STOPOVER ECOLOGY OF THE BLACKPOLL WARBLER, *Dendroica striata*, DURING SPRING MIGRATION ON THE COASTAL PLAIN OF VIRGINIA

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This project represents the culmination of a life long fascination with birds and birding. I remember seeing my first Blackpoll in my parent's backyard. It was the spring of 1984. Decades later I continue to be in awe of the amazing journey of North America's longest distance migrant.

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ABSTRACT

High quality stopover sites along the migratory path are critical to migrant songbird populations because arrival timing on the breeding grounds impacts breeding success. Both sexes gain a reproductive advantage by arriving on the breeding territory with extra fat reserves (Sandberg and Moore 1996) obtained during stopovers. During the spring, Blackpoll Warblers, *Dendroica striata*, stopover in large numbers on Virginia's coastal plain (Burleigh 1934). In this study, I set out to examine the energetic value of the region to migrant Blackpoll Warblers by examining the geographic patterns of migration, generalizing foraging ecology of Blackpoll Warblers, and determining whether this region represents a source of energy for migrants. It appears Blackpoll Warblers are responding to available energy resources, and that this region represents a source of energy for Blackpoll Warblers during the spring migration.

GENERAL INTRODUCTION

INTRODUCTION

Bird migration is closely tied to seasonal food resources (Alerstam 1990). The annual surge in insect populations across the northern temperate zone provides an enormous food resource for breeding songbirds. Numerous species have evolved to take advantage of this resource, by migrating from the tropics to breed in nearctic regions (Alerstam 1990). There are tradeoffs associated with this migration. Instead of remaining in a harsh climate throughout the year, Neotropical migrants breed in areas with abundant arthropod resources, and winter in areas of mild climate and relatively constant food source. However, migrants encounter unpredictable wind, weather, and food conditions along the migratory pathway.

Blackpoll Warblers breed near the ground in stunted spruce forests and alder thickets across the northern tier of Alaska and Canada, and at high elevations in the Canada's Maritime Provinces and New England. In the winter, the population resides along the edges of lowland tropical forests in Columbia, Peru, Bolivia, and Brazil (Curson et al. 1994). Annual migration for Blackpoll Warblers can exceed 16,000 km roundtrip (Nesbit et al., 1995).

The route of fall migration has been the subject of much debate in the last 40 years. Blackpoll Warblers have been found to stage in large numbers in New England and the Canadian Maritime Provinces, storing enormous fat loads for several weeks. The birds then depart with favorable winds out over the Atlantic (Nesbit et al 1963, McNair and Post 1993, Nesbit et al. 1995). This route is currently accepted as the standard migratory path (Hunt and Eliason 1999), but there has been debate as to whether it is followed by the bulk of the population (Murray 1989). Blackpolls have been shown to be physiologically capable of completing this migratory route (Nesbit et al. 1995), and birds have been found along the proposed trajectory on the island of Bermuda (Nesbit 1963). Additionally, numerous offshore sightings (Cherry et al. 1985) substantiate the route. The spring migration route has not been well studied.

High quality stopover sites along the migratory path are critical to migrant songbird populations because arrival timing on the breeding grounds impacts breeding success. For males, arrival timing is directly linked to productivity (Klomp 1970), and it is important that they return to the breeding area during a specific window of time. The most productive individuals are the ones that have good food availability at the time of nesting, and have nests hatching at the time of greatest food abundance (Perrins 1970). In order to achieve hatching within this window of time, it is important that males arrive early enough to establish and defend territories, and attract mates (Francis and Cooke 1986, Gauthreaux 1982). Females are not under extreme competition for mates and territories, but depend equally on high quality stopover sites, because they face high energetic costs associated with egg production. Early female arrival is directly correlated with breeding success as well (Murphy 1986). Both sexes gain a reproductive advantage by arriving on the breeding territory with extra fat reserves (Sandberg and Moore 1996) obtained during stopovers.

During spring migration, stopover sites are critical to Blackpoll Warblers. An individual may stop in a location in an attempt to fulfill energetic requirements (Moore et al. 1995), though exact mechanisms for fine scale site selection are not known. Larval arthropods are thought to provide the best source of energy for migrants because of their high water content and caloric value (Graber and Graber 1983). It is unlikely that individuals that do not meet metabolic requirements for migration will survive the trip.

The spring stopover ecology of migrant warblers has been well studied along the Gulf of Mexico, where migrants make landfall and immediately begin utilizing arthropod resources to replenish fat lost during the crossing. Blackpoll Warblers, following spring trans-Gulf migration, had an average stopover length of 2.4-3.3 days (Kuenzi and Moore 1991). Migrants that stopped over for longer, gained more mass (Moore and Kerlinger 1987).

Previous work with Blackpoll Warblers during migratory stopover indicates that the species tolerates a wide range of habitats. In the Dominican Republic, Blackpoll Warblers were found in low mangrove thickets, foraging on larval arthropods (Latta and Brown 1999). In North Carolina, they were found in a mix of thickets, hardwood forests, and pine stands (Parnell 1969), and in Maryland they were found along mature hardwood forest edges, and in park-like settings with little or no understory (Morse 1979).

During the spring, Blackpoll Warblers stopover in large numbers on Virginia's coastal plain (Burleigh 1934). Along the coastal plain of Virginia, their arrival tends to coincide with annual spring leaf onset in deciduous trees (per ob.). Leaf onset is determined by a combination of factors including latitude, average spring temperatures, rainfall, and proximity to the coast. Trees on the Coastal Plain of Virginia will leaf before those in the Piedmont and in points further north. Consequently, it is possible that there may be a large supply of arthropods on the coastal plain during the time that Blackpoll Warblers are passing through the region.

Additionally, an overwater spring migratory route has been suggested for Blackpoll Warblers (Hunt and Eliason 1999). However, it is not known whether Blackpoll Warblers stopping over along Virginia's coastal plain have come directly across the Atlantic from the Antilles, or have arrived by using an overland route across the Southeastern US.

