

ASSESSING THE FUNCTION OF BROAD-SCALE MOVEMENTS MADE BY JUVENILE SONGBIRDS PRIOR TO MIGRATION

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Abstract. The post-fledging period represents a time of considerable energetic constraint and selection pressure for juvenile songbirds. Despite its potential importance for survival, this period remains one of the least studied stages of the annual cycle. Using radio telemetry and taking advantage of unique topographical characteristics at three spatially separated study sites, we assessed four hypotheses regarding the function of broad-scale, landscape-level movements for juveniles: (1) commencement of migration, (2) habitat optimization, (3) selection of a breeding territory, and (4) formation of a homing target. For the Blackpoll Warbler (*D. striata*), we found that movement was directed to the southeast at all three study sites but individuals were also associated with river valleys, providing support for the homing-target and habitat-optimization hypotheses. For the Yellow-rumped Warbler (*Dendroica coronata*), we found that movement was directed toward and down river valleys, following the unique orientation of the valleys at each study site, supporting the habitat-optimization hypothesis. Our results provide important insights into the function of broad-scale landscape-level movements for juvenile songbirds prior to migration, as well as their relative importance to individuals' success, both immediate and future.

Key words: foraging, homing, habitat use, orientation, post-fledging, pre-migratory.

Evaluando la Función de los Movimientos de Amplia Escala Previos a la Migración de Aves Canoras Juveniles

Resumen. El período posterior al emplumamiento representa un momento de restricciones energéticas considerables y de presión de selección para las aves canoras juveniles. A pesar de su importancia potencial para la supervivencia, este período sigue siendo uno de los estadios menos estudiados del ciclo anual. Usando radio telemetría y aprovechando las características topográficas únicas de tres sitios de estudio separados espacialmente, evaluamos cuatro hipótesis sobre la función de los movimientos de amplia escala a nivel de paisaje para los juveniles: (1) comienzo de la migración, (2) optimización del hábitat, (3) selección del territorio de cría, y (4) habilidad de regresar al hogar luego de la migración. Para *Dendroica striata*, encontramos que el movimiento fue dirigido hacia el sudeste en los tres sitios de estudio, pero los individuos también se asociaron con los valles de los ríos, apoyando las hipótesis de regreso al hogar y de optimización de hábitat. Para *D. coronata*, encontramos que el movimiento fue dirigido hacia y en dirección descendente de los valles de los ríos, siguiendo la orientación única de los valles de cada área de estudio, apoyando la hipótesis de optimización de hábitat. Nuestros resultados dan una idea importante sobre la función de los movimientos de amplia escala previos a la migración que ocurren a nivel de paisaje de las aves canoras juveniles, y de su importancia relativa para el éxito de los individuos, tanto inmediato como futuro.

INTRODUCTION

For juvenile migratory songbirds, the post-fledging period is a time of intense selective pressure (Morton 1992). Upon becoming independent from adults, but prior to commencing migration, individuals must locate and access resources to support metabolic maintenance, thermal regulation, pre-basic molt, and migratory fattening (Sullivan 1988, Weathers and Sullivan 1989, Morton 1991) while simultaneously avoiding predation (Sullivan 1989, Anders et al. 1997, Kershner et al. 2004). Individuals may also begin to prospect for resources to

be used the following year, such as breeding territories (Nocera et al. 2006, Betts et al. 2008). Thus the post-fledging period may have important implications for individuals' success and survival in both the short and long term (Anders et al. 1997, Robinson et al. 2004).

Despite the potential importance of the post-fledging period to individual success, it is one of the least studied stages of the annual cycle (Baker 1993, Kershner et al. 2004, Vitz and Rodewald 2006). Because information regarding the behavior and ecology of juveniles is limited, few attempts have been made to test relevant hypotheses concerning the distinct

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patterns of movement songbirds undertake at this time. For instance, several studies have documented broad-scale, landscape-level movements after fledging (hereafter meso movements, at the scale of kilometers) prior to migration (Morton 1991, Morton et al. 1991, Anders et al. 1998), yet their function remains poorly understood (Vega Rivera et al. 1998, Kershner et al. 2004). These movements may enable individuals to find habitat associated with resources needed immediately (e.g., food, shelter, predator relief); however, they could also function to determine the location of resources to be used the following year for breeding. Thus a more direct assessment of post-fledging meso movements is needed to determine their relative importance to individuals' success, both current and future.

In the literature, four hypotheses regarding the function of such meso movements have been commonly suggested; (1) migration commencement, (2) habitat optimization, (3) breeding-territory selection, and (4) homing-target formation. The migration-commencement hypothesis posits that meso movements represent initial migratory displacements (Rappole and Ballard 1987). The habitat-optimization hypothesis suggests meso movements enable individuals to discover and access productive foraging sites (Rappole and Ballard 1987, Morton et al. 1991) or habitat that provides an optimal thermal environment or shelter from predators (e.g., Walsberg 1986, Rodríguez et al. 2001). The territory-selection hypothesis, applied by Brewer and Harrison (1975) to males only, suggests meso movements are involved in locating sites for future breeding. Last, the homing-target hypothesis posits that the function of meso movements is to enable the bird to locate landmarks that it can use to return to the vicinity of the natal territory the following spring (Wiltschko and Wiltschko 1978, Baker 1993).

Using radio-telemetry in combination with unique topographical characteristics at three spatially separated study sites, we assessed the function of meso movements for juvenile Blackpoll (*Dendroica striata*) and Yellow-rumped (*D. coronata*) Warblers in the boreal forests of insular Newfoundland, Canada. We predicted that if meso movements represent initial migratory displacements, these moves should be oriented to the southwest at each study site, parallel to the known axis of migration (Richardson 1972). Alternatively, if meso movements serve in locating and accessing optimal habitat, we predicted movements should be oriented toward and along the first- and second-order rivers at each study site (i.e., down the elevational gradient); southeast at the northern site, northeast and southeast at the middle site, and northeast at the southern site (Fig. 1). We expected this pattern because river valleys and low elevations represent the most productive habitat in terms of insect availability—the Blackpoll Warbler is predominantly insectivorous during the fall (Hunt and Eliason 1999, Latta and Brown 1999), and the Yellow-rumped prefers insects to fruit when insects are abundant (Afik and Karasov 1995). They are also likely the most thermally favorable habitats

