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2 **The potential for comparative research across New World bird**
3 **migration systems**

4 Alex E. Jahn · Víctor R. Cueto

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7 **Abstract** For a migratory bird, the costs and benefits of
8 utilizing a given migratory strategy vary according to the
9 biotic (e.g., physiology) and abiotic (e.g., weather) con-
10 straints it experiences throughout the year. In the New
11 World, closely related migratory species migrate to
12 breeding grounds located across a wide range of latitudes,
13 from northern North America to southern South America.
14 Because the ultimate goal of a bird on spring migration is
15 to successfully arrive on the breeding grounds in a timely
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18 selection pressures, the behavior of birds on spring
19 migration. Variation across north temperate, tropical, and
20 south temperate latitudes in breeding strategies, breeding
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22 season has been well documented in various bird species.
23 Thus, such factors as migratory strategies, risk of mortality
24 on migration, and effects of climate change on migratory
25 patterns may also vary predictably, depending on the lati-
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27 migratory population breeds. Comparing such patterns
28 across the New World, using interdisciplinary approaches
29 and the latest in technological advances, holds promise for
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31 spectacular journeys.
32

Keywords Latitude · Neotropical austral migration · 33
Nearctic-Neotropical migration · Southern Hemisphere · 34
Tropics 35

How migratory birds successfully arrive at their destination 36
in a timely manner has been a question that ornithologists 37
have pursued for more than a century (reviewed by Bert- 38
hold 2001; Newton 2008), yet we still do not understand 39
the ecological basis of the decisions that define an indi- 40
vidual's migratory strategy (Barlein and Coppack 2006; 41
Hedenström 2008). At what speed to fly? How and where 42
to stopover? When to depart? When to arrive? 43

This is due in large part because: (1) most research on 44
bird migration has focused on specific behavioral and 45
physiological adaptations, whereas the avian migration 46
syndrome involves a varied set of behavioral and physio- 47
logical adaptations whose functions are difficult to eluci- 48
date on a piecemeal basis (Dingle 2006). In contrast, an 49
integrative, interdisciplinary approach has the potential to 50
yield novel insights into the evolution of the traits associ- 51
ated with migration (Barlein and Coppack 2006; Bowlin 52
et al. 2010), (2) implementing a standardized set of pro- 53
tocols across multiple study sites on different continents is 54
a daunting task requiring fluid communication between 55
researchers, (3) the technological limitations of following 56
individual birds across large distances has precluded such 57
research, and (4) most bird migration research has been 58
focused on a limited set of migration systems and species, 59
namely those that breed at north temperate latitudes, where 60
most researchers and financial resources are concentrated 61
(Jahn et al. 2004). 62

Across New World bird migration systems, numerous 63
species are derived from common ancestors (Levey and 64
Stiles 1992; Rappole 1995; Joseph 1997), such that 65

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66 comparing migration strategies across species affords a
 67 unique opportunity to evaluate the adaptive value of a
 68 given migration strategy, within a phylogenetic context
 69 (Dingle 2008). Factors that vary with latitude such as the
 70 length of the breeding season and distance to wintering
 71 grounds may be correlated with a migratory strategy.
 72 Indeed, latitudinal comparisons of breeding strategies
 73 (Martin et al. 2000; Russell et al. 2004; Auer et al. 2007;
 74 Dingle 2008), hormone levels (Robinson et al. 2010b),
 75 metabolic rates (Wiersma et al. 2007), and growth rates
 76 (Ricklefs 1976) have yielded many important insights into
 77 the evolution and regulation of life history strategies in
 78 general (reviewed by Robinson et al. 2010b). In contrast,
 79 such comparative research is still rare in studies of the
 80 strategies birds use to migrate, with comparisons between
 81 migration systems almost exclusively limited to why birds
 82 migrate (e.g., Boyle and Conway 2007; Jahn et al. 2012).
 83 Calls for comparative studies of adaptations for migra-
 84 tion across species and hemispheres have been advanced in
 85 the past (Piersma et al. 2005; Dingle 2008). We support
 86 such calls, and argue that, in the New World, such com-
 87 parative research offers the maximum potential to test the
 88 adaptive value of a given migratory strategy (Dingle 2008)
 89 because of the wide range of environmental challenges to
 90 migration found across the Americas, among a wide range
 91 of closely related taxa.