Objectives

Considering the abundance of the species in the region and previously described stopover patterns, I set out to examine the energetic value of the region to migrant Blackpoll Warblers. The objectives of this study were: (1) examine the geographic patterns of migration by looking at arrival dates, dates of peak density, and dates of departure at each of the three regions of the coastal plain, (2) to generalize foraging ecology of Blackpoll Warblers by describing foraging tactics used and characteristics of the prey the birds selected, (3) to determine whether this region represents a source of energy for migrants, by describing overall daily intake rates, and comparing those with field metabolic expenditure, and, lastly, (4) to lend support to the notion of an over-water spring migration route with a projected landfall for migrants near the outer coastal plain of Virginia.

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EFFECT OF GEOGRAPHY ON THE MIGRATION PHENOLOGY OF THE BLACKPOLL WARBLER IN COASTAL VIRGINIA

INTRODUCTION

For many bird species, the timing of arrival on the breeding grounds has a direct influence on reproductive performance (Moore and Kerlinger 1987). Individuals that arrive early are able to claim the highest quality breeding territories (Francis and Cooke 1986), attract mates more readily (Gauthreaux 1982), and often produce more offspring (Moore and Yong 1991). For species that migrate over long distances, "decisions" made en route presumably reflect both the potential benefits of early arrival and the risks associated with premature migration. Individuals that migrate too late may suffer a competitive disadvantage upon arrival. Individuals that migrate too early may face inhospitable conditions along the way that may have an adverse impact on their physical readiness for breeding or even survivorship (Francis and Cooke 1986). For this reason, the timing of arrival on specific staging areas may be just as essential to successful migration as the timing of ultimate arrival on the breeding grounds. For many insectivorous birds, the northward advance of spring migration has been presumed to shadow the moving front of spring and associated emergence of insect prey (Gauthreaux 1982).

The Blackpoll Warbler (Dendroica striata) is one of the most northerly breeding warblers in North America. Within many regions, this species is also one of the latest spring migrants (Hunt and Eliason 1999). The latitudinal pattern of spring arrival dates was described for Blackpoll Warblers early in the 20th century (Cooke 1915). Migrants begin to appear in the southeastern U.S. in mid to late April. The migration front advances northward at a rate of approximately 50 km per day until reaching the northern U.S when the advancement accelerates rapidly. Lincoln (1935) correlated isochronal migration lines with isotherms and suggested that Blackpolls were tracking the advancement of spring.

Although latitude has a dominant influence on broad-scale temperature patterns, numerous other factors such as elevation or land cover may contribute to local thermal profiles. In Virginia, an east-west climate gradient occurs across the coastal plain due to the moderating influence of the Atlantic Ocean. On average, the outer coastal plain receives 3.8 cm more annual rainfall and experiences an annual temperature that is 2° F higher when compared to the inner coastal plain (http://www.nws.noaa.gov). This relatively steep climate gradient occurs over a distance of only 170 km and translates into a detectable difference in the timing of leafout. The extent to which spring migrants respond to this gradient has not been investigated. The purpose of this study was to examine the influence of geographic position within this coastal gradient on the migration phenology for the Blackpoll Warbler.

METHODS

During the spring of 2000, nine 30-ha spot-mapping grids were used to investigate the distribution and arrival time of Blackpoll Warblers during spring migration on the Coastal Plain of Virginia. Three replicate grids were chosen within the outer Coastal Plain (approximately 76.1 long. 36.8 lat.), the middle Coastal Plain (approximately 76.7 long. 37.3 lat.), and the inner Coastal Plain (approximately 77.4 long. 37.5 lat.). All grid sites were large residential areas that contained hardwood-dominated forests of middle age (40-80 yr age class) and extensive road systems. Forest sites were chosen for study based on stand age and canopy composition. All sites contained hardwood-dominated overstories. Common canopy species included various oaks (Quercus spp.), hickories (Carya spp.), red maple (Acer rubrum), American beech (Fagus grandifolia), and tulip poplar (Liriodendron tulipifera).

Spot-mapping grids were established between 1 April and 9 April, 2000. Grids were rectangular, 30-ha plots measuring 385 m by 800 m. We conducted censuses of grids between 17 April and 3 June, 2000. Each grid was surveyed twice within a 7 day time block. We surveyed all sites within a geographic region (e.g. outer coastal plain) during the same day. Working within three-day time blocks, we randomly surveyed among the regions. For example, in a three-day time block, the outer coastal plain sites were surveyed on day one, the middle coastal plain sites were surveyed on day two, and the inner coastal plain sites were surveyed on day three. On a given survey day, the three 30-ha plots within the region were also randomly surveyed. Surveys of individual sites took between 1 and 1.5 hrs to complete. Surveys commenced 0.5 hr after sunrise and were completed by 13:00. We surveyed all sites 14 times during the study period.

Spot-mapping grids were surveyed by walking slowly along roadways and plotting all Blackpoll Warblers detected, as accurately as possible, on a detailed grid map. A large majority of birds were detected by song. These birds were located with 7X35 power binoculars and plotted. This survey technique resulted in a heavy bias toward males.

Blackpoll density and migration phenology were compared using a one-way ANOVA with geographic location as the grouping variable. Peak bird density was standardized to birds/10 ha. Differences in phenology were examined using arrival and peak dates as dependent variables. Arrival date for each site was considered to be the date on which 10% of the birds had been detected for the season. This parameter was used instead of the date of first detection to reduce the influence of outliers.

RESULTS

In coastal Virginia, Blackpoll Warbler migration was nearly confined to the month of May. The first migrant was observed on 29 April and the last on 1 June. More than 90% of all birds included were observed in the 15-d period between 5 and 20 May. Considering all study areas together, migration peaked around mid May with a study-wide average of 4.6 birds/10 ha. Peak densities did not differ between geographic areas (one-way ANOVA, $F = 2.25$, $P > 0.05$).

Migration phenology varied with location across the coastal plain (Figure 1). Birds using the outer coastal plain had an earlier migration compared to those using the middle and inner coastal plain. Arrival dates for Blackpoll Warblers varied with geography. Migrant Blackpolls were first detected on the outer coastal plain followed by the more inland regions. The average date on which 10% of the individuals had been detected for the season (termed "arrival date") was significantly different (one-way ANOVA, F-statistic = 20.80, $P < 0.05$) between geographic areas.

