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Morphological response of songbirds to
100 years of landscape change in North America

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Abstract. Major landscape changes caused by humans may create strong selection pressures and induce rapid evolution in natural populations. In the last 100 years, eastern North America has experienced extensive clear-cutting in boreal areas, while afforestation has occurred in most temperate areas. Based on museum specimens, I show that wings of several boreal forest songbirds and temperate songbirds of non-forest habitats have become more pointed over the last 100 years. In contrast, wings of most temperate forest and early-successional boreal forests species have become less pointed over the same period. In contrast to wing shape, the bill length of most species did not change significantly through time. These results are consistent with the "habitat isolation hypothesis", i.e., songbirds evolved in response to recent changes in the amount of available habitat and associated implications for mobility. Rapid morphological evolution may mitigate, without necessarily preventing, negative consequences of habitat loss caused by humans through direct exploitation or climate change.

Key words: Rapid evolution; Landscape Ecology; Wing shape; Morphology; Forest fragmentation; Habitat loss; Museum specimens.
INTRODUCTION

Whether species can adapt rapidly to unprecedented environmental change caused by humans has become a major concern for ecologists (Rice and Emery 2003). Animals are able to evolve behavioral and morphological adaptations rapidly enough to track anthropogenic environmental change over decades or centuries, as illustrated by classic studies of industrial melanism in moths (Ford 1937), bill size (Grant and Grant 1989) and wing shape (Vanhooydonck et al. 2009) in Darwin's finches, and migratory behavior (Berthold et al. 1992). Such rapid evolution may be facilitated by behavioral innovations (Lefebvre et al. 2004) and may ultimately help population or even species to persist (Nicolakakis et al. 2003, Bell and Gonzalez 2009). However, gene flow may often inhibit the ability of local populations to adapt to local or regional environmental dynamics (Storfer 1999). The generality with which animals undergo rapid evolution in response to environmental change remains unknown.

Forest loss and fragmentation have been major conservation concerns in recent decades, although their evolutionary consequences generally have been ignored except for gene flow reduction (Ashley et al. 2003). Forest loss and fragmentation should select for higher mobility in animals, due to increased habitat isolation (Fahrig 2003), at least when colonization of fragments remains possible for the most mobile individuals. In birds, high mobility is often associated with pointed wings (Dawideit et al. 2009), because they result in more energy-efficient sustained flight (Bowlin and Wikelski 2008). Wing "pointedness" can evolve rapidly within species (Egbert and Belthoff 2003, Fiedler 2005), and is highly responsive not only to migratory distance (Winkler and Leisler 1992) but also to the amount of regional movement (Senar et al. 1994). By imposing new
constraints on dispersal and other daily movements of birds, forest fragmentation may require hundreds of additional kilometers of travel for individual birds each year, creating a new selective pressure for more pointed wings, especially in the case of non-migratory species. Conversely, reduced habitat fragmentation should favor rounder wings, given the high cost of take-off (Swaddle and Lockwood 2003) or foraging with more pointed wings, especially for species foraging close to the ground or in thick vegetation (Savile 1957, Marchetti et al. 1995).

North-eastern North America offers a unique "natural experiment" with which to examine evolutionary change in birds in response to habitat loss and fragmentation. The temperate part of this region (south of the Laurentian hills) suffered severe deforestation in the 19th century, followed by a reverse trend of afforestation in the 20th century (Foster and Motzkin 2003). In contrast, boreal forests of eastern North America (Canadian shield, Abitibi and Lac-St-Jean lowlands) have been subjected to extensive clear-cuts for most of the 20th century, leading to a sharp decline of old coniferous forests and their replacement by younger mixed and deciduous stands (Imbeau et al. 2001, Boucher et al. 2009). If songbird fitness is reduced by the isolation caused by forest loss and fragmentation — as often implied and sometimes shown in the extensive literature on the subject (Fahrig 2003) — we should expect evolutionary change in flight-related attributes such as wing shape in parallel with major changes in habitat isolation (habitat isolation hypothesis).

Using museum specimens, I examined changes in the morphology of forest birds of north-eastern North-America since the beginning of the 20th century. More specifically, I tested the following predictions: over the last century, species mostly...
found in boreal, mature coniferous forests and temperate non-forest habitats evolved more pointed wings in response to increased fragmentation, whereas species associated with temperate mature forests and boreal early-successional forests evolved less pointed wings because of relaxed selection for mobility. Additionally, I examined whether the above predictions were better supported in non-migratory species than in neotropical migrant species. Finally, I tested for temporal trends in culmen (bill) length as a "control", to contrast temporal changes due to mobility with effects of landscape changes unrelated to isolation.