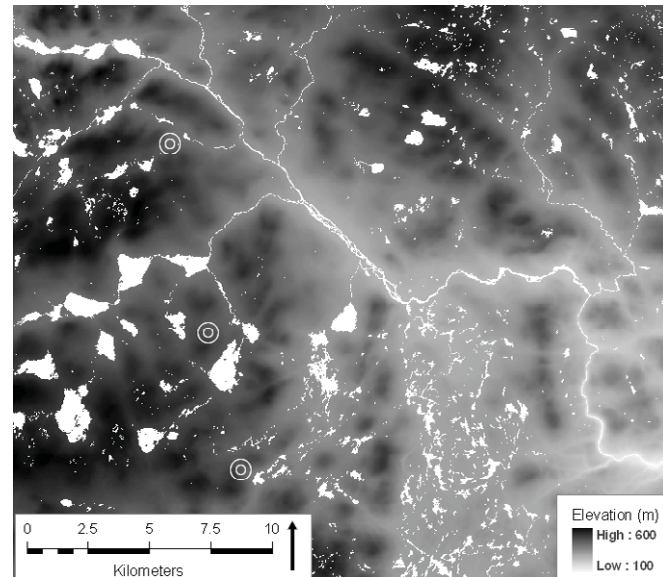


FIGURE 1. Digital elevation model and locations (circles) of study sites in northwestern Newfoundland. Black represents higher elevations; lighter gray represents lower elevations. White areas represent lakes and first- or second-order rivers. The black arrow depicts geographic north.

(lowest winds, warmest temperatures) in the broader landscape (Hodkinson 2005, Seagle and Sturtevant 2005, Högberg et al. 2006). If meso movements represent males prospecting for future breeding territories, we expected movement to be oriented nearly randomly at each site (i.e., to be dispersed in direction) because potential breeding sites are available throughout our study area (Taylor and Krawchuk 2006). If meso movements function to establish a homing target, we predicted that individuals should move at angles perpendicular to the known axis of migration. Such an orientation would increase an individual's probability of encountering recognizable landmarks during the following spring migration over the probability of its encountering a parallel target that could be missed altogether (Baker 1993). Through assessing these hypotheses, we provide new insights into the function of meso movements and their relative importance to both the immediate and future individual success of juvenile songbirds.

METHODS

STUDY SPECIES

The Blackpoll and Yellow-rumped Warblers are small (13 g) insectivorous songbirds with similar phenologies. The subspecies of the Yellow-rumped we studied (*D. c. coronata*) breeds from north-central Alberta through to Newfoundland and south to West Virginia; it winters in the eastern U.S., Mexico, and Central America (Hunt and Flashpohler 1998). The Blackpoll breeds throughout the boreal forest of northern North America and winters in Bolivia, Perú, Colombia,

TABLE 1. Sample sizes for movement-orientation analysis (by study site and year) of juvenile Blackpoll and Yellow-rumped Warblers during the post-fledging period in northwestern Newfoundland, 2005–2006.

	2005	2006
Blackpoll Warbler		
Northern site	6	5
Middle site	8	4
Southern site	1	6
Yellow-rumped Warbler		
Northern site	6	5
Middle site	12	6
Southern site	4	6

Venezuela, Guyana, Suriname, and northwestern Brazil (Hunt and Eliason 1999). During the breeding season both species commonly forage in the canopies of mature conifers in the forest interior, riparian edge, forest edge, and, to lesser extent, open habitats (Hunt and Flashpohler 1998, Hunt and Eliason 1999, Whitaker and Montevecchi 1999). After fledging, juveniles of both species are commonly associated with dense understory and overstory vegetation (Mitchell et al. 2010), and like adults, commonly forage in the canopies of mature conifers (Mitchell, unpubl. data). Recent evidence suggests that clearcut forest may represent low-quality habitat for juveniles of both species (Mitchell et al. 2009).

STUDY AREA

Our research took place in the northwest of the island of Newfoundland, Canada. This area is vegetated with old-growth forest interspersed with water courses, ponds, lakes, rocky outcrops, peatlands, patches of coniferous scrub, and patches

of regenerating clearcuts (logged in 1999 and 2000). Forests are dominated by balsam fir (*Abies balsamea*) with lesser amounts of black spruce (*Picea mariana*), white spruce (*P. glauca*), and white birch (*Betula papyrifera*; Damman 1983, Thompson et al. 2003). At the time of study, clearcuts covered 6% of the landscape, were irregular in size and shape (20–100 ha), and were characterized by abundant coarse woody debris and low densities of both mature white birch and regenerating balsam fir. Clearcuts were not homogeneously distributed throughout the landscape; they extended 5 km west of the northernmost study site (see baseline sampling below), 1.5 km west of the middle study site, and 1.5 km west, 3 km east, and 3 km south of the southernmost study site. The Humber River watershed directly south of our study area was also heavily harvested.

BASELINE SAMPLING

In 2005, we captured 25 Blackpoll and 26 Yellow-rumped Warblers between 20 July and 5 August. In 2006, we captured 23 Blackpoll and 22 Yellow-rumped between 26 July and 7 August (Table 1). All captures were part of a concurrent passive mist-netting study examining the movement and demography of boreal songbirds (Whitaker et al. 2008). Captures took place at three study sites (northern, middle and southern; Fig. 1) located approximately 5 km apart along a north–south axis. Each site had distinctive topography attributable to river valleys with different orientations (Fig. 1) that enabled us to compare observed movement orientations and habitat associations with those we expected under the four hypotheses regarding the function of post-fledging meso movements (Table 2).

Upon capture, the birds were aged on the basis of plumage criteria (Pyle 1997) and fitted with a unique combination of three color bands, a numbered U.S. Fish and Wildlife

TABLE 2. Hypotheses and predictions used to assess the function of meso movements by juvenile Blackpoll and Yellow-rumped Warblers during the post-fledging period in northwestern Newfoundland.

Hypotheses	Predictions		
	Orientation ^a	Distance to river	Change in elevation
Migration commencement	SW at each study site (i.e., parallel to the known axis of migration)	NA ^b	NA
Habitat optimization	northern study site, SE middle study site, SE and NE southern study site, NE (i.e., parallel to the orientation of the first- and second-order rivers at each site)	from actual locations should be less than from random locations	decrease from actual locations should be greater than from random locations
Breeding-territory selection (males only)	random at each study site	NA	NA
Homing-target formation	SE at each study site (i.e., perpendicular to the known axis of migration)	NA	NA

^aWith respect to displacement from initial point of capture.

^bNA, not applicable.

Service aluminum band, and a 0.53-g transmitter (Holohil Systems Ltd., Carp, Ontario; model BD-2N, median battery life 17 days). Transmitters were affixed to birds with a figure-eight leg-loop harness (Rappole and Tipton 1991). The total weight of the harness and radio equaled 0.66 g, 5% of a warbler's body mass. Radio tagging was initiated when family groups began to break apart and juveniles began to disperse, as indicated by increased rates of capture of juveniles in the concurrent netting study; the birds' exact natal origin was unknown. All procedures were approved by the Animal Care Committee of Acadia University in accordance with Canadian Council on Animal Care guidelines and adhered to the legal requirements of Environment Canada.

