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Tracking mated pairs in a long-distance migratory songbird: migration schedules are not synchronized within pairs

Bridget J. M. Stutchbury [a, *], Kevin C. Fraser [b], Cassandra Silverio [a], Patrick Kramer [a], Bob Aeppli [c], Nanette Mickle [d], Myrna Pearman [e], Anne Savage [f], James Mejeur [f]

[a] Department of Biology, York University, Toronto, ON, Canada
[b] Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada
[c] Purple Martin Conservation Association, Erie, PA, U.S.A.
[d] Woodbridge, VA, U.S.A.
[e] Ellis Bird Farm, Lacombe, AB, Canada
[f] Disney's Animals, Science and Environment, Lake Buena Vista, FL, U.S.A.

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In long-distance migrants, it has been hypothesized that re-pairing in spring is facilitated if, on the wintering grounds, formerly mated individuals maintain close proximity or occupy ecologically similar habitat, which then results in more synchronized spring migration schedules. For songbirds, pair members have long been thought to migrate independently, but only recently has it been possible to directly track start-to-finish migration to test this prediction. We used light-sensor geolocators to track paired versus nonpaired purple martins, *Progne subis subis*, that breed in North America and winter in South America. In 6 of 12 pairs, pair members departed on autumn migration within 4 days of each other, but pairs rarely occupied nearby stopover sites in Central America and were separated by an average of 560 km upon arrival in Brazil. Formerly paired birds were not significantly more similar in autumn or spring migration timing, or winter roost location, compared with nonpaired birds tracked from the same colonies and years. Formerly mated pairs who were closer together in Brazil, or who occupied regions with similar amounts of forest cover, did not have more synchronized spring migration schedules. Only 1 of 12 pairs that were tracked remated after migration. Intense competition for nesting cavities combined with disparate spring migration schedules of former pairs probably contributes to the high divorce rate.

Long-term breeding partnerships occur in diverse taxa including invertebrates, fish, mammals and most often in birds due to their high levels of parental care (Black, 1996). The fitness benefits of long-term pairing versus divorce has received extensive study but with conflicting results. Divorce is widespread in monogamous animals and occurs when two previously paired individuals are alive and present in the same area during the next breeding season but one or both mate with a new partner. Some studies have found evidence that divorce can be a selfish tactic by one partner to trade up and increase reproductive fitness through improved mate or territory quality (Culina, Radersma, & Sheldon, 2014; Otter & Ratcliffe, 1996). But other studies have found that divorce is not beneficial to either pair member, yet is still common (reviewed in: Adkins-Regan & Tomaszycki, 2007; Choudhury, 1995; Sánchez-Macouzet, Rodríguez, & Drummond, 2014). For instance, in alpine marmots, *Marmota marmota*, 'forced' divorce occurs when one pair member is aggressively evicted by a newcomer, while the remaining pair member gains no increase in reproductive success with its new mate (Lardy, Cohasa, Figueroab, & Allainéa, 2011).

For migratory birds, breeding season partnerships sometimes remain intact year-round and over thousands of kilometres (Newton, 2008). However, for most species, little is known about pair associations on migration, and it is unclear to what extent events on migration affect synchrony of spring migration schedules and likelihood of divorce. Spatial separation of formerly mated birds during the migratory journey may lead to asynchronous spring migration schedules and increase the likelihood of divorce (Choudhury, 1995). In Scopoli's shearwaters, *Calonectris diomedea*, pairs do not migrate together but their migration destinations are similar (Müller, Massa, Phillips, & Dell'Omo, 2015). Shearwaters have lifelong pair bonds, and distances between nonbreeding areas of paired individuals are smaller than among unpaired birds

* Correspondence: B. J. M. Stutchbury, Department of Biology, York University, Toronto, ON M3J 1P3, Canada.
E-mail address: bstutch@yorku.ca (B. J. M. Stutchbury).

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(Müller et al., 2015). It has also been hypothesized that co-occupancy of ecologically similar winter sites by formerly mated pairs, even when widely separated in space, can lead to similar spring migration schedules and thus facilitate re-pairing the next breeding season (Gunnarsson, Gill, Sigurbjörnsson, & Sutherland, 2004). Observations of banded black-tailed godwits, *Limosa limosa islandica*, revealed synchronized arrival (<3 days separation) at breeding sites of pairs even though pair members were observed at wintering sites hundreds of kilometres apart (Gunnarsson et al., 2004). Utilization of winter sites with similar resource quality may indirectly align migration schedules and increase the likelihood of re-pairing.

It has long been assumed that, in migratory passerines, mated pairs do not associate on migration (Newton, 2008). Evidence for this comes almost entirely from observations of spring arrival at breeding sites. In passerines, males typically arrive earlier than most females due to intense competition for territories and mates; individuals of either sex that arrive at breeding sites too late may find their former mate already paired (Morbey, Coppack, & Pulido, 2012). But it is unknown to what extent passerine pairs remain in close proximity while on migration, or even whether they occupy similar stopover or wintering sites. Male–female associations are observed more often than expected at migratory stopover or wintering sites, and some of these birds have been observed to behave as mated pairs and in some cases to defend winter territories together (reviewed in Newton, 2008). It has recently become possible to track small birds on migration (Stutchbury, Tarof, et al., 2009) and, with large-scale deployments, to track mated pairs after the breeding season ends. Arizaga, Willemoes, Unamuno, Unamuno, and Thorup, (2014) recently reported intriguing evidence in barn swallows, *Hirundo rustica*, for one mated pair in which the two individuals appeared to have remained in close proximity throughout their round-trip journey from northern Spain to West Africa (10 000 km, over 7 months).

