that showed signs of breeding activity (swollen cloacal protuberances or vascularized brood patches) were removed from the “migrant” sample. We believe that the resulting sample of birds for these species represents primarily migrant individuals, although some locally breeding birds could be mixed in with the migrant sample. At least one of the yellow warblers we captured had measurements indicative of the locally breeding Cuban yellow warbler or *gundlachi* subspecies; however, 6 of the 7 individuals had fat deposits consistent with birds preparing for or participating in migration.

We estimated the minimum stopover length (MSL) of recaptured birds by subtracting the date of first capture from the date of last capture (Cherry 1982). This method assumes that birds were captured on their first day at the study site and again on the day before leaving the study site. This assumption is most likely false and true stopover length is almost certainly longer than our calculated MSL (Kaiser 1999, Shaub et al. 2001). However, MSL is a standardized index that has been reported among many studies and is useful for comparing patterns of stopover among species, sites, and seasons. We refer to birds captured again after their initial capture as "recaptures" and all birds that were only captured once during a season as "single-captures." Birds that were captured a second time on the same day as their initial capture were excluded from all subsequent recapture analyses due to the potentially negative effects of this much handling on migrant condition (Mueller and Berger 1966). For recaptures, we calculated changes in body mass as the percentage change in body mass from initial to final capture using the equation

$$\text{percentage change} = (\text{final mass} - \text{initial mass}) * \text{initial mass}^{-1} * 100.$$

For changes in fat scores for recaptures we subtracted the final fat score from the initial fat score. Since most birds captured during migration are single-captures, we performed linear regressions of mass versus time of day to see if the slope of these regressions could be used to estimate daily mass gain from single-captures (Winker 1995, Dunn 2000, Jones et al. 2002).

Diet Data Collection and Fecal Sample Analysis

The 3 primary methods of diet sampling in field ornithology are (1) collection of birds to examine prey items in stomachs, (2) use of emetic to force birds to regurgitate prey items from their stomach, and (3) examination of fecal samples. All 3 methods are subject to possible biases of differential digestibility of prey items, with soft-bodied or small prey items being more infrequent in diet samples (Rosenberg and Cooper 1990). This bias is assumed to be strongest in fecal samples due to the longer amount of time available for digestion before a sample is produced relative to the freshness of prey items in stomachs or emetic samples (Major 1990). Although initial results from emetic studies suggested low mortality rates (Poulin and Lefebvre 1995), Johnson et al. (2002) showed lower recapture rates for birds that were given emetic and suggested that, because of the difficulty of finding dead birds, mortality due to this method may be higher than initially reported. We chose to examine fecal samples to characterize the diet of migrants because it was minimally invasive. Previous studies have found undigested fragments of small, soft-bodied prey items (such as flies) identifiable to the taxonomic level of family (Waugh 1979, Waugh and Hails 1983), and this method was probably sufficient to document all arthropod taxa that may have been present in the diets of Florida Keys migrants (Chapman and Rosenberg 1991).

We collected fecal samples by searching the cloth bags used to transport migrants to the central banding station. Each bag was turned inside out and carefully searched for fecal material, which was transferred into a small, labeled, plastic bag for storage. Fecal samples were then frozen and stored for analysis at the end of each field season. Fecal samples were generally single, relatively solid, well-contained packets. Some fecal samples were composed of multiple fragments, which were all collected and stored in the same bag. Within each bird species, only fecal samples of similar size were selected for analysis and incomplete samples were discarded. Fecal samples were analyzed under 10- to 30-power dissecting microscopes. After thawing, each sample was placed in a Petri dish and a small drop of water was added to loosen the sample for analysis. Samples were then teased apart with a sharp probe to separate fruit pulp, insect pulp, and undigested arthropod parts. Arthropod parts were identified primarily from photographs and line drawings from 3 references, which are listed here in decreasing order of usefulness (Chapman and Rosenberg 1991, Calver and Wooler 1982, and Ralph et al. 1985). In addition, arthropod parts were compared with parts from a reference collection of local, whole arthropods that we collected during arthropod abundance sampling at our study sites. This was particularly useful for identification by direct visual comparison of legs and wings found in fecal samples.

We used the method of Calver and Wooler (1982) to quantify the minimum number of individual arthropods represented by undigested parts in each fecal sample. For example, fangs and legs were the most common fragments used to identify spiders. A single spider has 8 legs and 2 fangs. If a fecal sample contained 2 fangs and 6 legs (of similar size), this was considered representative of only a single spider, even though it is possible that the fangs and legs came from different individuals. If the sample contained 2 fangs and 10 legs, this was considered representative of 2 spiders. If a sample contained 2 fangs and 3 legs, yet the 2 fangs were of different size, this was considered representative of 2 individuals. This method gave a conservative, minimum estimate of the number of individual arthropods in each fecal sample. Numbers of arthropods were probably underestimated because birds most likely ingested many arthropods of similar size, and these would be indistinguishable in individual fecal samples. For example, a prairie warbler may eat 7 ants of the same species in quick succession. The fecal sample that we collected for this individual may include only 19 legs (since the remaining legs might not be passed until in the next excretion). We would consider this fecal sample as representing only 4 individual ants (19 legs/6 legs per ant = >3 individuals).

Remains of both gastropods (shell fragments) and adult Lepidoptera (wing scales) were so fragmented that it was not possible to quantify the number of individual prey items of these 2 categories in each fecal sample. Migrant diet for these 2 prey categories is summarized only as the percentage of samples where the prey category was present. For all prey categories where numbers of individual arthropods in fecal samples were quantifiable, we calculated the proportion of each prey category in the diet of each species following the method of Chapman and Rosenberg (1991). In summary, the proportionate number of individuals of each prey category was determined separately for each fecal sample. Then, diets for each species were determined as the average of proportions of each prey category across all fecal samples for each species. This method is preferable to summing the number of individual arthropods in all samples pooled, which tends to overestimate the relative frequency of taxa that are particularly numerous in a few individual samples.

For each fecal sample, we determined the presence of fruit by the presence of seeds, capillaries, or fruit pulp. Fruit pulp differed in both texture and color from undigested insect pulp, and fecal samples with fruit often had a dark bluish to purplish coloration. We identified individual seeds to tree species by comparing them to dried seeds from hardwood hammock trees that were collected by researchers at the Tavernier Science Center (National Audubon Society, Tavernier, Florida) working with white-crowned pigeons (Bancroft and Bowman 1994). For each tree species in the reference collection we measured or categorized the following characteristics for 6 individual seeds: length, width, color (light vs. dark), flatness (flatted vs. not flattened), shape (oval, round, teardrop, wedge, bowl), and texture (smooth, rough, grooved, veined, or pitted). We entered these measurements into a database and then queried this database for the same characteristics of seeds we found in fecal samples. Queries tended to narrow possible tree species to 1–5 species. We then visually compared seeds from fecal samples to dried seeds in the reference collection to make final identifications.

Foraging Observations

We collected migrant foraging observations opportunistically in both seasons. Most observations were collected on trails outside of the main banding grid during the hours of mist-net operation. A small number of observations were collected along mist-net lanes in the hour following daily mist-netting after the nets had been closed. Individual birds were followed and observed through binoculars, and their foraging behavior was recorded by speaking into a portable micro-cassette recorder in real time. Foraging observations on cassettes were transcribed to data sheets in real time at the end of each migration season. During each foraging observation, information was collected on foraging rates, substrates, heights, and tree species used. Each time a bird changed its perch to a new location, this was recorded as a hop. Each time the bird moved to a new tree species, this event was recorded. Each time a bird made a movement that was indicative of an attack on a prey item, this was recorded as an attack. It was not possible to consistently determine the outcome of individual attacks (successful or not) so foraging attacks indicate a mix of successful and unsuccessful attacks on prey items. However, we view summaries of foraging attacks as indicative of the substrates, heights, and tree species where prey items were most likely acquired for each species.

For each foraging attack we recorded the substrate and height at which the attack took place. Foraging substrates included live leaves, dead leaves, bark, flowers, mid-air, or the ground. Because some species forage on the ground by pecking at the surface and others pick through leaves to access a deeper stratum of the leaf litter (Strong 2000), we divided attacks on the ground into 2 different categories: ground peck (surface) or ground turn (subsurface). Foraging heights were recorded relative to canopy height where the observation took place with an attack at the very top of a canopy tree receiving the value of 10. Therefore, an attack half the distance to the canopy was recorded as a 5, an attack at 3 m height in an area where the canopy was 10 m tall was considered a 3, and so on. This required each observer to regularly check the height of the canopy where foraging observations took place. During data analysis, foraging heights were reduced to 4 categories: ground, low (heights 1–3), middle (heights 4–6), and high (heights 7–10). To summarize foraging heights and substrates for each species, we first calculated the proportion of foraging attacks at each height or substrate for each individual foraging observation. We then averaged these proportions across all foraging observations for each species to characterize foraging height and substrate preferences among species. This approach was preferable to summing events across all observations pooled because there was considerable variation in the length of each individual foraging observation, and we wanted to avoid biasing summaries by observation length. We removed from summaries of foraging behavior 7 foraging observations that were shorter than 20 seconds.

Arthropod Sampling and Food Availability

We used a slight modification of methods described by Johnson (2000) to collect arthropod samples from live foliage, hereafter referred to as branch clipping. We used 2 custom-built extension poles to collect arthropod samples. One pole had a frame designed to hold a 13-gallon, white, plastic garbage bag in an open and horizontal position. After raising this pole to the desired height of the sample, the bag was quickly slipped over vegetation at the tip of a branch and closed by pulling on a string from the ground. The second pole was equipped with a pruning saw that was operated from the ground by cord and pulley. This saw was then used to clip branches just below the closed bag. Samples were lowered to the ground, the bag was closed with a twist-tie and labeled, and samples were placed in a freezer overnight to kill or immobilize all arthropods. The following day, bags were cut open lengthwise along their seams, spread out on a table with good lighting, and inspected for arthropods. Each leaf cluster of each branch clipping was carefully inspected (both visually and with magnifying glasses) and all arthropods were removed from either the vegetation or the surface of the bag and placed in a Petri dish for identification. Arthropods were identified to prey category under a dissecting microscope and each arthropod was measured to the nearest millimeter from the tip of the head to the tip of the abdomen using a measurement grid placed beneath the dish. Primary references used for arthropod identification were Borror et al. (1981) and Milne (1980). Arthropods of all common taxa were stored in jars of 70% ethyl alcohol and archived as voucher specimens at the Florida State collection of arthropods in Gainesville, Florida.

We collected 40 branch clippings per sampling event during 4 different sampling events (once every 2 weeks) each migration season. Branch-clip samples were taken from the 8 most common trees at the Upper Keys site and 8 of the 12 most common trees at the Lower Keys sites. Samples were not taken in the Lower Keys from Joewood (to avoid damage to a state-endangered species), saffron plum (thorns and the dense physical structure of this plant made sampling impossible), sea grape (bags would not fit over wide branch tips), or Florida thatch palm (fronds did not fit in sample bags). Within each tree species, samples were taken from heights selected by a random number table. Individual trees were selected by locating trees of the appropriate species closest to a random bearing from a random center point. In the Upper Keys, our extension poles could not reach upper canopy vegetation (the maximum height of the extended pole was 8 m, and some canopy trees in the Upper Keys study site were 13 m tall). Therefore, when canopy samples were called for by the random number table, we collected samples from the highest possible location we could reach. In this sense, our branch-clipping method was inadequate to sample the highest vegetation in the Upper Keys. This would bias results based on this sampling method if arthropod abundance varied between lower and upper branches of canopy trees. We did not sample live foliage arthropods when vegetation was wet after rains or during high winds.

Numbers of arthropods did not vary among sampling events within each season; therefore, we pooled all samples from each migration field season to describe arthropod relative abundance and prey category composition in branch-clipping samples. Different tree species had different masses and sample lengths due to differences in specific gravities and physical structure among species. Therefore, we did not standardize numbers of arthropods per sample by mass or length because the effect of tree species would introduce too much bias. Rather, we attempted to collect standard sample amounts per tree species, and we present our results as average numbers of arthropods per sample. We consider this a good index of the relative density of individual arthropods, which we consider a meaningful measure of relative food availability for migrant insectivores among tree species and between sites and seasons.

We collected arthropods from the leaf litter using standard collection methods described in Strong and Sherry (2001). We repeatedly sub-sampled leaf litter at random directions and distances from a random central point. For each sub-sample, we used a 10-inch putty knife to scoop leaf litter into the cylinder of a 0.1-m-diameter metal coffee can. Leaf litter was then transferred from the coffee can into a 1-gallon plastic bag until the bag was half full. One half-full bag was considered a single leaf-litter sample. Generally, 4–6 sub-samples of leaf litter were adequate to complete a single sample. Eight samples were taken during each sampling event in the Upper Keys, and 6 samples were taken during each sampling event in the Lower Keys. Since birds forage at or just under the surface of the leaf litter, care was taken to only collect the top horizon of leaf litter and not the soil beneath. Care was also taken not to collect samples near disturbed areas, such as trails, that may influence the natural abundance of leaf-litter arthropods. New areas were sampled at each study site during each sampling event to reduce the possibility of decreasing arthropod abundance over the course of a season during repeat sampling of leaf litter at a single site. We did not collect leaf-litter arthropods after rains when the leaf litter was wet.

After collecting leaf-litter samples in the field, each sample was placed in a Berlese funnel (Strong 2000), which was operated for 20–24 hours to extract arthropods from the leaf litter. In a test of the effectiveness of our funnels, we did not find any arthropods remaining in the leaf litter (which was picked through very carefully by hand with magnifying glasses) of 6 different samples after 20 hours of extraction. Numbers of arthropods did not vary among sampling events within each season; therefore, we pooled all samples from each migration field season to describe arthropod relative abundance and prey category composition in leaf-litter samples. Since the number of samples taken varied between the Upper Keys and Lower Keys we summarized relative abundance of leaf-litter arthropods as average numbers of individual arthropods per sample.

We collected arthropods in dead-leaf clusters (aerial leaf-litter) during spring 2003 only. This foraging substrate was used infrequently by most species, but regularly by worm-eating warblers, and is an important foraging substrate for worm-eating warblers during winter (Greenberg 1987). We walked random bearings within the study site and collected dead-leaf clusters into 1-gallon plastic bags until each bag was half full. We collected only clusters with less than 100 leaves each to insure that each sample represented a large number of independent dead-leaf clusters. We extracted arthropods from dead-leaf samples using Berlese funnels. We did not use this method to summarize relative abundance between sites or seasons. Therefore, we do not present relative numbers of arthropods per sample using this method, but rather pool data from all samples to describe prey size and prey taxa composition for this foraging micro-habitat.

We defined food availability as the abundance of potential prey items in micro-habitats used by an insectivore while searching for food (Wolda 1990). Therefore, we used results from our diet sampling to only include prey taxa actually occurring in migrant diet in estimates of food availability. After removing prey taxa that were not present in migrant diet, we used our foraging data to associate the appropriate arthropod abundance sampling technique (branch clipping or leaf litter) with each species. For example, leaf-litter sampling was considered a measure of food availability for Swainson's warblers and ovenbirds because >99% of all foraging attacks for these species was on the ground. Similarly, branch clipping was considered a measure of food availability for species that focused most of their foraging attacks on live foliage.

Data Analysis

Normality and homogeneity of variance was examined for all sample groups prior to statistical tests. When parametric assumptions were not met, we applied the appropriate non-parametric procedures (Zar 1998). Means and standard deviations are reported throughout this report. In some cases, medians and inter-quartile ranges may have been more appropriate summary statistics to report due to skewed distributions; however, we report means and standard deviations to allow for comparisons of our data with previous studies that have reported means and standard deviations. A statistical significance level was set at $\alpha = 0.05$ for all tests unless otherwise indicated. We used correspondence analysis to investigate dietary and foraging relationships among species (Sall and Lehman 1996, Krebs 1999). All statistical procedures were performed in either JMPIN version 3.2.6 (Sall and Lehman 1996) or Statistica version 6.1 (Statsoft 1995). Tables and figures were created in Excel 2000. All data were originally entered and stored in an Access database.

RESULTS

Mist-netting Effort, Species Composition, and Relative Abundance

We opened mist-nets for 20,987 net hours during the 5 migration seasons of this study. Nets were operated an average of 45.3 days per spring migration during 2002–2004 (3 spring field seasons) and an average of 56.5 days per fall migration during 2002–2003 (2 fall field seasons) (Table 1). Nets were open for a relatively consistent sampling period each field season of 4.83 ± 0.40 hours per day beginning 10–15 minutes before sunrise. However, there was considerable variation in total mist-net hours per field season (standard deviation of 1,678 net hours per season) due to variation in the frequency of individual net closures among field seasons. Nets within the more open, lower stature vegetation of the Lower Keys study site were more exposed to wind than the more protected study site in the Upper Keys. Thus, nets were more frequently closed in the Lower Keys due to high winds. Spring 2004 was particularly windy, and we were able to open a lesser number of nets per day during this season. Consequently, total net-hours for this season were more than 50% less than for all other field seasons, even though roughly the same number of days, and hours per day, were sampled among seasons. Because the number of net hours varied among field seasons, comparisons of mist-net captures across sites and seasons are made using the effort-standardized measure of captures (birds) per 1,000 mist-net hours (b/1,000 mnh).

In all 5 seasons combined we captured 2,760 individuals of 58 different migrant species. We also captured 241 individuals of 13 different locally breeding species (Appendix A). Based on the total number of individuals captured across all seasons, the 7 most abundant species made up 62.7% of all migrant captures (Table 2). These, plus an additional 8 species, made up 83.6% of all migrant captures. Fewer than 25 individuals were captured for

Table 1. Dates (start date, end date, and total number of days) and hours (h/day, total net hours) of mist-netting efforts at 2 different hardwood hammock study sites (Upper Keys and Lower Keys) in the Florida Keys during 5 different migration seasons (spring 2002, fall 2002, spring 2003, fall 2003, and spring 2004).

First day	Last day	Year	Season	Site	Number of days netting	Number of days closed	Hours/day netting	Total net hours
28 Mar	17 May	2002	Spring	Upper Keys	49	2	5.32	6,250
25 Aug	23 Oct	2002	Fall	Upper Keys	58	1	4.84	6,858
31 Mar	14 May	2003	Spring	Upper Keys	44	1	5.08	5,346
31 Aug	25 Oct	2003	Fall	Lower Keys	55	1	4.60	5,805
1 Apr	13 May	2004	Spring	Lower Keys	43	4	4.30	2,526

Table 2. Total number of mist-net captures and capture rates (birds per 1,000 mist net hours [b/1,000 mnh]) for the 15 most commonly captured species during spring and fall migration (combined) in hardwood hammocks of the Florida Keys (Upper Keys and Lower Keys study sites combined), 2002–2004. Species are sorted from highest to lowest overall capture rates.

