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

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## ARTICLE INFO

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.

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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

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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

that aerial insectivores forage over large areas during the daytime and it corresponds to approximate longitudinal error in geolocator-derived estimates of breeding sites of this species (Fraser et al., 2012). Regional forest cover within 50 km of estimated roost sites ranged widely from >95% in heavily forested regions of northwestern Brazil to <30% in the more developed southern and eastern portions of the purple martin winter range (Fraser et al., 2012).

Statistics were performed with SPSS v.23 (IBM, Armonk, NY, U.S.A.). Statistics reported for t test used bootstrap method in SPSS (1000 bootstrap samples) and no assumption of equal variances.

## RESULTS

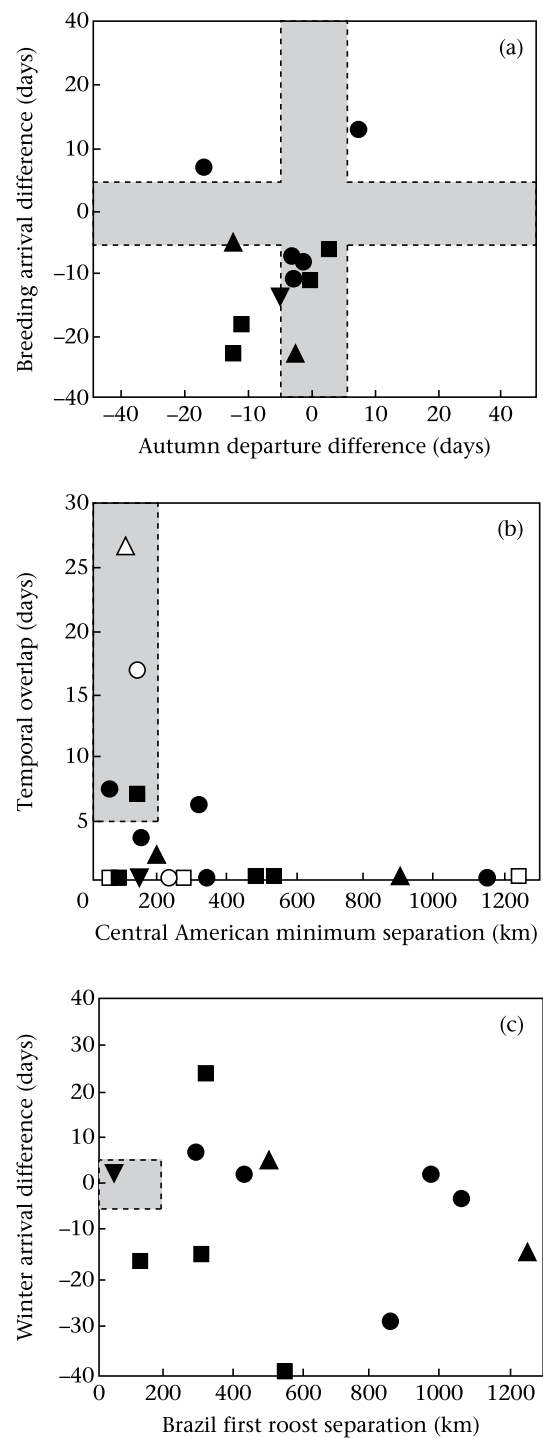### Pair Migration Timing and Wintering Sites

For autumn migration, 6 of 12 pairs departed within 4 days of each other (Fig. 1a), and the mean ($\pm$95% CI) temporal separation of departure was 6.8 $\pm$ 3.1 days ($N = 12$) for all pairs. During autumn migration, purple martins typically have one or two prolonged (>7 days) stopovers in the Yucatan Peninsula of Mexico or in Central America (Fraser, Stutchbury, et al., 2013). For the 12 tracked pairs, the mean ($\pm$95% CI) stopover duration was 14.8 $\pm$ 5.7 days at the first location and 12 $\pm$ 6 days ($N = 9$) at the second location in Central America. If pair members associate on migration, then these stops should coincide in time and space. The mean $\pm$ 95% CI minimum distance between pair members' first stopover sites (Fig. 1b) was 382 $\pm$ 199 km, and the mean temporal overlap at these sites was only 2.2 $\pm$ 1.96 days. The first stopover sites for members of two pairs in Central America were separated by <200 km and overlapped by >5 days, so given geolocator error, these pairs could have been in the same place for a prolonged period (e.g. Fig. 2a). There were also two pairs that could have had prolonged co-occupancy at their second stopover sites in Central America (Fig. 1b).

