



Effects of Spring Migration Distance on Tree Swallow Reproductive Success Within and Among Flyways

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During migration, animals may experience high rates of mortality, but costs of migration could also be manifested through non-lethal carry-over effects that influence individual success in subsequent periods of the annual cycle. Using tracking data collected from light-level geolocators, we estimated total spring migration distance (from the last wintering sites to breeding sites) of tree swallows (*Tachycineta bicolor*) within three major North American flyways. Using path analysis, we then assessed direct and indirect effects of spring migration distance on reproductive performance of individuals of both sexes. When these data were standardized by flyway, females fledged 1.3 fewer young for every 1,017 km they traveled, whereas there was no effect of migration distance on reproductive success in males. In comparison, when these data were standardized across all individuals and not by flyway, longer migrations were associated with 0.74 more young fledged for every 1,017 km traveled by females and 0.26 more young fledged for every 1,186 km migrated by males. Our results suggest that migration distance carries over to negatively influence female reproductive success within flyways but the overall positive effect of migration distance across flyways likely reflects broader life-history differences that occur among breeding populations across the tree swallow range.

Keywords: tree swallow, migration, geolocation, migration distance, path analysis, young fledged

INTRODUCTION

Migration is widespread throughout the animal kingdom (reviewed in Newton, 2008) and likely evolved as an adaptation to optimize resource use (Alerstam et al., 2003; Alerstam, 2011). However, traveling between locations, many of which are thousands of kilometers apart, is also considered to be costly (Wikelski et al., 2003). Such costs are primarily thought to be “direct” in the form of higher mortality when compared to non-migratory periods of the annual cycle (Lok et al., 2014), though the migratory period may not be the only period with the highest mortality rates (Leyrer et al., 2013; Rakhimberdiev et al., 2015a; Senner et al., 2019). Among those individuals that survive migration, the cost of traveling such long distances may also carry over to influence reproductive success the following season (Harrison et al., 2011). Determining the existence and strength of these carry-over effects and how they may vary within and among populations will contribute to our understanding of long-term population dynamics and how life-history trade-offs shape broad-scale migration patterns (Norris and Marra, 2007; Harrison et al., 2011; Betini et al., 2013).

Many species of birds migrate different distances, even within a single breeding population (Fraser et al., 2012; McKinnon et al., 2013; Knight et al., 2018; McKinnon and Love, 2018). Only a few avian studies have examined carry-over effects of migration distance on individual reproductive success following a breeding season, and most have focused on whether migration distance is related to timing of arrival at a breeding site (Hötker, 2002; Bregnballe et al., 2006; Gunnarsson et al., 2006; Alves et al., 2012; Briedis et al., 2019), the start of breeding (Lok et al., 2016; Kentie et al., 2017), and breeding productivity (Bearhop et al., 2005; Bregnballe et al., 2006; Lok et al., 2016; Kentie et al., 2017). For example, in great cormorants, *Phalacrocorax carbo* (Bregnballe et al., 2006), and pied avocets, *Recurvirostra avosetta* (Hötker, 2002), birds wintering farther south arrived later at breeding sites. For pied avocets, early arrival led to higher breeding success (Hötker, 2002), whereas this relationship was not observed in great cormorants (Bregnballe et al., 2006). More southerly wintering black-tailed godwits, *Limosa limosa* that crossed the Sahara, started breeding earlier than those wintering farther north that did not cross the Sahara, but there was little effect of migration distance on reproductive success (Kentie et al., 2017). Male Eurasian spoonbills, *Platalea leucorodia*, that migrated longer distances began breeding later and subsequently produced fewer and lower quality chicks, and recruited fewer young (Lok et al., 2016). Similarly, in a study on songbirds, European blackcaps, *Sylvia atricapilla*, wintering farther north, as estimated from stable isotopes, produced larger clutches and fledged more young compared to those wintering farther south (Bearhop et al., 2005). Collectively these studies suggest that non-lethal effects of migration distance on reproduction might depend on the species or ecological context, and strongly emphasize that further study is needed across a wider range of taxa and among multiple populations.