RADIO TRACKING

Tracking began 24 hr after the transmitter was attached. We located the birds via homing (following a signal up to and observing an individual) as well as through four aerial telemetry flights. For all tracking, we used TR-4 receivers (Telonics, Inc., Mesa, AZ) and two- (Telonics) or three-element (Advanced Telemetry Systems, Isanti, MN) hand-held antennae. Locations were obtained opportunistically between 06:00 and 20:00. We attempted to locate tagged birds every 1 to 3 days, but because of the spatial extent of movement, there were gaps of more than 3 days between successive locations for 10% of all observations (median number of days between locations 1.26, range 0.60–12.91). We recorded locations with Garmin eTrex Venture Global Positioning System units (Olathe, KS) set to record UTM coordinates (WGS 84, zone 21N). When an individual's signal was lost (because of predation, migration, or radio failure), we surveyed the study area via triangulation from hilltops every 2 to 3 days for the remainder of the study. A 660-km² area encompassing our study site was also searched during each aerial telemetry flight. Tracking took place from initial captures until 25 August in 2005 and 27 August in 2006. Birds were tracked until their radio signal was lost or the individual was found dead (from exposure or predation; $n = 17$). In 2006, we stopped following one individual for logistical reasons.

Although we did not evaluate the effects of radio transmitters directly, we have no evidence they had an adverse effect on the birds' movement or survival. The distances tagged birds moved were comparable to those reported for other species that were not fitted with radio transmitters (e.g., Morton 1991, Morton et al. 1991). Also, Leonard et al. (2008) used the same attachment method and found no effect of radio transmitters on movement rate or annual survival of adult Blackpolls or Northern Waterthrushes (*Parkesia noveboracensis*).

DEFINING MESO MOVEMENTS

We defined meso movements of the Blackpoll and Yellow-rumped Warblers as rates of >898 and >643 m day⁻¹, respectively; we termed rates less than these values "residency"

movements and did not use them in the final analyses. To derive these cut-off values, we used two quantitative and empirical lines of evidence (see Mitchell et al. 2010). First, we identified "natural breaks" in the distributions of observed movement rates in plots of the density of these rates. These breaks are represented by troughs separating adjacent humps in each density curve (i.e., the second hump represents the distribution of meso-movement rates), as well as by gaps in the rug plots beneath each density curve (Fig. 2A, 3A). These humps appear to be small, but their size is relative to the number of residency movements, i.e., if fewer residency movements had been measured, the difference in the humps would be more apparent. To derive exact cut-off values, we then examined the differences in the 1% quantile values of the movement-rate distributions; cut-off values were defined by the 1% quantile value where a large difference in successive quantiles was followed by a series of small differences (Fig. 2B, 3B). Using these criteria, we classified 30 of 48 Blackpolls and 39 of 48 Yellow-rumps as making meso movements. Of the Blackpolls that made meso movements, 15 individuals made one meso movement and 15 made two or more. Of the Yellow-rumps that made meso movements, 14 made one meso movement, and 25 made two or more. Only those individuals that made meso movements were included in our analyses (Table 1).

STATISTICAL ANALYSIS

All statistical analyses were completed in R 2.8.0 (R Core Development Team 2006). To assess the function of meso movements, we modeled ORIENTATION (model terms in capital letters) with spherically projected multivariate linear models (SPML; Presnell et al. 1998 Scapini et al. 2002). Code for the SPML models was provided by Scapini et al. (2002). ORIENTATION was based on the trajectory from the point of initial capture to final location (zero degrees equals north). We used only these specific points to derive orientation because, currently, SPML models are not parameterized to account for random effects (i.e., repeated measures of orientation of individuals) and because the majority of displacement and thus displacement orientation can be accounted for by meso movements but not by finer-scale residency movements, which did not deviate from a uniform circular distribution (Rayleigh test: residency: $P = 0.73$; meso: $P = 0.02$). STUDY_SITE, YEAR, and the number of observations (NUM_OBS) were included as predictors. YEAR was included to control for possible annual differences in movement related to annual variation in resource distribution (e.g., invertebrate abundance; Keane and Morrison 1999). NUM_OBS was included to account for potential differences in orientation between individuals for which we had few observations and those for which we had many. Sample sizes were too low for interactions between main effects to be assessed (Table 2). We fitted models for each species separately.

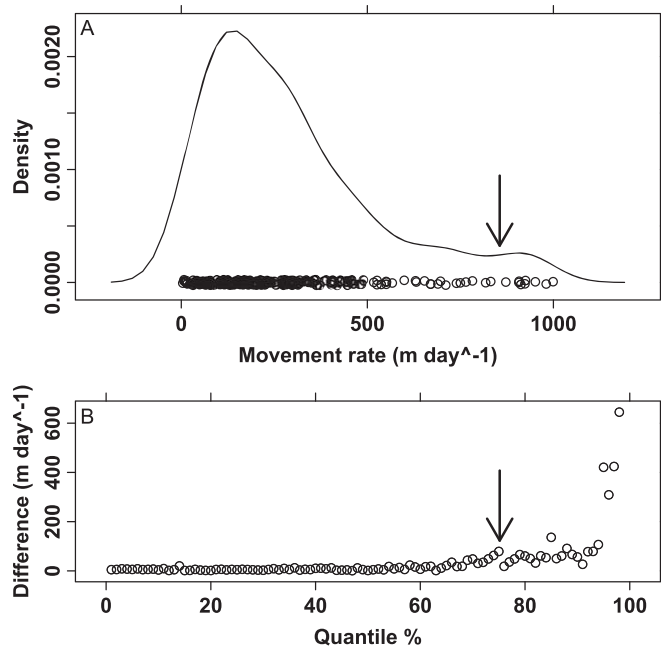


FIGURE 2. (A) Density and rug plots illustrating the bimodal distribution of rates of movement of juvenile Blackpoll Warblers during the post-fledging period in northwestern Newfoundland, 2005–2006. Arrow indicates location of the natural break in the distribution distinguishing residency and meso movements. (B) Difference in 1% quantile values of rates of movement of juvenile Blackpoll Warblers for the same values as in (A). Arrow indicates location of the natural break (large difference followed by series of small differences) in the distribution distinguishing residency and meso movements.