Only 1 of 12 pairs (8.3%) showed coordinated arrival in time (<5 days) and space (<200 km) at their first roost site in Brazil (Fig. 1c). This pair was also the only pair that subsequently remated in the next breeding season, but the male and female did not remain together over the course of the winter and did not have synchronized spring migration (Fig. 2b). The mean ($\pm$ 95% CI) distance between former pair members' first long-term (>30 days) roost site in Brazil was 560 $\pm$ 217 km (Fig. 3b). The timing of autumn or spring migration, or the location of the first winter roost was not significantly more similar for formerly paired birds than for randomly chosen nonpaired birds from the same years and colonies (Table 1, Supplementary Fig. S1).

### Spatial Proximity, Habitat Similarity and Spring Migration Synchronization

During spring migration, males departed from Brazil before their former mates in 10 of 12 cases (Fig. 4a). These 10 males also arrived at their breeding sites, on average ($\pm$95% CI), 13 $\pm$ 4 days before their former mates (Fig. 4b). In two pairs, the female departed first (20 and 14 days earlier) and arrived first (7 and 13 days earlier, respectively). Mean ($\pm$95% CI) distance between pairs at their final roosts sites, just prior to onset of spring migration, was 843 $\pm$ 278 km (Fig. 4a, b) and was not positively correlated with absolute difference in either spring departure date (Spearman rank correlation: $r_S = 0.35$, $P = 0.91$) or arrival date ($r_S = 0.04$, $P = 0.91$) of formerly paired individuals.

Regional forest cover within 50 km of the estimated last roost site in Brazil ranged from 14.5% to 99.8% among all pairs tracked (Fig. 4c, d) as a result of the large geographical area collectively occupied by these individuals (Fig. 3b). Absolute difference in regional forest cover between formerly mated pairs at their last