METHODS

I measured 851 specimens of fully grown (> 1 month post fledging) birds of 21 species from the Cornell University Museum of Vertebrates and the Canadian Museum of Nature. Specimens used here were collected between 1900 and 2008, throughout their species' geographic distribution (exceptions described below). I selected all species meeting the following requirements: 1) > 10 specimens ranging over most of the last 100 years, 2) small enough to be measured with digital calipers, and 3) unambiguous association to one of the following four groups: boreal mature forests, temperate mature forests, boreal open areas (< 20 y old forest stands, shrubs, crops, or pastures), and temperate open areas, based on Birds of North America monographs (Poole 2005). Two exceptions were Red-breasted Nuthatch (*Sitta canadensis*) and Brown Creeper (*Certhia americana*); these species breed extensively both in temperate and boreal forests. Nuthatch specimens from both regions were measured but were analyzed separately. In the case of Brown Creeper, I analyzed only specimens collected in Maryland, New
Hampshire, New York, and Ohio. Only specimens collected east of the Mississippi were measured in the case of species whose range extended to western North America. I measured the distance between the carpal joint of the right wing and the distal end of (a) the outermost secondary feather, and (b) wing tip (unflattened wing chord). I used the ratio of distances $100*(b-a)/b$, also known as "primary projection", to evaluate wing pointedness (Fig. 1). Left wings were used for measurement when right wings were damaged or absent from the specimen ($n = 24$). I also measured the total length of the culmen (bill) from skull to the distal end of the upper mandible. All measurements were made with digital calipers under a dissecting microscope. Specimens with apparent molt of flight feathers or extensive feather wear were infrequent ($n < 30$) and discarded from analyses. A random sample of 128 specimens was measured twice (non-sequentially, i.e., "blind"), to assess measurement error. Median differences between measurements of the same specimens were 0.25 mm, 0.30 mm and 0.16 mm for secondary feathers, wing chord and total culmen respectively, yielding intra-class correlation coefficients (measurement repeatabilities) $> 98.9\%$. I estimated temporal changes in primary projection for single species with linear models using the following covariates: year of collection and sex. Mean temporal changes in primary projection for each of the four species groups were obtained from mixed-effects linear models, with year of collection as covariate, and species and sex within species as random effects (SAS Institute 2009). In the case of mature forest species, migratory status (migrant or not) was also included as a fixed-effect covariate (species from open habitats were all migrant). Mean changes in culmen length for each of the four species groups were assessed with year of collection as a covariate and species and sex within species as random effects. Model residuals were
examined visually through diagnostic plots and no strong departures from normality or homoscedasticity were noted. I did not use independent, phylogeny-based contrasts in the analysis, because I assume that phylogenetic relationships among species did not greatly influence significance testing, given the very short time periods involved, and the presence of temporal change in a broad variety of the taxa examined.

RESULTS

Primary projection of half of the species selected for study changed significantly over the last century (Table 1). Only one of the 11 significant temporal trends (Wilson's Warbler, Wilsonia pusilla, Table 1) was opposite to the prediction from the habitat isolation hypothesis (binomial test, $P = 0.01$). In accordance with predictions, songbirds of temperate mature forests evolved rounder wings, while those of boreal mature forests evolved more pointed wings, after inter-specific and sexual differences were accounted for (Table 1; Fig. 2). Primary projection trends for birds of open areas such as fields and young forests were opposite to those of mature forest species of the same region, again consistent with predictions. Temporal trends differed greatly among the four species groups (mixed model, year × group interaction, $F_{3,803} = 32.1, P < 0.0001$).

Additionally, there was evidence for regional differences in wing shape trends within species: Red-breasted Nuthatch had increasingly pointed wings in boreal areas, and rounder wings in temperate regions over the last century (region × year interaction $F_{1,74} = 7.4, P = 0.008$). Migratory status was unrelated to change in wing shape in the temperate mature forest species (year × migratory status interaction: $F_{1,250} = 1.08, P = 0.3$).
However, over the last century, increase in primary projection was greater by 1.74% (± 0.86 SE) in residents than in migrants in the case of boreal mature forest species ($F_{1,364} = 4.02, P = 0.046$). Wings of mature forest species were more pointed than those of species in young successional or open habitats ($F_{1,890} = 330.0, P < 0.0001$) suggesting an influence of foraging substrate. In contrast to wing shape, culmen length seldom changed over the last 100 years. It changed only in mature boreal species, with five of the six species having longer culmens (mean = 0.47 mm per 100 y, SE = 0.21, $t_{357} = 2.2, P = 0.03$).

**DISCUSSION**

These documented changes in avian wing morphology over the last century are remarkably consistent with the hypothesis that forest loss and fragmentation induces strong selection pressure for mobility. Only Wilson's Warbler did not fit the expectation of the habitat isolation hypothesis, possibly because of misclassification of its habitat, which is often riparian (Ammon and Gilbert 1999), or undocumented pressure on movements, such as possible changes in wintering areas. These results provide new evidence in support of the thesis that habitat loss and fragmentation have lasting consequences on avian behavior, fitness and ultimately, evolution (see also Lens et al. (1999)). That the physiological advantages of elongated wings (Bowlin and Wikelski 2008) and the isolation cost of habitat fragmentation (Fahrig 2003) would result in rapid evolution of wing morphology is not trivial; alternatively, the selective pressure may have been insufficient or overcome by gene flow, resulting in no measurable evolutionary response. Few studies on birds have shown fitness consequences of habitat
fragmentation, especially in terms of increased isolation (as opposed to effects that fragmentation may have on habitat quality). However, in a meta-analysis of 80 avian species, Lampila et al. (2005) showed that habitat fragmentation does have fitness implications. Specifically, they showed that pairing success was the reproductive variable most influenced by forest fragmentation, suggesting that fitness consequences of habitat fragmentation are mostly the result of habitat isolation.