Species	All captures (*n*)	b/1,000mnh
Ovenbird	563	24.8
Western palm warbler	225	10.6
American redstart	250	10.3
Common yellowthroat	233	8.7
Prairie warbler	176	8.3
Worm-eating warbler	186	8.1
Black-throated blue warbler	198	7.6
Northern waterthrush	129	5.6
Black-and-white warbler	129	4.7
Gray catbird	107	4.2
Northern parula	85	4.0
Swainson's warbler	58	2.6
Blackpoll warbler	46	2.1
Red-eyed vireo	36	1.7
Hooded warbler	31	1.3

each of the remaining 42 migrant species (73.7% of all species captured). Fewer than 5 individuals were captured for 23 species (40.4% of all species captured), and a single individual was captured for 12 species (21.1% of all species captured). For all subsequent summaries using mist-net capture rates, we pool capture data from the 2 spring migration seasons where we mist-netted in the Upper Keys (2002 and 2003) and present average capture rates for the Upper Keys in spring based on these 2 field seasons combined.

We captured an average of 38 species during fall migration and 26 species during spring migration. Combining all field seasons, 48 migrant species were captured during fall and 36 during spring. Ovenbirds, worm-eating warblers, northern waterthrushes, northern parulas, prairie warblers, and Swainson's warblers were captured more frequently during fall than spring, whereas western palm warblers and blackpoll warblers were captured more frequently during spring. Combining all seasons, we captured 43 species in the Upper Keys and 44 species in the Lower Keys. Ovenbirds, worm-eating warblers, Swainson's warblers, and black-and-white warblers were captured more frequently in the Upper Keys than the Lower Keys, whereas western palm warblers, blackpoll warblers, northern parulas, prairie warblers, red-eyed vireos, common yellowthroats, and American redstarts were captured more frequently in the Lower Keys. Capture rates were higher during fall than spring and higher in the Lower Keys than in the Upper Keys (Table 3). However, this pattern varied among site-season-species combinations (Appendix A). During fall migration, more birds were captured in the Upper Keys (142 b/1,000 mnh) than the Lower Keys (119 b/1,000 mnh). However, the opposite was true of spring migration, when many more birds were captured in the Lower Keys (183 b/1,000 mnh) than the Upper Keys (48 b/1,000 mnh).

Table 3. Capture rates (birds/1,000 mist-net hours) of migrant songbirds during fall and spring migration (Upper Keys and Lower Keys study sites combined) and in the Upper Keys and Lower Keys (fall and spring migration combined) in hardwood hammocks of the Florida Keys, 2002–2004. More detailed results for each study site in each season are presented in Appendix C.

Species	Total	Fall	Spring	Upper Keys	Lower Keys
Ovenbird	24.8	36.7	6.6	34.2	10.4
Western palm warbler	10.6	3.2	21.7	0.3	26.2
American redstart	10.3	11.5	8.5	8.1	13.7
Common yellowthroat	8.7	7.3	10.8	6.1	12.6
Prairie warbler	8.3	10.6	4.8	0.9	19.4
Worm-eating warbler	8.1	11.2	3.3	11.8	2.4
Black-throated blue warbler	7.6	8.4	6.4	8.5	6.2
Northern waterthrush	5.6	8.1	1.9	4.8	6.8
Black-and-white warbler	4.7	4.3	5.3	5.9	2.9
Gray catbird	4.2	3.9	4.7	4.0	4.4
Northern parula	4.0	6.1	0.8	2.6	6.1
Swainson’s warbler	2.6	4.0	0.5	4.3	0.1
Blackpoll warbler	2.1	0.0	5.4	0.1	5.3
Red-eyed vireo	1.7	2.8	0.1	0.5	3.5
Hooded warbler	1.3	1.6	0.8	0.8	2.0
All other migrants	9.8	11.4	7.4	5.8	15.8
Total	114.4	131.0	89.1	98.8	138.0

Age and Sex Ratios

Fourteen species with more than 20 captures were reliably aged during fall migration and 4 of these same species could also be reliably aged during spring migration. During fall migration, immature birds were significantly more common than adults for 9 of 14 species (Table 4), and 65% of all birds were immatures during fall migration (range of 41–85% by species). During spring migration, adult American redstarts were significantly more common than immatures; however, no significant differences were found in the number of adult versus immature birds for the other 3 species reliably aged during spring migration (Table 4). Immature birds had been significantly more common than adults for 2 of these same species during fall migration (black-throated blue warblers and prairie warblers).

Table 4. Age distributions for 14 species that could be reliably aged during fall migration and 4 species that could be reliably aged during spring migration, from mist-net captures in hardwood hammocks of the Florida Keys, 2002–2004.

Species	Season	Adult	Immature	Unknown	Total	Percent aged	Percent immature	P^a
American redstart	Fall	65	62	19	146	87.0	48.8	ns
Black-and-white warbler	Fall	32	22	0	54	100.0	40.7	ns
Black-throated blue warbler	Fall	33	68	5	106	95.3	67.3	***
Common yellowthroat	Fall	17	66	10	93	89.2	79.5	****
Gray catbird	Fall	14	34	0	48	100.0	70.8	**
Hooded warbler	Fall	3	17	0	20	100.0	85.0	**
Northern parula	Fall	18	54	4	76	94.7	75.0	****
Northern waterthrush	Fall	46	52	3	101	97.0	53.1	ns
Ovenbird	Fall	171	243	51	465	89.0	58.7	***
Prairie warbler	Fall	48	81	5	134	96.3	62.8	**
Red-eyed vireo	Fall	11	23	1	35	97.1	67.6	*
Swainson's warbler	Fall	18	28	5	51	90.2	60.9	ns
Worm-eating warbler	Fall	65	68	9	142	93.7	51.1	ns
Western palm warbler	Fall	6	33	2	41	95.1	84.6	****
American redstart	Spring	67	29	8	104	92.3	30.2	****
Black-and-white warbler	Spring	40	28	7	75	90.7	41.2	ns
Black-throated blue warbler	Spring	43	34	15	92	83.7	44.2	ns
Prairie warbler	Spring	19	10	13	42	69.0	34.5	ns

[a] **** = $P < 0.0001$, *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ns = not significant, for X^2 tests for each species/season combination that the observed ratio of adults to immature birds differs from a 50:50 ratio.

For the 4 species that could be reliably aged during both spring and fall migration, there were some season- and site-specific differences in age ratios (Table 5). Immature birds of all 4 species were captured in higher proportions than adults during fall migration in the Lower Keys. In the Upper Keys, however, adult American redstarts and black-and-white warblers were captured in higher proportions than immatures during fall migration. A much higher proportion of adult black-throated blue warblers were captured during fall migration in the Upper Keys than the Lower Keys. Immature prairie warblers were much more common than adults during fall migration at both sites. Seven species could be reliably sexed during at least 1 migration season in the Florida Keys. Males made up a significantly higher proportion of all captures than females for 4 out of 7 of these species (Table 6). For these 7 species, an average of 62.5% of all captures were males (range 54.3–68.9% by species). For the 4 species that could be reliably sexed during both spring and fall migration, there were no seasonal or site-specific differences in sex ratios ($P >$ 0.20).

Table 5. Seasonal (fall and spring) and site-specific (Upper Keys and Lower Keys) differences in the proportion of immature American redstarts, black-and-white warblers, black-throated blue warblers, and prairie warblers captured in mist-nets in hardwood hammocks of the Florida Keys, 2002–2004.

	Upper Keys		**Lower Keys**			
Species	**Fall**	**Spring**	**Fall**	**Spring**	X^{2a}	***P***
American redstart	26.3	33.3	67.1	23.3	30.6010	<0.0001
Black-and-white warbler	34.9	39.3	70.0	50.0	4.5660	0.2064
Black-throated blue warbler	53.9	41.4	91.7	71.4	29.2240	<0.0001
Prairie warbler	80.0	50.0	61.3	32.0	9.6890	0.0214

[a] Chi-square tests with H_o that the percentage of immature birds of each species captured was equal among site/season combinations.

Table 6. Sex ratios of the 7 species that could be reliably sexed during migration in the hardwood hammocks of the Florida Keys, 2002–2004.

Species	**Female**	**Male**	**Unknown**	**Total**	**Percent sexed**	**Percent male**	P^a
American redstart	69	153	28	250	88.8	68.9	****
Black-and-white warbler	58	69	2	129	98.4	54.3	ns
Blackpoll warbler	15	30	1	46	97.8	66.7	*
Black-throated blue warbler	89	108	1	198	99.5	54.8	ns
Hooded warbler	11	19	1	31	96.8	63.3	ns
Northern parula	25	51	8	84	90.5	67.1	**
Prairie warbler	56	93	27	176	84.7	62.4	**

[a] **** = $P < 0.0001$, ** = $P < 0.01$, * = $P < 0.05$, ns = not significant, for X^2 tests for each species that the observed proportion of males and females is equal.

Migration Timing

During both spring and fall migration, mist-net captures were more common in the hours around sunrise than later in the morning (Fig. 2). This pattern was more exaggerated in fall than in spring. In fall, 63.7% of all captures occurred within the first 2 hours of sunrise, compared to 50.3% in spring. Captures later in the day were also more common in spring, when 29.5% of all captures were within the last 2 hours of mist-netting compared to 21.8% in fall.

Daily capture rates were highly variable with some days contributing very little to the season's migrant capture total and other days (fallouts) contributing as much as 12.2% of the season's migrant capture total in a single day (Fig. 3). In general, daily mist-net captures were more variable in spring than fall. During spring migration, 18.1% of all days contributed more than 4% to the season's total capture, versus only 6% in fall. More than a quarter of all days during spring migration (27.5%) contributed <0.5% to the season's total capture, compared to 10.4% of all days in fall.

Seasonally, spring migration peaked in the last 2 weeks of April, while fall migration peaked toward the end of September (Fig. 4). Fall migration had a more protracted peak and migrants were common through most of September. Migration was also more strongly peaked in spring than in fall. Nearly 30% of the season's total could pass through in a single week in spring, where typically no more than 20% would pass through during a single week in fall. There were significant differences in the overall timing of spring migration among the 3 different field seasons ($X^2 = 153.27$, $P < 0.0001$, df = 2, Kruskal-Wallis ANOVA). Spring migration in the Lower Keys was earlier than spring migration in the Upper Keys. Within the 2 field seasons at the Upper Keys site, spring 2002 was slightly later than spring 2003, although this difference was small. The overall timing of fall migration did not differ significantly between the 2 fall field seasons (Z = 1.3357, $P = 0.1817$, df = 1, 2-sample Wilcoxon rank sum test).

There were differences in the timing of migration among species in both seasons (Tables 7 and 8). The number of days for passage of 80% of any given species' season total was shorter in spring (average 22.1 days for 12 common spring species) than during fall (average 28.6 for 14 common fall species). In spring, hooded warblers, prairie warblers, and western palm warblers were early-season migrants and American redstarts, northern waterthrushes, common yellowthroats, and blackpoll warblers were late-season migrants. The other 5 common spring migrants all had median passage dates during the

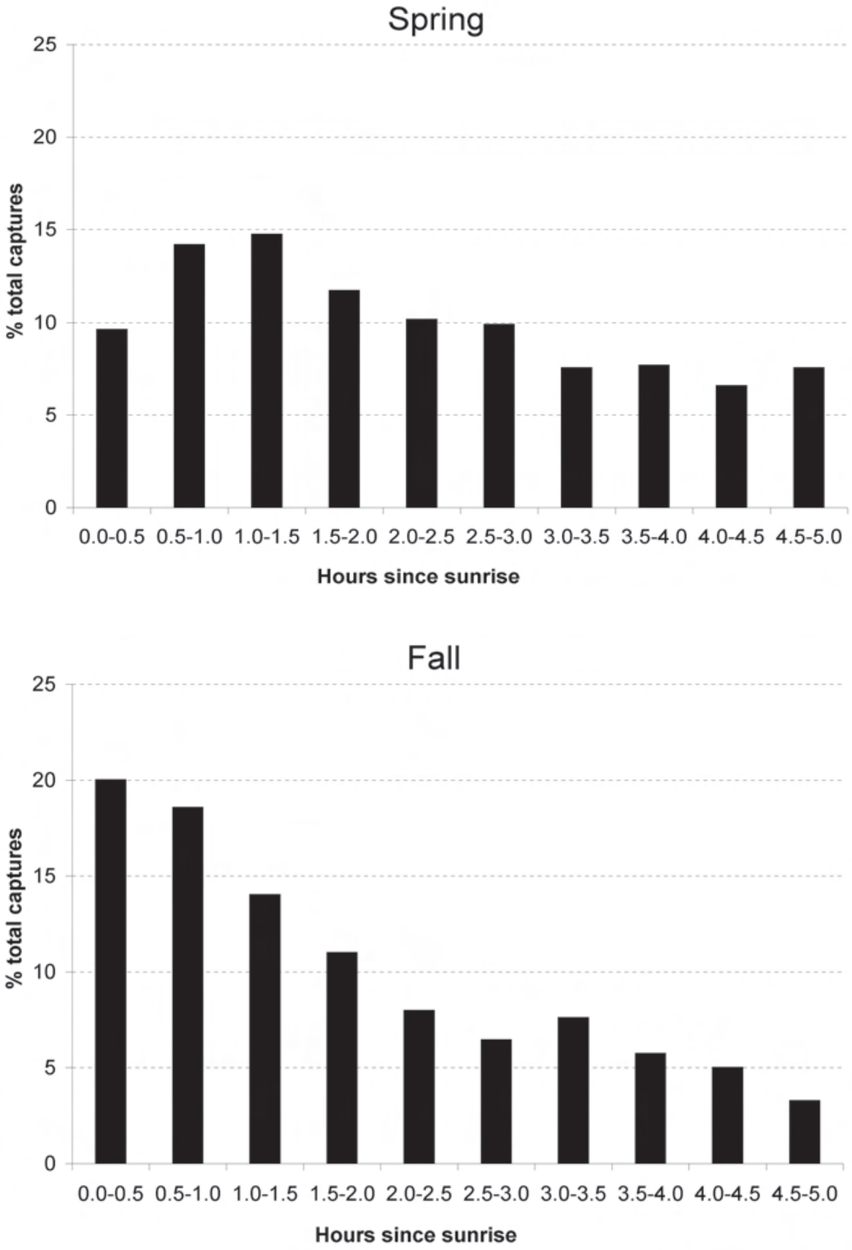


Fig. 2. Percent of all mist-net captures by time of day (by half-hour periods) for both spring and fall migration in hardwood hammocks of the Florida Keys, 2002–2004. Individuals captured between 00 and 29 minutes after the hour were assigned to the first half-hour period and individuals captured between 30 and 59 minutes after the hour were assigned to the second half-hour period.

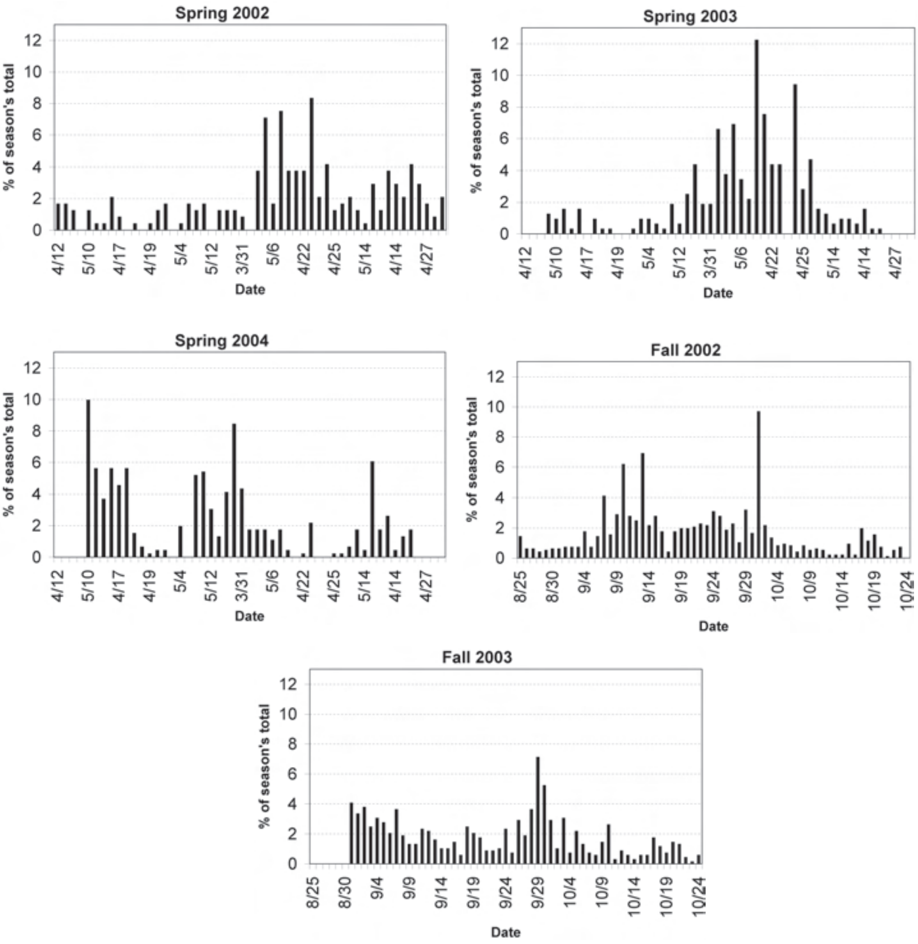
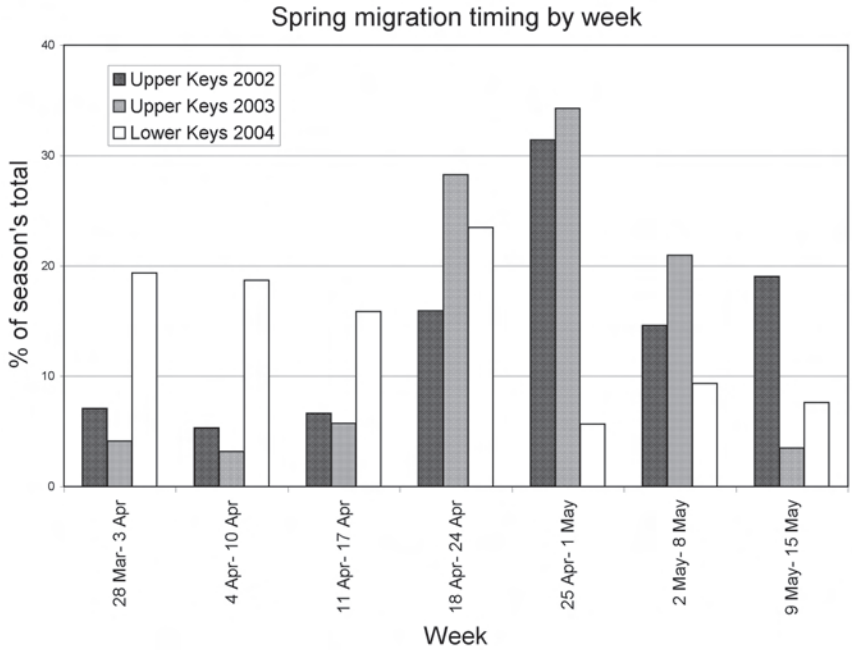


Fig. 3. Seasonal differences in daily mist-net capture rates (expressed as a percentage of the entire season's total on the y-axis) during migration in the hardwood hammocks of the Florida Keys, 2002–2004.

peak of migration between 23 April and 28 April. In fall, hooded warblers and prairie warblers were early-season migrants and American redstarts, black-throated blue warblers, common yellowthroats, western palm warblers, and gray catbirds were late-season migrants. Median passage dates for the remaining 7 common species were centered around the peak of migration between 14 September and 24 September.