**Figure 1.** Migration timing, Central American stopovers and wintering sites of formerly paired purple martins ($N = 12$). Symbol shape represents different study sites (Alberta: triangle; Florida: inverted triangle; Pennsylvania: circle; Virginia: square). (a) Difference in autumn departure date (male minus female) and spring arrival date; shaded box is a visual aid to identify pairs with similar (<5 days) timing. Negative differences indicate that the male migrated earlier than the female. (b) Number of days on which formerly paired birds overlapped temporally at their first (closed symbol) and second (open symbol) stopover sites in Central America and minimum distance separating the estimated roost sites based on longitude only; shaded box shows pairs that were less than 200 km apart and who overlapped in time by more than 5 days. (c) Difference in arrival date (male minus female) at the first roost site in Brazil and the distance separating the roost sites; shaded box shows pairs that arrived close in time (<5 days) and space (<200 km). Winter roost site locations of individuals were calculated as average geolocator positions for at least 30 days while apparently stationary. Geolocator accuracy averaged over multiple breeding sites is about 40 km in latitude and 50 km in longitude; accuracy at wintering sites is unknown.
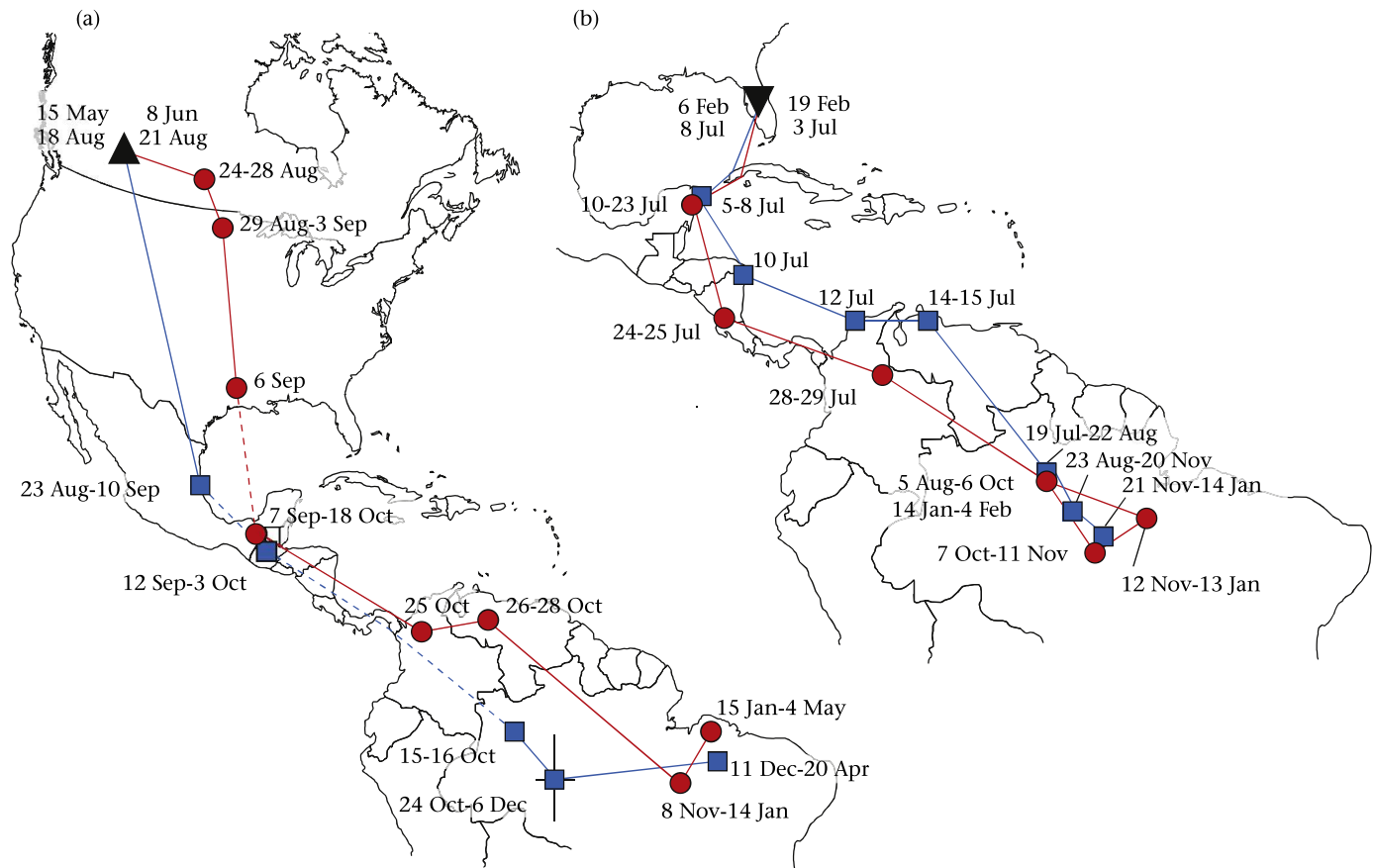
**Figure 2.** (a) Autumn migration timing and a subset of stopover sites of a purple martin pair (male: squares; female: circles) tracked from Alberta. Dashed line indicates the period during the autumn equinox when latitude could not be determined; estimated locations during this period are based on longitude alone. The typical standard deviation in latitude and longitude of a winter roost site (error bars around the roost site) in Brazil is shown for one winter roost site. (b) Autumn migration timing and a subset of stopover sites for a pair (male: squares; female: circles) from Florida; this pair was the only one to remate the next breeding season.
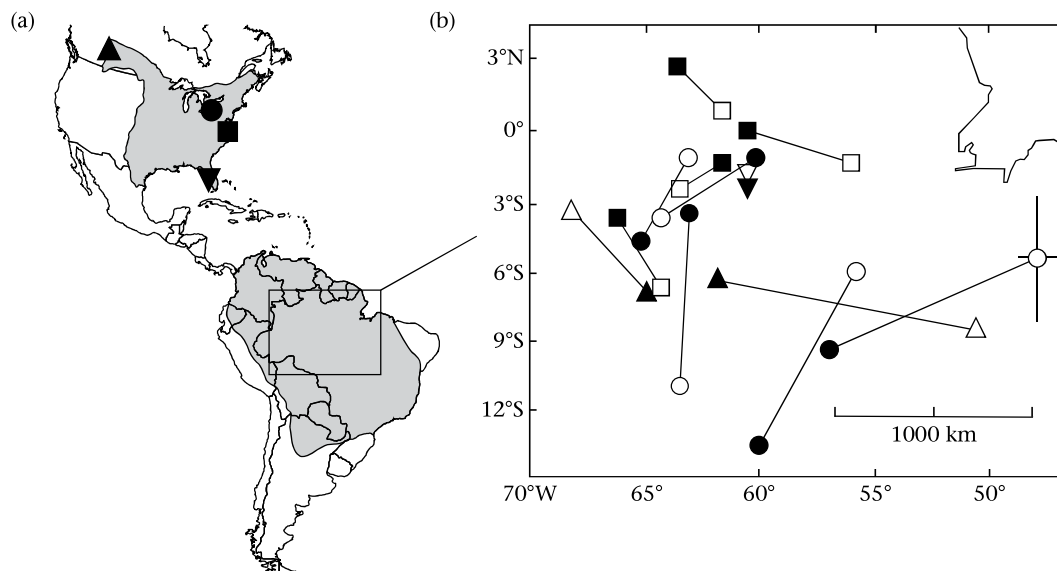


**Figure 3.** (a) Map of breeding sites (solid symbols) from which paired purple martins were tracked; grey shading shows breeding range in North America and wintering range in South America. (b) First winter roost location in Brazil with lines connecting roost sites of pairs; symbols indicate breeding site (male: solid; female: open). Points are the average latitude and longitude during roost occupancy; the typical geolocator position error (± SD) is also shown for one representative bird in eastern Amazon.