Prior to fitting models, we assessed the circular normality of observed orientations for each study site and year ($\alpha = 0.10$) with Watson's test for the von Mises (circular normal) distribution by using the CircStats package (Lund and Agostinelli 2009). This same package was used for the Rayleigh test described above. Where models contained two factors (e.g., STUDY_SITE and YEAR), we assessed additivity (parallel-ogram rule; Scapini et al. 2002) visually prior to fitting the model by plotting the parameter estimates (x , y coordinates) of each factor-level mean simultaneously. Model selection was based on an information-theoretic approach (Akaike information criterion, AIC), where models were retained in the final set if the difference between AIC values for the best-fit model (i.e., the model with the lowest AIC value) and the model in question was ≤ 2 (Burnham and Anderson 2002). We considered all subsets of the models (range of predictors 1–3) in the selection procedure because of their biological feasibility. To assess the possibility that the largest models in the final sets for each species were over-fit (see Guthery et al. 2005), we also used likelihood-ratio tests (LRTs) to assess the contribution of each term to the reduction in the model's overall deviance. Like the AIC approach, LRTs balance the reduction in the model's deviance with the number of parameters fit in the model by

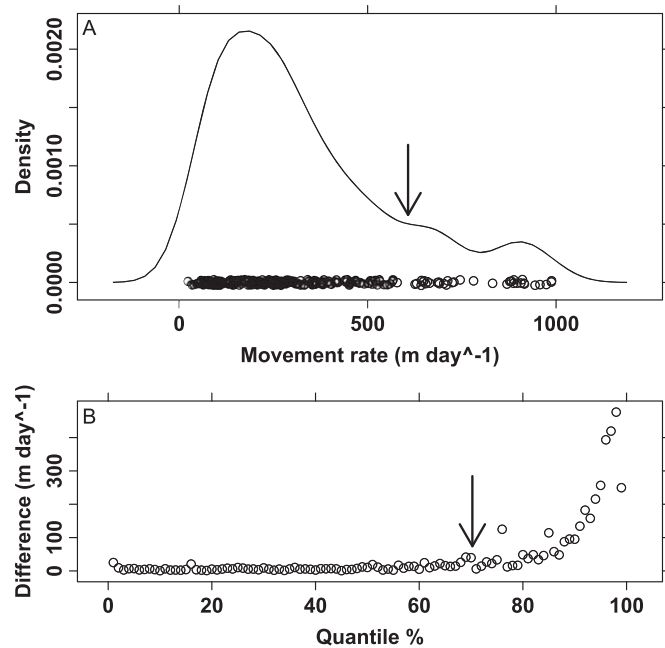


FIGURE 3. (A) Density and rug plots illustrating the bimodal distribution of rates of movement of juvenile Yellow-rumped Warblers during the post-fledging period in northwestern Newfoundland, 2005–2006. Arrow indicates location of the natural break in the distribution distinguishing residency and meso movements. (B) Difference in 1% quantile values of rates of movement of juvenile Yellow-rumped Warblers for the same values as in (A). Arrow indicates location of the natural break (large difference followed by series of small differences) in the distribution distinguishing residency and meso movements.

applying a penalty for each additional parameter estimated (Murtaugh 2009). Terms were deleted in order of significance of parameter estimates, the least significant terms being deleted first. When terms were deleted, we examined the sign, magnitude, and significance of the model's other terms to ensure they did not change.

To assess the foraging-optimization hypothesis further, we used randomization tests to compare the median distance from the closest river-valley bottom and the mean absolute change in elevation between locations bounding meso movements for both actual and randomly generated locations. This procedure enabled us to assess the extent to which the observed metric (distance and change in elevation) was a product of chance. We used median distance when assessing distance to the closest river-valley bottom because the distribution of distances was skewed toward lower values and means were not accurate measures of central tendency. We derived both distance to the closest river-valley bottom as well as change in elevation in R 2.8.0 (R Core Development Team 2008) with a digital elevation model based on 1:15 840 aerial photographs produced by the Newfoundland and Labrador Department of Natural Resources (last updated in 2000).

We selected random locations by using actual displacement distances for movements from the location of each bird's initial capture but in directions randomly chosen (from a uniform distribution) relative to the capture location. This procedure allowed us to bound the distribution of random displacement distances and the ultimate location of random points realistically. Each random placement of locations (Yellow-rumped: $n = 39$, Blackpoll: $n = 30$) was repeated 10 000 times. Values for these randomization tests are reported as P -values in the results.

RESULTS

For 2005 and 2006 pooled, we recorded 301 and 330 locations for the Blackpoll and Yellow-rumped Warblers, respectively. In neither the number of observations per individual nor displacement distance did the species differ (Blackpoll, median number of observations 6, range 2–20; Yellow-rumped, median number of observations 8, range 2–18; Wilcoxon

rank-sum test; $W = 698.50$, $P = 0.17$; Blackpoll, displacement distance 3076 m, range 131–16 082 m; Yellow-rumped, displacement distance 4071 m, range 377–9468 m; Welch two-sample t -test log of displacement distance: $t = 0.73$, $df = 65.48$, $P = 0.47$). For five individuals overall displacement distances were <1000 m, and for three of these (1 Blackpoll and 2 Yellow-rumped) they were <800 m. Of this subset, one individual of each species made a meso movement west of its capture location and subsequently moved back toward its capture location before contact was lost (GWM, unpubl. data). The other Yellow-rumped Warbler drifted east and made two meso movements to the west but was still located east of its initial capture location (GWM, unpubl. data). Nine other Yellow-rumps and 10 Blackpolls also made meso movements west of their capture location, but six and four of these, respectively, made subsequent meso movements back east of their initial capture location. Seventy two percent of the remaining meso movements ($n = 138$) were directed to the east (Fig. 4).