As with arrival dates, on average, Blackpoll Warbler densities varied with date across the coastal plain. Blackpoll numbers peaked on the outer coastal plain on 7 May, on the middle coastal plain on 14 May, and on the inner coastal plain on 17 May. This 10-d difference in the migration peak across the study area was statistically significant (one-way ANOVA, F-statistic = 35.15, $P < 0.005$). However, the time difference across the coastal plain was much shorter for arrival times compared to peak dates. The average arrival date for the outer coastal plain was 5 May compared to 10 May for the inner coastal plain.

Figure 1. Patterns in migration phenology for Blackpoll Warblers on the coastal plain of Virginia. Outer, middle, and inner refer to respective regions of the coastal plain. Dates presented indicate the beginning day of each survey block. Bars represent average densities among three spatial replicates.

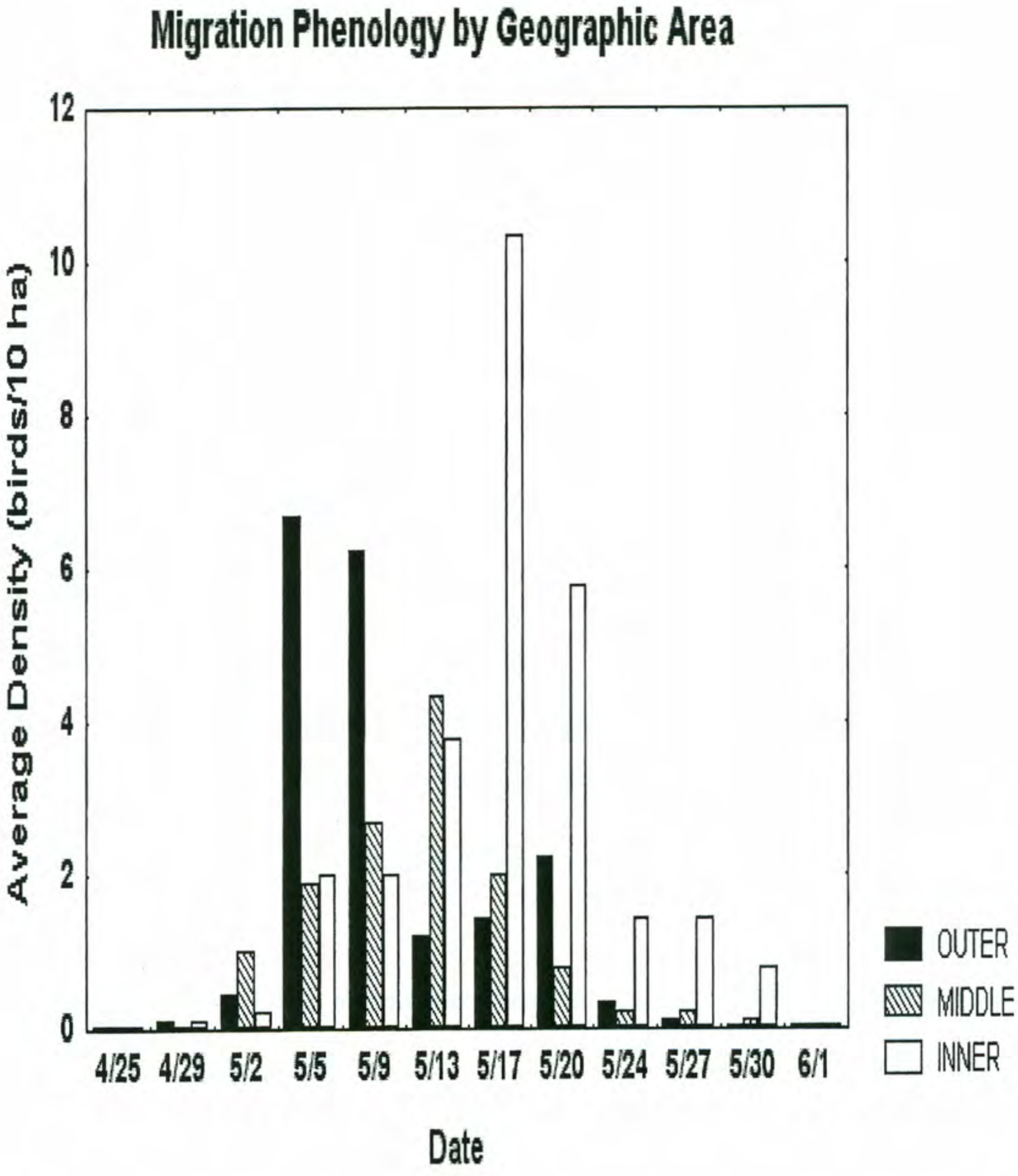
Migration Phenology by Geographic Area
Average Density (birds/10 ha)
12
10
8
6
4
2
0
4/25
4/29
5/2
5/5
5/9
5/13
5/17
5/20
5/24
5/27
5/30
6/1
Date
OUTER
MIDDLE
INNER

Figure 1.

DISCUSSION

Migrant Blackpoll Warblers that reach the mid-Atlantic region appear to pass through the outer coastal plain earlier than the inner coastal plain. This pattern, in conjunction with the climate gradient across this region, is consistent with the notion that birds are moving north in step with the emergence of insect prey. How Blackpolls are able to track this resource on such a fine temporal and spatial scale remains unclear.

Previous discussions of Blackpoll migration through Southeastern North America have indicated a broad-front movement that is advancing northward at a rate of approximately 50 km per day (Cooke 1915, Lincoln 1935). Although it is possible that birds are arriving broadly throughout the coastal plain and then differentially settling in specific geographic areas at different times, this seems unlikely. Birds not only arrived in geographic areas at different times, but they peaked at different times. In order for the proposed northerly movement pattern to be consistent with the observed patterns in phenology, the leading edge of the migration front would have to tilt strongly north along the coast such that birds moving along the outer coastal plain arrive and pass through earlier.

