1 Combined effects of migration distance, foraging method vegetation
2 density, and population density on wing shapes of boreal songbirds

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12 Combined effects of migration distance, foraging method vegetation 13 density, and population density on wing shapes of boreal songbirds

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15 **Abstract**

16 In birds, migration distance is known to influence morphological attributes that influence
17 flight performance, especially wing shape. However, wing shape is under the likely
18 influence of less documented factors such as foraging method, vegetation density and
19 isolation of individuals and populations. To better understand factors leading to
20 interspecific differences in wing shape, we measured the pointedness of wings (Kipp's
21 distance) of 1017 live birds of 22 species in an eastern Canadian boreal forest. We modeled
22 wing pointedness as a function of migration distances from eBird records, foraging, habitat,
23 and population density data from *Birds of North America* monographs. Long-distance
24 migrants and species living in low-density vegetation had more pointed wings than shorter-
25 distance migrants and dense-vegetation dwellers, in accordance to our predictions. After
26 accounting for vegetation density and migration distance, we found no link between the
27 extent of aerial foraging or mean breeding population density, an indicator of isolation, and
28 wing pointedness. Those results are consistent with a tradeoff between sustained flight
29 efficiency and maneuverability, but suggest that interspecific variation in wing shape due
30 specifically to foraging method or habitat isolation is nonexistent or obscured by other
31 factors.

32 **Keywords:** ORNITHOLOGY, COMPARATIVE, ECOLOGY, FLIGHT, LOCOMOTION,
33 MIGRATION, MORPHOLOGY

34 Introduction

35 Variation in wing shape is constrained by aerodynamic principles, but it remains highly
 36 variable from one species to another. In the case of birds, elongated wings with short
 37 secondary remiges and long primary remiges facilitate sustained flight (Bowlin and
 38 Wikelski 2008) while rounder wings are thought to facilitate maneuverability (Savile
 39 1957). Wing shape is associated to migratory performance in mammals and birds (Palmer
 40 1900; Norberg and Rayner 1987). This association has been shown with Palearctic warblers
 41 (Marchetti et al. 1995; Nowakowski et al. 2014), Nearctic thrushes (Dilger 1956) and
 42 swallows (Huber et al. 2016), seven Palearctic and Nearctic passerine genera (Mönkkönen
 43 1995), as well as shorebirds (Burns 2003; Minias et al. 2015). North American passerines
 44 may provide an exception to this rule (Keast 1980; Niemi 1985), but no quantitative
 45 evidence exists to assess this claim.

46 Once migration is completed, birds are subject to further selective pressure on
 47 functional traits related to flight, and at very different spatial scales (Huber et al. 2016). For
 48 species gleaning food on the ground, perched or in dense vegetation, the advantages of
 49 manoeuvrability may overwhelm the need for efficient sustained flight (Dilger 1956; Niemi
 50 1985). Isolation from conspecifics and concomitant movement may exert evolutionary
 51 pressure independent of migration distance, in favor of elongated wings (Desrochers 2010).
 52 While their roles are often speculated upon, foraging method, vegetation density and
 53 population isolation remain poorly documented correlates of avian wing shape.

54 In this study we link bird wing pointedness, more specifically the projection of
 55 primary flight feathers also known as Kipp's distance (Lockwood et al. 1998), and four
 56 important aspects of their ecology: migration distance, foraging method, breeding habitat
 57 density and isolation. With boreal forest songbirds, we test the following hypotheses: wings
 58 are more pointed in species 1) with longer migration distances; 2) more frequently using
 59 aerial foraging tactics such as hovering and sallying; 3) foraging in sparse vegetation; and
 60 4) found in low-density breeding populations.