Recently, we described a migratory network based on year-round movements of tree swallows (*Tachycineta bicolor*) originating from 12 breeding populations across their range

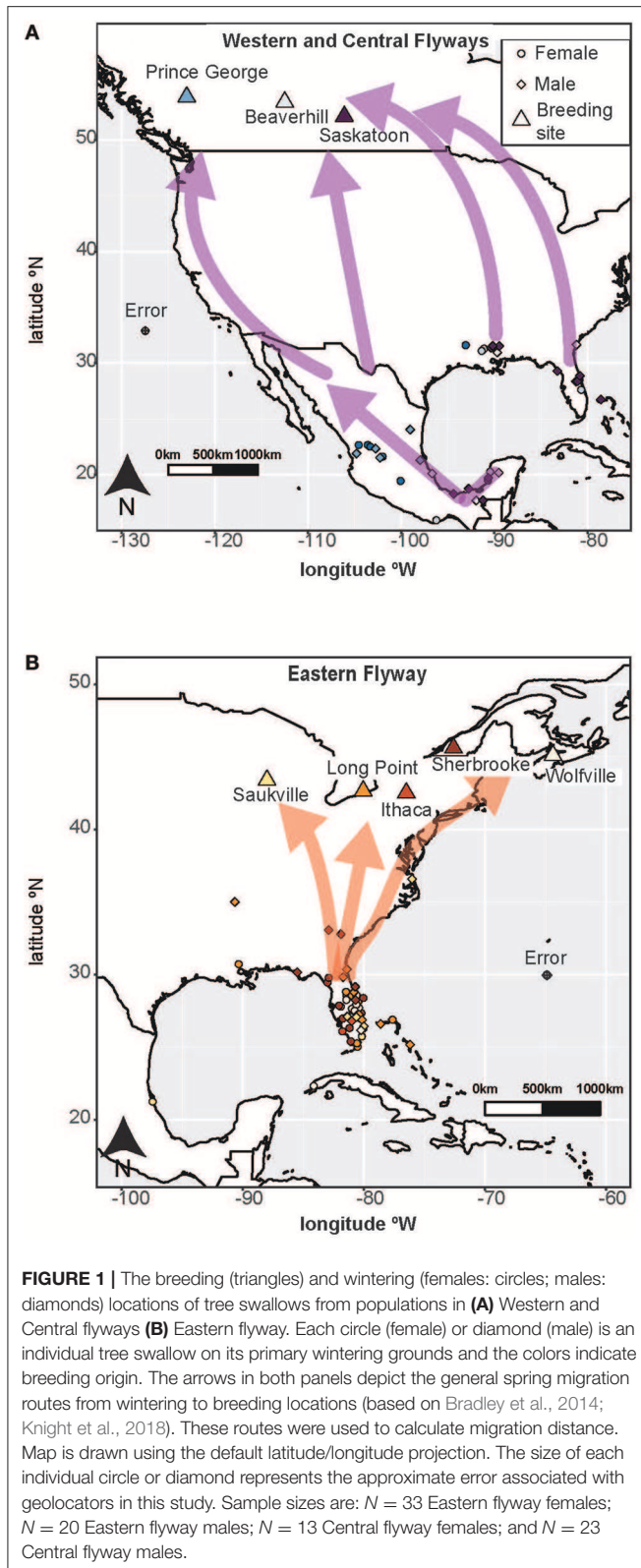
(Knight et al., 2018). In addition to linking breeding populations with stopover and wintering sites, we also identified three distinct migratory flyways (Knight et al., 2018). In the Western flyway, tree swallows breeding west of the Rockies migrated primarily to western Mexico, those in the Central flyway bred in central Canada or the U.S and either crossed the Gulf of Mexico to wintering sites in eastern Mexico, or wintered in Louisiana, Mississippi, or Florida (Central flyway). The Eastern flyway consisted of tree swallows that bred in eastern North America and primarily used wintering sites in Florida, the Caribbean Islands, or Cuba (Eastern flyway; **Figure 1**; Knight et al., 2018). In a subsequent study, the timing of arrival on the breeding grounds appeared to be most strongly influenced by both the latitude from which the birds departed and the latitude of the breeding site (Gow et al., 2019), suggesting that the distance an individual traveled could influence the timing of breeding. Whether and how spring migration distance could carry over to influence subsequent reproductive success is not known.

