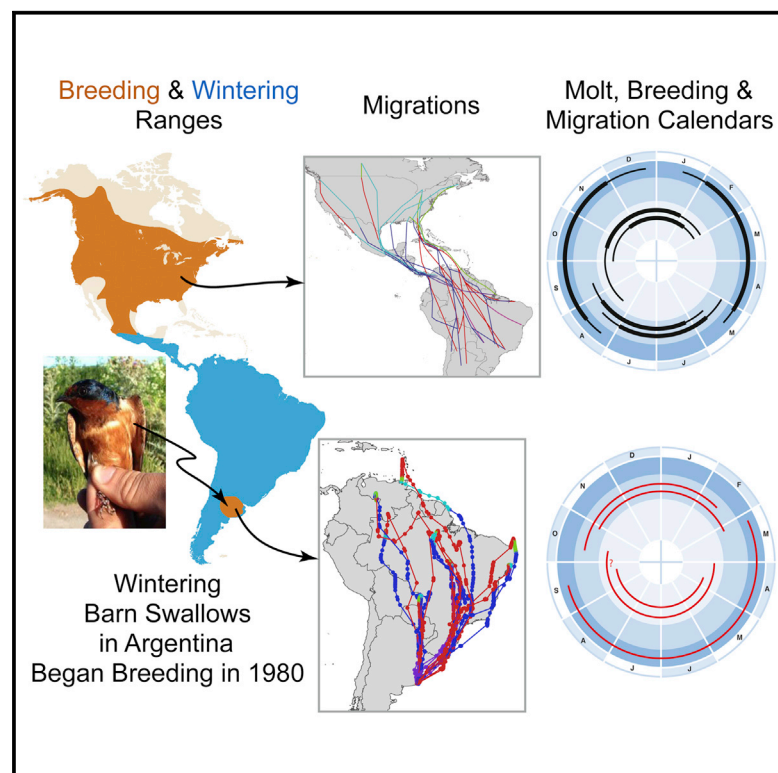


# Current Biology

## Long-Distance Range Expansion and Rapid Adjustment of Migration in a Newly Established Population of Barn Swallows Breeding in Argentina

### Graphical Abstract



### Authors

David W. Winkler, Facundo A. Gandoy, Juan I. Areta, Marshall J. Iliff, Eldar Rakhimberdiev, Kevin J. Kardynal, Keith A. Hobson

### Correspondence

dww4@cornell.edu

### In Brief

North American Barn Swallows began breeding on the southern edge of their wintering range 35 years ago. Winkler et al. show that these birds have quickly changed their migratory route and schedule and the timing of their annual cycle to take advantage of new nesting substrates (road bridges) in areas with temperate photoperiodic cycles.

### Highlights

- A widespread North American bird has begun breeding and spreading across Argentina
- This extends the breeding range 7,000 km into what was formerly the wintering range
- Paths quickly shifted to resemble those of other South American migratory birds
- The entire annual cycle has shifted by about 6 months

# Long-Distance Range Expansion and Rapid Adjustment of Migration in a Newly Established Population of Barn Swallows Breeding in Argentina

David W. Winkler,<sup>1,7,\*</sup> Facundo A. Gandoy,<sup>2</sup> Juan I. Areta,<sup>2</sup> Marshall J. Iliff,<sup>1</sup> Eldar Rakhimberdiev,<sup>3,4</sup> Kevin J. Kardynal,<sup>5</sup> and Keith A. Hobson<sup>5,6</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, Museum of Vertebrates and Laboratory of Ornithology, Cornell University, Corson Hall, Ithaca, NY 14853, USA

<sup>2</sup>Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO)-CONICET, Av. 9 de Julio 14, Rosario de Lerma 4405, Salta, Argentina

<sup>3</sup>Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, the Netherlands

<sup>4</sup>Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, 119992 Moscow, Russia

<sup>5</sup>Environment and Climate Change Canada, Wildlife and Landscape Research Directorate, 11 Innovation Boulevard, Saskatoon, SK S7N 3H5, Canada

<sup>6</sup>Department of Biology, University of Western Ontario, 1151 Richmond Street, London, ON N6A 5B7, Canada

<sup>7</sup>Lead Contact

\*Correspondence: [dww4@cornell.edu](mailto:dww4@cornell.edu)