61 **Materials and methods**

62 **Study Area**

63 We conducted field work at Forêt Montmorency, Quebec, Canada (47.4 N, 71.1W) during
 64 the summers 2013 and 2014. This forest has been managed for timber since the early
 65 1930's, with ecosystem management (Bélanger 2001; Gauthier et al. 2008) dominating the
 66 southern half of the territory, and large (100-150 ha) clearcuts dominating the northern half.
 67 Young stands (<20 y) are generally a dense mixture of deciduous and coniferous species
 68 (Mallik et al. 2014), but older stands are largely dominated by balsam fir (*Abies balsamea*
 69 (L.) Mill.), with occasional groves of spruce (*Picea glauca* (Moench) Voss, *Picea mariana*
 70 (Mill.) Britton), birch (*Betula papyrifera* Marsh.) and poplar (*Populus tremuloïdes* Michx.,
 71 *Populus balsamifera* L.).

72 **Wing pointedness**

73 We captured birds in mist nets at 30 sites throughout the 412 km² study area. We deployed
 74 nets between 5 am and 11 am over 2 or 3 consecutive days at each site. We used recordings
 75 of mobbing calls (Gunn et al. 2000) and species songs to increase capture rates. We
 76 banded, identified and measured birds with age and sex determined by plumage (Pyle
 77 1997). To facilitate the measurements of wing pointedness, we took one to three photos of
 78 the right wing flattened on a wing ruler for each bird, with a Nikon D80 digital SLR with a
 79 resolution of 10 Megabytes in 2013 and Nikon D7100 DSLR 24 megabytes in 2014. We
 80 took measurements in pixels from each photo with an image processing software, ImageJ
 81 (<http://imagej.nih.gov/ij/>). Two lengths were obtained: a) the total length of the folded,
 82 flattened, wing, and b) the length between the posterior end of the most distal secondary
 83 feather and the posterior end of the wing (Fig. 1). Wing pointedness was quantified as the
 84 ratio $b/(a+b)$ (Lockwood et al. 1998).

85 Repeated (blind) estimates of the wing pointedness of the same bird by the same
 86 author had a mean standard deviation of 0.27 mm ($n = 666$ birds), and a coefficient of
 87 variation of 1.6%. The mean standard deviation of wing pointedness estimates of the same
 88 bird measured separately by the two authors was 0.3 mm ($n = 20$ birds). We assume that

precision and accuracy of wing pointedness estimates were sufficiently high to yield useful interspecific comparisons.

Aerial Foraging, Vegetation Density, and Population Density

We characterized foraging method, vegetation density, and breeding population density with monographs from *The Birds of North America Online*, BNA (Rodewald 2015). For foraging method, we estimated for each species the proportion of time spent gleaning while perched or on the ground, hovering (picking prey in flight, from substrate), and sallying (flying from perch to catch flying prey, (Eckhardt 1979)). When available, quantitative estimates we used, otherwise we attributed 10% of the time for foraging methods depicted as “occasional” (including “common”, “frequent”, “sometimes”) and 5% for method rarely used (including “seldom”), leaving the rest to the most frequently used method. We calculated an aerial foraging index as a weighted sum, with weights of 1, 2, and 3 for gleaning, hovering and sallying respectively (possible range 1-3; Table 1).

For vegetation density, we made a systematic search of words qualifying density using the “Habitat” section of the BNA account of each species. The search was divided between breeding and winter ranges. We sought words related to shrub layers, "shrub", "bush", "scrub", "dense", "thick", and measured the location of first occurrence of one of these words (*n*th word in the Habitat section). The relative position of the word in the text (100% = first, 0% = last) was taken as an indicator of weight. We assume that keywords used earlier in the paragraph provided evidence for a stronger link to dense cover than those listed towards the end of the text. We added ratings computed for the breeding as well as the wintering season to obtain a vegetation density index for each species (Table 1).

We calculated the mean breeding population density of each species from all the breeding density estimates cited in the BNA species accounts (Table 1). In the case of the little-known Bicknell's Thrush (*Catharus bicknelli*) we used Rimmer et al. (1996) .