We tracked paired versus nonpaired purple martins, *Progne subis subis*, a transhemispheric migratory songbird that travels between breeding colonies in North America and wintering roosts in the Amazon basin (Tarof & Brown, 2013). Our objectives were to test (1) whether formerly mated pairs show more similar migration timing and wintering locations that nonpairs from the same colonies and years, and (2) whether closer proximity on the wintering grounds in Brazil, or more similar habitat, of formerly mated pairs is associated with more synchronous spring migration schedules.

METHODS

Study Species and Sites

Purple martins were captured at their nesting boxes and fitted with geolocators (British Antarctic Survey, Cambridge, U.K., models MK10, MK12, MK14, MK20, and Biotrack-equivalent models, Wareham, U.K.) during the nesting period (2007–2014, $N = 987$ geolocators) at multiple breeding sites in Canada (Alberta) and the U.S.A. (Florida, Minnesota, New Jersey, Pennsylvania, South Carolina, South Dakota, Texas, Virginia; for more details on methods see Fraser et al., 2012, Fraser, Silverio, et al., 2013). Geolocators were retrieved in the year following deployment, and while some malfunctioned, we obtained migration data for 222 different individuals. Most (80%) geolocators were deployed on birds in at least their second year of breeding, as identified by the distinct plumage characteristics of older birds (Tarof & Brown, 2013).

The return rate of individuals fitted with geolocators varied across years (25–48%) and was not lower than for birds not carrying geolocators (Fraser et al., 2012). If both members of a mated pair were captured, both were sometimes tagged with geolocators. Across all sites, 65 mated pairs ($N = 130$ individuals) were equipped with geolocators, but there were only 12 instances where both pair members returned the following year. These tracked pairs came from four of our nine deployment sites (Alberta, Pennsylvania, Virginia and Florida). Overall return rate of formerly paired geolocator birds, including cases where only a single bird returned, was 51/130 (39.2%). We randomly selected nonpaired birds (i.e. one male and one female) from the same colonies and years as the pairs we were able to track, to test whether paired birds associated more closely on migration that nonpaired birds.

Geolocator Analysis

Raw light data were corrected for clock drift (1–3 min) using BASTrak and analysed using TransEdit (British Antarctic Survey). We manually verified a sharp transition at each sunrise and sunset and deleted obvious shading events during the daytime. We used a light-level threshold of 32 (MK14, MK10) or 5 (MK12, MK20) to define sunrise and sunset transitions, and used live calibration data from birds after nesting but prior to migration to determine the average sun elevation that corresponded to this light-level threshold at the breeding site. Sun elevation values were averaged across breeding sites for each year to better represent average conditions for migrating birds at unknown locations. Latitude was not determined for 15 days before and after the spring equinox when daylength is similar everywhere. During this period, positions were estimated using longitude, which is appropriate for this species, as migratory routes have a large longitudinal component (Stutchbury, Tarof, et al., 2009; see Supplementary Fig. S1). Latitude and longitude coordinates were calculated with Locator software (British Antarctic Survey) using midnight locations, because purple martins are primarily diurnal migrants.

Migration movements were defined as those that shifted a bird's position >200 km latitude and >100 km longitude, and in a direction consistent with autumn and spring migration. Purple martins have a fast initial pace (400–500 km/day) during autumn migration (Fraser, Stutchbury, et al., 2013) and, therefore, pair members that departed 5 or more days apart would likely be separated by more than 1000 km by the time the later-departing individual began migrating. We considered that arrival at the wintering grounds, or at breeding sites, had occurred when the latitude and longitude ceased to shift in a direction consistent with migration and fluctuated around a narrow range of values less than 2 degrees longitude, consistent with a stationary bird. We considered autumn migration to have ceased when birds stopped for at least 7 days within the wintering range. Almost half of the purple martins shifted winter roost sites 1 month or more after first arriving at their wintering grounds in Brazil, moving an average of 700 km between roost sites (Fraser et al., 2012). Spring arrival date was associated with sudden and frequent shading from nestbox use. To estimate geolocator accuracy, we calculated location for 2 weeks after nesting but prior to autumn migration and compared that with the known roost or breeding colony location. Geolocator accuracy prior to autumn migration, at multiple breeding sites, averaged about 40 km for latitude and 50 km for longitude (Fraser et al., 2012).

Winter Roost Regional Habitat Analysis

To compare wintering habitat of nonpairs and formerly mated pairs, we derived land-cover data for the purple martin wintering range in South America from Eva (2002). We calculated the percentage of forest cover within a 50 km radius of estimated wintering sites that had been occupied for at least 30 days (see also Fraser et al., 2012). This distance is ecologically appropriate given