ECOLOGICAL SOCIETY OF AMERICA

Ecology/Ecological Monographs/Ecological Applications

1

Morphological response of songbirds to

100 years of landscape change in North America

4

5   A. DESROCHERS

6

7   *Centre d'étude de la forêt, Université Laval, Pavillon Abitibi-Price, 2405 rue de la*

8   *Terrasse, Québec, Qc, G1V 0A6 CANADA; and Laboratory of Ornithology, Cornell*

9   *University, 159 Sapsucker Woods Road, Ithaca, NY 14850 USA. Tel. (418) 656-2131 ext.*

10   *2908. Email : andre.desrochers@sbf.ulaval.ca*

11

12   Running title: Morphological response to landscape change

13

14

15   Article type: Report

16   Word count: 156 (Abstract), 3133 (Main text incl. references, without Tables and

17   Figures).

18   Figures: 2

19   Tables: 1

20

21

22   *Abstract.* Major landscape changes caused by humans may create strong selection

23   pressures and induce rapid evolution in natural populations. In the last 100 years, eastern

24   North America has experienced extensive clear-cutting in boreal areas, while

25   afforestation has occurred in most temperate areas. Based on museum specimens, I show

26   that wings of several boreal forest songbirds and temperate songbirds of non-forest

27   habitats have become more pointed over the last 100 years. In contrast, wings of most

28   temperate forest and early-successional boreal forests species have become less pointed

29   over the same period. In contrast to wing shape, the bill length of most species did not

30   change significantly through time. These results are consistent with the "habitat isolation

31   hypothesis", i.e., songbirds evolved in response to recent changes in the amount of

32   available habitat and associated implications for mobility. Rapid morphological evolution

33   may mitigate, without necessarily preventing, negative consequences of habitat loss

34   caused by humans through direct exploitation or climate change.

35

36   *Key words: Rapid evolution; Landscape Ecology; Wing shape; Morphology; Forest*

37   *fragmentation; Habitat loss; Museum specimens.*

38

39   INTRODUCTION

40   Whether species can adapt rapidly to unprecedented environmental change caused by

41   humans has become a major concern for ecologists (Rice and Emery 2003). Animals are

42   able to evolve behavioral and morphological adaptations rapidly enough to track

43   anthropogenic environmental change over decades or centuries, as illustrated by classic

44   studies of industrial melanism in moths (Ford 1937), bill size (Grant and Grant 1989) and

45   wing shape (Vanhooydonck et al. 2009) in Darwin's finches, and migratory behavior

46   (Berthold et al. 1992). Such rapid evolution may be facilitated by behavioral innovations

47   (Lefebvre et al. 2004) and may ultimately help population or even species to persist

48   (Nicolakakis et al. 2003, Bell and Gonzalez 2009). However, gene flow may often inhibit

49   the ability of local populations to adapt to local or regional environmental dynamics

50   (Storfer 1999). The generality with which animals undergo rapid evolution in response to

51   environmental change remains unknown.

52   Forest loss and fragmentation have been major conservation concerns in recent

53   decades, although their evolutionary consequences generally have been ignored except

54   for gene flow reduction (Ashley et al. 2003). Forest loss and fragmentation should select

55   for higher mobility in animals, due to increased habitat isolation (Fahrig 2003), at least

56   when colonization of fragments remains possible for the most mobile individuals. In

57   birds, high mobility is often associated with pointed wings (Dawideit et al. 2009),

58   because they result in more energy-efficient sustained flight (Bowlin and Wikelski 2008).

59   Wing "pointedness" can evolve rapidly within species (Egbert and Belthoff 2003, Fiedler

60   2005), and is highly responsive not only to migratory distance (Winkler and Leisler 1992)

61   but also to the amount of regional movement (Senar et al. 1994). By imposing new

62   constraints on dispersal and other daily movements of birds, forest fragmentation may

63   require hundreds of additional kilometers of travel for individual birds each year, creating

64   a new selective pressure for more pointed wings, especially in the case of non-migratory

65   species. Conversely, reduced habitat fragmentation should favor rounder wings, given the

66   high cost of take-off (Swaddle and Lockwood 2003) or foraging with more pointed

67   wings, especially for species foraging close to the ground or in thick vegetation (Savile

68   1957, Marchetti et al. 1995).