Spring migration timing by week

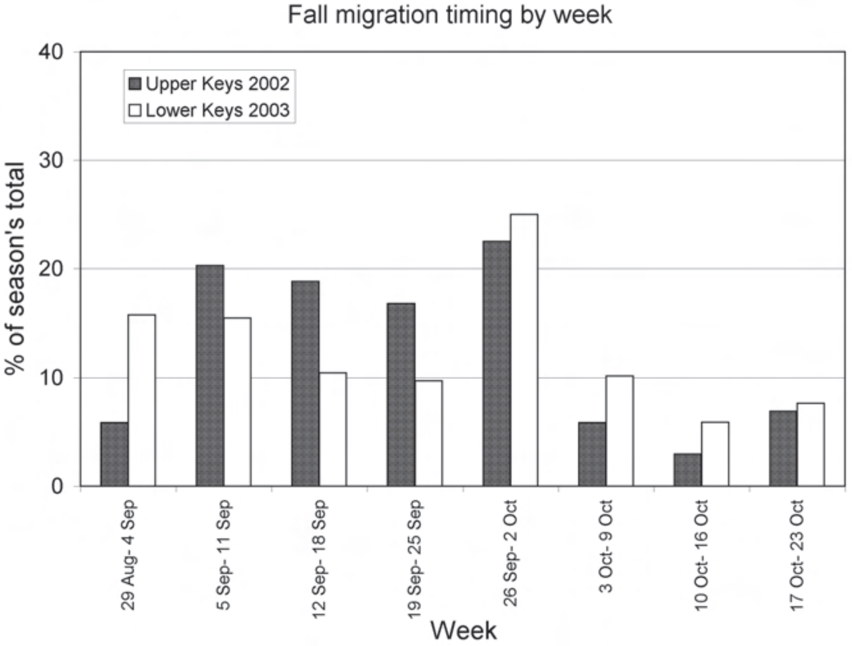

Fall migration timing by week

Fig. 4. Seasonal timing of spring and fall bird migration in hardwood hammocks of the Florida Keys, 2002–2004. Captures per week expressed as a percentage of the season's total.

Table 7. Median and bulk (central 80%) passage dates (and total number of days required for bulk passage) for 12 species of commonly captured spring migrants in hardwood hammocks of the Florida Keys, 2002–2004. Species are sorted by median passage date.

Species	**Median**	**Central 80% dates** **10%**	 **90%**	**Number of days for central 80%**
Hooded warbler	3 Apr	30 Mar	19 Apr	20
Prairie warbler	5 Apr	30 Mar	19 Apr	20
Western palm warbler	5 Apr	30 Mar	17 Apr	18
Worm-eating warbler	23 Apr	4 Apr	29 Apr	25
Black-and-white warbler	24 Apr	5 Apr	30 Apr	27
Gray catbird	24 Apr	14 Apr	29 Apr	15
Ovenbird	25 Apr	3 Apr	3 May	30
Black-throated blue warbler	28 Apr	18 Apr	5 May	17
American redstart	1 May	19 Apr	13 May	23
Northern waterthrush	1 May	14 Apr	13 May	28
Common yellowthroat	3 May	19 Apr	11 May	22
Blackpoll warbler	9 May	19 Apr	9 May	20
All migrants	23 Apr	1 Apr	6 May	35

Table 8. Median and bulk (central 80%) passage dates (and total number of days required for bulk passage) for 14 species of commonly captured fall migrants in hardwood hammocks of the Florida Keys, 2002–2004. Species are sorted by median passage date.

Species	**Median**	**Central 80% dates** **10%**	 **90%**	**Number of days for central 80%**
Prairie warbler	7 Sep	31 Aug	30 Sep	30
Hooded warbler	8 Sep	2 Sep	1 Oct	29
Northern parula	14 Sep	4 Sep	1 Oct	27
Worm-eating warbler	14 Sep	7 Sep	29 Sep	22
Ovenbird	15 Sep	4 Sep	1 Oct	27
Red-eyed vireo	15 Sep	6 Sep	3 Oct	28
Swainson’s warbler	19 Sep	5 Sep	5 Oct	30
Northern waterthrush	20 Sep	3 Sep	1 Oct	28
Black-and-white warbler	24 Sep	3 Sep	7 Oct	34
American redstart	30 Sep	4 Sep	18 Oct	44
Black-throated blue warbler	30 Sep	14 Sep	19 Oct	35
Common yellowthroat	3 Oct	21 Sep	18 Oct	27
Western palm warbler	6 Oct	26 Sep	20 Oct	24
Gray catbird	18 Oct	8 Oct	23 Oct	15
All migrants	21 Sep	4 Sep	10 Oct	36

Fat Stores and Body Mass at Arrival

We collected data on migrant condition for a single season at each study site with the exception of the Upper Keys, where we collected data during 2 different spring migration seasons (2002 and 2003). Neither body mass nor wing chord length varied between the 2 spring field seasons in the Upper Keys for any species. Therefore, body mass and wing chord data from both seasons were pooled. However, due to the change in fat scoring methods after the spring 2002 field season, as expected, fat scores differed between the spring 2002 and spring 2003 seasons ($Z = -4.7044$, $P < 0.0001$, df = 1, 2-sample Wilcoxon rank sum test). Thus, we include only data from the spring 2003 season for analyses of fat scores for the Upper Keys.

We investigated the relationship between overall size (using wing chord as a proxy) and body mass for 15 species. Regressions of wing chord versus body mass were significant for 10 of the 15 species with more than 30 captures at this site ($P < 0.05$). However, this relationship generally explained a small amount of the variation in body mass within a species (average r^2 of 0.13, range 0.05–0.28). Fat stores had a far greater influence on body mass than size (wing chord). All 15 species had significant relationships between fat scores and body mass (all P values < 0.01, many with $P < 0.0001$), and this relationship described a far larger proportion of the variation in body mass within a species (average r^2 of 0.43, range 0.18–0.73). Since body mass was much more strongly related to fat stores than size (or rather, wing chord as a proxy for size), we did not use wing chord to calculate a size-corrected body mass. We consider mass alone to be a good indicator of migrant condition. All subsequent tests for the effects of age, sex, season, or site on migrant condition are performed using the closely related dependent variables of mass and fat scores. Fat scores consistently showed a linear relationship with body mass. Residuals from linear regressions of fat scores versus body mass were normally distributed within each fat score (0–6) and had r^2 values ranging from 0.92 to 0.99. Therefore, we treated fat scores as a continuous rather than ordinal variable in subsequent data analyses.

Neither fat scores nor body mass were strongly or consistently affected by age or sex (or an age*sex interaction term). Therefore, all further summaries and analyses of body condition use species as the sampling unit, pooling data from all age/sex classes. For the 12 species where we looked for the effect of age on body mass, only adult ovenbirds and black-throated blue warblers had significantly higher body mass than immature birds. In both of these cases, mean differences in mass between the 2 age classes were both lower than 0.34 g. For the 5 species where we were able to look for the effect of sex on body mass, only male northern parulas had higher body masses than females (a difference of 0.66 g). For American redstarts the interaction term for age and sex was significant due to relatively low body masses of immature females (which ranged from 0.48 to 0.57 g lower than the other 3 age/sex classes).

A large proportion of migrants in the Florida Keys were initially captured with substantial fat stores. The mean fat score for all migrants was 2.2, and only 12% of all migrants had no visible fat, although fat stores varied among species (Table 9). Worm-eating warblers, red-eyed vireos, and gray catbirds all had high mean fat scores (2.8–3.3) compared to other migrants, and these 3 species also had a particularly low percentage of individuals with no visible fat (3–7%). American redstarts, blackpoll warblers, and hooded warblers had low mean fat scores (1.3–1.6) relative to other migrants and generally had higher percentage of individuals with no visible fat (7–32%).

Both body masses and fat scores of single-captures were often higher during fall than spring migration. Body mass was significantly higher in fall for 6 of the 11 species that had enough data for statistical tests (Table 10). The exception was the gray catbird, which had significantly higher body mass in spring. Only ovenbirds, prairie warblers, western palm warblers, and hooded warblers did not show seasonal variation in body mass. Fat scores followed the same pattern as body mass, with significantly higher scores in fall for 6 of 11 species, and higher fat scores in spring for gray catbirds (Table 11).

Table 9. Fat scores (mean ± 1 SD) and percent of individuals with no visible fat (lean birds) for individuals that were only captured once (single captures) during fall and spring migration in hardwood hammocks of the Florida Keys, 2002–2004. Species are sorted from highest to lowest mean fat score.

Species	***n***	**% lean**	**Mean fat score**	**SD**
Worm-eating warbler	140	3	3.3	1.3
Red-eyed vireo	35	3	3.1	1.4
Gray catbird	90	7	2.8	1.2
Common yellowthroat	168	10	2.6	1.5
Northern parula	73	7	2.5	1.2
Northern waterthrush	102	13	2.4	1.4
Prairie warbler	152	11	2.2	1.4
Swainson’s warbler	44	18	2.1	1.7
Black-and-white warbler	96	15	2.1	1.3
Ovenbird	442	12	2.0	1.2
Black-throated blue warbler	149	7	2.0	1.0
Western palm warbler	190	6	2.0	0.9
American redstart	207	19	1.6	1.1
Blackpoll warbler	42	7	1.5	0.7
Hooded warbler	28	32	1.3	1.2
All migrants	2,132	12	2.2	1.3

Table 10. Seasonal body masses (g) for single-captures during fall and spring migration in hardwood hammocks of the Florida Keys, 2002–2004. Body mass summary statistics are only presented for species with ≥10 captures per migration season.

	Fall		Spring		Difference	
Species	***n***	**Mean (±SD)**	***n***	**Mean (±SD)**	**fall-spring**	***P*[a]**
American redstart	132	7.78 (0.80)	94	7.35 (0.48)	0.44	****
Black-and-white warbler	49	10.76 (1.16)	63	9.87 (1.32)	0.88	****
Blackpoll warbler			42	10.89 (0.84)		
Black-throated blue warbler	90	9.44 (0.80)	85	9.23 (1.09)	0.21	**
Common yellowthroat	85	10.02 (1.15)	128	9.58 (0.98)	0.44	*
Gray catbird	48	36.31 (2.89)	56	39.00 (5.88)	-2.69	****
Hooded warbler	18	10.17 (1.29)	10	10.39 (0.96)	-0.22	ns
Northern parula	64	7.52 (0.90)				
Northern waterthrush	88	16.82 (1.83)	24	15.12 (2.19)	1.70	***
Ovenbird	389	18.88 (1.56)	83	19.20 (2.21)	-0.32	ns
Prairie warbler	116	7.48 (0.67)	35	7.26 (0.76)	0.21	ns
Red-eyed vireo	34	18.21 (2.84)				
Swainson's warbler	39	15.31 (1.75)				
Worm-eating warbler	104	14.37 (1.26)	37	12.99 (1.08)	1.38	****
Western palm warbler	36	9.45 (0.65)	154	9.65 (0.91)	-0.20	ns

[a] **** = $P < 0.0001$, *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ns = not significant, for *t*-tests with H_o that masses were equal between spring and fall migration. Tests were not performed for species that were commonly captured during only 1 migration season.

Table 11. Seasonal fat scores (mean ± 1 SD) and percent of individuals with no visible body fat (%lean birds) for migrants captured in hardwood hammocks of the Florida Keys, 2002–2004. Mean fat scores are only presented for species with ≥10 captures per migration season.

	Fall			Spring			Difference	
Species	***n***	**% lean**	**Mean (±SD)**	***n***	**% lean**	**Mean (±SD)**	**fall-spring**	***P*[a]**
American redstart	138	14	1.8 (1.1)	69	29	1.1 (0.9)	0.7	****
Black-and-white warbler	49	4	2.5 (1.1)	47	26	1.6 (1.2)	0.9	**
Blackpoll warbler				42	7	1.5 (0.7)		
Black-throated blue warbler	92	9	2.0 (1.0)	57	5	2.1 (1.0)	-0.1	ns
Common yellowthroat	88	10	2.8 (1.6)	80	9	2.3 (1.2)	0.6	**
Gray catbird	48	10	2.3 (1.1)	42	2	3.3 (1.0)	-1.0	****
Hooded warbler	18	17	1.7 (1.2)	10	60	0.5 (0.7)	1.2	**
Northern parula	66	8	2.4 (1.3)					
Northern waterthrush	90	14	2.4 (1.5)	12	0	2.2 (0.9)	0.3	ns
Ovenbird	393	12	2.0 (1.2)	49	8	2.4 (1.2)	-0.4	ns
Prairie warbler	118	11	2.3 (1.4)	34	12	1.7 (0.9)	0.7	*
Red-eyed vireo	34	3	3.1 (1.5)					
Swainson's warbler	40	18	2.1 (1.7)					
Worm-eating warbler	107	1	3.6 (1.2)	33	9	2.3 (1.2)	1.3	****
Western palm warbler	36	11	1.8 (1.0)	154	5	2.0 (0.9)	-0.3	ns

[a] **** = $P < 0.0001$, ** = $P < 0.01$, * = $P < 0.05$, ns = not significant, for 2-sample Wilcoxon rank sum tests with H_o that fat scores were equal in fall and spring migrations. Tests were not performed for species that were commonly captured during only 1 migration season.

Both body masses and fat scores were often higher in the Upper Keys than the Lower Keys, although patterns were complex and varied by species (Tables 12 and 13). Four of 11 species had significantly higher body mass in the Upper Keys than the Lower Keys and 4 species had significantly higher fat scores in the Upper Keys. However, American redstarts and hooded warblers had significantly lower fat scores in the Upper Keys, although this did not translate into site-specific differences in body mass for these same 2 species (Tables 12 and 13).

Table 12. Site-specific body masses (g) for single-captures in hardwood hammocks of the Florida Keys, 2002–2004. Body mass summary statistics are only presented for species with ≥10 captures per site.

	Upper Keys		**Lower Keys**		**Difference**	
Species	***n***	**Mean (±SD)**	***n***	**Mean (±SD)**	**Upper-Lower**	**P^a**
American redstart	125	7.62 (0.63)	101	7.58 (0.81)	0.03	ns
Black-and-white warbler	92	10.37 (1.35)	20	9.76 (1.07)	0.61	ns
Blackpoll warbler			40	10.85 (0.83)		
Black-throated blue warbler	140	9.42 (0.97)	35	9.03 (0.86)	0.39	*
Common yellowthroat	115	9.75 (1.04)	98	9.76 (1.11)	-0.01	ns
Gray catbird	68	38.45 (3.95)	36	36.46 (6.18)	1.98	ns
Hooded warbler	12	10.29 (0.95)	16	10.21 (1.34)	0.07	ns
Northern parula	31	7.99 (0.75)	1	7.21 (0.84)	0.77	***
Northern waterthrush	67	16.60 (2.26)	45	16.24 (1.62)	0.36	ns
Ovenbird	418	19.02 (1.66)	54	18.32 (1.81)	0.70	**
Prairie warbler	12	7.47 (0.51)	139	7.43 (0.71)	0.04	ns
Red-eyed vireo			28	18.01 (2.75)		
Swainson's warbler	45	15.29 (1.68)				
Worm-eating warbler	123	14.16 (1.29)	18	12.97 (1.37)	1.20	***
Western palm warbler			184	9.62 (0.86)		

[a] *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ns = not significant, for *t*-tests with H_o that masses were equal between the Upper Keys and Lower Keys. Tests were not performed for species that were commonly captured at only 1 site.

Table 13. Site-specific fat scores (mean ± 1 SD) and percent of individuals with no visible body fat (lean birds) for migrants captured in hardwood hammocks of the Florida Keys, 2002–2004. Mean fat scores are only presented for species with ≥10 captures per site.

	Upper Keys			Lower Keys			Difference	
Species	***n***	**% lean**	**Mean (±SD)**	***n***	**% lean**	**Mean (±SD)**	**Upper-Lower**	***P*[a]**
American redstart	103	28	1.4 (1.1)	104	11	1.7 (1.0)	-0.3	*
Black-and-white warbler	76	18	2.0 (1.3)	20	0	2.2 (0.9)	-0.1	ns
Blackpoll warbler					41	7 (1.4)	0.7	
Black-throated blue warbler	114	8	2.0 (1.0)	35	6	2.1 (1.2)	0.0	ns
Common yellowthroat	69	13	2.5 (1.5)	99	7	2.6 (1.4)	-0.1	ns
Gray catbird	53	2	2.9 (1.0)	37	14	2.6 (1.4)	0.3	ns
Hooded warbler	12	58	0.8 (1.1)	16	13	1.7 (1.1)	-0.9	*
Northern parula	31	0	3.0 (0.9)	42	12	2.0 (1.3)	1.0	***
Northern waterthrush	57	5	2.9 (1.2)	45	22	1.8 (1.5)	1.1	***
Ovenbird	388	10	2.1 (1.1)	54	26	1.5 (1.2)	0.6	***
Prairie warbler	11	9	2.4 (1.4)	141	11	2.2 (1.3)	0.2	ns
Red-eyed vireo				28	4	3.0 (1.3)		
Swainson's warbler	43	19	2.1 (1.7)					
Worm-eating warbler	122	2	3.4 (1.3)	18	6	2.7 (1.4)	0.7	*
Western palm warbler				187	6	2.0 (0.9)		

[a] *** = $P < 0.001$, * = $P < 0.05$, ns = not significant, for 2-sample Wilcoxon rank sum tests with H_0 that fat scores were equal in the Upper Keys and Lower Keys. Tests were not performed for species that were commonly captured at only 1 site.