<http://dx.doi.org/10.1016/j.cub.2017.03.006>

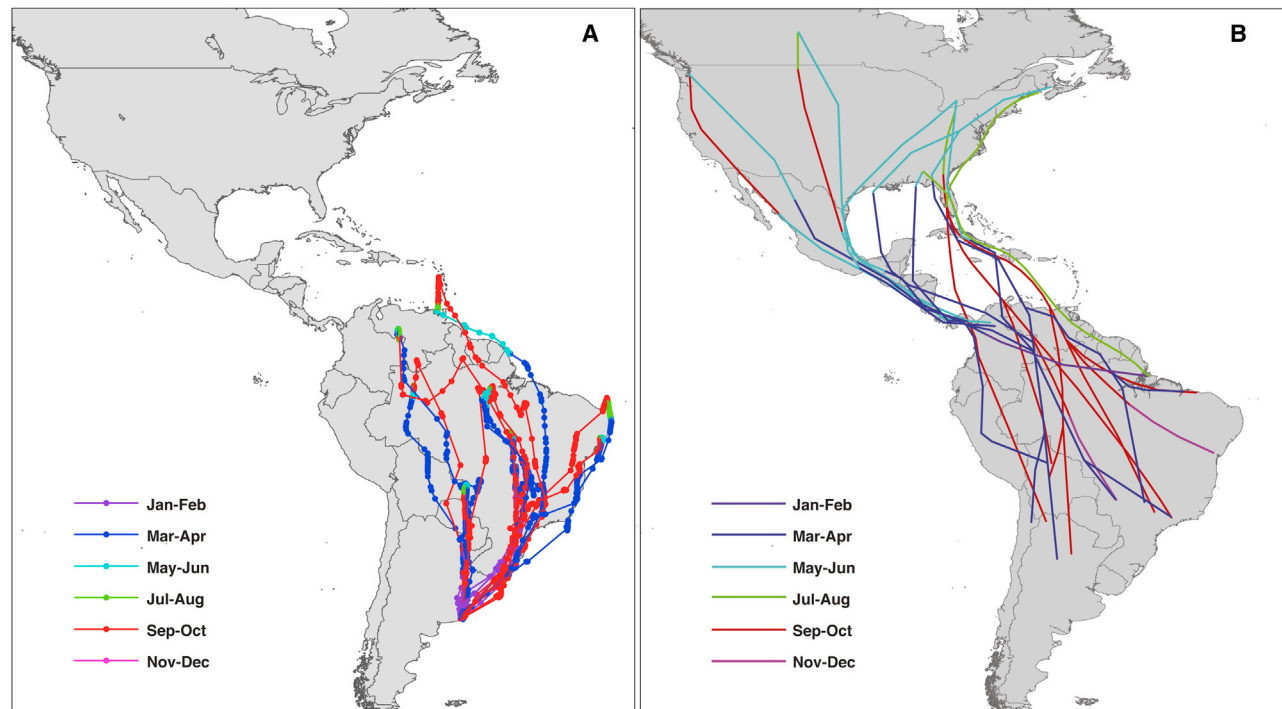
## SUMMARY

When bird populations spread, long-distance pioneering populations are often backfilled by a more slowly advancing front [1–3]. The Barn Swallow *Hirundo rustica*, a globally distributed passerine [4, 5], expanded its breeding range an exceptional 7,000 km when it began breeding 35 years ago in its regular wintering range in Argentina [6], subsequently expanding over 500 km from its starting point [7–11]. Trans-hemispheric breeding attempts have occurred previously in related swallows [12–14], but only this colonization has lasted. Comparative studies of birds show a remarkable diversity in patterns of change in migratory habits [15–21], and these Argentine-breeding swallows might retain ancestral patterns, breeding in Argentina but returning to North America for the austral winter. Feather isotopes from these birds are consistent with the alternative possibility that they migrate no farther than northern South America [22]. Because isotopic patterns cannot definitively distinguish these alternatives, we pursued a solar geolocator study [23, 24] to do so. Data from nine tagged birds show conclusively that Barn Swallows breeding in Argentina have rapidly changed their movements to migrate no farther north in austral winter than northern South America. The phenology of the annual cycles of molt, migration, and breeding for these Argentine-breeding swallows have all shifted by about 6 months, and we suggest that stimulatory day lengths and the proliferation of nesting substrates facilitated their colonization.