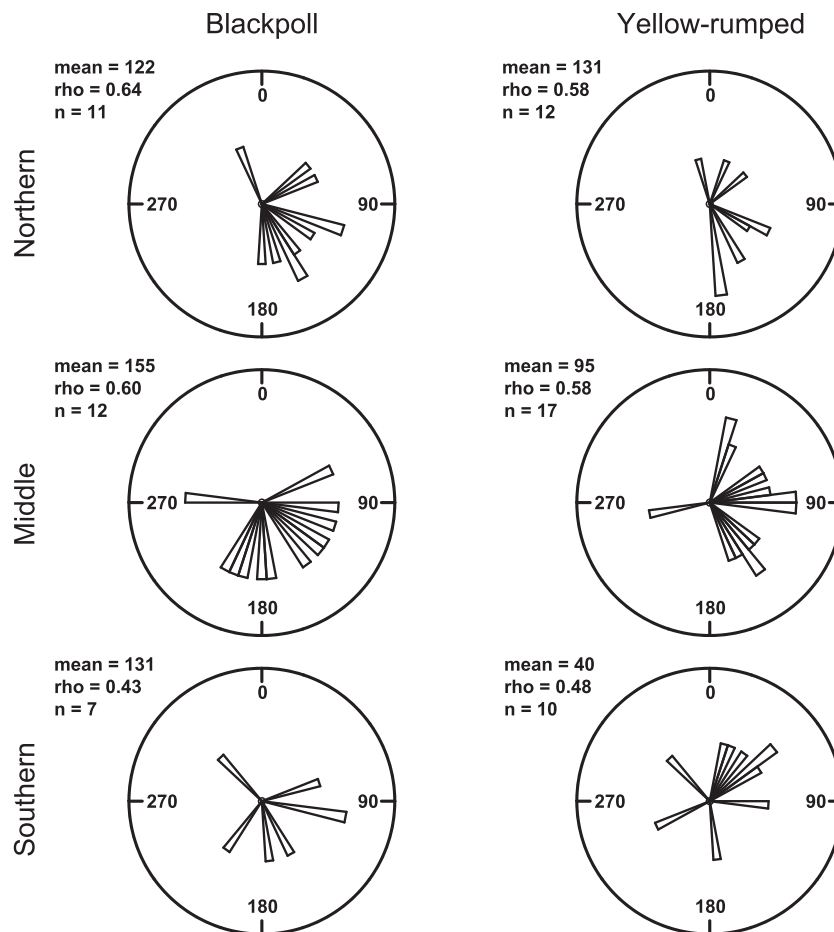


FIGURE 4. Circular histograms illustrating orientation of final locations by species and study site for juvenile Yellow-rumped and Blackpoll Warblers during the post-fledging period in northwestern Newfoundland, 2005–2006. Mean direction is in degrees relative to north (0°), ρ represents relative strength of orientation or an assessment of circular dispersion (i.e., 0 = random orientations, 1 = all observations in same direction), and n represents sample size.

TABLE 3. Top movement-orientation models from AIC model-selection procedure and results of likelihood-ratio test (LRT) for the largest model within this set for juvenile Blackpoll and Yellow-rumped Warblers during the post-fledging period in northwestern Newfoundland, 2005–2006. Models are presented in order of increasing AIC value. Order of predictors for LRT represents the order in which terms were considered on the basis of the significance of parameter estimates. Parameter estimates are not provided because they lack biological meaning, given the bivariate nature of spherical distribution, i.e., two parameters representing coordinates on the distribution are estimated for every predictor or factor level considered.

Rank	Model	AIC	n (β)	df
Blackpoll Warbler				
1	NUM_OBS	87.44	4	26
2	STUDY_SITE + YEAR + NUM_OBS	89.03	10	20
3	YEAR + NUM_OBS	89.37	6	24
Yellow-rumped Warbler				
1	STUDY_SITE	128.31	6	33
2	STUDY_SITE + YEAR	129.87	8	31

Predictor	Difference of likelihood	Difference of df	P (LRT)
Blackpoll Warbler			
YEAR	4.76	2	0.09
STUDY_SITE	5.65	4	0.22
NUM_OBS	10.54	2	<0.01
Yellow-rumped Warbler			
YEAR	2.44	2	0.30
STUDY_SITE	10.11	4	0.04

For the Blackpoll, all three final models indicated that movement orientation varied significantly with number of observations: individuals with fewer observations had a more north-easterly orientation than did individuals with a larger number of observations (Table 3, 4). Furthermore, the number of observations was the only term common to all three final models and was the only predictor that resulted in a significant increase in the models' deviance when removed ($\chi^2_1 = 9.1$, $P < 0.01$; χ^2_4 LRT = 10.54, $P < 0.01$; Table 3). Thus both AIC and the LRTs most strongly supported the model containing number of observations as the only predictor. Conversely, for the Yellow-rumped, both final models indicated that orientation of movement from the middle and southern sites differed (Fig. 4; Table 3); orientation of movement mirrored the orientation of river-valley bottoms at each site: southeast at the northern site, southeast to east-northeast at the middle site, and north-east at the southern site (Fig. 1, 4). Furthermore, study site was the only term common to both final models and was the only predictor that resulted in a significant increase in the models' deviance when removed ($\chi^2_1 = 2.9$, $P = 0.09$; χ^2_4 LRT = 11.9, $P = 0.04$; Table 3). Thus both AIC and the LRTs most strongly supported a final model containing only the term study site. A backward step-wise approach yielded the same results for both species. For the Blackpoll, the results of these analyses were unchanged when the individual with a displacement distance <800 m was removed from the dataset. For the Yellow-rumped, when the two individuals with displacement

distances <800 m were removed from the analyzed dataset, AIC specified the model containing only study site as the best, and the sign and magnitude of the parameter estimates remained unchanged. But the LRTs suggested that deleting study site resulted in a marginally insignificant increase in model deviance (χ^2_4 likelihood-ratio test = 7.9, $P = 0.10$).

For both species, median distance to the closest river-valley bottom was closer for observed than for random locations (probability of median value being less than or equal to the median distance for actual locations: Yellow-rumped, $P < 0.01$; Blackpoll, $P = 0.03$). Median distances of observed locations from river-valley bottoms were 981 and 1015 m for

TABLE 4. Summary statistics describing how orientation varied with the number of observations of juvenile Blackpoll Warblers during the post-fledging period in northwestern Newfoundland, 2005–2006. Mean direction is in degrees relative to north (0°), ρ represents relative strength of orientation (i.e., 0 = random orientations, 1 = all observations in same direction), and n represents sample size.