Recaptures and Stopover Length

Just over 9% (9.4%) of all migrants were recaptured at least 1 day after their initial capture. Recapture rates varied among species (Table 14, Appendix C). Among the commonly captured species, recapture rates were highest for worm-eating warblers and Swainson's warblers and lowest for common yellowthroats, American redstarts, and gray catbirds (for which not a single individual out of 109 initial captures was recaptured on a subsequent day).

Minimum stopover length did not vary between the Upper and Lower Keys (Z = -0.2323, $P = 0.8319$, df = 1, 2-sample Wilcoxon Rank Sum test). However, MSL was significantly longer in fall (4.8 ± 5.5, range 1–23 days) than in spring (3.1 ± 2.7, range 1–17 days) ($X^2 = 5.4512$, P = 0.0196, df = 1, 2-way Wilcoxon Rank Sum test). Minimum stopover length varied significantly among species ($X^2 = 25.1183$, $P = 0.0088$, df = 11, Kruskal-Wallis ANOVA for 12 species with more than 5 recaptures); however, the significance of this test was driven entirely by northern waterthrushes, which had longer MSL than 5 other species (black-throated blue warblers, northern parulas, prairie warblers,

Table 14. Recapture rates and sample sizes for the 20 most commonly captured species during migration in hardwood hammocks of the Florida Keys, 2002–2004.

Species	Total captures	Total recaptures	Percent recaptured
Ovenbird	570	56	9.8
American redstart	255	14	5.5
Western palm warbler	250	30	12.0
Common yellowthroat	238	9	3.8
Black-throated blue warbler	201	19	9.5
Worm-eating warbler	190	39	20.5
Prairie warbler	179	12	6.7
Northern waterthrush	131	10	7.6
Black-and-white warbler	130	13	10.0
Gray catbird	109	0	0.0
Northern parula	87	11	12.6
Swainson's warbler	58	11	19.0
Blackpoll warbler	46	3	6.5
Red-eyed vireo	36	1	2.8
Hooded warbler	31	3	9.7
Blue-grey gnatcatcher	24	2	8.3
Black-whiskered vireo	23	3	13.0
Indigo bunting	20	3	15.0
Prothonotary warbler	20	6	30.0
Swainson's thrush	20	3	15.0

western palm warblers, and common yellowthroats). All other species pairs did not have significantly different MSLs.

Thirty-four percent of all recaptures occurred the day following initial capture, MSL of 1 day. This pattern varied among species, and some species had a higher percentage of recaptures with MSL of 1 than others (Table 15). A high percentage of black-throated blue warbler (68.4%) and common yellowthroat (55.6%) recaptures had MSLs of 1, whereas worm-eating warblers, prairie warblers, and northern waterthrushes had relatively few recaptures with MSLs of 1 (17–20%). Individual birds with MSL of 1 did not gain mass or fat during stopover ($P > 0.30$ for 1-tailed paired *t*-tests of initial mass versus final mass; sample groups were all species combined and each of the 10 commonly recaptured species). However, birds that were recaptured more than 1 day after initial capture (recaptures with MSL > 1) tended to increase both mass and fat during stopover (results in paragraphs below). Original masses of these 2 different groups (individuals with MSL = 1 versus individuals with MSL >1) were similar ($P > 0.30$; *t*-tests for all 10 commonly recaptured species). Small sample sizes precluded valid statistical comparisons of rates of mass change for the 2 groups (MSL = 1 versus MSL > 1) for individual species; however, mean percent mass gain during stopover was higher for birds with MSL > 1 for 9 of 10 species (Table 16). Since it is possible that lower rates of mass gain for birds with MSL = 1 are related to the stress of initial capture in mist-nets (due to reduced foraging time, more time spent preening after handling, or other physiological stresses related to capture) we eliminated all individuals with MSL = 1 from subsequent summaries of mass or fat score changes during stopover to eliminate potential biases in these data related to the handling of birds during their initial capture (see also Shaub and Jenni 2000).

Table 15. Stopover lengths (mean ± 1 SD, range) for the 20 most commonly captured migrants in hardwood hammocks of the Florida Keys, 2002–2004. Individuals recaptured on the next day following their recapture minimum stopover length (MSL) = 1 were eliminated from the calculation of MSL summary statistics. The percent of individuals with MSL = 1 and the remaining number of individuals used in calculations (with MSL >1) are presented for each species.

Species	**% recaptures with MSL = 1**	**Recaptures (*n*) with MSL > 1**	**Mean MSL**	**SD MSL**	**Range MSL**
Ovenbird	35.7	35	4.7	5.4	1–23
American redstart	28.6	10	5.2	5.3	1–20
Western palm warbler	33.3	20	3.1	2.2	1–9
Common yellowthroat	55.6	4	2.4	2.1	1–7
Black-throated blue warbler	68.4	6	1.9	1.9	1–7
Worm-eating warbler	17.9	31	5.6	4.6	1–17
Prairie warbler	16.7	9	3.4	1.9	1–8
Northern waterthrush	20.0	8	9.7	8.2	1–23
Black-and-white warbler	30.8	9	4.4	4.1	1–15
Gray catbird					
Northern parula	36.4	6	2.5	1.4	1–4
Swainson's warbler	36.4	6	3.6	3.4	1–11
Blackpoll warbler	33.3	2			
Red-eyed vireo	0.0	1			
Hooded warbler	66.7	1			
Blue-grey gnatcatcher	50.0	1			
Black-whiskered vireo	0.0	3			
Indigo bunting	100.0	0			
Prothonotary warbler	16.7	5	6.5	5.9	1–17
Swainson's thrush	33.3	2			

Table 16. Percent change in body mass (g) during stopover of individuals with minimum stopover length (MSL) = 1 and MSL >1 that were captured during migration in hardwood hammocks of the Florida Keys, 2002–2004. Mean ± 1 SD, and range of percent changes in body mass are given only for species with a minimum of 4 observations per category.

	MSL = 1				MSL > 1			
Species	***n***	**Mean (±SD)**	**Low**	**High**	***n***	**Mean (±SD)**	**Low**	**High**
American redstart	4	-1.5 (5)	-5.9	3.2	10	4 (11)	-5.3	30.7
Black-and-white warbler	4	-1.6 (2)	-3.7	0.6	9	7.6 (5.2)	0.6	16.9
Black-throated blue warbler	13	2.1 (4)	-2.9	8.1	6	8.7 (9.2)	1.2	26.3
Northern parula	4	-1.9 (2)	-2.9	0.3	6	11.4 (6.2)	3.2	20.9
Northern waterthrush	2				8	1.9 (7.6)	-9.0	17.5
Ovenbird	20	-0.8 (5)	-15.6	5.1	35	4.3 (11)	-10.7	35.3
Prairie warbler	2				9	2.4 (8.6)	-16.6	14.0
Swainson's warbler	4	-2.1 (4)	-8.0	1.4	6	3.6 (4.5)	-3.3	10.2
Worm-eating warbler	7	0.9 (4)	-4.2	6.5	31	7.3 (9.6)	-9.9	38.1
Western palm warbler	9	2.9 (5)	-15.0	1.2	20	-1.9 (7.1)	-13.3	18.0

Body Condition Change During Stopover

Most birds were captured only once. Therefore, we regressed mass versus time of day for 15 different species within each season (fall or spring) or site (Upper or Lower Keys) with a sample size of more than 30 single-captures. After adjusting P values for multiple tests, only 4 of 47 tests showed a significant relationship between mass and time of day. In all cases r^2 was below 0.06, and 95% confidence intervals for slopes were very wide. Thus, we regard time of day as a poor predictor of body mass and do not calculate rates of mass gain from regression equations of mass versus time of day based on single-captures. All subsequent presentations of mass gain during stopover are based on recapture data for birds with MSL > 1 (see above).

Six of the 10 commonly recaptured species had significant increases in body mass during stopover and most species had a high percentage of individuals that gained mass (Table 17). Percent change in body mass varied by species (X^2 = 28.4071, P = 0.0008, df = 9, Kruskal-Wallis ANOVA); however, the significance of this test was driven by the strong difference in percent change in body mass between worm-eating warblers and western palm warblers. Only 3 species had more than 50% of recaptured individuals that lost body mass during stopover (northern waterthrush, western palm warbler, and prairie warbler). Three of the 10 commonly recaptured species increased fat scores significantly during stopover (Table 18). A much higher percentage of individuals increased, rather than decreased, fat scores during stopover for

Table 17. Percent changes in body mass (g) during stopover for the 10 most commonly recaptured species in hardwood hammocks of the Florida Keys, 2002–2004.

Species	Recaptures	Mean % mass change	SD	Range		% losing mass	*t*	*P*[a]
				Low	High			
American redstart	10	4.0	10.5	-5.3	31	40.0	1.1769	0.1347
Black-and-white warbler	9	7.6	5.2	6.6	17	0.0	4.4353	0.0011
Black-throated blue warbler	6	8.7	9.2	1.2	26	0.0	2.2299	0.0381
Northern parula	6	11.4	6.2	3.2	21	0.0	4.9911	0.0021
Northern waterthrush	8	1.9	7.6	-9.0	18	66.6	0.6440	0.2701
Ovenbird	35	4.3	10.6	-11.0	35	37.1	2.2770	0.0146
Prairie warbler	10	2.4	8.6	-17.0	14	20.0	0.8677	0.2040
Swainson's warbler	6	3.6	4.5	-3.3	10	16.6	2.0216	0.0496
Worm-eating warbler	31	7.3	9.6	-9.9	38	12.9	4.1589	<0.0001
Western palm warbler	20	-1.9	7.1	13.3	18	60.0	-1.2706	0.8904

[a] Results from 1-tailed paired *t*-tests of initial mass versus final mass for recaptures, assuming that migrants will gain mass during stopover.

Table 18. Changes in fat scores during stopover for the 10 most commonly recaptured species in the hardwood hammocks of the Florida Keys, 2002–2004.

Species	Recap-tures	Change in fat score			Losing fat (%)	Gaining fat (%)	No gain/ loss (%)	*t* ratio	*P*[a]
		Mean (±SD)	range						
			low	high					
American redstart	10	0.3 (0.8)	-1	1	20.0	50.0	30.0	1.152	0.1394
Black-and-white warbler	9	1.2 (1.0)	-4	4	0.0	77.7	22.3	3.770	0.0027
Black-throated blue warbler	6	0.7 (1.2)	-1	2	16.6	50.0	33.4	1.348	0.1177
Northern parula	7	1.8 (1.3)	0	4	0.0	85.7	14.3	3.652	0.0053
Northern waterthrush	8	0.0 (1.6)	-3	3	12.5	12.5	75.0	0.000	0.5000
Ovenbird	36	0.2 (1.4)	-4	3	30.6	36.1	33.3	0.692	0.2466
Prairie warbler	10	0.4 (0.8	-1	2	10.0	40.0	50.0	1.500	0.8390
Swainson's warbler	7	-0.1 (0.9)	-1	1	42.9	28.6	28.5	-0.420	0.6555
Worm-eating warbler	32	0.6 (1.5)	-4	4	15.6	43.8	40.6	2.089	0.0225
Western palm warbler	20	0.0 (0.8)	-1	2	25.0	20.0	55.0	0.000	0.5000

[a] Results from 1-tailed paired *t*-test of initial fat score versus final fat score assuming that migrants will increase fat scores during migration.

7 of these same 10 species. Changes in fat scores varied by species, with northern parulas having significantly higher increases in fat scores than both ovenbirds and western palm warblers (X^2 = 19.9104, *P* = 0.0185, df = 9, Kruskal-Wallis ANOVA for change in fat score by species).

A majority of individual birds (73.1%) gained mass during stopover. Only 5 individuals had >10% decrease in body mass, compared with 38 individuals that increased their body mass by >10%. Extreme increases in body mass were relatively common, and >20% increases in body mass occurred for 14 individuals (8.4% of all recaptures). Seven individuals increased their body mass by >30% during stopover (2 ovenbirds, 2 prothonotary warblers, 1 worm-eating warbler, 1 common yellowthroat, and 1 American redstart), and a single prothonotary warbler increased its mass by 51.2%. Changes in fat scores were highly variable, ranging from a decrease of 4 fat score levels to an increase of 5 levels. Only 19.3% of all migrants had lower fat scores at final recapture than at first capture, whereas 42.1% increased fat scores and 38.6% stayed within the same fat category (Table 18).

Overall percent mass gain was higher in the Upper Keys (3.9 ± 9.2%, range -10.7–38.1%) than the Lower Keys (2.9 ± 10.1%, range -16.6–51.2%). However, this difference was not statistically significant (Z = 1.7693, *P* = 0.0768, df = 1, 2-sample Wilcoxon rank sum test on percentage mass gain for all species combined), and there was no difference in changes in fat scores between the Upper and Lower Keys (Z = 1.5052, *P* = 0.1323, df = 1, 2-sample Wilcoxon rank sum test, all species combined). Percent mass gain was higher in fall (4.6 ± 9.8%, range -10.5–51.2%) than spring (0.7 ± 7.7%, range -16.6–30.7%) (Z = -2.9236, *P* = 0.0035, df = 1, 2-sample Wilcoxon rank sum test, all species combined). Sample sizes were too small for valid statistical comparisons of seasonal or site-specific changes in body mass or fat scores by species.

Recaptures in Subsequent Seasons

We recaptured 8 individual migrants in more than 1 season of banding in the Upper Keys (5 ovenbirds, 2 black-and-white warblers, and 1 worm-eating warbler). In our 5 days of mist-netting and intensive surveys between the fall 2002 and spring 2003 field seasons in the Upper Keys, we recaptured a single banded bird, a gray catbird that had been banded during spring 2002. During this effort we captured 2 new black-and-white warblers. We also detected 1 ovenbird, 1–2 northern parulas, 1 American redstart, 1 orange-crowned warbler, and 5–6 black-and-white warblers. The study site was very quiet, and we are confident that we captured or detected most of the birds present during this sampling period. Thus, we suspect that at least some, if not most, of the migrants recaptured in subsequent seasons in the Upper Keys represent individuals stopping over in the same patch of hardwood hammock in subsequent migrations rather than individuals wintering at the site. We recaptured 9 individual migrants in more than 1 season of banding in the Lower Keys (4 American redstarts, 2 ovenbirds, 1 northern waterthrush, 1 common yellowthroat, and 1 western palm warbler). We were not able to survey for migrants between the fall 2003 and spring 2004 field seasons in the Lower Keys. We did not recapture a single bird in the Lower Keys that was originally banded in the Upper Keys. We did not recapture a single bird that had been banded at a site away from the Florida Keys.

Diet

We analyzed 419 fecal samples from 20 different migrant species. We counted 1,624 arthropod prey items (an average of 3.9 arthropods per fecal sample) and identified 1,573 (96.9%) individual arthropods into 16 different prey categories (Table 19). Appendix D lists diet sample sizes by species, site, and season. Spiders were most commonly identified by fangs and legs; ants by whole heads, mandibles, and legs; and beetles by elytra, legs, whole heads, or mandibles. A number of other structures were helpful in identifying some of the less common orders (e.g., mandibles of lepidopteron larvae, psuedoscorpion pincers, or homopteran ribs) (Table 20).

Ants were the most commonly identified arthropod prey item (31.7% of all individual arthropod prey items), followed by beetles (24.8%) and then spiders (20.1%). These 3 prey categories made up 76.6% of all prey items. Non-formicidae hymenopterans (wasps) made up 6.6% of all prey items. The 12 other prey categories each contributed <2.8% to the total number of prey items identified in fecal samples. When average proportions of prey categories were calculated for all migrant diet samples combined, beetles become the most common prey item (27.6%), followed by ants (26.2%) and spiders (21.7%). These 3 groups made up 75.5% of the total migrant diet sample. With the addition of non-formicidae hymenopterans, orthopterans, and lepidoptera larvae, these 6 categories made up 89% of all migrant prey. Beetles were present in 63% of all individual fecal samples, spiders in 54%, ants in 52%, and hymenoptera (wasps) in 22%. All other prey categories were present in <10% of all fecal samples (Table 19).

Only 17% of all samples had evidence of fruit in migrant diet (e.g., fruit pulp, capillaries, or seeds) although the proportion was high for gray-cheeked thrushes (100%), red-eyed vireos (86%), Swainson's thrushes (83%), and gray catbirds (63%). These species also had a relatively low average number of arthropods per fecal sample (2.3 arthropods per sample for all 4 species

Table 19. Contribution of 19 different arthropod prey categories (number of individuals, percent of diet samples with prey category present, and percent of each prey category comprising the overall diet of migrants) to migrant diet. Prey items were identified from fecal samples taken from all bird species combined during migration in hardwood hammocks of the Florida Keys, 2002–2004.

Scientific name of prey category	Common name of prey category	Individual arthropods in samples (*n*)	Samples with category present (%)	Contribution of category to diet (%)
Formicidae	Ants	515	52	26.2
Coleoptera	Beetles	402	63	27.6
Aranae	Spiders	327	54	21.7
Hymenoptera	Wasps	107	22	7.7
	Unknown adult arthropods	51	11	
Orthoptera	Crickets and grasshoppers	45	10	3.3
Lepidoptera	Caterpillars	47	10	2.5
Acari	Ticks and mites	31	4	1.0
Hemiptera	True bugs	27	6	2.1
Psuedoscorpiones	Psuedoscorpions	29	5	1.4
Diptera	Flies	18	4	1.3
Homoptera	Cicadas and leafhoppers	10	2	0.4
	Unknown larvae	7	2	0.6
	Unknown vertebrates	2	0	0.1
Odonata	Dragonflies and damselflies	3	1	0.2
Blattodea	Roaches	2	0	0.1
Chilopoda	Centipedes	1	0	0.0
Gastropoda	Snails		18	
Lepidoptera	Butterflies		8	
Total items in diet		1,624		

Table 20. Useful arthropod parts (percent used for positive identifications of each prey category) for identifying different prey categories in fecal samples from migrants in hardwood hammocks of the Florida Keys, 2002–2004. Parts only useful for a single prey category are listed in notes beneath the table.