## RESULTS AND DISCUSSION

Path reconstructions for the nine nesting Barn Swallows tagged in southern Buenos Aires province from which we retrieved good data were unequivocal: none of the birds went any farther north in the austral winter than coastal Venezuela, and some went no farther than central Brazil (Figure S1). When viewed together (Figure 1A), the broad range of routes and spatial dispersion exhibited by these nine birds is impressive: none went to the same place or followed exactly the same path to get there. Nevertheless, individuals appeared to follow two fairly distinct routes, at least at more southerly latitudes. Six of the birds traversed the tropics along the coast (Figure S1), then either continued north of São Paulo along the coast or across the sparsely forested areas of the Cerrado north of that state to northern South America. The other three birds headed straight north of Buenos Aires province, traversing the tropics along the drainages of the Paraná and Uruguay rivers, and either stayed there or continued across the densely forested Amazon to the Llanos and coasts of northern South America (Figure S1). Though they moved less during the austral winter (Figure S2), most birds continued moving throughout the non-breeding season, and we chose not to designate a given wintering area for any of them. In their movements, though, they all moved north of the breeding grounds by at least 20 degrees of latitude (Figure S2A), and their longitudes spanned most of the breadth of South America (Figure S2B). The estimated mean annual journey was 8,797 km (SD = 3,159 km; range: 4,506–14,628 km; Table S1). Despite spatial heterogeneity in routes and locations, all birds departed the breeding grounds during a 3-week period between February 13 and March 6 and returned to the breeding grounds between September 25 and October 26 (Table S1).

The routes and timing of the migrations of the Argentine-breeding birds contrast strongly with those for North American breeders [25] (Figure 1B), emphasizing the dramatic change in migratory biology that these birds have so quickly achieved.



**Figure 1. Reconstructed Paths for Barn Swallows Tagged with Geolocators**

(A and B) Paths for Argentina nesting colonies (A) reconstructed from FLIGHTR (see text) and those from nesting colonies in North America (B) redrawn from [25]. Segments in each of the paths are colored to show the calendar months for each, with a common coloring scheme for both. See also Table S1 and Figures S1 and S2.

The approximately 6-month changes in the timing of northward and southward migration reinforce what is known about the phenology of the remainder of the life cycle, a remarkable mirror-image timing of events compared to that of the recent ancestors in North America [26] (Figure 2).

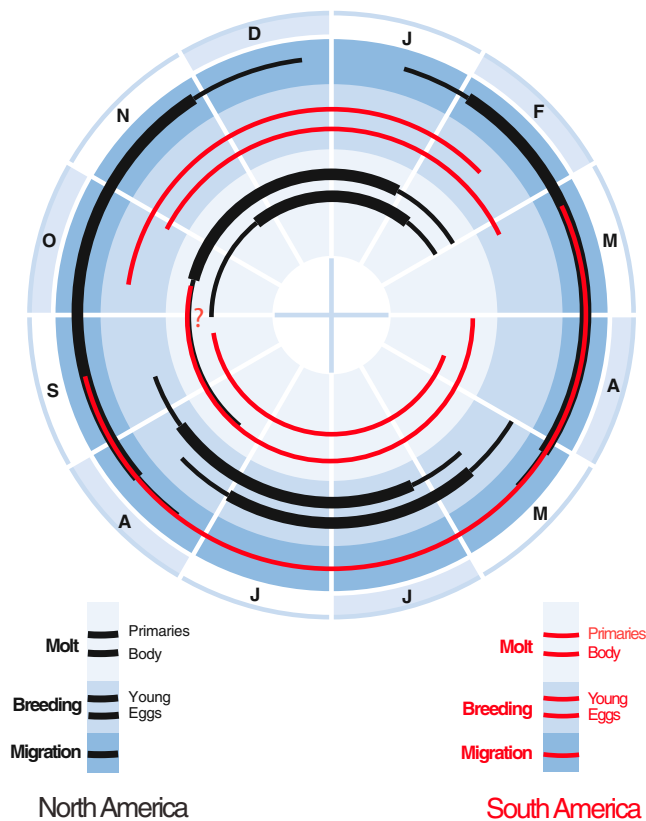
This study confirms that Barn Swallows in this recently established population in southern South America have dramatically changed their migratory timing and orientation in less than 35 years, overwintering in new destinations in northern South America. These Argentine Barn Swallows are now following a migratory pattern and choice of wintering areas that is very much like that of other migrant birds from the temperate zone of South America [23, 27–29]. Recent work on North American Barn Swallows based on solar geolocators [25] indicates that those in eastern Canada are likely completing an annual round-trip journey of over 20,000 km. In contrast, the Argentine birds are making shorter round-trip journeys averaging only a third that distance and never exceeding 14,600 km. This substantial reduction in distance traveled may represent an important advantage of their new route and includes avoiding the long crossing of the Gulf of Mexico or western Atlantic that at least some North American Barn Swallows endure [25, 30].