The idea that both northwestern and northeastern breeding populations are entering the continent via a route through the extreme southeast implies that the populations are diverging in mid-continent and then advancing toward their respective breeding areas (Lincoln 1935). It is also possible that these two populations are arriving in North America using distinctly different routes. Blackpolls that make up the eastern breeding population may be making an over-water flight from the Caribbean directly to the mid-Atlantic. As has been shown in fall migration, Blackpolls are capable of long oceanic flights (Nesbit 1970). In coastal Virginia, Blackpoll Warblers reached average peak densities approaching or exceeding 1 bird/ha. Bird densities fall off dramatically moving west beyond the coastal plain (Kain 1987). Limited observations just to the south in coastal North Carolina suggest that Blackpolls are much less common during spring migration (LeGrand 1975). If Blackpolls are actually making landfall in coastal Virginia, the difference in phenology observed may represent an advancement front that is moving inland from the coast rather than northward from the southeast. Further work is needed to determine the specific route taken to reach this staging area. Such information would provide further insight into the role that the mid-Atlantic region plays in the life cycle of this species.

Regardless of how Blackpoll Warblers arrive in coastal Virginia, birds appear to be able to respond to the steep climate gradient and to take advantage of the early coastal warming. Birds that stage on the outer coastal plain may be able to gain a competitive advantage. By migrating earlier these birds may arrive earlier on the breeding grounds or may achieve breeding readiness at an earlier date.

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FORAGING ECOLOGY OF BLACKPOLL WARBLERS DURING SPRING MIGRATION WITHIN THE MID-ATLANTIC

INTRODUCTION

More than one half of all North American land birds migrate from breeding areas in temperate latitudes to winter areas in Mexico, Central America, the Caribbean, and South America (Keast 1980). Such long-distance movements may be very energetically demanding (Berthold 1975, Blem 1980). The vast majority of nearctic-neotropical migratory birds are physically incapable of carrying enough energy to complete non-stop flights between breeding and winter areas (Nisbet et al. 1963, Berthold 1975, Dawson et al. 1983., Pettersson and Hasselquist 1985). To overcome this problem, migrants make periodic stops en route to replenish energy reserves. Once in stopover areas, migrants encounter unfamiliar landscapes and uncertain conditions. Individuals that are able to successfully negotiate these conditions presumably increase their probability of successfully completing migration. Since successful migration is a prerequisite for future breeding, choices about stopover areas, as well as, decisions made within stopover areas have profound fitness consequences for migrants.

One of the most important characteristics of stopover areas is the quality of available habitats. In order for migrants to successfully complete migration, individuals must locate geographic areas that provide a net energy gain. These so-called energy sources allow birds to accumulate the energy needed to make advances toward breeding areas. Migrants should avoid geographic areas where they can not break even energetically. Such so-called energy sinks have a negative impact on migrant condition and may delay migration. For many species breeding in north temperate latitudes, the timing of arrival on the breeding grounds has a direct influence on reproductive performance (Gauthreaux 1982). Individuals that arrive early are able to claim the highest quality breeding territories (von Haartman 1968, Slagsvold 1976), and attract mates more readily (Francis and Cooke 1986), and have greater breeding success (Eliason 1986).

Relatively little information is currently available on the distribution of areas where land bird migrants accumulate the energy needed to fuel migration. Equally little information is available on how migrants interact with habitats in order to extract needed energy. Such information is important both to the achievement of a broader understanding of the energetic underpinnings of migration and to the conservation of stopover habitats. The focus of this study is to evaluate energy budgets and to describe the foraging ecology of male Blackpoll Warblers within spring stopover habitats in coastal Virginia.

METHODS

During the course of a broader ecological investigation of migrant Blackpoll Warblers, behavioral observations were made of individuals within forested habitats. In 1999, observations of migrant Blackpolls were made within a large forested patch in Richmond, Virginia. In 2000, this investigation was expanded to include nine, 30-ha spot-mapping grids selected within the mid-Atlantic Coastal Plain (one grid included the forested block used in 1999).

Forest sites were chosen for study based on stand age and canopy composition. All sites contained hardwood-dominated overstories that appeared to be of middle age (40-80 yr age class). Common canopy species included various oaks (Quercus spp.), hickories (Carya spp.), red maple (Acer rubrum), American beech (Fagus grandifolia), and tulip poplar (Liriodendron tulipifera). Three replicate grids were chosen within the outer coastal plain of Virginia (approximately –76.14 long. 36.84 lat.), the middle coastal plain (approximately –76.71 long. 37.27 lat.), and the inner coastal plain (approximately –77.44 long. 37.54 lat.). Spot-mapping grids were established between 1 April and 09 April, 2000. Grids were rectangular, 30-ha plots measuring 385 m by 800 m. All grid sites were large residential areas that contained an extensive road system. Based on observations made within the coastal plain in 1999, residential areas provide ideal stopover habitats for Blackpoll Warblers because of their broken canopies with extensive edge.

Individual birds were observed to quantify time budgets. Observers walked slowly through study areas until an individual was encountered. Focal birds were followed for a period of 2 min and observed using 7X35 power binoculars. Every effort was made to maintain contact with birds while minimizing disturbance. All observations were recorded in real time on a micro-cassette recorder and later transcribed using a stopwatch. Behaviors were classified into 4 categories: (1) foraging, (2) inactive, (3) singing, and (4) chasing. Birds were considered to be foraging if they were actively searching through vegetation or pursuing prey. Birds that were simply perched and not engaged in other activities were classified as inactive. Individuals that were aggressively pursuing other birds were classified as chasing. Behavioral observations were made between 5 May and 28 May in 1999 and between 1 May and 3 June, 2000. During both years, observations were made from sunrise to 11:30.

In order to quantify foraging behavior, additional information was collected during foraging bouts. Foraging data included foraging tactic, foraging success, prey type, prey size, and handling time. Foraging tactics considered here include leaf gleaning, branch gleaning, picking/probing, hawking, and hovering (terminology used here follows Robinson and Holmes 1982). A bird was considered to be successful performing a specific foraging tactic if it captured a single prey item. All prey items observed fell into four taxonomic categories including adult Dipterans, adult Lepidopterans, larval Lepidopterans (caterpillars), and Arachnids. Prey size was estimated in intervals of ½ bill length (approximately 5 mm). Handling time was considered to be the time interval between prey capture and prey ingestion or escape.