92 An overview of New World bird migration systems

93 Broadly speaking, five forms of long-distance bird migra-
 94 tion exist in the New World: (1) migration between north
 95 temperate breeding grounds of North America and Neo-
 96 tropical wintering grounds (i.e., Nearctic-Neotropical
 97 migration, or North American Temperate-Tropical migra-
 98 tion; sensu Joseph 1997), (2) migration within north tem-
 99 perate latitudes of North America (i.e., North American
 100 Cool-Temperate migration; sensu Joseph 1997), (3)
 101 migration within tropical latitudes (i.e., intratropical
 102 migration; Faaborg et al. 2010), (4) migration between
 103 south temperate breeding grounds and tropical wintering
 104 grounds of South America (i.e., South American Temper-
 105 ate-Tropical migration; sensu Joseph 1997), and (5)
 106 migration within south temperate latitudes of South
 107 America (i.e., South American Cool-Temperate migration;
 108 sensu Joseph 1997). These last two systems comprise
 109 Neotropical austral migration (Cueto and Jahn 2008;
 110 hereafter “austral migration”), in which birds migrate
 111 wholly within South America.

112 We evaluated the number of species shared by the
 113 Nearctic-Neotropical and austral migration systems using
 114 the database of Parker et al. (1996). Fifty-three genera have
 115 species that migrate in both of these systems, of which 17

genera have at least 2 species migrating in each system 116
 (Table 1). Notably, 23 species have populations migrating 117
 in both systems (Table 1). One group that stands out is the 118
 Tyrannidae (New World flycatchers). This is a highly 119
 migratory family in both North and South America, with 120
 25 % of species migratory in North America (Rappole 121
 1995) and 23 % migratory in South America (Chesser 122
 1994). 123

Environmental and avian life history variation 124 across the New World 125

There is well-documented latitudinal variation in New 126
 World avian life history strategies, climate and primary 127
 productivity: 128

1. A slower life history strategy in the south: South 129
 temperate and tropical breeding birds tend to have 130
 smaller clutch sizes (Martin 1996; Martin et al. 2000, 131
 2006; Jetz et al. 2008; Yom-Tov et al. 1994; Auer et al. 132
 2007), a longer time to independence (Russell et al. 133
 2004), and higher adult survival (Rowley and Russell 134
 1991; Martin 1996; Johnston et al. 1997) than north 135
 temperate breeders (reviewed by Wiersma et al. 2007; 136
 Robinson et al. 2010b). 137
2. Reduced seasonality in the south: The Southern 138
 Hemisphere is primarily covered by oceans, while 139
 the Northern Hemisphere is characterized by large 140
 landmasses. As a result, the Southern Hemisphere’s 141
 climate is more buffered, with a milder and drier 142
 climate than most of the Northern Hemisphere (Yom- 143
 Tov et al. 1994; Dingle 2008). In the New World, 144
 seasonality in temperate South America is diminished 145
 relative to similar latitudes north of the equator 146
 (Paruelo et al. 1998, 2007). As a result, compared to 147
 North America, food resources for many South 148
 American bird species are likely to be available for a 149
 longer period of time during the breeding season 150
 relative to northern latitudes, as documented in Aus- 151
 tralia (Rowley and Russell 1991). This strongly 152
 suggests a weaker (i.e., more gradual and less 153
 pronounced) spring flush in food resources for birds 154
 at south temperate latitudes relative to similar latitudes 155
 north of the Equator (Rowley and Russell 1991). 156
3. Higher inter-annual variability in primary productivity 157
 in the south: south temperate latitudes are character- 158
 ized by higher variability in net primary production 159
 than north temperate latitudes, in part due to the El 160
 Niño Southern Oscillation (Goetz et al. 2000). This 161
 could translate to more unpredictable food levels for 162
 migrant species that breed at south temperate latitudes 163
 relative to those at north temperate latitudes. 164

Table 1 Number of species shared by the Neotropical austral and Nearctic-Neotropical migration systems