69   North-eastern North America offers a unique "natural experiment" with which to

70   examine evolutionary change in birds in response to habitat loss and fragmentation. The

71   temperate part of this region (south of the Laurentian hills) suffered severe deforestation

72   in the 19th century, followed by a reverse trend of afforestation in the 20th century (Foster

73   and Motzkin 2003). In contrast, boreal forests of eastern North America (Canadian

74   shield, Abitibi and Lac-St-Jean lowlands) have been subjected to extensive clear-cuts for

75   most of the 20th century, leading to a sharp decline of old coniferous forests and their

76   replacement by younger mixed and deciduous stands (Imbeau et al. 2001, Boucher et al.

77   2009). If songbird fitness is reduced by the isolation caused by forest loss and

78   fragmentation — as often implied and sometimes shown in the extensive literature on the

79   subject (Fahrig 2003) — we should expect evolutionary change in flight-related attributes

80   such as wing shape in parallel with major changes in habitat isolation (habitat isolation

81   hypothesis).

82   Using museum specimens, I examined changes in the morphology of forest birds

83   of north-eastern North-America since the beginning of the 20th century. More

84   specifically, I tested the following predictions : over the last century, species mostly

85 found in boreal, mature coniferous forests and temperate non-forest habitats evolved

86 more pointed wings in response to increased fragmentation, whereas species associated

87 with temperate mature forests and boreal early-successional forests evolved less pointed

88 wings because of relaxed selection for mobility. Additionally, I examined whether the

89 above predictions were better supported in non-migratory species than in neotropical

90 migrant species. Finally, I tested for temporal trends in culmen (bill) length as a

91 "control", to contrast temporal changes due to mobility with effects of landscape changes

92 unrelated to isolation.

93

94   METHODS

95 I measured 851 specimens of fully grown (> 1 month post fledging) birds of 21 species

96 from the Cornell University Museum of Vertebrates and the Canadian Museum of

97 Nature. Specimens used here were collected between 1900 and 2008, throughout their

98 species' geographic distribution (exceptions described below). I selected all species

99 meeting the following requirements : 1) > 10 specimens ranging over most of the last 100

100 years, 2) small enough to be measured with digital calipers, and 3) unambiguous

101 association to one of the following four groups: boreal mature forests, temperate mature

102 forests, boreal open areas (< 20 y old forest stands, shrubs, crops, or pastures), and

103 temperate open areas, based on Birds of North America monographs (Poole 2005). Two

104 exceptions were Red-breasted Nuthatch (*Sitta canadensis*) and Brown Creeper (*Certhia*

105 *americana*); these species breed extensively both in temperate and boreal forests.

106 Nuthatch specimens from both regions were measured but were analyzed separately. In

107 the case of Brown Creeper, I analyzed only specimens collected in Maryland, New

108   Hampshire, New York, and Ohio. Only specimens collected east of the Mississippi were

109   measured in the case of species whose range extended to western North America.

110   I measured the distance between the carpal joint of the right wing and the distal

111   end of (a) the outermost secondary feather, and (b) wing tip (unflattened wing chord). I

112   used the ratio of distances 100*(b-a)/b, also known as "primary projection", to evaluate

113   wing pointedness (Fig. 1). Left wings were used for measurement when right wings were

114   damaged or absent from the specimen ($n = 24$). I also measured the total length of the

115   culmen (bill) from skull to the distal end of the upper mandible. All measurements were

116   made with digital calipers under a dissecting microscope. Specimens with apparent molt

117   of flight feathers or extensive feather wear were infrequent ($n < 30$) and discarded from

118   analyses. A random sample of 128 specimens was measured twice (non-sequentially, i.e.,

119   "blind"), to assess measurement error. Median differences between measurements of the

120   same specimens were 0.25 mm, 0.30 mm and 0.16 mm for secondary feathers, wing

121   chord and total culmen respectively, yielding intra-class correlation coefficients

122   (measurement repeatabilities) > 98.9 %. I estimated temporal changes in primary

123   projection for single species with linear models using the following covariates: year of

124   collection and sex. Mean temporal changes in primary projection for each of the four

125   species groups were obtained from mixed-effects linear models, with year of collection as

126   covariate, and species and sex within species as random effects (SAS Institute 2009). In

127   the case of mature forest species, migratory status (migrant or not) was also included as a

128   fixed-effect covariate (species from open habitats were all migrant). Mean changes in

129   culmen length for each of the four species groups were assessed with year of collection as

130   a covariate and species and sex within species as random effects. Model residuals were

131   examined visually through diagnostic plots and no strong departures from normality or

132   homoscedasticity were noted. I did not use independent, phylogeny-based contrasts in the

133   analysis, because I assume that phylogenetic relationships among species did not greatly

134   influence significance testing, given the very short time periods involved, and the

135   presence of temporal change in a broad variety of the taxa examined.