There are several factors that influence reproductive performance (i.e., number of young fledged), and ultimately population dynamics (Cox et al., 2018). These include reproductive traits, such as clutch size (Dunn et al., 2000; Millet et al., 2015), timing of events such as arrival at breeding locations (e.g., Norris et al., 2004), or start of breeding (i.e., first egg dates; Hochachka, 1990; Verhulst and Nilsson, 2008; Millet et al., 2015). Understanding the relationships among these factors and how they directly or indirectly affect reproductive success could provide mechanisms through which spring migration distance and the duration of spring migration may influence productivity. Here, we evaluated (1) the potential for spring migration distance to affect reproductive performance among populations, (2) how this may vary between major flyways, and (3) whether migration distance had different effects on each sex. We used path analysis (Shipley, 2009) to first quantify the direct effects of spring migration distance on timing of arrival to breeding sites, first egg date, clutch size, and the number of young fledged, and then estimated possible indirect effects of spring migration distance on the number of young fledged via the other reproductive metrics. We evaluated these effects by sex controlling for flyway (identified in Knight et al., 2018), and then compared these results to analyses when data from all flyways were combined. From the direct and indirect effects estimates from the path models, we then generated predictions of the total effect of migration distance on the number of young fledged.

MATERIALS AND METHODS

Study Sites and Data Collection

Between 2010 and 2014, we equipped 561 adult tree swallows with an archival light-level geolocator (hereafter referred to as “geolocators”) at the 12 breeding sites (Fairbanks, Alaska, 65.90°N, 147.70°W; Vancouver, British Columbia, 49.21°N, 123.18°W; Prince George, British Columbia, 53.85°N, 123.02°W; Beaverhill, Alberta, 53.40°N, 112.50°W, Saskatoon, Saskatchewan, 52.17°N, 106.10°W; Ames, Iowa, 42.11°N, 93.59°W; Saukville, Wisconsin, 43.40°N, 88.00°W; Boone, North Carolina, 36.21°N, 81.67°W; Long Point, Ontario, 42.62°N,



80.46°W; Ithaca, New York, 42.50°N, 76.50°W; Sherbrooke, Québec, 45.55°N, 72.60°W; Wolfville, Nova Scotia, 45.10°N, 64.39°W). Overall, we retrieved 161 geolocators, 133 of which

were free from malfunctions. Each bird was tracked for a 1-year period. Of these 133, we obtained reproductive history from 105 individuals. Birds from Vancouver, Alaska, Iowa, and North Carolina were not included in this study, either because of small sample size or because individuals at these sites were outliers based on migration distances within their respective flyway. Eighty-nine individuals (46 females and 43 males) were therefore used in this study.

Geocator Analysis and Definition of the Last Wintering Site

Light data from geolocators were analyzed using the BASTag package 0.1.3 (Wotherspoon et al., 2013) and FlightR package version 0.3.6 (Rakhimberdiev et al., 2015b) with R version 3.2.3 (R Core Development Team, 2016). The FlightR package works well for open area birds, and it uses a state-space hidden Markov model to estimate daily locations. For step-by-step details about geocator deployment and analysis see Knight et al. (2018). Given the well-defined light transitions, geocator error was minimal (46 ± 90 km in latitude and 52 ± 90 km in longitude; Gow et al., 2019). Geocator error was calculated based on averaged location estimates from the breeding site (Gow et al., 2019). We followed the definitions in Gow et al. (2019) for determining wintering site, and identifying departure and arrival at sites. Briefly, locations were determined by calculating the mean location of all daily locations from a stationary period. We considered birds to have departed from the wintering site if they made a large (≥ 250 km) northward movement, lasting for at least 2 d, away from a stationary position. Given that tree swallows may use more than one wintering site (Knight et al., 2018), the last wintering site was defined as the last location that a tree swallow spent at least 28 d. Breeding arrival date was defined as the first day tree swallows had location estimates consistently matching those of the known breeding site.