Number of observations	Mean direction	ρ	n
2–4	106.04°	0.42	10
4–8	147.42°	0.53	11
8–20	147.20°	0.82	9

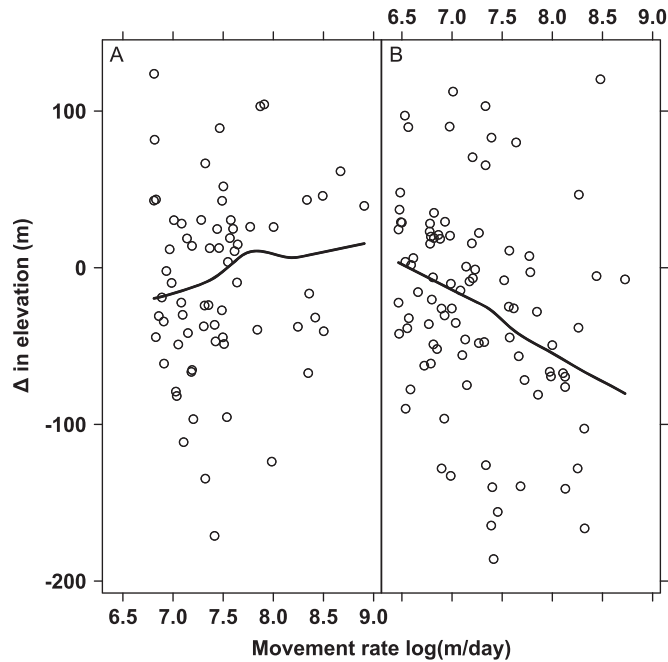


FIGURE 5. Change in elevation between locations bounding meso movements of juvenile (A) Blackpoll Warblers and (B) Yellow-rumped Warblers during the post-fledging period in northwestern Newfoundland, 2005–2006. Circles represent observed differences in elevation. Trends illustrated with locally weighted regression lines.

the Yellow-rumped and Blackpoll, respectively. For random locations, the median distances from river-valley bottoms were 1104 and 1096 m for the Yellow-rumped and Blackpoll, respectively. Furthermore, changes in elevation during meso movements resulted in greater decreases in elevation relative to randomizations for the Yellow-rumped ($P < 0.01$; Fig. 5b) but not the Blackpoll ($P = 0.28$; Fig. 5a). Mean change in elevation for observed locations was -24 m for the Yellow-rumped and -9 m for the Blackpoll, while the mean change in elevation for random locations was -7 m for the Yellow-rumped and -4 m for the Blackpoll.

DISCUSSION

Our results demonstrate that post-fledging movements of the Blackpoll and Yellow-rumped Warblers are similar in their association with river valleys, but we found species-specific differences as well. At all three study sites Blackpoll Warblers maintained a southeasterly orientation as they traversed the landscape and were closely associated with river-valley habitat, although the birds did not follow the exact trajectory of the river valleys they encountered. In contrast, at each study site Yellow-rumped Warblers moved both toward and along river valleys, moving down the elevational gradient of the rivers. The clear orientation of both species toward the east fails to support our predictions for either the migratory-commencement hypothesis (southwest) or the breeding-territory-selection hypothesis

(random). However, the association of the Blackpoll with river valleys as well as its population-level movement at an angle perpendicular to the axis of migration is consistent with our predictions for both the habitat-optimization and homing-target-formation hypotheses, respectively, while the close association of the Yellow-rumped with river valleys and continued movement down an elevational gradient is consistent with our predictions for the habitat-optimization hypothesis.

The post-fledging period is a time of considerable energetic constraint and predation risk (Sullivan 1988, Weathers and Sullivan 1989, Anders et al. 1997). Although we did not evaluate the hypothesis directly, we posit that river-valley habitat in the boreal forest, particularly at low elevations, might mitigate these stresses. For example, lower elevations can be correlated with significantly higher productivity and in turn prey availability (Bormann et al. 1970, Seagle and Sturtevant 2005, Högberg et al. 2006). During fall migration, the Blackpoll forages primarily on insects (Parish 1997, Latta and Brown 1999). Similarly, although the Yellow-rumped feeds on fruit during the fall, insects are thought to be its preferred prey (Malmberg and Willson 1988, Afik and Karasov 1995). As both species appear to forage preferentially on insects, river valleys may represent optimal foraging habitat. Alternatively or additionally, low-elevation sites may offer an optimal thermal environment in terms of temperature and shelter from wind, helping the birds maintain a positive energy balance (Walsberg 1986, Hodkinson 2005). Unfortunately, we were unable to quantify habitat-specific predation risk or broad-scale patterns of predator distributions, as both variables may have also influenced the patterns we observed. For example, in a previous analysis, we found that at the stand level the Yellow-rumped (but not the Blackpoll) is associated with dense overstory cover (Mitchell et al. 2010). If a denser overstory in river valleys or at low-elevation sites provides more cover from predators, this might also explain the Yellow-rumped Warbler's close association with low elevations. Future research should assess which of these habitat characteristics are most important for survival.

The Yellow-rumped appeared to respond to river-valley habitat more strongly than did the Blackpoll. Although Blackpolls were located in the vicinity of river valleys, they did not move downslope continuously, as we found in alternative analyses of habitat use (Mitchell et al. 2010). Such behavior may reflect an ability of the Blackpoll to increase its fat load more efficiently than can the Yellow-rumped (Holberton and Dufty 2005), resulting in less dependence upon the most productive habitat available and with the consequent freedom to explore habitat away from river valleys for other purposes. Alternatively, as discussed above, lower elevations may be associated with some other habitat feature (e.g., temperature/shelter; see above) that is important to the Yellow-rumped but less so to the Blackpoll. Again, further research is needed to

determine how the availability of river-valley habitat influences these species.

At northern latitudes breeding is more synchronous than at lower latitudes, limiting birds' opportunities to prospect for future breeding habitat at currently active nests (Nocera et al. 2006). By developing a homing target in the fall, birds may be able to return promptly the following spring to an area for which they have a measure of breeding success, albeit that of their natal territory and territories immediately adjacent, (Baker 1993, Dale et al. 2006), facilitating rapid territory establishment and commencement of breeding. For example, Dale et al. (2006) observed second-year male Ortolan Buntings (*Emberiza hortulana*) attempting to establish breeding territories at or around their natal territories in early spring. If these males were unsuccessful, it was only then that they began dispersing more broadly throughout the landscape. Also, Whitaker et al. (2008) found that in our study area between-year apparent survival of the Yellow-rumped Warbler was lower than that of the Blackpoll, suggesting that either dispersal distances were greater or that survival was lower for the Yellow-rumped. This is the result expected if Blackpolls are better able to home to a specific area in the landscape the following spring via formation of a homing target, provided that both adults and juveniles follow similar behavioral processes during the post-fledging period.

The pre-formative molt of the Blackpoll Warbler does not differ by sex (Pyle 1997). Therefore, we were unable to reliably sex the individuals we studied, although presumably females constituted about 50% of our sample. In migratory species, natal dispersal of females is generally greater than that of males (Clark et al. 1997, Winkler et al. 2005), so is it reasonable to infer that female Blackpolls are also forming a homing target? We present two reasons why we believe this to be a reasonable inference. First, although distances of females' natal dispersal may be larger, the extent of these differences is usually only several kilometers (e.g., Winkler et al. 2005), meaning that individuals are returning to the general area of their natal territories. If females inherit local and regional adaptations (e.g., timing of breeding) to a particular area, forming a homing target to return to that area to breed the following year could maximize fitness (Caro et al. 2009). Second, there may be no cost associated with returning to the same area, if, for example, first-year birds are able to recognize relatives (e.g., Wheelwright and Mauck 1998).