136

137   RESULTS

138   Primary projection of half of the species selected for study changed significantly over the

139   last century (Table 1). Only one of the 11 significant temporal trends (Wilson's Warbler,

140   *Wilsonia pusilla*, Table 1) was opposite to the prediction from the habitat isolation

141   hypothesis (binomial test, $P = 0.01$). In accordance with predictions, songbirds of

142   temperate mature forests evolved rounder wings, while those of boreal mature forests

143   evolved more pointed wings, after inter-specific and sexual differences were accounted

144   for (Table 1; Fig. 2). Primary projection trends for birds of open areas such as fields and

145   young forests were opposite to those of mature forest species of the same region, again

146   consistent with predictions. Temporal trends differed greatly among the four species

147   groups (mixed model, year × group interaction, $F_{3,803} = 32.1$, $P < 0.0001$).

148

149   Additionally, there was evidence for regional differences in wing shape trends within

150   species: Red-breasted Nuthatch had increasingly pointed wings in boreal areas, and

151   rounder wings in temperate regions over the last century (region × year interaction $F_{1,74} =$

152   7.4, $P = 0.008$). Migratory status was unrelated to change in wing shape in the temperate

153   mature forest species (year × migratory status interaction: $F_{1,250} = 1.08$, $P = 0.3$).

154   However, over the last century, increase in primary projection was greater by 1.74 %

155   ($\pm$ 0.86 SE) in residents than in migrants in the case of boreal mature forest species

156   ($F_{1,364} = 4.02$, $P = 0.046$). Wings of mature forest species were more pointed than those

157   of species in young successional or open habitats (Table 1; $F_{1,890} = 330.0$, $P < 0.0001$)

158   suggesting an influence of foraging substrate. In contrast to wing shape, culmen length

159   seldom changed over the last 100 years. It changed only in mature boreal species, with

160   five of the six species having longer culmens (mean = 0.47 mm per 100 y, SE = 0.21,

161    $t_{357} = 2.2$, $P = 0.03$).

162

163   DISCUSSION

164   These documented changes in avian wing morphology over the last century are

165   remarkably consistent with the hypothesis that forest loss and fragmentation induces

166   strong selection pressure for mobility. Only Wilson's Warbler did not fit the expectation

167   of the habitat isolation hypothesis, possibly because of misclassification of its habitat,

168   which is often riparian (Ammon and Gilbert 1999), or undocumented pressure on

169   movements, such as possible changes in wintering areas. These results provide new

170   evidence in support of the thesis that habitat loss and fragmentation have lasting

171   consequences on avian behavior, fitness and ultimately, evolution (see also Lens et al.

172   (1999)). That the physiological advantages of elongated wings (Bowlin and Wikelski

173   2008) and the isolation cost of habitat fragmentation (Fahrig 2003) would result in rapid

174   evolution of wing morphology is not trivial; alternatively, the selective pressure may

175   have been insufficient or overcome by gene flow, resulting in no measurable evolutionary

176   response. Few studies on birds have shown fitness consequences of habitat

177   fragmentation, especially in terms of increased isolation (as opposed to effects that

178   fragmentation may have on habitat quality). However, in a meta-analysis of 80 avian

179   species, Lampila et al. (2005) showed that habitat fragmentation does have fitness

180   implications. Specifically, they showed that pairing success was the reproductive variable

181   most influenced by forest fragmentation, suggesting that fitness consequences of habitat

182   fragmentation are mostly the result of habitat isolation.

183   Of course, there are possible alternative explanations, given the large number of

184   factors responsible for avian wing morphology (Marchetti et al. 1995). Although primary

185   projection is not known to systematically change with age, wing length does change with

186   age in some species (Alatalo et al. 1984) and may have confounded temporal trends.