We used several published relationships to convert observed prey intake to energy gain. We first calculated the dry weight for individual prey items using relational equations derived in Sample et al. 1993. These relationships allow for the estimation of dry weight based on insect size according to the equation $\log(y) = b + a \log(x)$ where y = weight (gm) and x = body length (mm). Separate equations were used for each of the prey taxa observed. Dry weights for all prey items consumed during each 2-min observation period were then summed to yield a total intake weight per period. Total dry weights were then converted to metabolizable energy using relationships derived in Nagy 1987. This relationship estimates that 18.0 kj of metabolizable energy are contained in 1 gm dry weight of insects for a passerine bird. This value is more appropriate than the pre-ingestion energy content of prey because it represents actual energy gain. Energetic estimates for 2-min observation periods were expanded to a daily rate based on the average day length (853 min) during the study period. This approach assumes that migrant Blackpoll Warblers are foraging at a constant rate throughout the day.

A field metabolic rate (FMR) was calculated and used to estimate the energetic requirements of a Blackpoll Warbler during migration. FMR was calculated using an equation relating body weight and FMR for a small passerine. The equation $\log(y) = 0.949 + 0.749 \log(x)$ where y = FMR and x = body weight was used along with a weight of 12.6 gm for an average Blackpoll Warbler.

RESULTS

Time budgets were computed for 176 male Blackpoll Warblers observed for a total of 21,120 s (Figure 1). Sample sizes were 25 and 151 for, 1999 and 2000 seasons, respectively. On average, foraging activity accounted for the largest portion (55.7%) of the overall time budget followed by inactive perching (20.5%) and singing (17.5%). Chasing (3.4%) and prey handling (2.8%) accounted for the balance of the observation time. Other activities observed included overt aggression and preening. The composition of time budgets did not differ between years ($X2 < 1.0$, $P > 0.05$). Elements of the time budget were not always discreet or mutually exclusive. For example, foraging activity was frequently broken up by singing bouts or chasing behavior.

The composition of time budgets varied considerably between individuals. Only 50 individuals (28.4%) exhibited all 5 activities during the 2-min observation period. However, the majority of individuals (78.4%) engaged in at least 4 activities while under observation. None of the birds spent the entire observation period engaged in a single activity. Chasing was the least common behavior observed (51.1% of individuals observed) followed by prey handling (73.3%), inactive perching (88.6%), and singing (92.6%). Foraging was the most widespread activity with nearly 100% of individuals spending at least some portion of their time searching for food. According to time spent, foraging was the dominant activity in 76.7% of all time budgets.

Figure 1. Mean time budget of 176 male Blackpoll Warblers during migratory stopover on the coastal plain of Virginia. Activities are shown in seconds spent during a 2-minute observation period. Shaded areas indicate SE. Whiskers indicate SD.

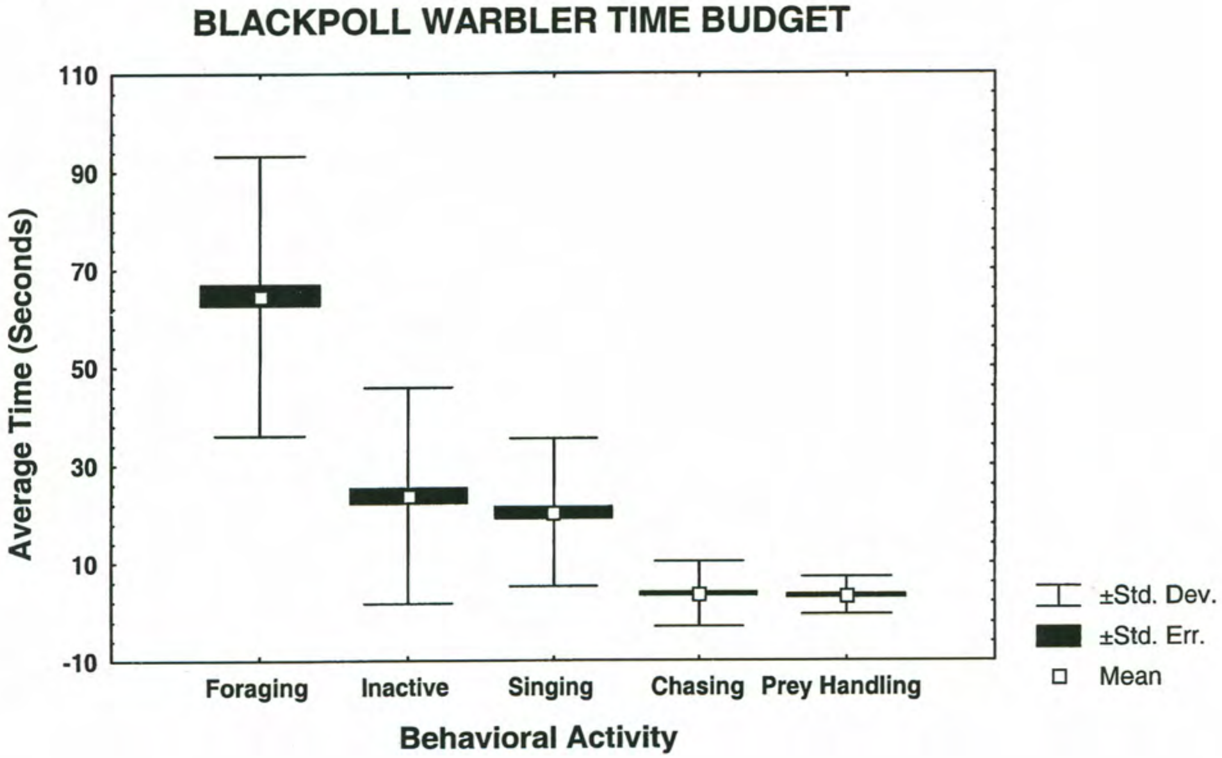
BLACKPOLL WARBLER TIME BUDGET
Average Time (Seconds)
110
90
70
50
30
10
-10
Foraging
Inactive
Singing
Chasing
Prey Handling
Behavioral Activity
±Std. Dev.
±Std. Err.
Mean

Figure 1.