We assessed four hypotheses regarding the function of post-fledging meso movements. As evidenced by our results, our predictions for the habitat-optimization and homing-target-formation hypotheses were not mutually exclusive, nor were they necessarily mutually exclusive of the migration-commencement hypothesis. However, aside from these non-independent hypotheses, our predictions, based on a specific set of assumptions about our study system, were independent. If this basic set of assumptions is changed, however, some of

our predictions become confounded. For example, instead of prospecting for future breeding territories in habitat across the broader landscape, juveniles may prospect for territories only in the most productive habitat available (i.e., river valleys at low elevations). Under this scenario, our predictions for the habitat-optimization and breeding-territory-selection hypotheses would be similar. This scenario further assumes, however, that first-year males are not usurped by older dominant conspecifics the following year, eliminating any benefit associated with prospecting in these areas (e.g., Hill 1988, Holmes et al. 1996). Further research on the pre-breeding movements of first-year males is ultimately needed for this possibility to be assessed definitively.

Another assumption of our study was that homing targets are oriented perpendicular to the axis of migration (Baker 1993). Again, if this assumption is incorrect, some of our predictions become confounded. For example, birds might use river valleys as a target for homing, as rivers constitute a large landscape feature that presumably could be recognized easily (Bingman et al. 1992), confounding the habitat-optimization and homing-target-formation hypotheses. Alternatively, if birds can detect latitude (e.g., by using the earth's magnetic field Fransson et al. 2001), a north-south-oriented homing target to which a bird could turn once it reaches an appropriate latitude may make sense (Baker 1993), confounding the migration-commencement and homing-target-formation hypotheses. Although the latter possibility may be moot, as we did not find support for the migration-commencement hypothesis, the former might have important implications for the interpretation of our results. For example, during the spring, Yellow-rumped Warblers migrating from the south will likely encounter at least one river associated with the watershed in which they hatched, which could facilitate homing to the natal area. If this were the sole function of association with river valleys, however, we should expect meso movements to be directed both up and down the elevational gradient, yet we observed downslope movement only, suggesting that regardless of our assumptions in this particular case, our results still support the habitat-optimization hypothesis.

In conclusion, our assessment of meso movements during the post-fledging period provides important insights into their function and relative importance for both immediate and future success of juveniles. In our study region, both species were associated with river valleys, suggesting the importance of this habitat for meeting immediate resource needs. The Blackpoll, however, also appeared to form a homing target, suggesting the importance of resources (e.g., local landmarks) that are not necessarily linked to immediate metabolic demands. Further research is needed to determine the mechanisms behind the close association of these warblers with river valleys and low-elevation habitat and whether or not this behavior influences an individual's current survival or its future success.

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LITERATURE CITED

- AFIK, D., AND W. H. KARASOV. 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76:2247–2257.
- ANDERS, A. D., D. C. DEARBORN, J. FAABORG, AND F. R. THOMPSON III. 1997. Juvenile survival in a population of neotropical migrant birds. *Conservation Biology* 11:698–707.
- ANDERS, A. D., J. FAABORG, AND F. R. THOMPSON III. 1998. Post-fledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115:349–358.
- BAKER, R. R. 1993. The function of post-fledging exploration: a pilot study of three species of passerines ringed in Britain. *Ornis Scandinavica* 24:71–79.
- BETTS, M. G., A. S. HADLEY, N. RODENHOUSE, AND J. J. NOCERA. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society B* 275:2257–2263.
- BINGMAN, V. P., K. P. ABLE, AND P. KERLINGER. 1982. Wind drift, compensation, and the use of landmarks by nocturnal bird migrants. *Animal Behavior* 30:49–53.
- BORMANN, F. H., T. G. SICCAMA, G. E. LIKENS, AND R. H. WHITTAKER. 1970. The Hubbard Brook ecosystem study: composition and dynamics of the tree stratum. *Ecological Monographs* 40:373–388.
- BREWER, R., AND K. G. HARRISON. 1975. The time of habitat selection by birds. *Ibis* 117:521–522.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach, Springer Verlag, New York.
- CARO, S. P., A. CHARMANTIER, M. M. LAMBRECHTS, J. BLONDEL, J. BALHAZART, AND T. D. WILLIAMS. 2009. Local adaptations of timing of reproduction: females are in the driver's seat. *Functional Ecology* 23:172–179.
- CLARKE, A. L., B.-E. SÆTHER, AND E. RØSKAFT. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438.
- DALE, S., Ø. STEIFETTEN, T. S. OSIEJUK, K. LOSAK, AND J. P. CYGAN. 2006. How do birds search for breeding areas at the landscape level? Interpatch movements of male Ortolan Buntings. *Ecography* 29:886–898.
- DAMMAN, A. W. H. 1983. An ecological subdivision of the island of Newfoundland, p. 163–206. *In* G. R. South [ED.], *Biogeography and ecology of the island of Newfoundland*. Junk Publishers, The Hague, Netherlands.
- FRANSSON, T., S. JAKOBSSON, P. JOHANSSON, C. KULLBERG, J. LIND, AND A. VALLIN. 2001. Bird migration: magnetic cues trigger extensive refueling. *Nature* 414:35–36.
- GUTHERY, F. S., L. A. BRENNAN, M. J. PETERSON, AND J. J. LUSK. 2005. Information theory in wildlife science: critique and viewpoint. *Journal of Wildlife Management* 69:457–465.
- HILL, G. E. 1988. Age, plumage brightness, territory quality, and reproductive success in the Black-headed Grosbeak. *Condor* 90:379–388.
- HÖGBERG, M. N., D. D. MYROLD, R. GIESLER, AND P. HÖGBERG. 2006. Contrasting patterns of soil N-cycling in model ecosystems of Fennoscandian boreal forests. *Oecologia* 147:96–107.
- HODKINSON, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80:489–513.
- HOLBERTON, R. L., AND A. M. DUFTY JR. 2005. Hormones and variation in life history strategies of migratory and nonmigratory birds, p. 437–444. *In* R. Greenberg and P. Marra [EDS.], *Birds of two worlds: the ecology and evolution of temperate–tropical migration*. Johns Hopkins University Press, Baltimore.
- HOLMES, R. T., P. P. MARRA, AND T. W. SHERRY. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65:183–195.
- HUNT, P. D., AND B. C. ELIASON. 1999. Blackpoll Warbler (*Dendroica striata*), no. 431. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- HUNT, P. D., AND J. FLASHPOHLER. 1998. Yellow-rumped Warbler (*Dendroica coronata*), no. 376. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- KEANE, J. J., AND M. L. MORRISON. 1999. Variation in resource use by Black-throated Gray Warblers. *Condor* 101:67–75.
- KERSHNER, E. L., J. W. WALK, AND R. E. WARNER. 2004. Post-fledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. *Auk* 121:1146–1154.
- LATTA, S. C., AND C. BROWN. 1999. Autumn stopover ecology of the Blackpoll Warbler (*Dendroica striata*) in thorn scrub forest of the Dominican Republic. *Canadian Journal of Zoology* 77:1147–1156.
- LEONARD, T. D., P. D. TAYLOR, AND I. G. WARKENTIN. 2008. Landscape structure and spatial scale affect space use by songbirds in naturally patchy and harvested boreal forests. *Condor* 110:467–481.
- LUND, U., AND C. AGOSTINELLI [ONLINE]. 2009. The CircStats package. Version 0.2-4. <<http://cran.r-project.org/web/packages/CircStats/index.html>> (1 June 2009).
- MALMBORG, P. K., AND M. J. WILSON. 1988. Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodland. *Condor* 90:173–186.
- MITCHELL, G. W., P. D. TAYLOR, AND I. G. WARKENTIN. 2010. Multi-scale postfledging habitat associations of juvenile songbirds in a managed landscape. *Auk* 127:354–363.
- MITCHELL, G. W., I. G. WARKENTIN, AND P. D. TAYLOR [ONLINE]. 2009. Movement of juvenile songbirds in harvested boreal forest: assessing residency time and landscape connectivity. *Avian Conservation and Ecology* 4(1):5. <<http://www.ace-eco.org/vol4/iss1/art5/>> (1 June 2009).
- MORTON, M. L. 1991. Postfledging dispersal of Green-tailed Towhees to a subalpine meadow. *Condor* 93:466–468.
- MORTON, M. L. 1992. Effects of sex and birthdate on pre-migration biology, migration schedules, return rates and natal dispersal in the Mountain White-crowned Sparrow. *Condor* 94:117–133.
- MORTON, M. L., M. W. WAKAMASTSU, M. E. PEREYRA, AND G. A. MORTON. 1991. Post-fledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. *Ornis Scandinavica* 22:98–106.
- MURTAUGH, P. A. 2009. Performance of several variable-selection methods applied to real ecological data. *Ecology Letters* 12:1061–1068.
- NOCERA, J. J., G. J. FORBES, AND L.-A. GIRALDEAU. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. *Proceedings of the Royal Society of London B* 273:349–355.