187   However, there was no measurable change in the proportion of first-year birds through

188   time in the 578 specimens measured for which age determination was reliable (logistic

189   regression: $P > 0.17$ in each group of species), thus making age-related bias in the

190   samples very unlikely. A second alternative explanation is that changes in primary

191   projection may simply reflect phenotypic, as opposed to genetic, change (Gienapp et al.

192   2008). However, body measurements are highly heritable, with narrow-sense h^2 generally

193   between ~ 0.6 – 0.7 in the case of wing length, which as in this study combines but does

194   not distinguish skeletal and feather components (Boag and van Noordwijk 1987). Thus,

195   although various stresses on feather or skeletal growth may account for the patterns

196   observed, heritable variation almost certainly accounted for part of the temporal change

197   in primary projection. A third alternative hypothesis is that size measurements often vary

198   geographically and population shifts over constant collecting locations have been

199   responsible for the temporal trends, but this is unlikely given the broad geographic extent

200   of sampling locations for most species. Furthermore, if population shifts occurred, they

201   would have been non-random with respect to landscape changes; otherwise they would

202   have obscured the differences in temporal trends among species groups. Finally, changes

203   in primary projection possibly reflect changes in habitat other than isolation per se (e.g.,

204   food resources). The difference in primary projection between mature forest species and

205   open/shrub species supports this idea, but the lack of temporal trends in culmen length in

206   species found outside mature boreal forests is inconsistent with the idea that changes in

207   foraging strategy are the main driving force behind temporal trends in wing shape.

208   Museum specimens have been used previously to document rapid evolutionary

209   change in birds (Smith et al. 1995) and mammals (Pergams and Ashley 1999). However,

210   museum specimens remain a relatively untapped data source that could provide key

211   information relevant to the fate of birds and other species in response to rapidly changing

212   environments. The assumption that species do not respond adaptively to rapid

213   environmental change caused by humans is frequent and probably wrong in many cases,

214   and several authors have warned that this may lead to species mismanagement (Ashley et

215   al. 2003, Rice and Emery 2003, Stockwell et al. 2003, Bell and Gonzalez 2009). As with

216   their ability to adapt to climate change (Walther et al. 2002), birds' ability to adapt

217   rapidly to forest loss and fragmentation may mitigate, without necessarily preventing, the

218   risk of regional extirpation of extinction. Further research should investigate the potential

219   for rapid evolution in response to habitat fragmentation in other parts of the World, in

220   particular the tropics, where recent decline in habitat area, as well as lack of dispersal

221   ability in birds, are sometimes drastic. Hopefully this research will contribute to the

222 emerging drive towards "evolutionary-enlightened management" (Ashley et al. 2003) of

223 species in the hope of reducing the risk of regional extirpation or extinction.

224

225

226

233

234 LITERATURE CITED

235

236 Alatalo, R. V., L. Gustafsson, and A. Lundberg. 1984. Why have young passerine birds

237   shorter wings than older ones? Ibis 126:410-415.

238 Ammon, E. M. and W. M. Gilbert. 1999. Wilson's Warbler.*in* A. Poole, editor. The birds

239   of North America Online. Cornell Lab of Ornithology, Ithaca, NY, USA.

240 Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O'Dowd, S. M. Gende, and J. S.

241   Brown. 2003. Evolutionarily enlightened management. Biological Conservation

242   111:115-123.

243 Bell, G. and A. Gonzalez. 2009. Evolutionary rescue can prevent extinction following

244   environmental change. Ecology Letters 12:doi 10.1111/j.1461-

245   0248.2009.01350.x.

246 Berthold, P., A. J. Helbig, G. Mohr, and U. Querner. 1992. Rapid microevolution of

247   migratory behavior in a wild bird. Nature 360:668-670.

248 Boag, P. T. and A. J. van Noordwijk. 1987. Quantitative genetics. Pages 45-78 *in* F.

249   Cooke and P. A. Buckley, editors. Avian genetics: a population and ecological

250   approach. Academic Press, London, UK.

251 Boucher, Y., D. Arseneault, L. Sirois, and L. Blais. 2009. Logging pattern and landscape

252   changes over the last century at the boreal and deciduous forest transition in

253   Eastern Canada. Landscape Ecology 24:171-184.

254 Bowlin, M. S. and M. Wikelski. 2008. Pointed wings, low wingloading and calm air

255   reduce migratory flight costs in songbirds. PLoS ONE 3:1-8.