Definitions of Reproductive Metrics and Flyways

Tree swallows breed in natural tree cavities or nest boxes throughout the southern half of Canada and the north/central United States; they generally have clutches of 4–7 eggs (Winkler et al., 2011). All tree swallows in our study were single-brooded, although some females attempted a second clutch if their first nest was depredated. Tree swallow clutch sizes increase with breeding latitude (Dunn et al., 2000). At each study site, nest boxes were checked every 1–7 days (with most sites checking nests every 1–3 days) to obtain the following breeding information from individuals in the year following geocator deployment: first egg date (date on which the first egg of the first clutch of the season was laid), clutch size (number of eggs laid in the first clutch of the season), and number of young fledged (number of young estimated to have survived to fledging). All failed nests were counted as zero in our analyses. We determined breeding arrival date (date bird first arrived at the breeding site), and spring migration distance for each tree swallow carrying a geocator. We calculated spring migration distance as the great circle distance between the last overwintering site and the

breeding site (i.e., spring migration distance; **Figure 1**; Bradley et al., 2014). The arrows in **Figure 1** show the general pathways used to calculate migration distance for each population. Most tree swallows migrated during the spring equinox making it difficult to estimate the true travel route. Thus, for consistency among individuals we calculated migration distance using several points along the migration pathways for tree swallows defined by Bradley et al. (2014; **Figure 1**). The connections between wintering and breeding sites are available in Knight et al. (2018).

We interpreted clutch size and the number of young fledged differently between sexes. For females, clutch size and the number of young fledged are direct measures of reproductive success. However, because there is rampant extra-pair paternity in tree swallows (e.g., 50–89%; Lifjeld et al., 1993; Barber et al., 1996; Kempenaers et al., 2001; Whittingham and Dunn, 2001; O'Brien and Dawson, 2007), the number of young fledged likely does not represent realized (i.e., genetic) reproductive success of males. Realized reproductive success would account for both a male's potential paternity lost within his nest and potential paternity gained via extra-pair fertilizations outside the social pair bond. Given that we did not have genetic paternity data from our sites, we could not include realized reproductive success of males in our study. Thus, for males, the number of young fledged within the social pair bond (the variable we measured and included in our study) more accurately reflects the quality of the social partner rather than true reproductive success in a given season. First egg dates and clutch size also mainly reflect the quality of the social partner rather than true reproductive parameters for males, meaning that the only reproductive variable that is solely influenced by males was breeding arrival date. Breeding arrival date may have subsequent carry-over effects that may influence the quality of the social mates that a male is able to acquire.

A network analysis by Knight et al. (2018) showed how breeding populations segmented into three migratory flyways: Western, Central, and Eastern. We chose to combine the Western and Central flyways because of the small sample of birds in the Western flyway ($n = 11$) and because these two flyways had similar means and standard deviations (s.d.) of migration distance (Western: $3,833 \pm 795$ km; Central: $4,217 \pm 1,082$ km; **Table 1**). We eliminated 4 populations from our analyses that had a small sample size (Vancouver, BC and Ames, IA) and/or represented extreme southern and northern regions of the tree swallows' range (Fairbanks, AK and Boone, SC). The populations we included from the Western and Central flyways (hereafter referred to as the Central flyway for simplicity) were Prince George, BC, Beaverhill, AB, and Saskatoon, SK ($N = 36$; female = 13; male = 23; **Figure 1A**), and those in the Eastern flyway were Saukville, WI, Long Point, ON, Ithaca, NY, Sherbrooke, QC, and Wolfville, NS ($N = 53$; female = 33; male = 20; **Figure 1B**).