Family/Genus	Neotropical austral migrants	Nearctic-Neotropical migrants	Species with populations in both migration systems
Anatidae			
<i>Dendrocygna</i>	2	2	<i>D. bicolor</i>
<i>Cygnus</i>	1	1	
<i>Anas</i>	8	10	<i>A. cyanoptera</i>
<i>Oxyura</i>	1	1	
Podicipedidae			
<i>Podiceps</i>	1	2	
Phalacrocoracidae			
<i>Phalacrocorax</i>	3	3	
Ardeidae			
<i>Botaurus</i>	1	1	
<i>Nycticorax</i>	1	2	<i>N. nycticorax</i>
<i>Butorides</i>	1	1	
Cathartidae			
<i>Cathartes</i>	1	1	<i>C. aura</i>
Accipitridae			
<i>Elanoides</i>	1	1	<i>E. forficatus</i>
<i>Ictinia</i>	1	2	<i>I. plumbea</i>
<i>Circus</i>	1	1	
<i>Accipiter</i>	3	2	<i>A. striatus</i>
<i>Buteo</i>	2	8	
Falconidae			
<i>Falco</i>	2	4	<i>F. peregrinus</i>
Rallidae			
<i>Gallinula</i>	1	1	<i>G. chloropus</i>
<i>Porphyrio</i>	1	1	<i>P. martinica</i>
<i>Fulica</i>	3	1	
Charadriidae			
<i>Charadrius</i>	2	5	
Haematopodidae			
<i>Haematopus</i>	1	1	
Scolopacidae			
<i>Gallinago</i>	1	1	
Laridae			
<i>Larus</i>	3	13	
<i>Gelochelidon</i>	1	1	<i>G. nilotica</i>
<i>Sterna</i>	2	4	
<i>Thalasseus</i>	1	3	<i>T. maximus, T. sandvicensis</i>
Rynchopidae			
<i>Rynchops</i>	1	1	<i>R. niger</i>
Columbidae			
<i>Columbina</i>	1	1	
<i>Patagioenas</i>	1	2	
Cuculidae			
<i>Coccyzus</i>	3	2	
Caprimulgidae			
<i>Caprimulgus</i>	3	3	
Trochilidae			
<i>Anthracothorax</i>	1	1	

Table 1 continued

Family/Genus	Neotropical austral migrants	Nearctic-Neotropical migrants	Species with populations in both migration systems
Alcedinidae			
<i>Megaceryle</i>	1	1	
Tyrannidae			
<i>Camptostoma</i>	1	1	
<i>Empidonax</i>	1	13	
<i>Contopus</i>	1	4	
<i>Pyrocephalus</i>	1	1	<i>P. rubinus</i>
<i>Legatus</i>	1	1	<i>L. leucophaeus</i>
<i>Myiodynastes</i>	1	2	<i>M. maculatus</i>
<i>Tyrannus</i>	3	7	<i>T. melancholicus</i>
<i>Myiarchus</i>	2	4	<i>M. tuberculifer</i>
Tityridae			
<i>Pachyramphus</i>	2	1	
Vireonidae			
<i>Vireo</i>	1	12	<i>V. olivaceus</i>
Hirundinidae			
<i>Stelgidopteryx</i>	1	1	
<i>Progne</i>	3	5	<i>P. chalybea</i>
<i>Tachycineta</i>	3	2	
Troglodytidae			
<i>Troglodytes</i>	1	2	<i>T. aedon</i>
Turdidae			
<i>Turdus</i>	2	1	
Motacillidae			
<i>Anthus</i>	2	2	
Emberizidae			
<i>Zonotrichia</i>	1	7	
Cardinalidae			
<i>Piranga</i>	1	2	<i>P. flava</i>
Icteridae			
<i>Sturnella</i>	2	2	
Fringillidae			
<i>Carduelis</i>	1	4	
Total	88	158	23

Genera in bold are those with at least two species migrating in each migration system. Based upon Parker et al. (1996; in Stotz et al. 1996); taxonomy according to the American Ornithologists' Union checklists of North and South American birds

165 Therefore, three factors might be noted: (1) annual
166 productivity (i.e., number of eggs and young produced) is
167 lower but adult survival is higher in the tropics/south
168 temperate latitudes versus north temperate latitudes, (2)
169 food resources are likely available for a longer part of the
170 south versus north temperate breeding season, and (3) there
171 is higher interannual climatic variation at south versus
172 north temperate breeding grounds. Such a pattern strongly
173 suggests that substantial variation should also exist in the
174 migratory strategies of populations breeding north versus
175 south of the Equator.