### Plasticity of Migration

We know from the geolocator-bearing birds that this change in migratory behavior was acquired in no more than 35 years, and perhaps simple genetic changes were selected for that took the ancestral migratory route and merely truncated it in

northern South America. Work on the genetics of migratory behavior in European passerines [31, 32] has suggested that migratory routes can be decomposed into orientation and duration components. The duration component has been shown to be responsive to selection in captive-reared warblers, and Argentine-bred Barn Swallows could have been subject to similar selection in the wild. However, changes in orientation would not have been amenable to a gradual selection for northerly migration post-fledging in Argentine-reared juveniles: any birds persisting with post-fledging migration in a southerly direction (the direction shown post-fledging in the ancestral North American breeders) would almost certainly perish over the Atlantic Ocean to the south.

A thorough analysis of the breeding life histories of the Argentine-breeding birds is underway (F.A.G., unpublished data), and once sufficient data are collected, they will tell whether the swallows breeding in South America are producing more offspring than they would have if their ancestors had stayed in North America. All that can be said for now is that the bulk of the expanding population appears to be coming from endemic population growth. The Argentine-breeding birds have a molt schedule that appears to be the mirror image of that of their northern counterparts, with molt occurring in the austral non-breeding season (Figure 2). Thus, the vast majority of individuals captured in Argentine breeding colonies are not molting. However, occasional birds are captured undergoing flight-feather molt or retaining vestiges of juvenile plumage that suggest that these are recent immigrants from North American breeding



**Figure 2. Graphical Summary of the Phenology of Argentine-Breeding Barn Swallows**

Timing of the annual cycle for birds breeding in Argentina (in red) overlain on the annual cycle for North American Barn Swallows in central North America [26]. Letters around the circle represent months of the year, starting with December (D) and January (J) at the top center, and the arcs represent parts of the annual cycle occupied by each activity, starting with molt innermost, then breeding and migration with larger radii. The thickness of the arcs represents the approximate proportion of the northern population engaged in the activity at the time. Information for Argentine-breeding birds (F.A.G., unpublished data) is still too sparse to estimate these relative proportions.

colonies (F.A.G., unpublished data). That these molting birds are new immigrants from North America is made more likely by the observation that the population genetics of the Argentine population does not suggest a strong founder effect with rigid reproductive isolation from the North American gene pool [33]. Thus, it appears that there may be infrequent but sustained continued immigration from wintering birds of North American origin, most likely from eastern North America [25] (Figure 1B), some of which co-occur with Argentine breeders in the southern summer. This continued genetic connection to northern-breeding populations of the same species makes the possibility of rapid genetic fixation of altered migration duration and orientation much less likely than if it were a totally isolated population.

Migration is flexibly responsive to an array of environmental cues (e.g., [34]), making it able to change without the need for underlying genetic change. It thus seems most likely that the rapid change in migration observed in the Argentine Barn Swallows is due to phenotypic changes that did not require large changes in the frequencies of associated genes. There is considerable

evidence for individual variation in the pace and phenology of migration within populations of this species, and swallows are generally diurnal migrants, often feeding while en route and responding to many cues not available to nocturnal migrants [30]. It is likely that Barn Swallows retain sufficient flexibility in their migratory decision-making that, if feeding conditions in northern South America were sufficiently good, they could stay there rather than take the risk of a long migration to North America. Thus, Argentine-bred Barn Swallows may still retain the potential of returning to North America in the austral winter, but as individuals they may each elect not to do so. Clearly, the migratory behavior and movement patterns of northern-reared swallows recruiting to colonies in Argentina would be informative and could illuminate the routes of causation leading to this rapid change in migration. We are actively pursuing such research.