Order	Leg	Head	Mandible	Wing	Body	Whole	Abdomen	Pronotum	Eye
Acari	0	0	6	0	12	82	0	0	0
Aranae[a]	36	0	0	0	1	1	1	0	0
Coleoptera[b]	20	12	13	0	1	1	0	2	0
Diptera	10	33	0	29	0	0	0	0	24
Formicidae	27	34	22	0	8	1	5	0	0
Hemiptera	34	10	0	3	31	0	3	14	3
Homoptera[c]	0	9	0	9	0	18	0	0	0
Hymenoptera	31	18	18	23	3	2	2	0	2
Lepidoptera (adult)	0	3	0	6	0	0	0	0	0
Lepidoptera (immature)	0	0	100	0	0	0	0	0	0
Orthoptera	73	6	0	6	0	0	2	0	2
Psuedoscorpiones[d]	0	0	0	0	0	0	0	0	0
Unknown larvae	0	0	57	0	29	0	0	0	0

[a] Forty-seven percent of all Aranae were identified by fangs.

[b] Thirty-nine percent of all Coleoptera were identified by elytra.

[c] Sixty-four percent of all homoptera were identified by ribs.

[d] One-hundred percent of all Psuedoscorpiones were identified by pinchers.

combined) leading to a relatively low total number of arthropod prey items (range 12–32 arthropod prey items per species). Thus, these 4 primarily fruit-eating species are not included in subsequent summaries of diets, which focus on the 11 species of arthropod specialists for which we had more than 10 fecal samples per species (Table 21). All other species had <23% samples with fruit in them and higher numbers of arthropods per fecal sample (range 3.2–6.5). We found seeds of 14 different plant species in migrant fecal samples; however, seeds of only 2 tree species were present in more than 5 fecal samples (black torch and strangler or shortleaf figs). We were able to identify seeds to tree species for all fecal samples collected in the Upper Keys. We were unable to identify seeds in 16 different fecal samples (representing an unknown number of tree species) in the Lower Keys because our reference collection was not as complete for this region.

The relative proportion of the 3 most common arthropod prey categories (ants, beetles, and spiders) varied among foraging groups and species (Table 22). Ants were much more common in fecal samples of prairie warblers (40%), ovenbirds (36%), and black-throated blue warblers (34%) than all other species. Ants were particularly uncommon in fecal samples from Swainson's warblers (7%) and worm-eating warblers (17%). Beetles were relatively common in fecal samples of Swainson's warblers (45%) and ovenbirds (39%), and relatively uncommon in black-throated blue warblers (15%) and blackpoll warblers (19%). Spiders were relatively common in fecal samples of northern parulas (37%), worm-eating warblers (36%), and Swainson's warblers (32%), and relatively uncommon in ovenbirds (10%). Numbers of individual snails and adult Lepidoptera could not be quantified in fecal samples, yet fragments of these prey items were often present. Snail shell fragments were frequently

Table 21. Sample sizes (number of samples and number of total arthropods) and sample contents (number of arthropods per sample and percent samples with fruit) for fecal samples collected from migrants in hardwood hammocks of the Florida Keys, 2002–2004.

Species	Samples	Total arthropods	Arthropods per sample	Samples with fruit (%)
American redstart	44	195	4.4	20
Black-and-white warbler	29	128	4.4	14
Blackpoll warbler	10	65	6.5	0
Black-throated blue warbler	31	103	3.3	10
Common yellowthroat	26	99	3.8	23
Northern parula	26	94	3.6	8
Northern waterthrush	22	51	2.3	9
Ovenbird	73	258	3.5	11
Prairie warbler	41	300	7.3	7
Swainson's warbler	12	43	3.6	0
Worm-eating warbler	40	127	3.2	3

Table 22. Diet summaries for warblers captured during migration in the hardwood hammocks of the Florida Keys, 2002–2004, including fecal sample sizes, percent frequency occurrence of important prey categories in fecal samples, and the proportion of the 3 most important prey taxa (ants, beetles, and spiders) in calculated migrant diets.

		Samples with prey category present (%)					% contribution to diet		
Species	**Samples**	**Ants**	**Beetles**	**Spiders**	**Snails**	**Adult Lepidoptera**	**Ants**	**Beetles**	**Spiders**
American redstart	44	50	68	57	18	9	19	27	19
Black-and-white warbler	29	59	83	66	34	14	24	31	26
Blackpoll warbler	10	100	80	100	10	10	27	19	23
Black-throated blue warbler	31	68	45	74	7	7	34	15	30
Common yellowthroat	26	62	81	62	8	15	25	27	18
Northern parula	26	50	77	81	4	12	21	28	37
Northern waterthrush	22	50	50	50	27	0	22	31	25
Ovenbird	73	59	71	32	33	3	36	39	10
Prairie warbler	41	76	59	59	0	5	40	22	20
Swainson's warbler	12	17	92	67	0	17	7	45	32
Worm-eating warbler	40	40	68	70	38	8	17	28	36

present in the fecal samples of worm-eating warblers (38%), black-and-white warblers (34%), ovenbirds (33%), northern waterthrushes (27%), and American redstarts (18%), and relatively infrequent (<10% of samples) for all other species. Adult Lepidoptera, while present in fecal samples from 10 of 11 species, were relatively infrequent for all species (average of 9% of samples per species, range 0–17%).

Dietary relationships of migrant insectivores in the hardwood hammocks of the Florida Keys are shown in Fig. 5. This analysis is based on only the proportions of beetles, spiders, and ants in migrant diet. The inclusion of additional prey categories did not improve the amount of variation explained by models and did not graphically alter the relationships among species. Swainson's warblers and ovenbirds had dissimilar diets from other migrants. Both species ate a high proportion of beetles; however, ovenbirds also ate a large proportion of ants and a very small proportion of spiders, while Swainson's warblers were the opposite, eating a large proportion of spiders, but very few ants. Prairie warblers, blackpoll warblers, and black-throated blue warblers grouped together due to the large proportion of ants in their diet; blackpolls and black-throated blues grouped together more closely due to a secondary preference for spiders and low dietary proportions of beetles. Northern parulas and worm-eating warblers grouped together due to a varied diet, but with a high proportion of spiders. Common yellowthroats, American redstarts, northern waterthrushes, and black-and-white warblers grouped closely together due to similarly varied diets, with relatively even proportions of all 3 major prey categories in their diet.

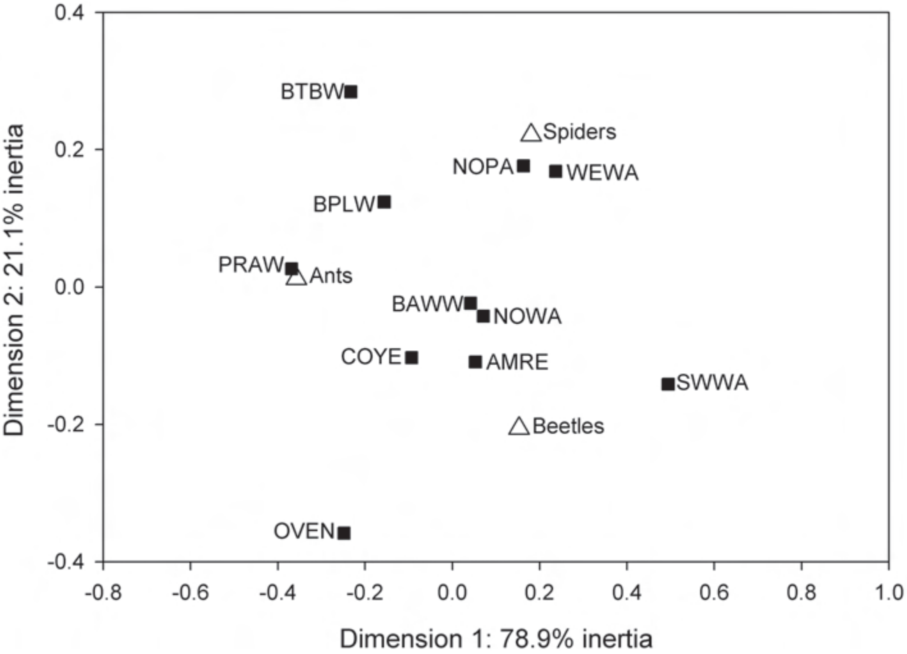


Fig. 5. Correspondence analysis plot displaying dietary relationships among migrant warblers captured in mist-nets in hardwood hammocks of the Florida Keys, 2002–2004. Triangles indicate the 3 most common prey categories (spiders, ants, and beetles). Squares indicate diets for individual species. Squares for species with diets proportionately rich in 1 prey taxa are clustered closest to triangle for that category (e.g., the prairie warbler triangle is nearly on top of the ants triangle). Distance of species squares from different prey category triangles reflect their relative use of each prey category. Squares for species with diets that are evenly proportioned among the 3 main prey categories fall in between all 3 triangles (e.g., black-and-white warblers). AMRE = American redstart, BAWW = black-and-white warbler, BPLW = blackpoll warbler, BTBW = black-throated blue warbler, COYE = common yellowthroat, NOPA = northern parula, NOWA = northern waterthrush, OVEN = ovenbird, PRAW = prairie warbler, SWWA = Swainson's warbler, and WEWA = worm-eating warbler.

Foraging Relationships

We collected 216 foraging observations on 16 different migrant species. Foraging observations ranged in duration from 20 seconds to 9 minutes, with an average observation time of 2 minutes and 12 seconds. Each observation recorded an average of 9.6 foraging attacks (range 0–66 foraging attacks per observation). We present summarized observations for 10 of the most common migrant species where we had >4 foraging observations with ≥5 foraging attacks and for which we also have good diet and/or stopover data. Foraging rates (e.g., attacks per minute and hops per minute) varied among species (Table 23). For species with a sample size of ≥5 foraging observations, Swainson's warblers and ovenbirds (both ground-foraging birds)

Table 23. Foraging rates (and foraging observation sample sizes) for 10 common species of warblers observed in the hardwood hammocks of the Florida Keys, 2002–2004.

Species	Number of observations	Minutes observed	Number of attacks	Attacks per minute	Hops per minute
American redstart	6	12	62	5.3	24.7
Black-and-white warbler	16	57	272	5.3	31.7
Blackpoll warbler	10	38	139	4.5	14.8
Black-throated blue warbler	3	5	17	3.3	22.9
Common yellowthroat	5	21	72	4.6	19.8
Northern parula	7	21	75	4.2	18.8
Ovenbird[a]	15	50	341	7.9	
Prairie warbler	17	48	192	4.7	20.3
Swainson's warbler[a]	2	4	72	19.8	
Worm-eating warbler	13	31	227	9.0	16.5

[a] Ovenbirds and Swainson's warblers forage by walking on the ground; therefore, hops per minute are not reported for these species.

tended to make higher numbers of foraging attacks per minute than all other species. Among species that foraged primarily in vegetation, black-and-white warblers tended to change perches most frequently (31.7 hops/minute), whereas blackpoll warblers (14.8 hops per minute) and worm-eating warblers (16.5 hops/minute) tended to search more slowly and methodically for prey items.

Foraging observations took place opportunistically along trails and were not randomized with respect to tree species. This said, 63% of all foraging attacks in the Upper Keys were observed in 2 different tree species, stopper (32%) and wild tamarind (31%). In the Lower Keys, 54% of all foraging attacks were observed in buttonwood, 11% in saffron plum, and 9% in dilly. Nearly all observations in dilly were foraging attacks on flowers. All other tree species contributed <7% of all observed foraging attacks at each site. All observations of birds feeding in flower clusters were during spring migration. Birds were observed foraging at flower clusters only in wild tamarind in the Upper Keys and dilly in the Lower Keys.

Foraging heights varied across species (Table 24). Swainson's warblers and ovenbirds foraged almost exclusively on the ground; common yellowthroats, black-and-white warblers, and worm-eating warblers tended to forage in the lower third of vegetation; black-throated blue warblers and prairie warblers in the middle third; and American redstarts and blackpoll warblers in the upper third. Northern parulas foraged both in the middle third and upper third of the vegetation.

Table 24. Foraging heights (percent of foraging attacks per category) for 10 species of warblers observed during migration in hardwood hammocks of the Florida Keys, 2002–2004.

Species	Ground	Low	Mid	High
Swainson's warbler	100	0	0	0
Blackpoll warbler	0	0	33	67
Ovenbird	99	1	0	0
American redstart	4	2	28	66
Northern parula	0	9	44	47
Prairie warbler	0	19	52	29
Black-throated blue warbler	0	33	53	13
Worm-eating warbler	11	61	23	5
Black-and-white warbler	3	63	26	2
Common yellowthroat	25	66	1	9

Foraging substrates also varied considerably among species (Table 25). Although ovenbirds and Swainson's warblers both foraged on the ground, ovenbirds foraged primarily by pecking at the surface of the leaf litter, and Swainson's warblers by turning over leaves and probing beneath them. Black-and-white warblers foraged almost exclusively in bark. The remaining species all foraged primarily on live vegetation, with a range of secondary substrate preferences. American redstarts frequently made aerial foraging attacks. Worm-eating warblers foraged on a mix of live foliage, bark, and dead-leaf clusters. Blackpoll warblers and black-throated blue warblers foraged secondarily at flower clusters. Correspondence analysis created 5 different groupings based on foraging substrate, illustrating differences in substrate use among Swainson's warblers (leaf-litter sub-surface), ovenbirds (leaf-litter surface), black-and-white warblers (bark), worm-eating warblers (dead-leaves and bark), and all other species (live foliage, flowers, and air) (Fig. 6).

Table 25. Percent of foraging attacks per substrate for 10 species of migrant warblers observed in hardwood hammocks of the Florida Keys, 2002–2004. Species are sorted from highest to lowest percentage of attacks on live foliage.

Species	Live leaf	Dead leaf	Bark	Flower	Air	Ground peck	Ground turn
Northern parula	95	0	0	0	5	0	0
Prairie warbler	78	1	15	0	5	0	0
Blackpoll warbler	70	0	7	23	0	0	0
Black-throated blue warbler	69	0	11	20	0	0	0
Common yellowthroat	65	0	10	0	0	25	0
American redstart	39	0	2	15	40	4	0
Worm-eating warbler	32	27	28	0	2	9	2
Black-and-white warbler	2	3	91	0	1	1	2
Ovenbird	1	0	0	0	0	85	14
Swainson's warbler	0	0	0	0	0	14	86

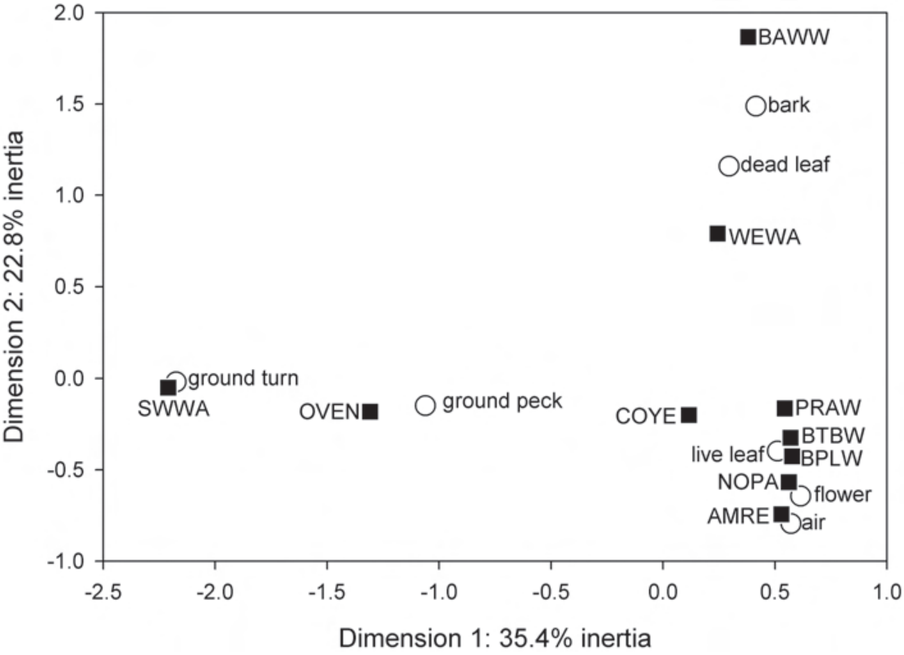


Fig. 6. Correspondence analysis plot displaying foraging substrate use by migrant warblers captured in mist-nets in hardwood hammocks of the Florida Keys, 2002–2004. Open circles indicate the 7 most common foraging substrates used by migrants: bark; dead-leaf clusters (aerial leaf litter); live leaves; flowers; air; and 2 different categories for foraging attacks on the ground, ground peck (surface of the leaf litter) and ground turn (sub-surface of the leaf litter). Squares indicate species use of different foraging substrates. Squares for species that foraged mostly on single substrates are clustered closest to the circle for that category (e.g., the Swainson's warbler square is nearly on top of the ground turn circle). Distance of species squares from different substrate circles reflect their relative use of each substrate. AMRE = American redstart, BAWW = black-and-white warbler, BPLW = blackpoll warbler, BTBW = black-throated blue warbler, COYE = common yellowthroat, NOPA = northern parula, OVEN = ovenbirds, PRAW = prairie warbler, SWWA = Swainson's warbler, and WEWA = worm-eating warbler.

Food Availability

We included only the arthropod orders that commonly occurred in migrant diet in arthropod abundance sample summaries. For branch-clip samples we included only orders that represented >3% of the diet for >3 species. For leaf-litter samples we included only the orders that represented >3% of the diet of either ovenbirds or Swainson's warblers. Thus, comparisons of seasonal arthropod abundance for branch-clip samples include spiders, beetles, ants, hymenoptera (wasps), flies, snails, hemipterans, lepidoptera larvae, lepidoptera adults, and orthopterans. Seasonal arthropod abundance summaries for leaf-litter samples include ants, beetles, spiders, hymenoptera (wasps), snails, adult lepidoptera, larval lepidoptera, and orthopterans. Summaries of prey category composition of dead-leaf samples include spiders, beetles, ants, hymenoptera (wasps), gastropods, lepidoptera larvae, diptera, orthopterans, and hemiptera.

Arthropod abundance varied both seasonally and by site (Table 26). Live-foliage arthropods were much more abundant during fall in the Upper Keys than in all other site/season combinations, which did not differ from each other ($X^2 = 115.1957$, $P < 0.0001$, df = 3, Kruskal Wallis ANOVA with site/season as the independent variable, number of arthropods per branch-clip sample as dependent variable). Leaf-litter arthropod abundance varied by both site (Z = -6.1795, $P < 0.0001$, df = 2, 2-sample Wilcoxon Rank sum test) and season (Z = -3.0726, $P = 0.0021$, df = 2), with higher numbers of arthropods in the Upper Keys and during fall migration.