Potential questions

We offer three questions relevant to understanding how migratory birds cope with the challenges to a life on the move, for which comparative research across the New World could provide new insights:

Which mechanisms drive spring migratory strategies?
Because the ultimate goal of spring migration is to arrive successfully on breeding grounds and reproduce, events occurring during the breeding season may exert a selection pressure on spring migratory strategies. For example, due

186 to a steep decline in reproductive success as the breeding
187 season progresses (e.g., Murphy 1986, 1988; Regosin and
188 Pruett-Jones 1995; Martin 1987), many migrants have a
189 limited window of time in which to successfully reproduce,
190 such that properly timing arrival on breeding grounds is
191 very important to successful reproduction (Lack 1968;
192 Møller 1994; Kokko 1999; Smith and Moore 2005; Visser
193 et al. 2006).

194 Optimal migration theory distinguishes between three
195 limiting factors molding migration strategies (Alerstam and
196 Lindström 1990; Åkesson and Hedenström 2007; He-
197 denström 2008): (1) Time-selected migration: migrants are
198 most limited by available time to breed, such that arriving
199 on breeding grounds as early as possible is of highest fit-
200 ness value; (2) Energy-selected migration: migrants are
201 most limited by adequate food resources during the jour-
202 ney; and (3) Predation-selected migration: migrants are
203 most limited by the risk of predation during migration.
204 Most optimal migration models assume that time minimi-
205 zation is the most relevant currency for a migrant, and that
206 selection favors a maximization of migration speed (He-
207 denström 2008).

208 However, because the amount of time available to breed
209 varies with latitude, often with a wider temporal window in
210 which to breed at lower latitudes, the costs of arriving at low
211 latitude breeding grounds a little “late” may not be as severe
212 (and the benefits of on-time arrival not as great) as for
213 populations that breed at higher latitudes. Furthermore,
214 because there is (1) a larger reproductive payoff (i.e., number
215 of young produced) at north temperate latitudes than at
216 tropical or south temperate latitudes, and (2) potentially more
217 predictable food resources in spring at north temperate lati-
218 tudes than at south temperate latitudes (see above), migratory
219 birds breeding at north temperate latitudes may be willing to
220 take more risks on spring migration to arrive first, employing
221 a more time-selected migratory strategy than those breeding
222 at tropical and south temperate latitudes, which may be more
223 energy- or predator-selected. As a result, although differences
224 in the speed of migration between years may exist (e.g.,
225 Marra et al. 2005), species that breed at north temperate
226 latitudes should on average migrate faster in spring than
227 those to tropical or south temperate latitudes.

228 Such a strategy could translate to other differences
229 between Nearctic-Neotropical and austral migrants. For
230 example, although seasonal carry-over effects have been
231 shown in a handful of Nearctic-Neotropical migrants (e.g.,
232 American Redstarts, *Setophaga ruticilla*; Marra et al.
233 1998), if the migratory period of intratropical and austral
234 migrants is much longer, seasonal carry-over effects could
235 be “washed out” before the beginning of the next phase of
236 their annual cycle.

237 *During which part of the annual cycle is mortality high-*
238 *est? Although high mortality during migration and winter*

239 has long been suspected for migratory birds breeding at north
240 temperate latitudes (Sherry and Holmes 1996, 2002), little
241 information is available on mortality during migration for
242 austral migrants. Because of the generally shorter migration
243 distances of austral migrants, many of which have overlap-
244 ping breeding and winter ranges (Chesser 1994; Stotz et al.
245 1996), and because austral migrants generally migrate over
246 land and do not have to cross any major topographical bar-
247 riers (Chesser 1994) versus Nearctic-Neotropical migrants,
248 many of which cross the Gulf of Mexico, mortality during
249 migration may not be as high for austral migrants. Addi-
250 tionally, if austral migrants are not as time-limited as
251 Nearctic-Neotropical migrants (see above), they may take
252 fewer risks on spring migration, leading to decreased mortal-
253 ity during that part of their annual cycle, relative to their
254 northern counterparts. Rather, given the relatively high
255 nestling mortality rates of birds breeding in the Neotropics
256 (e.g., Mezquida and Marone 2001), the greatest bottleneck to
257 survival for intra-tropical migrants and austral migrants may
258 be during the nestling stage.