**Table 1**
Mean (±95% confidence interval) absolute difference in migration timing (days) and distance between first winter roost sites of former mated pairs ($N = 12$) and randomly chosen pairings of male and female purple martins, from the same years and colonies, who were not former mates ($N = 31$)

| Migration variable | Formerly paired | Nonpaired | t | P |
|---|---|---|---|---|
| Departure on autumn migration (days) | 6.8±3.1 | 7.7±6.6 | 0.43 | 0.60 |
| Arrival at first roost in Brazil (days) | 15.6±6.6 | 14.3±11.6 | 0.49 | 0.65 |
| Distance between first roosts (km) | 560±217 | 615±502 | 0.58 | 0.95 |
| Distance between last roosts (km) | 843±278 | 792±589 | 0.27 | 0.55 |
| Difference in regional forest cover (%) at last roost | 18.8±9.4 | 15.5±15.9 | 0.60 | 0.57 |
| Departure on spring migration (days) | 16.2±3.5 | 14.4±8.8 | 0.74 | 0.45 |
| Arrival at breeding site (days) | 12.5±3.7 | 12.3±8.1 | 0.12 | 0.39 |

Winter roost site locations of individuals were calculated as average geolocator positions for at least 30 days while apparently stationary. Regional forest cover (%) determined within 50 km radius around the estimated roost location. Statistics reported for *t* test using bootstrap method (1000 bootstrap samples) and no assumption of equal variances.
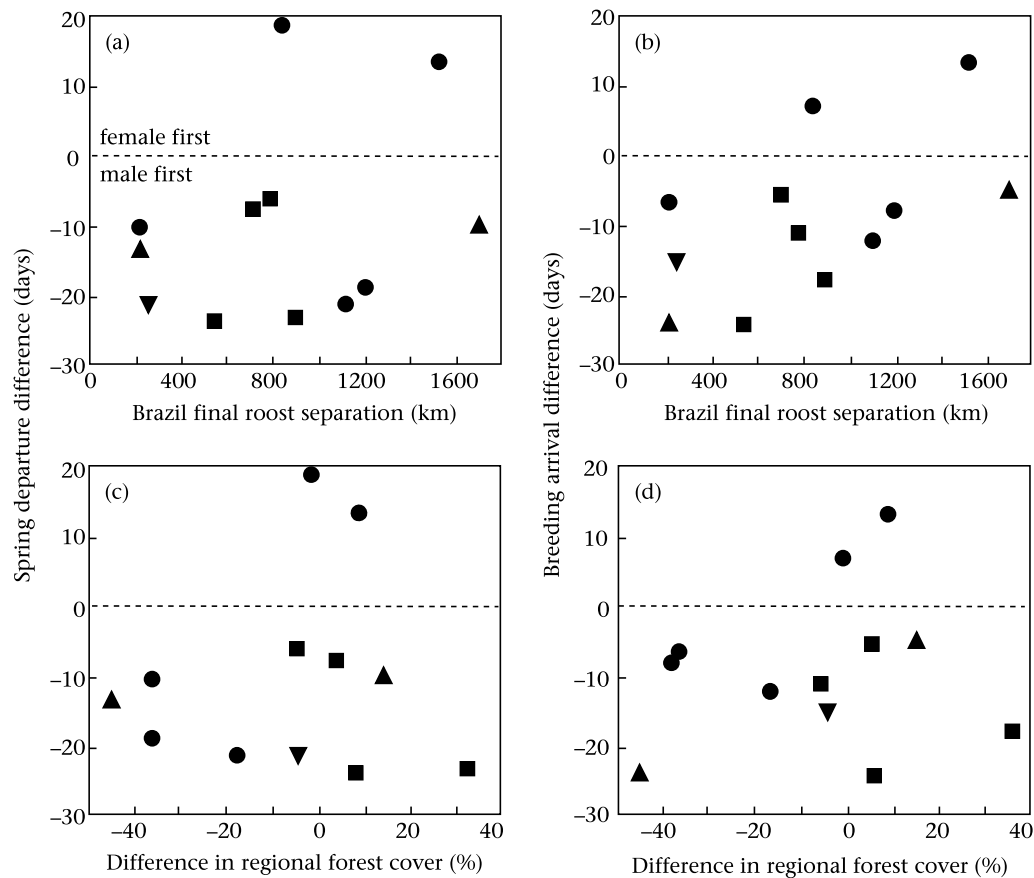