Migrant Blackpoll Warblers used 5 primary foraging tactics during stopover in Virginia. Leaf gleaning was the most commonly used tactic representing the largest portion of both bouts observed and time spent (Table 1). Blackpolls physically searched through large numbers of leaves in search of prey. Leaf gleaning was followed in importance by branch gleaning, probing/picking, hawking, and hover gleaning. Aerial pursuit of prey was not a dominant foraging tactic and did not occur over long distances. Hover gleaning was typically used to extract prey from leaves that were not reachable from branches.

Over the course of the study period, 121 male Blackpoll Warblers were observed to take 382 prey items. Common prey items included caterpillars (56.5%), adult dipterans (36.6%), moths (6.5%), and arachnids (0.3%). The distribution of prey sizes was highly skewed with items less than ½ bill length representing a large majority (Figure 2). Most of these small prey were larval Lepidopterans and adult Dipterans. The largest prey items taken were adult Lepidopterans. Blackpolls seemed to have difficulty catching and handling larger prey items. Average handling time for 0-5mm length prey was <1.0 sec, while prey of 16-20mm length had an average handling time > 10.0 sec. Larger prey were also more likely to escape.

There was a general relationship between prey taxa and foraging tactic (Table 2). Most of the caterpillars were taken by gleaning while searching at close range through leaves and twigs. Adult moths were taken opportunistically by hawking as they flew near a foraging Blackpoll. Dipterans were taken using all foraging tactics. A large portion of

TABLE 1. Relative frequency and time spent for different foraging tactics.

Foraging Tactic	**Foraging Bouts (N)**	**Foraging Bouts (% of total)**	**Foraging Time (sec)**	**Foraging Time (% of total)**
Leaf Gleaning	485	38.0	5,890	54.9
Branch Gleaning	387	30.3	3,035	28.3
Picking/Probing	230	18.0	1,213	11.3
Hawking	114	8.9	365	3.4
Hovering	61	4.8	224	2.1
Total	**1,277**		**10,727**	

Figure 2. Size classes (in 5mm increments) of arthropod prey taken by Blackpoll Warblers during migratory stopover (N=382).

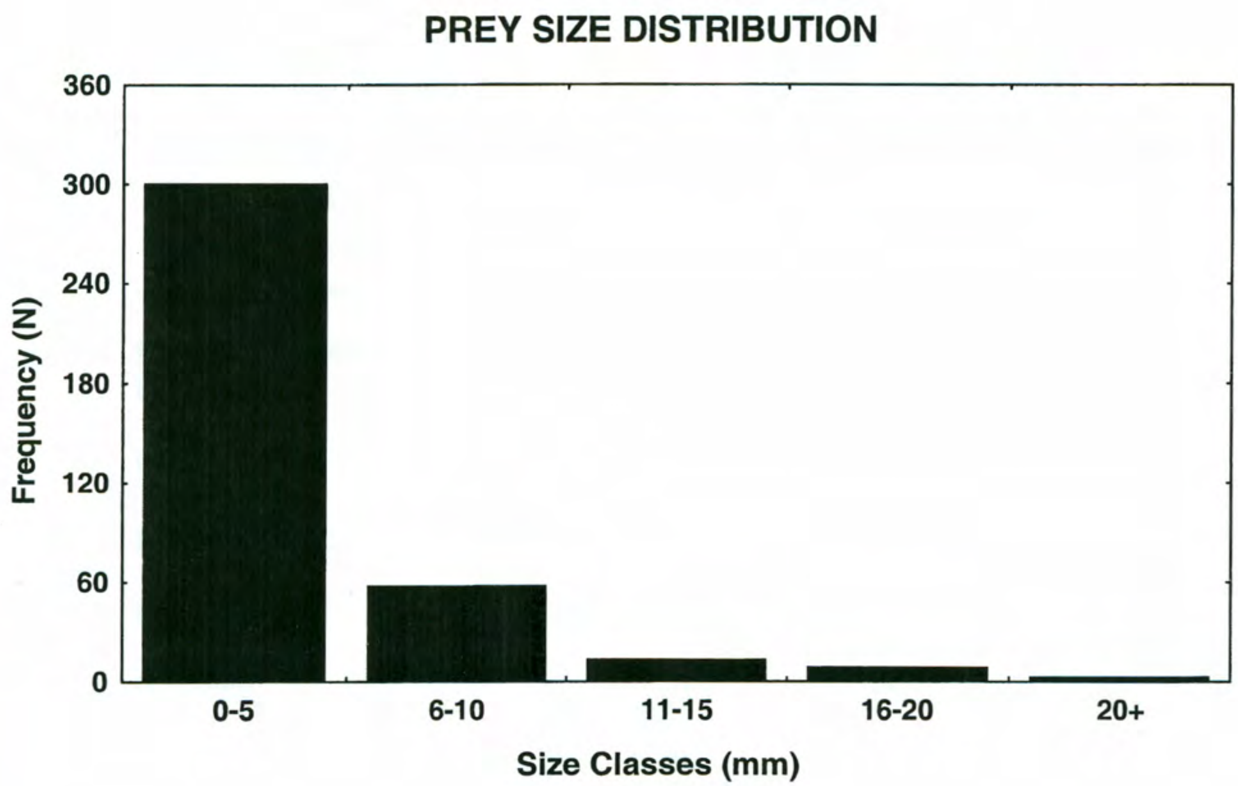
PREY SIZE DISTRIBUTION
360
300
240
180
120
60
0
Frequency (N)
0-5
6-10
11-15
16-20
20+
Size Classes (mm)

Figure 2.

TABLE 2. Foraging tactics and taxa of prey items used by Blackpoll Warblers. Values indicate number of prey items taken.

Foraging Tactics	Lepidopteran Larvae	Lepidopteran Adult	Dipteran	Arachnid
Leaf Gleaning	144	0	32	0
Branch Gleaning	32	0	16	0
Picking/Probing	38	0	11	1
Hawking	0	25	63	0
Hovering	2	0	18	0
Total	**216**	**25**	**140**	**1**

these were taken using repeated flights into swarms near the canopy surface. Others were taken directly from the substrate surface.