Of course, there are possible alternative explanations, given the large number of factors responsible for avian wing morphology (Marchetti et al. 1995). Although primary projection is not known to systematically change with age, wing length does change with age in some species (Alatalo et al. 1984) and may have confounded temporal trends. However, there was no measurable change in the proportion of first-year birds through time in the 578 specimens measured for which age determination was reliable (logistic regression: $P > 0.17$ in each group of species), thus making age-related bias in the samples very unlikely. A second alternative explanation is that changes in primary projection may simply reflect phenotypic, as opposed to genetic, change (Gienapp et al. 2008). However, body measurements are highly heritable, with narrow-sense $h^2$ generally between $0.6 – 0.7$ in the case of wing length, which as in this study combines but does not distinguish skeletal and feather components (Boag and van Noordwijk 1987). Thus, although various stresses on feather or skeletal growth may account for the patterns observed, heritable variation almost certainly accounted for part of the temporal change in primary projection. A third alternative hypothesis is that size measurements often vary geographically and population shifts over constant collecting locations have been responsible for the temporal trends, but this is unlikely given the broad geographic extent
of sampling locations for most species. Furthermore, if population shifts occurred, they would have been non-random with respect to landscape changes; otherwise they would have obscured the differences in temporal trends among species groups. Finally, changes in primary projection possibly reflect changes in habitat other than isolation per se (e.g., food resources). The difference in primary projection between mature forest species and open/shrub species supports this idea, but the lack of temporal trends in culmen length in species found outside mature boreal forests is inconsistent with the idea that changes in foraging strategy are the main driving force behind temporal trends in wing shape.

Museum specimens have been used previously to document rapid evolutionary change in birds (Smith et al. 1995) and mammals (Pergams and Ashley 1999). However, museum specimens remain a relatively untapped data source that could provide key information relevant to the fate of birds and other species in response to rapidly changing environments. The assumption that species do not respond adaptively to rapid environmental change caused by humans is frequent and probably wrong in many cases, and several authors have warned that this may lead to species mismanagement (Ashley et al. 2003, Rice and Emery 2003, Stockwell et al. 2003, Bell and Gonzalez 2009). As with their ability to adapt to climate change (Walther et al. 2002), birds’ ability to adapt rapidly to forest loss and fragmentation may mitigate, without necessarily preventing, the risk of regional extirpation of extinction. Further research should investigate the potential for rapid evolution in response to habitat fragmentation in other parts of the World, in particular the tropics, where recent decline in habitat area, as well as lack of dispersal ability in birds, are sometimes drastic. Hopefully this research will contribute to the
emerging drive towards "evolutionary-enlightened management" (Ashley et al. 2003) of species in the hope of reducing the risk of regional extirpation or extinction.

ACKNOWLEDGMENTS

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LITERATURE CITED


Table 1 Change in primary projection in 21 songbird species, 1900-2008. Migratory status based on winter distribution:

Residents (R) = year-round in their breeding range, Short-distance (SD) = mostly in continental US, long-distance (LD) = in the Caribbean or south of continental US.

<table>
<thead>
<tr>
<th>Species</th>
<th>Migratory status</th>
<th>Primary projection (% of wing chord)*</th>
<th>Change in Primary projection (/100 y)</th>
<th>SE</th>
<th>Error df</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
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<td></td>
<td></td>
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<td></td>
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<tr>
<td>Red-breasted Nuthatch, <em>Sitta canadensis</em></td>
<td>R</td>
<td>25.4</td>
<td>-1.65</td>
<td>1.78</td>
<td>17</td>
<td>-0.92</td>
<td>0.369</td>
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<td>30.2</td>
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<td>47</td>
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<td>26.4</td>
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<td>2SE</td>
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<td>365</td>
<td>7.09</td>
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<td>0.96</td>
<td>56</td>
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<td>1.42</td>
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<td>0.372</td>
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<td>7.31</td>
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<td>11</td>
<td>2.57</td>
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* Corrected for year (set to 1950).
Figure Legends

**FIG. 1.** Measurements used to calculate primary projection in wings of museum specimens, showing the distance between the carpal joint of the right wing and the distal end of (a) the outermost secondary feather, and (b) wing tip (unflattened wing chord).

Photo of female Scarlet Tanager, by A. Desrochers.

**FIG. 2.** Change in primary projection in wings of four groups of eastern North American songbirds since 1900. Species groups based on breeding range and habitat. Scales are identical to facilitate comparisons.