Both prey size and relative proportions of different prey categories varied across arthropod sampling methods (Fig. 7). Arthropods in aerial leaf-litter samples (3.1 ± 0.7 mm) and branch-clipping samples (3.0 ± 1.8 mm) were larger then arthropods in ground leaf-litter samples (2.1 ± 0.5 mm) ($X^2 = 38.1209$, $P < 0.0001$, df = 2, Kruskal Wallis ANOVA on prey size per sample). Ground leaf-litter samples had high proportions of both beetles (34.5%) and spiders (30.2%), lesser numbers of ants (17.0%) and lepidopteron larvae (10.4%), and very low proportions of all other prey types. Branch-clipping

Table 26. Seasonal and site-specific differences in arthropod abundance (number of arthropods per sample) in branch-clipping and leaf-litter arthropod samples collected during migration in the hardwood hammocks of the Florida Keys, 2002–2004.

	Upper Keys				Lower Keys			
	Fall		Spring		Fall		Spring	
	mean	SD	mean	SD	mean	SD	mean	SD
Branch clipping	5.7	4.6	3.3	5.5	2.4	2.8	2.2	2.1
Leaf litter	26.8	11.8	17.4	10.1	10.9	7.5	6.5	5.5

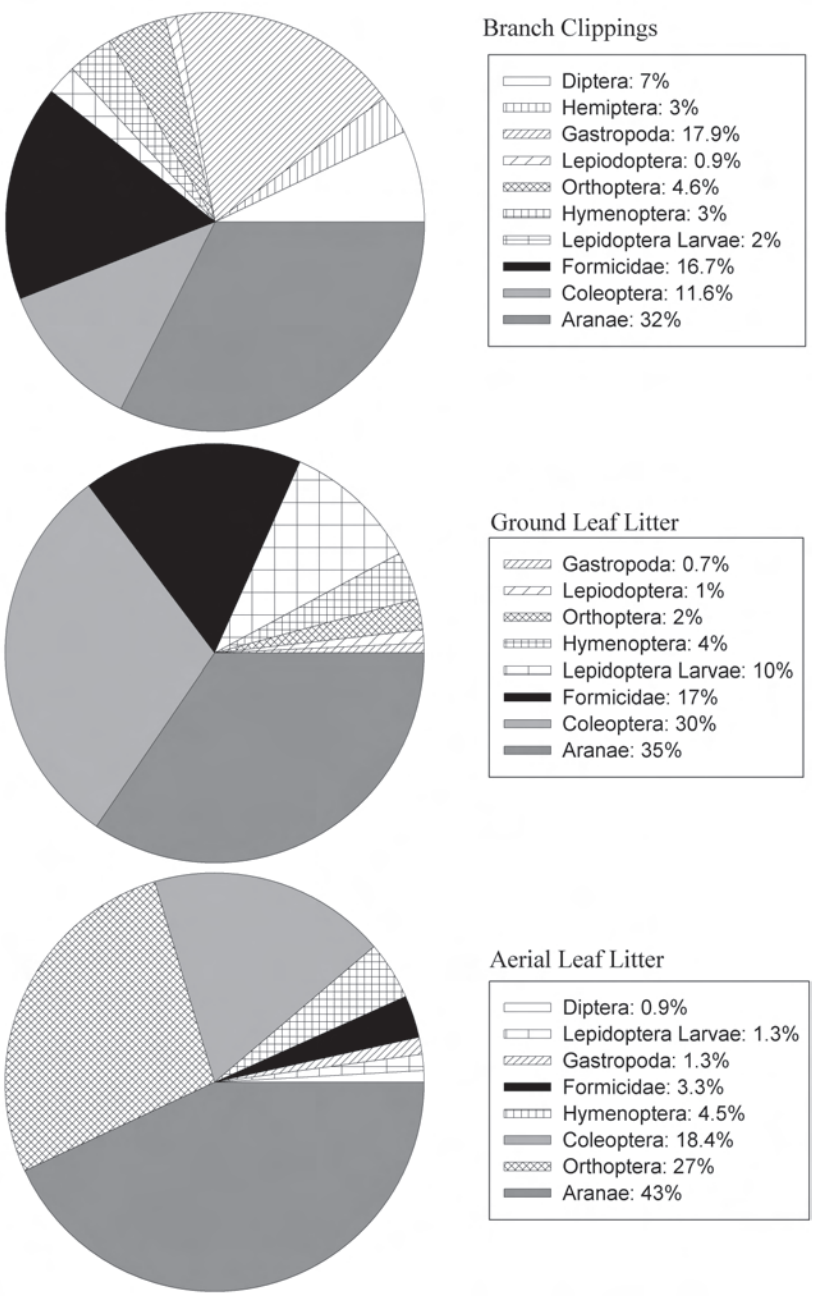


Fig. 7. Proportions of prey taxa in 3 different types of arthropod abundance samples taken in hardwood hammocks of the Florida Keys, 2002–2004

samples had high proportions of spiders (32.4%), followed by lesser numbers of snails (17.9%), ants (16.7%), beetles (11.6%), and flies (7.1%). All other prey types contributed <5% to the branch-clipping samples. Aerial leaf samples had the highest proportion of spiders (43%) of all arthropod sampling methods, followed by relatively high numbers of orthoptera (27.3%), and lesser numbers of beetles (18.4%). All other prey types made <5% of the aerial leaf-litter arthropod samples.

Live-foliage arthropod abundance varied by tree species within some site/season combinations (Table 27). During fall in the Upper Keys, both pigeon plum and stopper samples had higher numbers of arthropods than poisonwood and Jamaica dogwood samples (X^2 = 25.9021, P = 0.0005, df = 7). During fall in the Lower Keys, samples from buttonwood had higher numbers of arthropods than samples from dilly (X^2 = 21.8133, P = 0.0007, df = 7). Arthropod numbers did not differ significantly among tree species during spring migration at either site (X^2= 7.2531, P = 0.2981, df = 6 for the Upper Keys; X^2 = 9.5196, P = 0.2175, df = 7 for the Lower Keys).

Table 27. Arthropod abundance (numbers of arthropods per branch-clipping sample) for 14 different tree species sampled during spring and fall migration in hardwood hammocks in the Florida Keys, 2002–2004. Jamaica dogwood trees are deciduous and did not have leaves available for sampling during our spring migration sampling period.

	Fall			**Spring**		
Species	**Samples (*n*)**	**Mean**	**SD**	**Samples (*n*)**	**Mean**	**SD**
Upper Keys						
Crabwood	23	6.8	4.2	21	5.0	10.9
Gumbo limbo	15	2.9	1.7	6	2.2	1.2
Jamaica dogwood	11	3.8	2.0			
Pigeon plum	24	7.7	6.5	19	3.6	3.0
Poisonwood	12	2.8	2.0	6	1.5	0.8
Stopper species	32	7.5	5.5	21	2.8	1.6
Strongbark	12	5.3	3.3	2	1.5	0.7
Wild tamarind	27	4.8	2.8	20	2.6	1.9
Lower Keys						
Black bead	10	1.8	0.8	10	1.7	1.9
Black mangrove	10	1.2	0.6	14	3.9	3.9
Black torch	14	2.5	1.8	10	1.9	1.3
Buttonwood	18	4.2	3.8	14	2.3	1.9
Dilly	14	1.3	0.5	10	1.8	0.9
Poisonwood	10	2.0	1.1	6	2.2	1.9
Red mangrove	10	1.5	0.7	7	1.3	0.5
Stopper species	14	3.1	5.3	16	1.4	0.6

DISCUSSION

Mist-net Inventory of Species Composition and Relative Abundance

This study provides the first systematic quantification of the migration of Nearctic-Neotropical migrant landbirds in hardwood hammocks of the Florida Keys using mist-nets. Aside from providing data on relative abundance and species richness, mist-nets were invaluable for collecting physiological data on individual migrants (e.g., mass, fat loads, diet samples) that are critical to understanding stopover biology. Mist-nets also afforded the opportunity to discern the age of a number of species in the hand that are not possible to age with binoculars in the field. Bicknell's thrushes are virtually impossible to separate from gray-cheeked thrushes by birdwatchers in the field; however, there are unambiguous measurements that separate the 2 species in the hand (Oulette 1993, Pyle 1997). The use of mist-nets allowed us to document the first state records for this species that have been accepted by the Florida Ornithological Society's records committee (Brand et al., in press). Mist-nets were particularly valuable to demonstrate that Swainson's warblers, a species on the Partners in Flight watch list (Rich et al. 2004) and thought to be uncommon during migration in the Florida Keys (Pranty 1996), are indeed relatively common during fall migration in hardwood hammocks of the Upper Keys. Because Swainson's warblers are particularly difficult to observe during migration, and birdwatchers infrequently visit mid- to large-sized patches of hardwood hammock, this information would have been nearly impossible to come by without using mist-nets.

Many species that migrate through the Florida Keys have winter ranges that are centered on the Caribbean, a region currently undergoing extreme deforestation, presenting conservation challenges (Wunderle and Waide 1994). Twelve of the 15 most commonly captured species during this study have large proportions of their wintering range in the Caribbean, and the Caribbean is the core winter range for North American breeding populations of black-throated blue warblers, prairie warblers, and Swainson's warblers. Worm-eating warblers winter primarily in the Caribbean, but also in Central America. Ovenbirds, American redstarts, western palm warblers, common yellowthroats, northern waterthrushes, black-and-white warblers, gray catbirds, and northern parulas have larger wintering ranges and are common in winter in the Caribbean and throughout Mexico and Central America. The Florida Keys present an excellent opportunity for monitoring a large number of species that winter in the Caribbean.

Several migrant species common in the Florida Keys have large portions of their North American breeding areas in boreal Canada, well north of monitoring efforts that are part of the Breeding Bird Survey (Hussell and Ralph 1998). These species include blackpoll warbler, western palm warbler, northern waterthrush, red-eyed vireo, black-and-white warbler, ovenbird, and American redstart. Mist-netting during migration could be an effective method for monitoring long-term population changes for these species that are difficult to monitor during the breeding season because of remote northern breeding areas (Dunn et al. 1997, Hussell and Ralph 1998).

In addition, hardwood hammocks in the Upper Florida Keys may present a unique opportunity to study the stopover biology of Swainson's warblers, which are not captured in high numbers at other sites during migration. Because of differences in habitat and/or capture rates between our 2 study sites (Table 3), migration monitoring would be more effective in the Upper Keys for some species (Swainson's warblers, worm-eating warblers, and black-and-white warblers) and more effective in the Lower Keys for others (northern parula, prairie warbler, blackpoll warbler, and western palm warbler). Some of these species are more abundant during fall; however, blackpoll warblers are only common in the Florida Keys during spring migration.

Although mist-netting is a standard sampling technique in field ornithology, it has been criticized for providing a biased picture of relative abundance. Specifically, mist-nets are ineffective for capturing birds that forage high in the canopy (Remsen and Good 1996). At both sites, all of our mist-nets were set within 3 m of the ground. Our foraging observations indicated that several common migrant species spent most of their time foraging high in the vegetation (northern parulas, prairie warblers, blackpoll warblers, and American redstarts). Thus, capture rates for these species (particularly at our Upper Keys study site where canopy height ranged from 8 to 12 m) are probably low relative to the true number of individuals of these species using hardwood hammocks in the Keys. This bias was probably strongest in spring in the Upper Keys, where many species foraged in the flower clusters of wild tamarind near the tops of trees. Although infrequently captured at our study sites, Cape May warblers are relatively common during spring migration in the Florida Keys (Pranty 1996), and we believe that mist-nets were particularly ineffective in capturing this species due to its preference for foraging high in the canopy.

Age and Sex Ratios

Of the 14 species reliably aged during fall migration in the Keys, an average of 65% of all individuals was young (first-year) birds (range 41–85% by species) (see Table 4). This is a relatively low percentage of young birds compared to most other sites that have reported age ratios during fall migration. Most banding stations along the Atlantic and Pacific coasts have reported between 85 and 95% young birds during fall migration (Drury and Keith 1962, Murray 1966, Morris et al. 1996 for the Atlantic Coast; Ralph 1971, Stewart et al. 1974 for the Pacific Coast). Ralph (1981) hypothesized that experienced adult birds were more likely to migrate inland, avoiding the hazards of water barriers, and that the concentration of young birds along the coast was due to their inexperience. Ralph (1981) also suggested that sites that captured a higher percentage of adult birds may be closer to the center of a migration route for a species, and sites that capture high percentages of young birds may be closer to the periphery of a species' migration route.

Of 5 inland sites that reported age ratios, 2 reported a high percentage of young birds and 3 reported a relatively low percentage of young birds. Jones et al. (2002) reported age ratios for migrants captured at Long Point, an inland site on the shoreline of Lake Ontario. Of the 10 species that were common between this study and our study, an average of 84% of all birds were young (range 67–92% by species). Rimmer and McFarland (2000) reported age ratios for another inland (high-elevation) banding station in Vermont that also captured a large proportion of young birds (average of 91.6% young, range 72–100% for 6 species common to both studies). Relatively low proportions of young birds in fall migration have been reported for only 3 sites. Yong and Finch (2002) reported only 48% immature birds in their sample of migrants captured along the Rio Grande in New Mexico; Woodrey and Moore (1997) reported 76% young birds in fall migrants captured in coastal Louisiana; and Winker (1995) reported an average of 59% young birds in fall migrants captured at an inland site in the Yucatan (average calculated from 6 species in common with our study).

Yong and Finch (2002) proposed 3 explanations for the relatively low proportion of young birds captured at their site that seem relevant for evaluating the relatively low proportion of young birds captured in the Florida Keys: (1) low proportions of immature birds reflect low reproductive success across the source range for migrants, (2) high mortality of young birds before arrival in the Florida Keys may explain lower proportions of young birds compared to more northern sites, and (3) the actual migration route used by adults and young birds may differ. We view factor 1 as an unlikely explanation because the breeding ranges of species captured in the Florida Keys span most of eastern North America, and low productivity in one region would most likely be balanced by high productivity in another. Factor 2 seems plausible because the proportion of young birds in a migrant sample tends to be lower at southern sites during fall migration and because both inland sites at northern latitudes (Long Point and inland Vermont) reported high proportions of young birds. Factor 3 is essentially a rephrasing of Ralph's hypothesis that low proportions of immature birds reflect areas more central to the migration route of a species. This is a possibility in the Florida Keys because both young and adult birds of many species captured in the Keys are close to their final core wintering areas in the Caribbean. More geographically widespread data across North America are necessary to assess the relative merits of these 3 hypotheses to explain geographic variation in age ratios at stopover sites. For the sake of long-term monitoring of migrants by mist-netting at stopover sites, relatively high proportions of adults in migrant samples at southern locations may better reflect overall population trends for a species as opposed to sites at northern latitudes that capture large proportions of young birds, which may better reflect annual variation in the regional production of young.

Interestingly, we found adult black-and-white warblers, American redstarts, and black-throated blue warblers to be proportionately more common than young birds during fall migration in the Upper Keys. This site-season combination also had the highest food availability of all the migration field seasons of this study. Several studies have shown that adult birds tend to secure higher quality territories than young birds during winter through behavioral dominance (Gauthreax 1978, Terrill 1987, Marra 2000). It is possible that the high proportion of adult birds captured in the Upper Keys during fall migration may be related to the behavioral dominance of adults at a site with high food resource levels. More seasons of banding and food availability data collection at this and/or additional sites in the Florida Keys would be interesting to address the hypothesis that age ratios may vary at stopover sites in response to food availability.

We have no ready explanation for the high proportion of male birds captured during this study. Sex ratios differed significantly from 50:50 for a number of species (average 63% male for 7 species, range 54–69%). Male birds of some species have shown behavioral dominance over females in securing higher quality wintering territories (Marra et al. 1998, Marra 2000). If our mist-netting took place in habitats superior to surrounding habitats, it is possible that behavioral dominance of males may explain the skewed sex ratios observed at this site. Again, more seasons of banding and food availability sampling at a greater number of sites in the Florida Keys would be necessary to assess this possibility.

Few species can be reliably aged during spring migration and very few migration sites have reported age ratios for both spring and fall migration. Since mortality during fall migration and winter may be much higher for inexperienced young birds than for adults (Greenberg 1980, Ketterson and Nolan 1988, Rappole et al. 1989), lower proportions of young birds should be expected during spring migration. Morris et al. (1994) reported high proportions of young birds during both spring and fall migration at a stopover site on an island in coastal Maine, suggesting that this site may be avoided by adults and more frequently used by inexperienced young birds in both seasons. For the 4 species that could be reliably aged during spring migration in the Florida Keys, we captured lower proportions of young birds during spring than during fall migration (average 25%, range 10–34% young birds), perhaps reflecting greater over-winter or migration mortality of young birds between fall migration and spring migration of the following year.

Migration Timing

Our seasonal mist-netting periods were adequate to sample most common species of migrant landbirds in the Florida Keys. However, fair numbers of prairie warblers may have already passed through the Keys by the time we began our daily fall banding in late August, and large numbers of western palm warblers most likely continued to arrive in the Florida Keys well after our fall banding season ended during the third week of October. In the Upper Keys, the first 2.5 weeks of spring banding were very slow and future spring banding efforts may wish to start in mid-April rather than late March (see Fig. 4). However, early spring banding in the Upper Keys did produce the only spring captures of a few uncommon species (Swainson's warbler and Louisiana waterthrush). In the Lower Keys, we captured higher numbers of birds in early spring due to our improved ability to capture western palm warblers and prairie warblers at this site. Few birds were captured after the first week in October during both seasons of this study, and future fall banding efforts may wish to terminate fall banding seasons slightly earlier than we did. The relatively long banding seasons of this inventory allowed us to capture the maximum number of species occurring in the Florida Keys both early and late during both migrations. Shorter seasons may be adequate for future studies of stopover biology or monitoring for common migrants. Tables 7 and 8, which present the seasonal timing of migration by species during both migrations, will be useful for planning the dates of future banding studies in the Florida Keys.

During both seasons, mist-net capture rates fell off precipitously in late morning as temperatures increased, and mist-netting was generally unproductive after 1100 hr. Many migrants became active again late in the afternoon as temperatures cooled down, and it is possible that opening nets again later in the day, if logistically feasible, would markedly increase either capture or recapture rates. The relatively short daily mist-netting period of this study may have made it difficult to document mass gain of single-captures over the course of a single day since relatively few captures occurred more than 4 hours after sunrise, perhaps an inadequate amount of time for migrants to gain large amounts of mass.