The relationship between foraging tactic and prey taxa leads to an unexpected pattern in prey capture rate and energy intake rate (Table 3). Although leaf gleaning, branch gleaning, and picking/probing were the dominant foraging tactics (collectively representing 86.3% of foraging bouts and 94.5% of time spent foraging), they provided the lowest capture and intake rates. By comparison, hovering and hawking provided the highest capture and intake rates. The difference in return reflects the fact that hovering and hawking are tactics directed to prey that have been detected whereas gleaning and probing, as used here, represent exploratory foraging tactics. The differences also reflect a disparity in prey size. Most of the large prey items were captured by hawking.

Migrant Blackpoll Warblers exceeded their estimated metabolic energy requirements by nearly a factor of 2. Blackpolls ingested an average of 1.47 x 10-2 g of prey (dry weight) per 2-min observation period or 6.25 g per day. This prey biomass is equivalent to 113.1 kj/d. Estimated Field Metabolic Rate for a 12.6 g Blackpoll Warbler is 59.3 kj/d.

TABLE 3. Foraging rates as a function of foraging tactics. Energy refers to estimated metabolizable energy. Projected rates were calculated based on one hours worth of each activity.

Foraging Tactic	Prey Items (N)	Estimated Energy (kj)	Estimated Energy/Item (kj/N)	Capture Rate (Items/h)	Intake Rate (kj/h)
Leaf Gleaning	176	4.59	32	107.6	2.80
Branch Gleaning	48	2.64	16	56.9	3.13
Picking/Probing	49	2.06	11	321.4	6.11
Hawking	88	29.89	63	145.4	294.8
Hovering	20	2.44	18	3600.0	39.20
Total	**382**	**41.62**	**140**	**128.2**	**13.97**

DISCUSSION

The observations of migrant Blackpoll Warblers presented here are consistent with the notion that this species depends on surface gleaning to obtain food. Gleaning accounted for a large portion of foraging bouts, total foraging time, and prey captures. This pattern is consistent with observations within other migration stopover areas (Morse 1979, Graber and Graber 1983, Latta and Brown 1999), as well as, on breeding (Morse 1979) and winter (Sick 1971) grounds. Migrants in coastal Virginia captured most prey from the surface of leaves and branches using near-perch maneuvers. Blackpolls also used more active foraging tactics such as gleaning from surfaces while hovering or hawking. These tactics are also described as minor foraging behaviors in other studies. Latta and Brown (1999) describe these tactics as representing less than 10% of foraging maneuvers during fall migration in the Dominican Republic. Morse (1979) describes these tactics as being more common during migration in Maryland compared to on the breeding grounds of New Hampshire.

Although active foraging tactics represented a minor portion of the foraging bouts and time spent foraging, they accounted for a dominant portion of the estimated energy intake. Hawking and hover gleaning were very rewarding in terms of both capture rate and energy intake rate. This success was partly due to the fact that these expensive foraging tactics were often directed toward large, valuable prey items. The fact that these tactics make a significant contribution to the overall energy budget has not been acknowledged elsewhere within stopover areas.

Blackpoll Warblers in coastal Virginia took a large number of small (< 5mm) prey items. The majority of these prey items were caterpillars. This finding is consistent with previous studies elsewhere that have examined prey use during migration (e.g. Morse 1979, Graber and Graber 1983, Latta and Brown 1999). A large number of these caterpillars were gleaned from newly emerged leaf clusters, a pattern also consistent with previous investigations conducted during spring migration.

Graber and Graber (1983) estimated that migrant Blackpoll Warblers achieved a daily energy intake of 322 kj in central Illinois. They suggest that caterpillar density was so high in this location that Blackpolls may have been approaching the upper limit of intake rate. They speculate that the intermittent rest periods observed were needed to digest prey. Estimated energy intake rate for coastal Virginia was 113.1 kj/d. Although this value is much lower than that reported for Illinois, it is dramatically higher than the estimated Field Metabolic Rate of 59.3 kj/d for this species. Blackpolls foraging in Virginia captured a prey item every 28.1 s on average. This capture rate is comparable to the Dominican Republic where migrant Blackpolls captured a prey item every 21.4 s.

The technique used here to estimate foraging rate includes some implicit assumptions. We first assume that sample observation periods give a reasonable representation of how Blackpoll Warblers spent their time during stopover. Although it is impossible to fully assess this assumption, the relatively large number of individuals sampled provides some level of confidence to the average time budgets presented. The remarkable degree of agreement between time budgets presented here and those calculated for Blackpolls within other stopover areas also provides some confidence in their general values. Male Blackpolls in coastal Virginia spent an average of 55.7% of their time foraging. This value is remarkably consistent with migrant Blackpolls in

Illinois that spent 54.0% of their time foraging (Graber and Graber 1983) and Blackpolls observed in New Hampshire that spent 49% of their time foraging (Morse 1979).

In order to calculate daily energy intake rates, an additional assumption was made that Blackpoll Warblers were foraging at a consistent average rate throughout the daylight hours. A mid-day depression in foraging activity has been well documented for a number of warbler species (e.g. Hutto 1981). The timing of foraging samples, in this study, was restricted to the morning hours. If migrant Blackpoll Warblers in coastal Virginia reduce foraging activity during any portion of the day, the net result of this assumption is an overestimate of daily intake rate. Graber and Graber (1983) suggested that migrant Blackpolls in Illinois exhibited a 3-hour lull in foraging activity in the middle of the day. Such a foraging lull in this study would result in a 20% reduction in daily energy intake. Although this reduction would reduce the magnitude of the estimated energy surplus achieved by migrant Blackpolls in coastal Virginia, it would not influence the direction of the energy budget.

The coastal plain of Virginia appears to be a source of energy for male Blackpoll Warblers during spring migration. Even considering a possible overestimate in energy intake, individuals more than offset their metabolic costs. The relative importance of this physiographic region to the overall life cycle of specific populations remains to be determined.