Path Analysis

Prior to executing the path analysis, we undertook two types of data standardizations to help separate the potential effects of breeding location on life-history variation from the effects on individuals migrating farther than other individuals within their flyway. First, we standardized each variable by flyway (sexes pooled) by subtracting the mean then dividing by the standard

TABLE 1 | Summary of migration distances among breeding sites across sexes and separated by females and males.

All	Breeding site	Min	Max	Mean	Median	s.d.	Flyway	N
	Prince George, BC	3,677	4,713	4,295	4,272	286	Western	11
	Beaverhill, AB	3,291	4,879	4,128	4,260	575	Central	11
	Saskatoon, SK	3,157	4,696	4,096	4,163	551	Central	14
	Ithaca, NY	1,767	1,956	1,878	1,895	80	Eastern	4
	Long Point, ON	1,496	2,247	1,778	1,733	199	Eastern	19
	Saukville, WI	1,783	2,188	2,047	2,078	147	Eastern	6
	Sherbrooke, QC	1,683	2,478	2,158	2,211	227	Eastern	14
	Wolfville, NS	2,540	3,209	2,697	2,630	201	Eastern	10
Female								
	Prince George, BC	3,677	4,698	4,213	4,202	335	Western	6
	Beaverhill, AB	3,291	4,811	4,041	4,354	703	Central	5
	Saskatoon, SK	4,671	4,681	4,676	4,676	7	Central	2
	Ithaca, NY	1,767	1,956	1,873	1,898	97	Eastern	3
	Long Point, ON	1,601	2,029	1,786	1,723	167	Eastern	10
	Saukville, WI	2,147	2,188	2,168	2,168	30	Eastern	2
	Sherbrooke, QC	2,006	2,478	2,242	2,256	150	Eastern	9
	Wolfville, NS	2,540	3,207	2,685	2,620	210	Eastern	9
Male								
	Prince George, BC	4,171	4,713	4,394	4,371	206	Western	5
	Beaverhill, AB	3,427	4,879	4,200	4,167	502	Central	6
	Saskatoon, SK	3,157	4,696	3,999	4,158	535	Central	12
	Ithaca, NY	1,893	1,893	1,893	1,893	NA	Eastern	1
	Long Point, ON	1,496	2,247	1,769	1,803	240	Eastern	9
	Saukville, WI	1,783	2,124	1,987	2,020	145	Eastern	4
	Sherbrooke, QC	1,683	2,297	2,006	2,119	279	Eastern	5
	Wolfville, NS	2,800	2,800	2,800	2,800	NA	Eastern	1

The minimum (min), maximum (max), mean, median, standard deviation (s.d.), flyways and samples sizes (N) are indicated. All distances are in km. Flyways were identified by Knight et al. (2018).

deviation (i.e., z-transformation). This allowed us to control for flyway effects. Second, we z-transformed these data across all individuals independent of flyway. If there was a positive effect of migration distance on first egg date, clutch size, or young fledged when the dataset was standardized across all individuals, then this may indicate the relationship was due to life-history factors rather than migration distance *per se*. In contrast, when standardizing by flyway, if there is a negative relationship between migration distance on first egg date, clutch size or young fledged, then this may suggest a potential carry-over effect of migration distance.

Following this standardization, we evaluated the direct and indirect effects of migration duration, migration distance, breeding arrival date, first egg date, and clutch size on the number of young fledged using a multi-level path modeling framework (Shipley, 2000, 2009). We included a random effect of "breeding site" to account for local-level effects across the 8 breeding populations. All mixed effects models were fitted with a Gaussian distribution, as the response variables best fit this distribution, using the nlme package (Pinheiro et al., 2018) in R 3.5.2 (R Core Development Team, 2018). We identified the most parsimonious path model based on Akaike's Information

Criterion corrected for sample size (AICc; Shipley, 2000, 2009, 2013). We evaluated four different sets of path models, separated by sex and standardization method (i.e., standardized by flyway or standardized across individuals).