### Flexibility of Breeding Phenology and Site Choice

Any northern-reared birds breeding in Argentina would also pose many interesting questions about the biology of the pioneering individuals. Do immigrant birds begin breeding during the first season they enter Argentine colonies, or are they initially confused, associating with a colony at first, but only breeding there after a full year has passed? Are the immigrants always young that fledged in the north less than 6 months earlier? Or do adults that have bred somewhere in the north sometimes recruit as breeders in Argentina?

No matter the age of immigrants, how does shifting the annual photoperiodic clock by a full 6 months affect other aspects of their biology? Given the occurrence of late-summer gonadal recrudescence and “autumnal sexuality” in northern songbirds [35–37], is a shift of 6 months actually the easiest clock shift to achieve? And is it possible that photoperiodism explains the origin of this new population near the southern edge of its formerly exclusive wintering range? Is it only here, south of the Tropic of Capricorn, that birds encounter photoperiods like those in a northern spring, stimulating gonadal activity that leads to courtship and nest building?

If so, a natural question might be why mud-nesting swallows have only begun breeding in southern South America relatively recently. Mean air temperatures, and especially minimum temperatures, in southern Buenos Aires province have increased over the past 50 years [38], and this may have had an encouraging effect on swallow breeding there. But likely an even bigger incentive to increased breeding is the proliferation of paved roads and concrete bridges across the province in the past 100 years. Throughout the world, the commonest substrates for the construction of nests by mud-nesting swallows are concrete bridges and stucco or concrete building walls under eaves. Concrete bridges in Argentina were first built in the 1890s, but they did not become the most commonly used bridge construction until the 1930s [39]. Thus, Barn Swallows would not have found substrates for attaching their nests before the 20<sup>th</sup> century, and the first recorded nests were observed about 50 years after nesting substrate first started becoming widely available.

### Migration Dosing in Long-Distance Migrants

Bildstein [40, 41] has argued that populations of migrating raptors have repeatedly produced extra-limital breeding populations when migrating individuals settle and begin breeding in

what had formally been only wintering or migratory passage areas. These extra-limital breeding populations can eventually speciate in what he calls “migration dosing” of the diversification process (see also [42]). Viewed from this evolutionary perspective, the Argentine Barn Swallow colonization may be the first step to speciation. Similar mechanisms could have been behind the origin of several far-northern and far-southern species pairs in skuas (*Stercorarius* spp.) and terns (*Sterna* spp.) [43]. Thus, rather than interpret this new swallow population as an oddity of a single clade of passerine birds, this colonization of a far southern site by a population of long-distance migrants from the opposite hemisphere may be the initial phase of an evolutionary process that has occurred in other clades at other times.

## EXPERIMENTAL PROCEDURES

We attached solar geolocation loggers to Argentine breeding Barn Swallows in three successive breeding seasons, and we had recovery rates of tagged birds near 50% in most years. Despite excellent recapture rates, technical problems with the loggers in the first two seasons yielded no useful data for geolocation. In the third geologging attempt, during the 2013–2014 breeding season, 71 tags, 22 from Migrate Technology and 49 prototype tags from Eli Bridge (University of Oklahoma), were attached to swallows (41 female, 27 male, 1 juvenile, 2 unknown age and sex; mean mass = 18.32 g) mist-netted in colonies under three bridges in Buenos Aires Province near El Moro (38.085664° S, 58.498100° W) and one near Cristiano Muerto (38.645503° S, 59.696069° W) on January 6, 7, and 8, 2014. The tags weighed  $0.65 \pm 0.1$  g, including flexible polymer leg loops for Rappole harnesses (see [24]) used to affix the tags to the backs of the swallows. In the next breeding season, in November 2014, 27 of these individuals (18 females, 9 males) were recaptured. Of these, three no longer wore their loggers, resulting in 24 tags recovered. A lower percentage of recovery of the Cristiano Muerto tags may have been due to some birds relocating elsewhere for nesting because of flooding at the previous year's nest site. All bird handling and tagging were performed under approved IACUC Protocol of Cornell University No. 2001-0051.