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GENERAL DISCUSSION

The results of this study indicate that location within the coastal plain of Virginia affects the phenology of Blackpoll Warbler migration. The results show significant differences in arrival time and peak density among the regions of the coastal plain. Observed peak densities of Blackpoll Warblers were staggered by 10 days between areas on the outer coastal plain, and areas on the inner coastal plain. Birds appear to be able to respond to the steep climate gradient and to take advantage of the early coastal warming. The birds may be able to gain a competitive advantage by arriving earlier on the breeding grounds. One possible explanation for the observed migration pattern is that arthropod resources may follow leaf emergence patterns.

It remains to be determined how the Coastal Plain of Virginia fits with the overall migration strategy for Blackpoll Warblers. Hunt and Eliason (1999) suggest the possibility of an over-water spring migration route, from the Greater Antilles to southeastern Atlantic states. We do not know if Blackpoll Warblers arriving on the coastal plain of Virginia have faced a large geographic barrier by coming across the Atlantic Ocean, or if they have taken an overland route. However, our results are consistent with a pattern of overwater migration. Relatively low densities of the species in the Carolinas (LeGrand 1975, Parnell 1969, Fussell 1996) also seem to support an overwater route. If Blackpolls are actually making landfall in coastal Virginia, the difference in phenology observed may represent an advancement front that is moving inland from the coast rather than northward from the southeast.

During both years of this study, Blackpoll Warblers foraged primarily by gleaning along leaves and branches, a pattern consistent with previous migration studies of this species (Latta and Brown 1999, Morse 1979). We found that leaf gleaning made up the majority of foraging attempts, followed by branch gleaning, picking, hawking, and hover gleaning. Foraging tactics used by Blackpoll Warblers were consistent across substrates, a pattern similar to that found for other warblers on the breeding grounds (Robinson and Holmes 1982). We also found that foraging tactics were dependent on the type of prey being captured, also consistent with Robinson and Holmes (1982).

This study mirrors the findings of previous research regarding prey size classes taken by Blackpoll Warblers, and time budgets for the species during stopover. The distribution of prey size classes taken by Blackpoll Warblers in this study are remarkably consistent with those reported previously (Graber and Graber 1983, Morse 1979). Previously published data indicate that size classes of insects selected by migrants are very specific, and often significantly different than size classes that were available (Marchetti et al. 1998), though our results may also suggest that Blackpoll Warblers are responding to availability within our sites. Though there was great individual variation, our observed time budgets for Blackpoll Warblers are consistent (X^2<1.0, P<.05) between years, and are similar to time budgets observed in Illinois during stopover (Graber and Graber 1983), and by Morse (1979) on the breeding grounds in New Hampshire and during migration in Maryland.

Blackpoll Warblers exhibit plasticity in their substrate choice during stopover (Hunt and Eliason 1999), and changes in substrate may be reflected by changes in foraging tactics (Morse 1979). The foraging tactics observed here were similar to those described in the literature during stopover, though we found greater instances of hovering and hawking tactics. Interestingly, the results indicate that although Blackpoll Warblers spent the bulk (84%) of their foraging time gleaning in the leaves and branches, this effort accounted for only 11% of the energy taken in by individuals. Hawking, done in only 3% of all foraging attempts, represented more than 82% of energy gain.

This disparity can be explained by differences in the energy values of prey items. Hawking is done in pursuit of adult Lepidopterans and Dipterans, high energy prey items. All of the adult Lepidopterans, and 45% of the Dipterans taken by Blackpoll Warblers in this study were obtained by hawking. Gleaning in leaves and branches does yield the greatest number of prey items (59%) of any tactic; however prey items obtained using this method tend to be of low energy value. Prey items taken while gleaning were primarily (78%) caterpillars. This can be compared to the diets of several species of warblers, including Blackpoll, observed by Graber and Graber (1983) and the diet of Blackpoll Warblers during a fall stopover (Latta and Brown 1999).

I suggest that Blackpoll Warblers are foraging in a manner consistent with available energy resources. During migratory stopover, birds exploit whatever food resources are available, and vary foraging tactics according to the type of prey an individual is pursuing (Robinson and Holmes 1982). Foraging patterns and rates observed in this study are consistent with patterns previously observed for Blackpoll Warblers during migratory stopover (Latta and Brown 1999, Morse 1979). Although movement rates have not been characterized for this species previously, Blackpoll Warblers have been described as 'slow and deliberate' foragers (Dunn and Garrett 1997). Our movement rates are comparable to those of other *Dendroica* species foraging on the breeding grounds (Robinson and Holmes 1982).

The results presented here indicate that the Coastal Plain of Virginia represents a source of energy for migrant Blackpoll Warblers. Intake rates for Blackpolls in this study exceeded their daily field metabolic rates. Birds were consuming almost twice their daily Field Metabolic Rate of 59.3 kj/day, a pattern consistent with the demands of migration. Our calculated intake rates (113.1kj/day) were much lower than the rate of 322kj/day previously calculated for migrant Blackpoll Warblers (Graber and Graber 1983). There are several possible explanations for the differences between this study and the Illinois study. In the Graber and Graber (1983) study, researchers used data from a site that experienced severe eruptive defoliation from insects in the year prior to and during the study. This insect eruption provided a super abundant food source that presumably was not available during our study, and may have affected warbler foraging rates. Another possible explanation for lower intake rates in our study may be that Blackpolls were under lower time and energetic constraints in Virginia than at locations like the Graber site in Illinois, further north along their migration route.

Further complicating the comparison of our data set to that of the Graber and Graber, was that during our analysis I assumed a constant foraging rate throughout the day. I included 55 non-foraging individuals into our time budget averages, which may have off-set a potential overestimate in intake rates. The possibility remains that I may have overestimated intake rates because I did not account for the mid-afternoon foraging depression associated with foraging rates in warblers. However, even with a 20% reduction in foraging rates to account for this depression, Blackpoll Warblers in this study were still exceeding their field metabolic requirements, and it appears the area is a source of energy for the birds.

In conclusion, there is a significant difference in the timing of migration of Blackpoll Warblers across the coastal plain of Virginia. It appears that birds are foraging in a manner consistent with the types of available arthropod resources present. It also appears that Blackpoll Warblers are gaining energy while stopping over, and that the coastal plain of Virginia represents a source of energy for these birds.

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