114 **Migration distance**

115 To assign average species migration distances, we used the eBird database (Sullivan et al.
116 2009). This site was developed by the Cornell Lab of Ornithology and the National
117 Audubon Society and contains millions of bird sightings throughout the world. We
118 obtained coordinates, rounded to the nearest degree of latitude and longitude, of each
119 observation in January and February (i.e. wintering) for all bird species considered in this
120 study, as well as the total observation effort in minutes. Multiple records of a species in the
121 same latitude/longitude on the same year were reduced to one to prevent bias due to
122 repeated observations (e.g. stragglers attracting large numbers of birders). For each eBird
123 entry ($n = 445,512$, Table 1), we calculated the great-circle distance from the geographic
124 center of the Forêt Montmorency using the ‘sp’ package of R software (Pebesma and
125 Bivand 2005; Bivand et al. 2013).

126 **Statistical analysis**

127 Studies comparing mean attributes from multiple species may suffer from a lack of true
128 replication because of phylogenetic proximity among subsets of the species. To account for
129 this, we obtained phylogenetic trees of the species studied, from Jetz et al. (2012). Because
130 of uncertainty in the relationship between DNA data and years since speciation,
131 phylogenetic trees are only approximations based on various assumptions about the rate of
132 phylogenetic divergence. Thus, we generated 10,000 phylogenetic trees (Fig. 2) and
133 established phylogenetic distances for each dyad from the 22 study species (Paradis et al.
134 2004).

135 We modeled the independent influences of migration distance, aerial foraging
136 index, vegetation density index, and population density on wing pointedness with a linear
137 model using phylogenetic Generalized Least Squares (pGLS). The pGLS method accounts
138 for the phylogenetic distance between species by using a distance covariance matrix which
139 gives more weight to differences in wing pointedness between remote species
140 phylogenetically than in wing pointedness of closely related species (Felsenstein 1985;
141 Grafen 1989; Harvey and Pagel 1991). We ran 10,000 pGLS models, corresponding to each
142 of the 10,000 phylogenetic trees of all species. We calculated summary statistics from those

10,000 models for regression coefficients, their standard error, and p values. Data analyses were conducted in R, using the ‘ape’ (Paradis et al. 2004), ‘nlme’ (Pinheiro et al. 2016), and ‘phylolm’ (Ho and Ané 2014).

Results

We considered 22 different bird species, that is, all species with at least five specimens captured ($n = 1017$; Table 1). Intraspecific variance of wing pointedness was significantly lower than interspecific variance ($F_{21,995} = 266.2$; $p < 0.001$), thus we assume that mean estimates for each species were sufficiently contrasted for comparative analysis. Vegetation density and aerial foraging indices were not significantly correlated ($r_s = 0.1$, $p = 0.6$, $n = 22$).

Wing pointedness was positively associated with migration distance (Fig. 3) and negatively associated to vegetation density (Fig. 4) with all phylogenetic trees (Table 2). Results were similar when the ‘outlier’ species with shortest and longest migration distances (Fig. 3) were removed. We found no relationship between wing pointedness, aerial foraging or breeding population density (Table 2) Results obtained with a multiple regression ignoring phylogenetic effects were highly similar for migration distance (estimate = $2.20\text{e-}5 \pm 5.9\text{e-}6$, $p < 0.001$), aerial foraging (estimate = $8.87\text{e-}4 \pm 2.0\text{e-}2$, $p = 0.9$), vegetation density (estimate = $-1.87\text{e-}2 \pm 7.1\text{e-}3$, $p = 0.02$), and breeding population density (estimate = $-2.38\text{e-}4 \pm 9.1\text{e-}3$, $p > 0.9$).

Discussion

As we predicted, wing pointedness was greater in species that performed longer migration and smaller in species living in more densely vegetated environments. However, the amount of aerial foraging and population density had no explanatory power. The low variance of estimates between GLS models suggests that interspecific differences in wing shape and length (i.e. wing pointedness) were not greatly affected by uncertainty in phylogenetic relationships.