256 Dawideit, B. A., A. B. Phillimore, I. Laube, B. Leisler, and K. Böhning-Gaese. 2009.

257   Ecomorphological predictors of natal dispersal distances in birds. Journal of

258   Animal Ecology 78:388-395.

259 Egbert, J. R. and J. R. Belthoff. 2003. Wing shape in House Finches differs relative to

260   migratory habit in eastern and western North America. Condor 105:825-829.

261 Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of

262   Ecology, Evolution, and Systematics 34:487-515.

263 Fiedler, W. 2005. Ecomorphology of the external flight apparatus of Blackcaps (*Sylvia*

264   *atricapilla*) with different migration behavior. Annals of the New York Academy

265   of Sciences 1046:253-263.

266   Ford, E. B. 1937. Problems of heredity in the Lepidoptera. Biological Reviews 12:461-

267   501.

268   Foster, D. R. and G. Motzkin. 2003. Interpreting and conserving the openland habitats of

269   coastal New England: insights from landscape history. Forest Ecology and

270   Management 185:127-150.

271   Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and

272   evolution: disentangling environmental and genetic responses. Molecular Ecology

273   17:167-178.

274   Grant, B. R. and P. R. Grant. 1989. Natural selection in a population of Darwin's Finches.

275   American Naturalist 133:377-393.

276   Imbeau, L., M. Mönkkönen, and A. Desrochers. 2001. Long-term effects of forestry on

277   birds of the Eastern Canadian boreal forests: a comparison with Fennoscandia.

278   Conservation Biology 15:1151-1162.

279   Lampila, P., M. Mönkkönen, and A. Desrochers. 2005. Demographic responses by birds

280   to forest fragmentation. Conservation Biology 19:1537-1546.

281   Lefebvre, L., S. M. Reader, and D. Sol. 2004. Brains, innovations and evolution in birds

282   and primates. Brain, Behavior, and Ecology 63:233-246.

283   Lens, L., S. van Dongen, C. M. Wilder, T. M. Brooks, and E. Matthysen. 1999.

284   Fluctuating asymmetry increases with habitat disturbance in seven bird species of

285   a fragmented afrotropical forest. Proceedings of the Royal Society of London.

286   Series B, Biological Sciences 266:1241-1246.

287   Marchetti, K., T. Price, and A. Richman. 1995. Correlates of wing morphology with

288   foraging behaviour and migration distance in the genus *Phylloscopus*. Journal of

289   Avian Biology 26:177-181.

290   Nicolakakis, N., D. Sol, and L. Lefebvre. 2003. Behavioural flexibility predicts species

291   richness in birds, but not extinction risk. Animal Behaviour 65:445-452.

292   Pergams, O. R. W. and M. V. Ashley. 1999. Rapid morphological change in Channel

293   Island deer mice. Evolution 53:1573-1581.

294   Poole, A., editor. 2005. The Birds of North America Online:

295   http://bna.birds.cornell.edu/BNA/. Cornell Laboratory of Ornithology, Ithaca,

296   NY, USA.

297   Rice, K. J. and N. C. Emery. 2003. Managing microevolution: restoration in the face of

298   global change. Frontiers in Ecology and the Environment 1:469-478.

299   SAS Institute. 2009. SAS software. Version 9.2. SAS Institute Inc., Cary, NC, USA.

300   Savile, D. B. O. 1957. Adaptive evolution in the avian wing. Evolution 11:212-224.

301   Senar, J. C., J. Lleonart, and N. B. Metcalfe. 1994. Wing-shape variation between

302   resident and transient wintering Siskins *Carduelis spinus*. Journal of Avian

303   Biology 25:50-54.

304   Smith, T. B., L. A. Freed, J. K. Lepson, and J. H. Carothers. 1995. Evolutionary

305   consequences of extinctions in populations of a Hawaiian Honeycreeper.

306   Conservation Biology 9:107-113.

307   Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution

308   meets conservation biology. Trends in Ecology & Evolution 18:94-101.

309   Storfer, A. 1999. Gene flow and endangered species translocations: a topic revisited.

310   Biological Conservation 87:173-180.

311   Swaddle, J. P. and R. Lockwood. 2003. Wingtip shape and flight performance in the

312   European Starling *Sturnus vulgaris*. Ibis 145:457-464.

313   Vanhooydonck , B., A. Herrel, A. Gabela, and J. Podos. 2009. Wing shape variation in

314   the medium ground finch (*Geospiza fortis*): an ecomorphological approach.