Nine of these tags, all Migrate Technology Intigeo P55B1-7 (0.60 g, 9–13 month battery), contained data, and these were offloaded, preprocessed in BASTag [44], and analyzed with FLIGHTR [45, 46] packages, in the R computing environment.

## ACCESSION NUMBERS

The data produced by this study are available on Movebank ([movebank.org](http://movebank.org), study name “Argentine Barn Swallows”). The data are published in the Movebank Data Repository and can be accessed through the following <http://dx.doi.org/10.5441/001/1.rt00m81v>.

## SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.03.006>.

## AUTHOR CONTRIBUTIONS

Conceptualization, D.W.W., F.A.G., J.I.A., M.J.I., E.R., K.J.K., and K.A.H.; Methodology, D.W.W., K.J.K., and E.R.; Investigation, D.W.W., F.A.G., J.I.A., M.J.I., K.A.H.; Writing – Original Draft, D.W.W.; Writing – Review & Editing, D.W.W., F.A.G., J.I.A., M.J.I., E.R., K.J.K., and K.A.H.; Funding Acquisition, D.W.W., J.I.A., F.A.G., and K.A.H.; Resources, F.A.G. and E.R.; Supervision, D.W.W. and J.I.A.

## ACKNOWLEDGMENTS

Thanks to the Gandoy family in Necochea for their hospitality; to Giselle Mangini, Emiliano Depino, and Federico Brisson for help in the field; and to

Valentina Ferretti, Arturo Petringa, and Daniel Alfredo Arano for help tracking down bridge history information. This work was supported in part by an NSF IDBR grant DBI-1152131 and by Program Support funds from Cornell to D.W.W., CONICET funding to J.I.A. and F.A.G., and an operating grant from Environment Canada to K.A.H. We thank James Fox of Migrate Technology for his expertise. D.W.W. thanks Eli Bridge for his help and support. Pablo Petracci and Gernot Huber shared their thoughts and knowledge of this system over the years, and the comments of Alex Jahn, Amy McCune, and two anonymous reviewers improved the manuscript. The base map in the Graphical Abstract was created by Cornell Lab of Ornithology using data from NatureServe.