Since the early speculations by Palmer (1900) and Seebohm (1901) (cited by Mönkkönen (1995)), at least a dozen studies have provided evidence for more pointed or

longer wings longer-distance migrants than conspecifics that migrate shorter distances (de La Hera et al. 2010; Rushing et al. 2014), or sedentary ones (Milá et al. 2008). Similar results were found in studies focusing on interspecific differences (Mönkkönen 1995; Minias et al. 2015). The present results, nearly half of which were obtained from north American warblers (Parulidae), are contrary to the earlier suggestions by Keast (1980) and Niemi (1985) that wing shape of those birds was unrelated to migration distance. Instead, this study adds to a growing body of evidence for a generally positive relationship between migratory behavior and wing attributes that facilitate sustained flight.

A notable exception to the wing shape – migration distance rule is the recent comparative analysis of eight swallow genera by Huber et al. (2016). They found a negative link between migration distance and wing pointedness, which they interpret as related to the swallows' aerial foraging behavior which resembles their migratory flight, contrary to most other species whose wing pointedness vs. migration has been investigated so far. Earlier studies also pointed to the importance of foraging behavior as a determinant of wing pointedness, in bats (Baagøe 1987) and birds (Savile 1957; Marchetti et al. 1995; Vanhooydonck et al. 2009). Contrary to expectation, our results did not suggest a link between wing pointedness and aerial foraging *per se*, possibly because of insufficient variation in foraging methods among the 22 species, a lack of precision in our assessment of aerial foraging, or a combination of both. It would therefore be premature to rule out an ecomorphological effect of foraging behavior in itself on wing shape, at least in boreal songbirds.

Vegetation density has long been proposed as influencing wing shape, with longer-winged species found in more open habitats (Linsdale 1938). Rounded wings are often thought to allow better maneuverability, an asset in cluttered habitats (Norberg 1979). Furthermore, less pointed wings could facilitate predator escape on takeoff (Swaddle and Lockwood 2003; Fernández and Lank 2007), also advantageous mostly in dense cover. The present study is the first to provide evidence for a direct relationship between vegetation density and wing pointedness, but it would be premature to generalize to a broader set of species, because here we focused on a specific group of birds, i.e., small-sized forest birds predominantly foraging on standing vegetation or the ground.

201 Contrary to our expectation, there was no significant link between population
202 density, which we assume reflects isolation (negatively), and wing pointedness. This could
203 be due to insufficient precision in breeding population densities measures caused by the
204 patchy records reported in BNA (Poole 2005) for most species. For example, those
205 estimates do not distinguish between situations where a species would be found in dense
206 clusters at the habitat patch scale, but scarce at the landscape scale, vs. uniformly scattered
207 pairs throughout a landscape. Such differences could greatly affect the level of isolation
208 experienced by individual members of the species. Furthermore, the population density of
209 certain bird species may vary greatly from one region to another, as well as between
210 wintering and nesting areas (Sherry and Holmes 1996). Unfortunately, there are few data
211 on population densities in the wintering grounds. Regardless of data availability, it is
212 perhaps unrealistic to expect that a species can be reduced to a single population density,
213 because of the substantial geographic variation which is likely to occur.

214 Despite the latter caveats, the use of a comparative approach between different
215 species of the same group still remains a useful approach to understand general patterns of
216 habitat use in association to wing morphology. The accumulation of evidence on correlates
217 of avian wing shape should not only lead to a better understanding of ecological differences
218 among species, but opens the way for more incisive comparative analyses testing
219 predictions about avian responses to ever-changing environments.

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Table 1. Species characteristics. Species ordered according to their estimated phylogenetic tree.