315   Biological Journal of the Linnean Society 98:129-138.

316   Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M.

317   Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to

318   recent climate change. Nature 416:389-395.

319   Winkler, H. and B. Leisler. 1992. On the ecomorphology of migrants. Ibis 134:21-28.

320

321

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

323   Residents (R) = year-round in their breeding range, Short-distance (SD) = mostly in continental US, long-distance (LD) = in the

324   Caribbean or south of continental US.

325

Species	Migratory status	Primary projection (% of wing chord)*	Change in Primary projection (/100 y)	SE	Error df	t	P
Temperate mature forest			**-2.73**	**0.45**	**251**	**-6.07**	**< 0.001**
Red-breasted Nuthatch, *Sitta canadensis*	R	25.4	-1.65	1.78	17	-0.92	0.369
White-breasted Nuthatch, *S. carolinensis*	R	30.2	-2.14	0.95	47	-2.24	0.030
Brown Creeper, *Certhia americana*	SD	23.7	-3.64	1.49	35	-2.44	0.020
Pine Warbler, *Dendroica pinus*	SD	26.4	-2.24	1.77	21	-1.26	0.221
Black-throated Blue Warbler *D. caerulescens*	LD	24.2	-4.59	0.81	44	-5.66	< 0.001
Cerulean Warbler, *D. cerulea*	LD	32.5	-1.47	2.72	15	-0.54	0.597

Hooded Warbler, *Wilsonia citrina*	LD	24.1	-2.79	1.75	25	-1.60	0.123
Scarlet Tanager, *Piranga olivacea*	LD	31.0	-1.56	0.94	40	-1.66	0.104
Boreal mature forest			**3.05**	**0.43**	**365**	**7.09**	**< 0.001**
Boreal Chickadee, *Poecile hudsonica*	R	18.5	4.23	1.29	73	3.28	0.002
Red-breasted Nuthatch, *S. canadensis*	R	24.5	3.24	0.96	56	3.36	0.001
Gray Jay, *Perisoreus canadensis*	R	20.1	4.56	1.42	45	3.22	0.002
Yellow-rumped Warbler, *D. coronata*	SD	25.8	1.73	1.07	51	1.62	0.111
Cape May Warbler, *D. tigrina*	LD	28.9	3.13	0.85	72	3.69	< 0.001
Bay-breasted Warbler, *D. castanea*	LD	30.4	2.10	0.84	63	2.50	0.015
Temperate open habitats			**3.42**	**1.30**	**94**	**2.63**	**0.010**

Eastern Meadowlark, *Sturnella magna*	SD	22.2	2.17	2.38	21	0.91	0.372
Field Sparrow, *Spizella pusilla*	SD	17.5	0.89	2.70	26	0.33	0.743
Henslow's Sparrow, *Ammodramus henslowii*	SD	16.4	12.5	5.84	20	2.14	0.045
Grasshopper Sparrow, *A. savannarum*	SD	20.0	4.20	2.06	24	2.04	0.052
Boreal open habitats			**-1.48**	**0.55**	**93**	**-2.70**	**0.008**
Lincoln's Sparrow, *Melospiza lincolnii*	LD	20.2	-0.94	1.56	16	-0.60	0.558
Magnolia Warbler, *D. magnolia*	LD	22.3	-1.85	0.64	37	-2.88	0.007
Mourning Warbler, *Oporornis philadelphia*	LD	23.6	-1.94	1.22	26	-1.59	0.123
Wilson's Warbler, *Wilsonia pusilla*	LD	21.9	7.31	2.84	11	2.57	0.026

326   * Corrected for year (set to 1950).

327 **Figure Legends**

328

329 **FIG. 1.** Measurements used to calculate primary projection in wings of museum

330 specimens, showing the distance between the carpal joint of the right wing and the distal

331 end of (a) the outermost secondary feather, and (b) wing tip (unflattened wing chord).

332 Photo of female Scarlet Tanager, by A. Desrochers.

333

334 **FIG. 2.** Change in primary projection in wings of four groups of eastern North American

335 songbirds since 1900. Species groups based on breeding range and habitat. Scales are

336 identical to facilitate comparisons.

337

Boreal mature forest

Temperate mature forest

Boreal open

Temperate open

Primary projection (%)

Year collected