Received: October 31, 2016

Revised: February 1, 2017

Accepted: March 2, 2017

Published: March 16, 2017

## REFERENCES

1. Hengeveld, R. (1989). *Dynamics of Biological Invasions* (Springer).
2. Veit, R.R., and Lewis, M.A. (1996). Dispersal, population growth, and the allee effect: dynamics of the House Finch invasion of eastern North America. *Am. Nat.* **148**, 255–274.
3. Gammon, D.E., and Maurer, B.A. (2002). Evidence for non-uniform dispersal in the biological invasions of two naturalized North American bird species. *Glob. Ecol. Biogeogr.* **11**, 155–162.
4. Dor, R., Safran, R.J., Sheldon, F.H., Winkler, D.W., and Lovette, I.J. (2010). Phylogeny of the genus *Hirundo* and the Barn Swallow subspecies complex. *Mol. Phylogenet. Evol.* **56**, 409–418.
5. Dor, R., Safran, R.J., Vortman, Y., Lotem, A., McGowan, A., Evans, M.R., and Lovette, I.J. (2012). Population genetics and morphological comparisons of migratory European (*Hirundo rustica rustica*) and sedentary East-Mediterranean (*Hirundo rustica transitiva*) barn swallows. *J. Hered.* **103**, 55–63.
6. Martinez, M.M. (1983). Nidificación de *Hirundo rustica erythrogaster* (Boddaert) en la Argentina. (*Aves*, Hirundinidae). *Neotropica* **29**, 83–86.
7. Morici, A. (2009). Nidificación de la Golondrina Tijerita (*Hirundo rustica*) en el partido de Puán, Buenos Aires, Argentina. *Nuestras Aves* **54**, 35–36.
8. Morici, A. (2012). Primeros registros de nidificación de la Golondrina Tijerita (*Hirundo rustica*) en la provincia de La Pampa, Argentina. *Nótulas Faunísticas* **96**, 1–7.
9. Idoeta, F.M., Roda, M.A., and Roesler, I. (2011). La Golondrina Tijerita *Hirundo rustica* sigue expandiendo su area de nidificación en Argentina. *Cotinga* **33**, 58–60.
10. Larracochea, G., Duran, H., and D'Acunto, C. (2012). Nidificación de la Golondrina Tijerita (*Hirundo rustica*) en el balneario Arroyo Pareja, Buenos Aires, Argentina. *Nuestras Aves* **57**, 18–19.
11. Grande, J.M., Santillán, M.A., Orozco, P.M., Liébana, M.S., Reyes, M.M., Galmes, M.A., and Cereghetti, J. (2015). Barn Swallows keep expanding their breeding range in South America. *Emu* **115**, 256–260.
12. Randall, R.M. (2013). House Martins make a home. *Af. Bird-life, March/April*, 58–59.
13. Petracci, P.F., and Delhey, K. (2004). Nesting attempt of the Cliff Swallow *Petrochelidon pyrrhonota* in Buenos Aires Province, Argentina. *Ibis* **146**, 522–525.
14. Salvador, S.A., Salvador, L.A., Gandoy, F., and Areta, J.I. (2016). La Golondrina Rabadilla Canela (*Petrochelidon pyrrhonota*) cría en Sudamérica. *Omitol. Neotrop.* **27**, 163–168.
15. Chesser, R.T. (2000). Evolution in the high Andes: the phylogenetics of Muscisaxicola ground-tyrants. *Mol. Phylogenet. Evol.* **15**, 369–380.
16. Helbig, A.J. (2003). Evolution of bird migration: a phylogenetic and biogeographic perspective. In *Avian Migration*, P. Berthold, E. Gwinner, and E. Sonnenschein, eds. (Springer-Verlag), pp. 3–20.