Scientific name	English name	N	Mean Wing pointedness	Aerial foraging index	Vegetation Density index	Mean Migration Distance (km)	Mean Breeding Density (Pairs/km ²)
<i>Setophaga coronata</i> L.	Yellow-rumped Warbler	66	0.232	1.45	0.85	3526 (74222)	44.4
<i>Setophaga virens</i> Gmelin	Black-throated Green Warbler	39	0.238	1.20	0.38	3771 (2989)	122.5
<i>Setophaga ruticilla</i> L.	American Redstart	37	0.196	2.20	3.02	3554 (4610)	163.7
<i>Setophaga striata</i> Forster	Blackpoll Warbler	128	0.292	1.15	1.08	4836 (230)	46.1
<i>Setophaga castanea</i> Wilson	Bay-breasted Warbler	26	0.283	1.15	0.97	4503 (427)	155.9
<i>Setophaga magnolia</i> Wilson	Magnolia Warbler	169	0.193	1.25	1.61	3759 (2316)	90.9
<i>Cardellina pusilla</i> Wilson	Wilson's Warbler	27	0.190	1.35	2.72	3932 (5636)	147.8
<i>Oreothlypis ruficapilla</i> Wilson	Nashville Warbler	45	0.214	1.15	0.55	3982 (2103)	56.3
<i>Oreothlypis peregrina</i> Wilson	Tennessee Warbler	18	0.265	1.15	1.82	4153 (3023)	251.2
<i>Geothlypis trichas</i> L.	Common Yellowthroat	12	0.161	1.15	3.14	3498 (21240)	98.0
<i>Junco hyemalis</i> L.	Dark-eyed Junco	49	0.197	1.00	2.97	2617 (95691)	95.8
<i>Zonotrichia albicollis</i> Gmelin	White-throated Sparrow	96	0.163	1.00	3.45	2159 (70635)	47.2
<i>Passerella iliaca</i> Merrem	Fox Sparrow	11	0.218	1.10	2.21	2957 (32735)	95.0
<i>Melospiza lincolni</i> Audubon	Lincoln's Sparrow	30	0.180	1.05	2.33	3703 (16018)	324.0
<i>Regulus satrapa</i> Lichtenstein	Golden-crowned Kinglet	22	0.213	1.60	2.41	2570 (39908)	169.6
<i>Regulus calendula</i> L.	Ruby-crowned Kinglet	50	0.194	1.90	1.99	3398 (68375)	185.0
<i>Catharus ustulatus</i> Nuttall	Swainson's Thrush	114	0.299	1.40	1.22	4930 (1147)	88.4
<i>Catharus bicknelli</i> Ridgway	Bicknell's Thrush	7	0.274	1.30	2.03	3138 (137)	129.7
<i>Poecile hudsonicus</i> Forster	Boreal Chickadee	13	0.159	1.20	0.00	0 (2154)	6.7
<i>Vireo philadelphicus</i> Cassin	Philadelphia Vireo	24	0.237	1.15	1.83	4047 (839)	38.6
<i>Empidonax flaviventris</i> Baird	Yellow-bellied Flycatcher	14	0.217	2.42	3.45	3927 (1042)	15.4
<i>Empidonax alnorum</i> Brewster	Alder Flycatcher	20	0.226	1.74	3.63	6519 (35)	54.9

Table 2. Means and ranges of GLS model estimates and p-values for 10,000 trees for relationship between wing pointedness, Aerial foraging Index, Vegetation Density Index, Migration Distance and Breeding Population Density ($N = 22$ species).

	Estimate	p
	-	
Aerial Foraging Index	0.0000100 [-0.00122,0.00148]	0.99 [0.94,1]
Vegetation Density Index	-0.0184 [-0.0190,-0.0181]	0.021 [0.018,0.024]
Migration Distance (per 1000 km)	0.0221 [0.0218,0.0225]	0.002 [0.0020,0.0024]
Breeding Population density (per 100 km ²)	0.016 [-0.035,0.078]	2]
		0.98 [0.93,1]

Figures

Fig. 1. Measurements used to calculate wing pointedness. Red markers (1,2 and 3) were tattooed on photos to facilitate measurements.

Fig. 2. A phylogenetic tree of the species in the study. Generated from the website "birdtree.org" (Jetz et al. 2014).

Fig. 3. Wing pointedness in relation with migration distance in kilometers. Each point denotes a species.

Fig. 4. Wing pointedness in relation with vegetation density index. Each point denotes a species.