Fat Stores and Body Mass at Arrival

Most migrants stopping over in the Florida Keys were already carrying substantial stores of body fat (fat scores at arrival = 2.2 ± 1.2) and very few fat-depleted birds (0 body fat score) were captured (12% of all migrants, range 2–32% by species). Fat scores from this study are not directly comparable with fat scores collected during other studies because of differences in categorical fat scales used among studies and uncontrolled differences in observers. It would greatly benefit stopover studies within the Nearctic-Neotropical migration system if a single fat-scoring protocol were adopted for North America, similar to the protocols adopted for widespread sampling migrants in the western Palearctic (Bairlein 1995, Shaub and Jenni 2000). Nevertheless, the percentage of fat-depleted birds (birds with no visible body fat) can be compared among studies. Morris et al. (1996) reported 52% fat-depleted birds during fall migration in Maine, Rimmer and McFarland (2000) reported 73% during fall migration in Vermont, and Yong and Finch (2002) reported 50% during fall migration along the Rio Grande in New Mexico. In contrast, Woodrey and Moore (1997) reported a very low percentage of fat-depleted birds at arrival (typically <5% fat-depleted birds per species) and high mean fat scores for 6 species of fall migrants in Louisiana prior to crossing the Gulf of Mexico; whereas Moore and Simons (1992) reported very high percentages of fat-depleted birds (80%) arriving on Gulf coastal islands after crossing the Gulf of Mexico in spring.

Although comparative data are still few, it seems that low fat loads may be the norm for fall migrants at northern or inland sites, or after water crossings, and higher fat loads may be carried by birds at southern sites before water crossings such as the Gulf of Mexico or the Caribbean Sea (this study). Within the Palearctic-African migration system both Biebach et al. (1986) and Finlayson (1981) reported a very low percentage (<5%) of fat-depleted birds and high mean fat scores during stopover at Saharan desert oases during spring and prior to desert crossings (in Gibraltar) in fall, lending support to the idea that migrants may carry higher fat loads when confronted with geographic barriers requiring long-distance flights with few or no opportunities to refuel (such as the Gulf of Mexico or the Sahara Desert). Field data from a larger number of geographically separated sites will be necessary to understand geographic patterns in fat loads carried during migration.

Body mass and fat scores were higher during fall migration than spring migration in the Florida Keys. Higher body mass and fat scores during fall migration may indicate regional differences in food availability between the 2 seasons. Fall migration takes place during the wet season in south Florida, a period of high arthropod and fruit abundance (Levings and Windsor 1982, Bancroft and Bowman 1994). Many migrants stopping over in the Florida Keys may have spent several days foraging at stopover sites with high arthropod abundance prior to arrival. In contrast, spring migration takes place towards the end of the dry season in the Caribbean, a period of relatively low arthropod and fruit abundance (Levings and Windsor 1982, Bancroft and Bowman 1994). Therefore, migrants may have spent time at relatively unproductive stopover habitats before arrival in the Florida Keys. Five of 7 foliage-gleaning insectivores had seasonally lower body masses in spring. By way of contrast, ovenbirds, which forage primarily in the leaf litter, did not have lower body mass in spring. Late in the dry season, leaf litter has been shown to be refuge from desiccation for many arthropod orders (Levings and Windsor 1982), whereas arthropod abundance decreases in live vegetation during late winter and early spring (Poulin et al. 1992, Sherry and Holmes 1996).

Four of 11 species had higher average body masses at arrival in the Upper Keys than the Lower Keys. Ovenbirds, worm-eating warblers, and black-throated blue warblers were also considerably more common in the Upper Keys; possibly because the well-developed under story, leaf litter, and aerial leaf-litter microhabitats of the Upper Keys provide more suitable stopover habitat for these species than the short-stature, densely structured vegetation of the Lower Keys. If single-capture birds are only present at the stopover site for 1 day, body mass at arrival should reflect habitat conditions at the previous day's stopover site or weather conditions during nocturnal migration, not local habitat conditions. However, the higher body mass of these species at more suitable habitats in the Upper Keys suggests that they may be spending some time at the site prior to initial capture or they may be stopping over at similar sites the night before.

Body Condition Change During Stopover

Since rates of mass gain may be indicative of habitat quality (Moore and Simons 1992), sampling biases inherent to both single-capture and recapture data deserve more serious study so that results and interpretations of studies of mass gain during stopover are framed appropriately. Single-captures make up the majority of migrants captured at stopover sites, and most birds captured during this study were captured only once. Therefore, several authors have attempted to estimate daily mass gain for single-captures from the slopes of regressions of mass versus time of day with the expectation that individuals of the same species that are captured later in the day will be heavier (e.g., Winker 1995; Dunn 2000, 2002; Jones et al. 2002). This method assumes that migrants arrive at night in an energy-depleted state and replenish body reserves and fat stores at stopover sites the following day well enough to recommence migration the night after arrival. Although these regressions are sometimes statistically significant, time of day typically describes a very small portion of variation in body mass. Since individual variation in body mass of single-captures is often large, these regression estimates typically provide imprecise estimates of mass gain, with confidence intervals ranging from extreme mass gains to extreme mass losses. In one study, regression estimates of mass change during stopover from single-captures provided estimates 29 times higher than actual observations of mass gain from recapture data (Yong and Finch 2002). Using the single-capture regression technique, we found few significant relationships between mass and time of capture in the Florida Keys, and these were all very weakly predictive. It is possible that we were not able to detect daily changes in mass due to the short daily sampling period of our mist-netting (~5 hours per day). However, we believe it is more likely that this method provides poor and unreliable estimates of daily mass gain due to the huge amount of individual variation in body mass of single-captures.

The proportion of birds that are recaptured during stopover studies is typically low (9.4% in this study). However, we believe that these data provide a more accurate description of mass gain during stopover (giving a better overall picture of habitat use and quality) than mass gain estimates from regressions from single-captures. We found differences in changes in body mass of recaptures among sites and seasons. Total percent changes in mass were higher during fall migration than spring migration. Higher total percent change in body mass during fall migration is probably related to the combination of higher daily rates of mass gain and slightly longer stopovers during fall migration. Total percent changes in body mass were also higher in the Upper Keys than the Lower Keys, but not significantly so at a critical α of 0.05 ($P \geq 0.0768$). However, daily percent changes in body mass were significantly higher in the Upper Keys. Stopover lengths did not vary between the Upper Keys and Lower Keys, suggesting a site-specific explanation for higher percent mass gains in the Upper Keys (see discussion on food availability). Since fat is the primary fuel used for migration, changes in body mass during stopover should be mirrored by changes in fat stores if migrants are replenishing fat supplies at stopover sites. Most species increased both body mass and fat stores during stopover in the Florida Keys, suggesting that food resources in hardwood hammocks were adequate to replenish energy stores depleted during nocturnal migration. However, prairie warblers and western palm warblers had relatively low percent increases in mass during stopover. It is possible that some of our migrant sample for these 2 species included resident prairie warblers or wintering western palm warblers that were not actively increasing mass for migration. It is also possible that the stopover sites we sampled in the Florida Keys are less suitable for refueling for these species than for other species with higher rates of mass gain.

Among our recaptured birds we found evidence of lower mass gains, or mass losses, for birds that had MSL = 1 compared to birds with MSL > 1. Others studies have demonstrated low initial mass gain at stopover sites; however, data describing this phenomenon have varied (and sometimes conflicted) among studies, and the physiological mechanisms underlying this pattern are still poorly understood (but see Gannes 2002). Shaub and Jenni (2000) found lower rates of mass gain for birds with MSL = 1 versus birds with MSL > 1 for 3 different species at 6 different sites across Europe. Gannes (2002) found low rates of mass gain for blackcaps (*Sylvia atricapilla*) up to 3 days after initial capture at an oasis stopover site in Israel. After a threshold of 3 days, blackcaps had much more positive rates of mass gain. Yong and Moore (1997) found low initial mass gains for thrushes during spring along the Gulf of Mexico. In contrast, Moore and Kerlinger (1987) showed high rates of initial mass gain for several species during spring migration immediately following the long-distance flight across the Gulf of Mexico, and Bairlein (1997) showed immediate positive mass gains for garden warblers (*S. borin*) during migration in Europe. This study provides additional evidence that daily mass gains during stopover are non-linear, with an initial period of low mass gains followed by a second period of higher mass gain. Variation in the occurrence or length of low initial mass gain periods among stopover sites makes comparison of changes in mass of recaptured birds among sites problematic. Including or removing birds with MSL = 1 in summaries of mass gain from recapture data strongly influenced our results (Table 16), and this issue deserves greater attention in further research.

Comparisons of mass gain among studies are further complicated by differences in methods for calculating or reporting changes in mass from recapture data. Specifically, a large number of different metrics have been used to report changes in mass, including total changes in mass in grams, mass gain in grams per day, total percent change in mass, percent change per day, or percent change in mass relative to lean body mass, which has been calculated in many different ways among studies. Therefore, we do not compare rates of mass gain observed during this study with other studies. To resolve this problem, we recommend that methods of migrant-condition data collection and analyses are standardized among sites, similar to the standardized field data collection protocols and multi-site analyses that have been applied in the Palearctic-African migration system (Bairlein 1995, Shaub and Jenni 2000).

Recaptures in Subsequent Seasons

Although long-distance migrants often show extreme site fidelity to breeding or wintering sites (Baker 1978), few studies have reported on site fidelity to stopover sites. Merom et al. (2000) found that 4.7% of all reed warblers (*Acrocephalus stentoreus*) banded during migration in Israel were later captured in the same reed beds in a subsequent season, implying considerable site fidelity. This may be expected of a wetland species in a dry region with few other options for stopover sites. Catry et al. (2004) reviewed long-term banding records from Portugal and found little evidence of stopover site fidelity for species with breeding or wintering ranges distant from the stopover site, implying large-scale variation in migration route or stopover site selection among years. However, stopover site fidelity was much more common for migrants that had breeding or wintering areas near the stopover site in Portugal. Kelly et al. (1999) found that migrant species with ranges near stopover sites were much more likely to be captured than species with breeding or wintering ranges distant from the stopover site. We are aware of no studies of Neotropical-Nearctic migrating warblers that report on stopover site fidelity. All 16 individuals that were recaptured during subsequent seasons in the Florida Keys were of 7 species that are common wintering birds in Cuba and elsewhere throughout the Caribbean (ovenbirds, black-and-white warbler, American redstart, worm-eating warbler, common yellowthroat, western palm warbler, and northern waterthrush).

Diet and Foraging Relationships

We frequently encountered fragments from all the common prey categories that occurred in our arthropod abundance samples in fecal samples collected from migrants. Although differential digestibility of arthropod orders may have influenced our results, fragments from the 3 most common prey categories in arthropod abundance samples (spiders, ants, and beetles) were all very common in fecal samples. Thus, we regard this method to be relatively accurate for describing the diet of migrants in the Florida Keys and for comparing diet samples among species. We found that dietary relationships among species were best characterized by the relative proportions of the 3 most-common prey categories because the inclusion of less-common prey categories in analyses did not alter our conclusions. Correspondence analysis suggested strong differences in the proportions and primary prey preferences of these 3 prey types among species. Ovenbirds and Swainson's warblers had distinct diets from other species due to the high proportion of beetles in their diet. However, their diets differed from each other due to strong secondary preferences for ants (ovenbirds) and spiders (Swainson's warblers). Prairie warbler diets differed from other species due to their strong primary preference for ants. Worm-eating warblers and northern parulas differed from other migrants due to their strong primary preference for spiders. The 6 other migrant species had more varied diets, with less strong primary prey preferences, resulting in their diets being more closely related to each other.

We suspect that there was very little inter-specific competition for prey among migrant species due to differences in diet and differences in foraging locations within hardwood hammocks in the Florida Keys. Although diets of some species pairs were similar (at our level of taxonomic distinction), foraging data indicated that these species probably found their prey in different foraging locations. For example, northern parulas and worm-eating warblers had similar diets, with large proportions of spiders; however, parulas most frequently foraged high up in live vegetation whereas worm-eating warblers foraged low in live vegetation, in dead-leaf clusters, and on the ground. Similarly, other species pairs (or groupings) with similar diets showed markedly different foraging relationships. Blackpoll warblers and black-throated blue warblers had similar diets, but foraged at very different heights. Blackpolls were almost always at the tops of canopy trees, while black-throated blue warblers foraged most frequently in low or mid-height understory vegetation. Northern waterthrushes, common yellowthroats, American redstarts, and black-and-white warblers had very similar diets; however, they foraged in very different substrates and at different foraging heights (Figs. 5 and 6, Table 24). Similarly, species that were grouped closely together by foraging substrates (Fig. 6) had either differences in diet (Fig. 5) or foraging heights (Table 24) that would reduce competition for similar prey taxa. Of course, it is possible that the prey taxa categories we chose to describe diet or foraging height and substrate preferences are not what drive competitive interactions among species. However, we did not observe aggressive interactions among species during this study, although aggressive interactions within species were common. This suggests that we may be correct in interpreting the interactions between diets and foraging data as evidence of dietary niche separation among species within the migrant community.

It is worth noting that our descriptions of migrant dietary relationships are based on proportions of numbers of individuals of different prey taxa in fecal samples. However, in our arthropod abundance samples, prey size varied among arthropod taxa and among foraging micro-habitats sampled for arthropod abundance. It is possible that biomass may be more closely related to rates of mass gain for migrants than numbers of individual prey items ingested. Therefore, we recommend that future studies of diet and food availability during stopover quantify both numbers of individuals and biomass in both diet and food availability samples using prey fragment/whole prey regressions to estimate prey size in diet samples (Calver and Wooler 1982) and then local or regional length/mass regressions (specific to each prey taxa) to estimate biomass for diet and food availability samples (Strong and Sherry 2000, Johnson and Strong 2000). It is possible that descriptions of migrant diet using biomass may have led to different conclusions of the dietary relationships among species in the Florida Keys.

We were surprised that fruit was not more prevalent in the diets of migrant birds in the Florida Keys because some of these same species become more frugivorous during migration in the northeastern U.S. (Parrish 1997). Insectivorous migrants that switch to diets of arthropods and fruit have sharper increases in mass (Parrish 1997, Bairlein 2002), and many species of hardwood hammock trees produce fruits during both migration seasons (Tomlinson 2002). We did not sample fruit availability during this study, and it is possible that fruits were not very abundant near our stopover sites (personal observations). Migrants may have concentrated on the more locally available resource of arthropods at our banding sites, where we collected diet samples. If this were true, the proportion of fruit we observed in diet samples may not be representative of the amount of fruit in the diet of migrants throughout the entire Florida Keys. We have observed migrants eating large numbers of fruits in short-leaf fig trees bearing heavy fruit during migration, suggesting that some migrants may eat more fruits when they are locally abundant. Perhaps migrants only focus on fruit when it is a super-abundant resource as it was at both sites in the northeastern U.S. where they showed increased frugivory (Parrish 1997, Suthers et al. 2000). It is also possible that previous studies overemphasized the role of frugivory in mass gain during stopover or that the amount of frugivory in the diet of passerines varies regionally for other reasons. More studies that quantify fruit in migrant diet from a wider range of locations in the Florida Keys and across North America are necessary to address this possibility.

We were also surprised that we did not find a wider range of seeds from different tree species in the fecal samples of migrants, because seeds of many tree species in the hardwood hammocks of the Florida Keys are bird-dispersed (Tomlinson 2002) and because the diet of white-crowned pigeons (the other major frugivore in the Florida Keys) is dominated by fruits of only 4 different tree species during the breeding season (Bancroft and Bowman 1994). Thanks to the reference collection of dried seeds at the Tavernier Science Center, we were able to identify all seeds that we encountered in the Upper Keys and many we encountered in the Lower Keys. Thus, from this short-term study it appears that migrant landbirds, although contributing to some seed dispersal, are not primarily responsible for dispersing fruits from a large number of hardwood hammock tree species in the Florida Keys. However, diet sampling from a larger number of sites may alter this conclusion. It is also possible that other groups of birds, such as summer or winter resident passerines (particularly gray catbirds, black-whiskered vireos, and northern cardinals), grey squirrels (*Sciurus vulgaris*) (in the Upper Keys), and raccoons (*Procyon lotor*) all contribute significantly to seed dispersal in tropical hardwood hammocks.

Food Availability

Newton (2004, 219) supplied the following summary of the reasoning behind claims that habitat quality of stopover sites can affect individual fitness or limit migrant populations: "food supplies at staging sites can be heavily depleted, slowing rates of fattening, which in turn delays migration…to the extent that it reduces breeding success, or prevents breeding altogether." Within this conceptual paradigm it is remarkable that more studies have not attempted to examine the relationships among food availability and mass gain. In fact, we know of only 2 studies that have investigated the relationship between food availability and mass gain during stopover (Bibby et al. 1976, Kelly et al. 2000). According to theories of optimal migration (Alerstam and Lindström 1990), migrants with more positive rates of mass gain during stopover should be more likely to successfully complete migration in a timely manner, which could have positive benefits for both survival and reproductive output. If food availability is related to mass gain during stopover, as this study suggests, more attention should be paid to the factors that influence food availability to inform management of habitats used by migrants. This study demonstrated that 3 groups of arthropods (spiders, beetles, and ants) made up a large proportion of the diets of migrants. Widespread sampling throughout the Florida Keys for these 3 arthropod prey types in the foraging micro-habitats defined within this study would help to assess the relative value of different sites (or habitats) as stopover sites. Complementary data collection of habitat or environmental parameters at these sites, such as rainfall, leaf-litter moisture content, vegetation density, tree species, or percent canopy cover, would perhaps allow for the description of forest types or management practices that are correlated with high arthropod abundances for migrants.

In this study, food availability was higher during fall migration than spring migration and higher in the Upper Keys than the Lower Keys. Correspondingly, body mass and fat scores at arrival, and rates of mass gain during stopover were also highest during fall migration and in the Upper Keys, suggesting that higher food availability was related to better migrant condition. Although condition at arrival may be related to regional or seasonal patterns in food availability rather than food availability at our study sites in the Keys, mass gain during stopover should be directly related to food availability at the stopover site. Thus, this study provides direct evidence that mass gain is related to food availability at a stopover site. Mass gain during stopover varied among species and some of this variation may be explained by patterns in arthropod abundance. Spiders were the most numerous prey items in branch-clipping samples, whereas both ants and beetles were relatively uncommon. Among the foliage gleaning species, those whose diet contained a high proportion of spiders had higher increases in body mass during stopover than species whose diet was made up of lower proportions of spiders and higher proportions of beetles or ants. Northern parulas, worm-eating warblers, and black-throated blue warblers had 37%, 36%, and 30% spiders in their diet, respectively. These species had mass increases during stopover ranging from 6.3% to 11.4%, and a range of 0%–12% of all individuals of these species lost mass during stopover. Although worm-eating warblers only had 32% of their foraging attacks in live vegetation, an additional 27% of their foraging attacks were in dead leaf clusters, which also had a very high proportion of spiders. Worm-eating warblers also had a high percent mass gain (7.3%), perhaps related to their preference for spiders and the relatively large size of prey items collected in the aerial leaf-litter micro-habitat. American redstarts, prairie warblers, and northern waterthrushes had 19%, 20%, and 25% spiders in their diet respectively. These species had mass increases during stopover ranging from 1.9% to 4%, and a range of 20–68% of all individuals of these species lost mass during stopover. It seems possible that species that were able to capitalize on the most abundant arthropod resource in live vegetation (spiders) were able to achieve the greatest mass gains.