259 *How does climate change affect migratory birds in dif-*
260 *ferent contexts?* Research at north temperate latitudes
261 demonstrates that many birds are migrating and arriving
262 earlier in spring (e.g., Hüppop and Hüppop 2003; Van-
263 Buskirk et al. 2009), expanding their ranges northward
264 (LaSorte and Thompson 2007), migrating later in fall (e.g.,
265 Sparks and Mason 2001; Gilyazov and Sparks 2002), and
266 changing the date of egg laying (e.g., McCleery and Perrins
267 1998; Dunn and Winkler 1999). Additionally, research
268 from the Northern Hemisphere indicates that the adaptive
269 value of the advancement of reproductive schedules could
270 be constrained because migration cycles are primarily
271 under the control of endogenous rhythms and periodic
272 cues, independent of temperature (Coppack and Both
273 2003). We know almost nothing about the sensitivity to
274 climate change of migratory species that breed at tropical
275 and south temperate latitudes, and the broad variation in
276 life history strategies among temperate versus tropical
277 species precludes generalizing how flexible migrants across
278 the planet are to climate change. Because genetic and
279 phenotypic variation in migratory traits is relatively high,
280 migrants in general may quickly adapt to climate change;
281 however, the strength of the response to selection may be
282 constrained by life history traits operating outside of the
283 migration period (Coppack and Both 2003).

284 Comparisons across New World migration systems also
285 offer a way to address migration-related questions other
286 than those listed above. For example, optimality models of
287 daily migration speed, fuel loads, and distance (Åkesson
288 and Hedenström 2007) could be compared across migration
289 systems to understand how robust such models are under
290 different conditions. Additionally, Sandberg and Moore
291 (1996) set forth several hypotheses to explain why

292 migratory birds arrive on the breeding grounds with extra
293 fat, several of which include predictions which rely upon
294 comparisons at high versus low latitudes. Extending such
295 comparisons to high latitudes south of the Equator could
296 test the generality of such hypotheses at a truly global
297 scale. Finally, because successful migration requires
298 accurate orientation/navigation, and because navigational
299 cues available to birds may vary across latitudes (e.g., the
300 Sun compass, and Earth's magnetic field), a comparison of
301 the navigational toolkit available to migrants breeding in
302 different hemispheres could unveil novel suites of navi-
303 gational mechanisms.

304 Conducting the type of research proposed here often
305 demands strong research collaborations and coordination
306 across several countries located on different continents,
307 posing formidable logistical obstacles to research, which
308 likely explains in large part the lack of such studies in the
309 literature on bird migration to date. However, modern day
310 ornithologists have at their disposal a wide range of tools
311 necessary to conduct research at spatial scales heretofore
312 unequalled. Emerging technologies permit unsurpassed
313 opportunities for tracking migratory birds (e.g., Stutchbury
314 et al. 2009; Robinson et al. 2010a), for collecting data on
315 their physiology and ecology (Cooke et al. 2004; Cagnacci
316 et al. 2010), and for harnessing the power of “citizen sci-
317 entists” via websites that allow data sharing (e.g., Bird-
318 Track, eBird, WorldBirds). Additionally, the advent of
319 high throughput genetic sequencing and the development
320 of phylogenies across a wide range of taxa increasingly
321 permit phylogenetic comparisons across various levels of
322 organization (i.e., population to family). Utilizing such
323 techniques while employing the comparative method to
324 evaluate patterns across migration systems promises many
325 novel insights into how and why birds migrate—and how
326 best to conserve them—in the twenty-first century.

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