17. Jahn, A.E., Levey, D.J., Hostettler, J.A., and Mamani, A.M. (2010). Determinants of partial bird migration in the Amazon Basin. *J. Anim. Ecol.* **79**, 983–992.
18. Piersma, T. (2011). Flyway evolution is too fast to be explained by the modern synthesis: proposals for an ‘extended’ evolutionary research agenda. *J. Ornithol.* **152**, 151–159.
19. Able, K.P., and Belthoff, J.R. (1998). Rapid ‘evolution’ of migratory behaviour in the introduced house finch of eastern North America. *Proc. R. Soc. B. Lon. Biol. Sci.* **265**, 2063–2071.
20. Berthold, P., Helbig, A.J., Mohr, G., and Querner, U. (1992). Rapid micro-evolution of migratory behaviour in a wild bird species. *Nature* **360**, 668–670.
21. Ogonowski, M.S., and Conway, C.J. (2009). Migratory decisions in birds: extent of genetic versus environmental control. *Oecologia* **161**, 199–207.
22. Garcia-Perez, B., Hobson, K.A., Powell, R.L., Still, C.J., and Huber, G.H. (2013). Switching hemispheres: a new migration strategy for the disjunct Argentinean breeding population of Barn Swallow (*Hirundo rustica*). *PLoS ONE* **8**, e55654.
23. Jahn, A.E., Levey, D.J., Cueto, V.R., Ledezma, J.P., Tuero, D.T., Fox, J.W., and Masson, D. (2013). Long-distance bird migration within South America revealed by light-level geolocators. *Auk* **130**, 223–229.
24. Bridge, E.S., Kelly, J.F., Contina, A., Gabrielson, R.M., MacCurdy, R.B., and Winkler, D.W. (2013). Advances in tracking small migratory birds: a technical review of light-level geolocation. *J. Field Ornithol.* **84**, 121–137.
25. Hobson, K.A., Kardynal, K.J., Van Wilgenburg, S.L., Albrecht, G., Salvadori, A., Cadman, M.D., Liechti, F., and Fox, J.W. (2015). A continent-wide migratory divide in North American breeding Barn Swallows (*Hirundo rustica*). *PLoS ONE* **10**, e0129340.
26. Brown, C.R., and Brown, M.B. (1999). Barn Swallow (*Hirundo rustica*). In *The Birds of North America*, P.G. Rodewald, ed. (Cornell Lab of Ornithology). <https://birdsna.org/Species-Account/bna/species/barswa>.
27. Zimmer, J.T. (1938). Notes on migrations of South American birds. *Auk* **55**, 405–410.
28. Joseph, L. (1997). Towards a broader view of Neotropical migrants: consequences of a re-examination of austral migration. *Ornitol. Neotrop.* **8**, 31–36.
29. Jiménez, J.E., Jahn, A.E., Rozzi, R., and Seavy, N.E. (2016). First documented migration of individual white-crested Elaenias (*Elaenia albiceps chilensis*) in South America. *Wilson J. Ornithol.* **128**, 419–425.
30. Winkler, D.W. (2007). Roosts and migrations of swallows (Hirundinidae). *Hornero* **21**, 85–97.
31. Berthold, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* **70**, 1–11.
32. Pulido, F. (2007). The genetics and evolution of avian migration. *BioSci.* **57**, 165–174.
33. Billerman, S., Huber, G.H., Winkler, D.W., Safran, R.J., and Lovette, I.J. (2011). Population genetics of a recent transcontinental colonization of South America by breeding Barn Swallows (*Hirundo rustica*). *Auk* **128**, 506–513.
34. Winkler, D.W., Jørgensen, C., Both, C., Houston, A.I., McNamara, J.M., Levey, D.J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D., and Piersma, T. (2014). Cues, strategies, and outcomes: how migrating vertebrates track environmental change. *Mov. Ecol.* **2**, 10.
35. Lincoln, G.A., Racey, P.A., Sharp, P.J., and Kandorf, H. (1980). Endocrine changes associated with spring and autumn sexuality in the Rook *Corvus frugilegus*. *J. Zool.* **190**, 137–153.
36. Dawson, A. (1983). Plasma gonadal steroid levels in wild starlings (*Sturnus vulgaris*) during the annual cycle and in relation to the stages of breeding. *Gen. Comp. Endocrinol.* **49**, 286–294.
37. Ball, G.F., and Ketterson, E.D. (2008). Sex differences in the response to environmental cues regulating seasonal reproduction in birds. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **363**, 231–246.
38. Merlotto, A., and Piccolo, M.C. (2009). Tendencia climática de Necochea-Quequén (1956-2006), Argentina. *Investig. Geográf.* **50**, 143–167.
39. CAMARCO (2011). Memoria de la infraestructura vial 1810-2010 (Cámara Argentina de la Construcción), 63 pp.
40. Bildstein, K.L. (2004). Raptor migration in the Neotropics: Patterns, processes and consequences. *Ornitol. Neotrop.* **15**, S83–S99.
41. Bildstein, K.L., and Zalles, J.I. (2005). Old World vs. New World long-distance migration in Accipiters, Buteos and falcons: the interplay of migration ability and global biogeography. In *Birds of Two Worlds: The Ecology and Evolution of Migration*, R. Greenberg, and P.P. Marra, eds. (Johns Hopkins University Press), pp. 154–167.
42. Curtis, O., and Koeslag, A. (2007). A confusion of buzzards: mystery surrounds buzzards breeding in the Western Cape. *Africa Birds and Birding, June/July*, 48–50.
43. Bridge, E.S., Jones, A.W., and Baker, A.J. (2005). A phylogenetic framework for the terns (Sternini) inferred from mtDNA sequences: implications for taxonomy and plumage evolution. *Mol. Phylogenet. Evol.* **35**, 459–469.
44. Wotherspoon, S., Sumner, M., and Lisovski, S. (2013). BASTag: basic data processing for light based geolocation archival tags. R package version 0.1-3.
45. Rakhimberdiev, E., Winkler, D.W., Bridge, E., Seavy, N.E., Sheldon, D., Piersma, T., and Saveliev, A. (2015). A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. *Mov. Ecol.* **3**, 25.
46. Rakhimberdiev, E., Saveliev, A., Piersma, T., and Karagicheva, J. (2017). FLIGHTR: an R package for reconstructing animal paths from solar geolocation loggers. *Methods in Ecology and Evolution*. <http://dx.doi.org/10.1111/2041-210X.12765>.