Arthropod abundance also varied among tree species. In the Upper Keys, arthropods were most abundant in wild tamarind, stopper, and pigeon plum. In the Lower Keys, arthropods were most abundant in buttonwood, saffron plum, and stopper. Correspondingly, a high proportion of foraging observations were of migrants in wild tamarind, buttonwood, and stopper, providing additional evidence that to some degree migrants foraged where food was the most abundant. Due to the high abundance of arthropods in buttonwood and the large proportion of foraging observations of migrants in this tree species, perhaps future studies of the stopover ecology of migrants in the Florida Keys should place more attention on buttonwood-dominated plant communities.

Our foraging data suggest that our arthropod sampling may be more indicative of food availability for some species than others. Greater than 99% of all foraging attacks for ovenbirds and Swainson's warblers occurred on the ground; thus, we believe that our leaf-litter arthropod samples adequately reflect the foraging micro-habitat where these species acquired their prey. Five species made at least 65% of their foraging attacks on live vegetation (Table 25). Black-and-white warblers foraged almost exclusively on bark, and we did not sample arthropod abundance for this micro-habitat. Worm-eating warblers foraged on a mix of live vegetation, dead-leaf clusters, and bark. Therefore, our arthropod sampling is most likely not as direct reflection of food availability for this species as for others. However, our auxiliary sampling of dead leaf arthropods may lend insight into which taxa worm-eating warblers acquire in this micro-habitat. American redstarts made 39% of their foraging attacks in live vegetation and 40% in the air. Thus, it may be necessary to sample aerial insects to fully describe food availability for this species. In addition, 3 species made 15–23% of their foraging attacks on flower clusters of wild tamarind or dilly. We have also observed migrants foraging intensively in the flowers of sea grape and willow bustic during spring migration. It may be instructive to do some targeted sampling of arthropods in the flower clusters of common hammock trees to see which food resources migrants may be acquiring from this micro-habitat. In order to fully quantify food availability for all species of migrant insectivores in the Florida Keys, one would need to combine branch-clip sampling, leaf-litter sampling, bark-arthropod sampling, dead-leaf cluster arthropod sampling, and aerial insect sampling, with perhaps some sampling of arthropods in flower clusters. It may also be necessary to weight different arthropod-abundance sampling methods by the foraging substrates and foraging heights where different species of migrants focus their efforts (see Johnson 2000). Clearly, it is important to collect foraging data to appropriately frame interpretations of migrant food availability.

CONCLUSION

Many aspects of migratory bird stopover ecology, physiology, and behavior show tremendous variation in both time and space. Because of this variation, results and interpretations of any short-term descriptive study such as this one should be seen as preliminary. Annual variation in weather during or prior to migration (influencing food availability at a variety of spatial scales) can have a huge impact on numbers of birds captured at stopover sites and patterns in stopover ecology that are documented through mist-net studies. Several common properties of migrant stopover data present challenges for analysis and interpretation. Abundance, physiology, or behavior of migrants may vary according to species, age, sex, season, site, year, or many other factors. Interactions among these factors are likely and will be difficult to detect with small sample sizes. In addition, much stopover data is characterized by tremendous individual variation within groups, strong deviations from normal distributions, homogeneity of variances, and other assumptions of parametric statistics. Odd data distributions and multiple factors with interactions often place statistical burdens on studies of stopover biology that cannot be resolved due to the small sample sizes generated during short-term studies. Thus, statistically robust patterns in stopover biology may only be described after a number of years of sampling.

In addition, the lack of comparative data from a number of different sites and regions (and a lack of standardized data collection among sites) make stopover data difficult to interpret at the important scales of region, flyway, or range. As in all ecological studies, it is often difficult to understand if statistically significant results are biologically relevant. For example, small yet statistically significant differences between adult and immature body mass at arrival may be easy to detect due to large sample sizes for single-captures; yet, it is hard to know if these differences are as important to understand as differences in mass gain among age classes, which may be difficult to detect due to the small sample sizes of recapture data.

Also, several authors have attempted to evaluate the results of stopover studies at single sites, or a network of sites, within the conceptual framework of an optimal migration theory (Alerstam and Lindström 1990, Alerstam and Hedenstrom 1998, Shaub and Jenni 2000) or by feeding migrant physiology data into theoretical flight performance models (Woodrey and Moore 1997, Dunn 2002). To date, theoretical models of passerine migration have done a relatively poor job of accounting for individual variation in migrant condition data or explaining migrant behavior at stopover sites for a wide range of species. More descriptive studies of the behavioral ecology and physiology of migrants at stopover sites from a larger range of locations (spanning several years of data collection) are necessary both to inform and to test theoretical models. Hopefully, this basic description of the stopover biology of migrants in the Florida Keys will inspire future work in this direction.

Finally, given the reliance of most of the Nearctic-Neotropical migrant landbird community in the Florida Keys on arthropods, it is extremely important that this prey base is not severely reduced by the application of aerial adulticides for mosquito control, which do not discriminate between mosquitoes, spiders, beetles, or ants. Since application of larvicides such as BTI (*Bacillus thuringiensis israelensis*) can potentially reduce non-target arthropod abundance (Emmel 1988) these should be very carefully evaluated before application is allowed in the hardwood hammocks or buttonwood transition zone habitats of the Florida Keys. If land managers value the diversity and abundance of migrant songbirds on their properties, careful experimental studies should be conducted on the effects of mosquito control adulticides and larvicides on non-target arthropod abundance before application of these insecticides is allowed in the Florida Keys.

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Appendix A. Total number of mist-net captures per site/season combination, and for the entire project, for each bird species captured in hardwood hammocks of the Florida Keys, 2002–2004. Also listed are scientific names and the migratory status (M = through migrants and B = locally breeding) of all species captured. Totals for the Upper Keys in spring included all individuals captured in spring 2002 and spring 2003 combined.

Migratory status	**Common name**	**Scientific name**	**Upper Keys**		**Lower Keys**		**Total captures**
			Fall	**Spring**	**Fall**	**Spring**	
M	Acadian flycatcher	*Empidonax virescens*	1				1
M	American redstart	*Setophaga ruticilla*	70	66	76	43	255
M	Barn swallow	*Hirundo rustica*			5		5
M	Black-and-white warbler	*Mniotilta varia*	43	63	10	14	130
M	Blue-gray gnatcatcher	*Polioptila caerulea*	11		12	1	24
M	Bicknell's thrush	*Catharus bicknelli*		2			2
M	Blackburnian warbler	*Dendroica fusca*			1		1
M	Blue grosbeak	*Passerina caerulea*				1	1
B	Blue jay	*Cyanocitta cristata*	1	5			6
M	Blackpoll warbler	*Dendroica striata*		2		44	46
M	Black-throated blue warbler	*Dendroica caerulescens*	69	78	38	16	201
M	Broad-winged hawk	*Buteo platypterus*		1			1
M	Black-whiskered vireo	*Vireo altiloquus*		13	8	2	23
M	Blue-winged warbler	*Vermivora pinus*	1				1
M	Canada warbler	*Wilsonia canadensis*	1				1
M	Clapper rail	*Rallus longirostris*			1		1
M	Cape May warbler	*Dendroica tigrina*		4	1	5	10
B	Common ground dove	*Columbina passerina*			1		1
B	Common grackle	*Quiscalus quiscula*	1	16		3	20
M	Cooper's hawk	*Accipiter cooperii*			1		1
M	Connecticut warbler	*Oporornis agilis*		3			3
M	Common yellowthroat	*Geothlypis trichas*	27	101	67	43	238
M	Chestnut-sided warbler	*Dendroica pensylvanica*			4		4
M	Chuck-will's widow	*Caprimulgus carolinensis*	7		3		10
B	Eastern screech owl	*Otus asio*	1				1
M	Eastern wood-pewee	*Contopus virens*	1		3		4
M	*Empidonax* flycatcher (unknown sp.)	*Empidonax* sp.			1		1
M	Gray-cheeked or Bicknell's thrush	*Catharus* sp.		1			1
B	Great-crested flycatcher	*Myiarchus crinitus*	1	7	3		11
M	Gray-cheeked thrush	*Catharus minimus*	1	3	2	2	8
B	Gray kingbird	*Tyrannus dominicensis*			1	1	2
M	Gray catbird	*Dumetella carolinensis*	32	39	17	21	109
M	Hooded warbler	*Wilsonia citrina*	6	8	14	3	31
M	House wren	*Troglodytes aedon*	1				1
M	Indigo bunting	*Passerina cyanea*	1	2		17	20
M	Kentucky warbler	*Oporornis formosus*	6		3		9
M	Louisiana waterthrush	*Seiurus motacilla*		2		1	3
M	Magnolia warbler	*Dendroica magnolia*	1	5	3		9
M	Mourning dove	*Zenaida macroura*			1		1
M	Mourning warbler	*Oporornis philadelphia*			1		1
M	Myrtle warbler	*Dendroica c. coronata*				1	1

Appendix A. Continued.

Migratory status	Common name	Scientific name	Upper Keys		Lower Keys		Total captures
			Fall	Spring	Fall	Spring	
M	Nashville warbler	*Vermivora ruficapilla*			1		1
B	Northern cardinal	*Cardinalis cardinalis*	35	59		1	95
M	Northern parula	*Parula americana*	31	3	48	5	87
M	Northern waterthrush	*Seiurus noveboracensis*	50	23	53	5	131
M	Ovenbird	*Seiurus aurocapillus*	393	87	76	14	570
M	Painted bunting	*Passerina ciris*		4	1	1	6
M	Prairie warbler	*Dendroica discolor*	10	4	126	39	179
M	Prothonotary warbler	*Protonotaria citrea*	3		10	7	20
B	Red-bellied woodpecker	*Melanerpes carolinus*	2	9	21	1	33
M	Red-eyed vireo	*Vireo olivaceus*	6	1	29		36
B	Red-shouldered hawk	*Buteo lineatus*	1	1			2
B	Red-winged blackbird	*Agelaius phoeniceus*		1	16	4	21
M	Ruby-throated hummingbird	*Archilocus colubris*		1		1	2
M	Scarlet tanager	*Piranga olivacea*	1		1		2
M	Sharp-shinned hawk	*Accipiter striatus*			1		1
M	Summer tanager	*Piranga rubra*	1		1	2	4
M	Swainson's thrush	*Catharus ustulatus*	6		12	2	20
M	Swainson's warbler	*Limnothlypis swainsonii*	51	6		1	58
M	Tennessee warbler	*Vermivora peregrina*			8		8
M	Trail's flycatcher	*Empidonax alnorum/traillii*			3		3
M	Veery	*Catharus fuscescens*	1	5	5		11
B	White-crowned pigeon	*Columba leucocephala*			6	1	7
B	White-eyed vireo	*Vireo griseus*	10	25	4	1	40
M	Worm-eating warbler	*Helmitheros vermivorus*	134	35	9	12	190
M	Wilson's warbler	*Wilsonia pusilla*			1		1
M	Wood thrush	*Hylocichla mustelina*	1	1			2
M	Western palm warbler	*Dendroica p. palmarum*	1	6	42	201	250
M	Yellow-brested chat	*Icteria virens*	1		1		2
M	Yellow-billed cuckoo	*Coccyzus americanus*	3	1	1	2	7
M	Yellow-bellied flycatcher	*Empidonax flaviventris*	1				1
B	Yellow-shafted flicker	*Colaptes a. auratus*	1	1			2
M	Yellow-throated warbler	*Dendroica dominica*			1	2	3
B	Yellow warbler	*Dendroica petechia*			7		7
Total captures			1,026	694	761	520	3,001
Total migrant species			973	570	716	501	2,760
Total breeding species			53	124	45	19	241

Appendix B. Scientific names for all plant species mentioned in this report.

Common name	Scientific name
Black bead	*Pithecullobium guadalupense*
Black mangrove	*Avicennia germinans*
Black torch	*Erithalus fruticosa*
Buttonwood	*Conocarpus erectus*
Crabwood	*Ateramnus lucidus*
Dilly	*Manilkara bahamensis*
Florida thatch palm	*Thrinax radiata*
Gumbo limbo	*Bursera simaruba*
Jamaica dogwood	*Piscidia piscipula*
Joewood	*Jacquinia keyensis*
Marlberry	*Ardisia escallonioides*
Pigeon plum	*Coccoloba diversifolia*
Poisonwood	*Metopium toxiferum*
Red mangrove	*Rhizophora mangle*
Saffron plum	*Bumelia celastrina*
Sea grape	*Coccoloba uvifera*
Spanish stopper	*Eugenia foetida*
White stopper	*Eugenia axillaris*
Strangler or short-leaf fig	*Ficus* sp.
Strongbark	*Bourreria succulenta.*
Torchwood	*Amyris elemifera*
White mangrove	*Laguncularia racemosa*
Wild lime	*Zanthoxylum fagara*
Wild tamarind	*Lysiloma latisiliquum*
Willow bustic	*Bumelia salicifolia*

Appendix C. Recapture data for all species captured at least once during migration in hardwood hammocks of the Florida Keys, 2002–2004.

Common Name	Total captures	Total recaptures	Percent recaptured	Recaptures (%) with MSL = 1	Recaptures (%) with MSL > 1	Recaptures (*n*) with MSL > 1
Acadian flycatcher	1	1	100.0	0.0	100.0	1
American redstart	255	14	5.5	28.6	71.4	10
Barn swallow	5	0	0.0			
Black-and-white warbler	130	13	10.0	30.8	69.2	9
Blue-gray gnatcatcher	24	2	8.3	50.0	50.0	1
Bicknell’s thrush	2	0	0.0			
Blackburnian warbler	1	0	0.0			
Blue grosbeak	1	0	0.0			
Blackpoll warbler	46	3	6.5	33.3	66.7	2
Black-throated blue warbler	201	19	9.5	68.4	31.6	6
Broad-winged hawk	1	0	0.0			
Black-whiskered vireo	23	3	13.0	0.0	100.0	3
Blue-winged warbler	1	0	0.0			
Canada warbler	1	0	0.0			
Clapper rail	1	0	0.0			
Cape May warbler	10	1	10.0	0.0	100.0	1
Cooper’s hawk	1	0	0.0			
Connecticut warbler	3	0	0.0			
Common yellowthroat	238	9	3.8	55.6	44.4	4
Chestnut-sided warbler	4	2	50.0	100.0	0.0	0
Chuck-will’s widow	10	0	0.0			
Eastern wood-pewee	4	0	0.0			
Unknown empidonax species	1	0	0.0			
Gray-cheeked or Bicknell’s thrush	1	0	0.0			
Gray-cheeked thrush	8	1	12.5	0.0	100.0	1
Gray catbird	109	0	0.0			
Hooded warbler	31	3	9.7	66.7	33.3	1
House wren	1	0	0.0			
Indigo bunting	20	3	15.0	100.0	0.0	0
Kentucky warbler	9	3	33.3	66.7	33.3	1
Louisiana waterthrush	3	1	33.3	0.0	100.0	1
Magnolia warbler	9	0	0.0			

Appendix C. Continued.

Common Name	Total captures	Total recaptures	Percent recaptured	Recaptures (%) with MSL = 1	Recaptures (%) with MSL > 1	Recaptures (*n*) with MSL > 1
Mourning dove	1	0	0.0			
Mourning warbler	1	0	0.0			
Myrtle warbler	1	0	0.0			
Nashville warbler	1	1	100.0	0.0	100.0	1
Northern parula	87	11	12.6	36.4	63.6	7
Northern waterthrush	131	10	7.6	20.0	80.0	8
Ovenbird	570	56	9.8	35.7	64.3	36
Painted bunting	6	0	0.0			
Prairie warbler	179	12	6.7	16.7	83.3	10
Prothonotary warbler	20	6	30.0	16.7	83.3	5
Red-eyed vireo	36	1	2.8	0.0	100.0	1
Ruby-throated hummingbird	2	0	0.0			
Scarlet tanager	2	0	0.0			
Sharp-shinned hawk	1	0	0.0			
Summer tanager	4	0	0.0			
Swainson’s thrush	20	3	15.0	33.3	66.7	2
Swainson’s warbler	58	11	19.0	36.4	63.6	7
Tennessee warbler	8	1	12.5	0.0	100.0	1
Trail’s flycatcher	3	0	0.0			
Veery	11	0	0.0			
Worm-eating warbler	190	39	20.5	17.9	82.1	32
Wilson’s warbler	1	0	0.0			
Wood thrush	2	0	0.0			
Western palm warbler	250	30	12.0	33.3	66.7	20
Yellow-breasted chat	2	0	0.0			
Yellow-billed cuckoo	7	0	0.0			
Yellow-bellied flycatcher	1	0	0.0			
Yellow-throated warbler	3	0	0.0			

Appendix D. Seasonal and site-specific sample sizes for fecal samples for all migrant species captured in hardwood hammocks of the Florida Keys, 2002–2004.

	Upper Keys		Lower Keys		Sites combined		Seasons combined		
Common name	**Fall**	**Spring**	**Fall**	**Spring**	**Fall**	**Spring**	**Upper Keys**	**Lower Keys**	**Total**
American redstart	9	11	13	11	22	22	20	24	44
Black-and-white warbler	16	12	0	1	16	13	28	1	29
Blue-grey gnatcatcher	5	0	0	0	5	0	5	0	5
Blackpoll warbler	0	0	0	10	0	10	0	10	10
Black-throated blue warbler	12	10	4	5	16	15	22	9	31
Common yellowthroat	0	11	5	10	5	21	11	15	26
Gray-cheeked thrush	0	0	0	3	0	3	0	3	3
Gray catbird	10	4	0	2	10	6	14	2	16
Hooded warbler	0	0	5	0	5	0	0	5	5
Kentucky warbler	3	0	0	0	3	0	3	0	3
Northern parula	15	0	11	0	26	0	15	11	26
Northern waterthrush	9	0	13	0	22	0	9	13	22
Ovenbird	31	9	31	2	62	11	40	33	73
Prairie warbler	5	0	26	10	31	10	5	36	41
Prothonotary warbler	2	0	4	0	6	0	2	4	6
Red-eyed vireo	5	0	9	0	14	0	5	9	14
Swainson’s thrush	0	0	4	2	4	2	0	6	6
Swainson’s warbler	12	0	0	0	12	0	12	0	12
Worm-eating warbler	29	11	0	0	29	11	40	0	40
Western palm warbler	0	0	0	8	0	8	0	8	8

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