- PARRISH, J. D. 1997. Patterns of frugivory and energetic condition in nearctic landbirds during autumn migration. *Condor* 99:681–697.
- PRESNELL, B., S. O. MORRISON, AND R. C. LITTELL. 1998. Projected multivariate linear models for directional data. *Journal of the American Statistical Association* 93:1068–1078.
- PYLE, P. 1997. Identification guide to North American birds, Part 1; Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.
- RAPPOLE, J. H., AND K. BALLARD. 1987. Postbreeding movements of selected birds in Athens, Georgia. *Wilson Bulletin* 99:475–480.
- RAPPOLE, J. H., AND A. R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- R Core Development Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RICHARDSON, W. J. 1972. Autumn migration and weather in eastern Canada: a radar study. *American Birds* 26:10–17.
- ROBINSON, R. A., R. E. GREEN, S. R. BAILLIE, W. J. PEACH, AND D. L. THOMSON. 2004. Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britain. *Journal of Animal Ecology* 73:670–682.
- RODRÍGUEZ, A., H. ANDRÉN, AND G. JANSSON. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* 95:383–396.
- SCAPINI, F., A. ALOIA, M. F. BOUSLAMA, L. CHELAZZI, I. COLOMBINI, M. ELFTARI, M. FALLACI, AND G. M. MARCHETTI. 2002. Multiple regression analysis of the sources of variation in orientation of two sympatric sandhoppers, *Talitrus saltator* and *Talorchestia brito*, from an exposed Mediterranean beach. *Behavioral Ecology and Sociobiology* 51:403–414.
- SEAGLE, S. W., AND B. R. STURTEVANT. 2005. Forest productivity predicts invertebrate biomass and Ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian landscapes. *Ecology* 86:1531–1539.
- SULLIVAN, K. A. 1988. Ontogeny of time budgets in Yellow-eyed Juncos: adaptation to ecological constraints. *Ecology* 69:118–124.
- SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *Journal of Animal Ecology* 58:275–286.
- TAYLOR, P. D., AND M. A. KRAWCHUK [ONLINE]. 2006. Scale and sensitivity of songbird occurrence to landscape structure in a harvested boreal forest. *Avian Conservation and Ecology* 1(1):5. <<http://www.ace-eco.org/vol1/iss1/art5/>> (DATE AVAILABLE?).
- THOMPSON, E. D., D. J. LARSON, AND W. A. MONTEVECCHI. 2003. Characterization of old “wet boreal” forests, with an example from balsam fir forests of western Newfoundland. *Environmental Review* 11:S23–S46.
- VEGA RIVERA, J. H., J. H. RAPPOLE, W. J. MCSHEA, AND C. A. HAAS. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. *Condor* 100:69–78.
- VITZ, A. C., AND A. D. RODEWALD. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biological Conservation* 127:477–486.
- WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. *Auk* 103:1–7.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs* 59:223–246.
- WHEELWRIGHT, N. T., AND R. A. MAUCK. 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. *Ecology* 79:755–767.
- WHITAKER, D. M., AND W. A. MONTEVECCHI. 1999. Breeding bird assemblages inhabiting riparian buffer strips in Newfoundland, Canada. *Journal of Wildlife Management* 63:167–179.
- WHITAKER, D. M., P. D. TAYLOR, AND I. G. WARKENTIN [ONLINE]. 2008. Survival of adult songbirds in boreal forest landscapes fragmented by clearcuts and natural openings. *Avian Conservation and Ecology* 3 (1):5. <<http://www.ace-eco.org/vol3/iss1/art5/>> (1 June 2009).
- WILTSCHKO, W., AND R. WILTSCHKO. 1978. A theoretical model for migratory orientation and homing in birds. *Oikos* 30:177–187.
- WINKLER, D. W., P. H. WREGE, P. E. ALLEN, T. L. KAST, P. SENESAC, M. F. WASSON, AND P. J. SULLIVAN. 2005. The natal dispersal of Tree Swallows in a continuous mainland environment. *Journal of Animal Ecology* 74:1080–1090.