**Figure 4.** Distance between the estimated final roost site in Brazil of formerly mated purple martin pairs and the difference in their timing (male minus female) of (a) onset of spring migration from Brazil and (b) arrival date at the breeding site in North America. Difference in regional forest cover (%) of final roost sites, within 50 km of the estimated location, and difference in timing of (c) onset of spring migration from Brazil and (d) arrival date at the breeding site. Points below the dashed horizontal line represent cases where the male's timing was earlier than the female's. Symbol shape represents different study sites (Alberta: triangle; Florida: inverted triangle; Pennsylvania: circle; Virginia: square).

estimated roost site (Fig. 4c, d) was not significantly correlated with absolute difference in either spring departure date ($r_S = 0.05$, $P = 0.89$) or arrival date ($r_S = 0.43$, $P = 0.16$).

## DISCUSSION

Although recent tracking evidence suggests that long-distance migratory songbird pairs sometimes remain in close proximity throughout their migration (Arizaga et al., 2014), we found that this was not the case for purple martins. In about half of the pairs we tracked, pair members departed on autumn migration within 4 days of each other, but these possible pair associations quickly broke down over the course of the journey. The timing of autumn stopovers in Central America, of arrivals to and departures from Brazil, and of arrivals back at the breeding site were rarely synchronized among former pair members. Arizaga et al. (2014) found that the day-to-day timing of shifts in longitude were nearly identical for both members of one mated pair of barn swallows, in stark contrast with an unmated pair that was also tracked. In the present study, sudden shifts in longitude during migration were not similarly timed either for pairs or for randomly chosen nonpaired purple martins (Supplementary Fig. S1).

Proximity on the wintering grounds, or similarity in habitat, could indirectly produce more synchronized spring migration schedules even if pairs do not actively associate during migration (Choudhury, 1995; Gunnarsson et al., 2004). We found that former

martin pairs did not winter significantly closer together than nonpairs. Purple martins form large nocturnal roosts on the wintering grounds, and as aerial insectivores, they forage over large areas during the daytime. The core wintering region for purple martins is the northwestern Amazon, where forest cover within 50 km of estimated roost sites typically exceeds 90% (Fraser et al., 2012). However, deforestation and agricultural development are extensive in other parts of the winter range. Recent studies of insectivorous songbirds in Europe and elsewhere have linked agricultural landscapes to population declines, with reduced food supply as the indirect mechanism (Hallmann, Foppen, Turnhout, de Kroon, & Jongejans, 2014; Paquette, Pelletier, Garant, & Bélisle, 2014). Despite wide variation in purple martins' exposure to agricultural landscapes on the wintering grounds, our tracking data indicated that neither proximity on the wintering grounds nor similarity in regional forest cover results in former pairs departing from Brazil closer together in time. Agricultural landscape cover in Brazil may influence aerial insect food supply, body condition or onset of spring migration in purple martins, but no field studies have yet examined these factors.

Divorce is more common in short-lived species (Cézilly & Nager, 1995) like purple martins, partly because of the relatively low probability that a mate will survive a full year. Adult annual survival is about 60% in purple martins, but breeding site fidelity of survivors is high (93%; Stutchbury, Hill, Kramer, Rush, & Tarof, 2009), so re-pairing at the breeding site is possible in theory. Nevertheless, Morton and Derrickson (1990) reported a divorce rate of 87% for purple martins, which is comparable to that reported here (92%) for a different colony. In our migration study, we did not make observations of pair formation in newly arrived individuals or study the behavioural interactions among divorced pair members and individuals who took their place. Purple martins are cavity nesters and have strong nest site and mate competition (Morton, Forman, & Braun, 1990; Stutchbury, 1991; Tarof & Brown, 2013). Pair formation typically occurs soon after arrival, and within-sex chases and prolonged fights over nesting cavities are commonly observed prior to egg laying for both males and females. The strong mismatch in spring migration schedules of formerly paired birds documented here, with arrival of former pairs separated by almost 2 weeks, may make re-pairing unlikely even when both pair members survive migration.

## Supplementary Material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.01.016.

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