We structured the path models based on previous knowledge of tree swallow ecology. For each set of path models, we started by fitting a global model, which included direct effects of spring migration duration, spring migration distance, breeding arrival date, first egg date, and clutch size on the number of young fledged. We removed terms associated with uninformative estimates for young fledged first, followed by those with uninformative estimates for clutch size, first egg date, breeding arrival date, and migration distance. We determined the order of deletion using AICc to assess the terms with the least support in each submodel using maximum likelihood estimation (MuMIn package; Barton, 2016; see **Figure S1** for path analysis submodels). We removed terms from the path model if their deletion did not increase the AIC by at least two units (**Table S1**). Models were not averaged because top models were all nested within preceding models (Arnold, 2010).

From the path analysis, we calculated direct effects of one variable on another as well as indirect effects (Mitchell, 1993). Indirect effects were calculated by taking the product of all possible pathways (path coefficients) from one variable to another. Direct effects occur between variables and are generated by path coefficients (regression beta coefficients). Because we standardized the dataset prior to conducting the path analysis we did not need to standardize the path coefficients. The total effect was calculated as the sum of all indirect and direct effects from one variable to another.

We compared migration distances between sex and standardization type using a linear mixed effects model (LMM). We included breeding site as a random effect. We used *post-hoc* pairwise differences to compare migration distances between the sexes standardized by flyway or across individuals.

Predicted Effects of Migration Distance on Young Fledged

Because total effect values summarize all direct and indirect pathways between migration distance to the number of young fledged, we also produced a predictive model. This model involved first summarizing the effect of migration distance on the number of young fledged using the total effect values and standard deviations (s.d.) for each variable (Bart and Earnst, 1999). For example, the effect of migration distance on number of young fledged was expressed as: s.d. (migration distance) = s.d. (young fledged*total effect). We took the mean migration distance and used it to predict differences in the number of young fledged across different migration distances. We only developed predictive models for the sex and standardizations in which there was at least one effect of migration distance on a reproductive metric.

This study was carried out in accordance with the principles of Animal Utilization Protocols or Animal Care Protocols and was approved by each University of the primary researcher for each field site.

RESULTS

Variation of Spring Migration Distance Between Flyways and Sexes

Tree swallows migrated on average $2,930 \pm 1,110$ km (range: 1,496–4,879 km). While males migrated farther and showed more variation in migration distances than females (males: $3,110 \pm 1,187$ km; females: $2,761 \pm 1,017$ km), there was no evidence the sexes arose from different distributions (LMM: $\beta = -61.89 \pm 82.44$, $t = -0.75$, $p = 0.45$; **Table 1**). Females migrated significantly farther and had different distributions in their migration distances in the Central flyway than the Eastern flyway (LMM: $\beta = 2,129 \pm 261$, $t = 8.14$, $p < 0.001$; **Table 1**), and a similar pattern was observed for males (LMM: $\beta = 2,201 \pm 161$, $t = 13.66$, $p < 0.001$; **Table 1**). Males spent more time on average migrating than females but this difference was not significant (LMM: $\beta = 5.58 \pm 4.67$, $t = 1.19$, $p = 0.24$; **Table 2**). In the Central flyway, females spent significantly more time on spring migration compared to the Eastern flyway (LMM: $\beta = 15.58 \pm 6.0$, $t = 2.60$, $p < 0.01$; **Table 2**). Although males in the Central flyway spent more days migrating in the spring than in the Eastern flyway, this was not significantly different (LMM: $\beta = 13.13 \pm 7.24$, $t = 1.81$, $p = 0.14$; **Table 2**).

Effect of Migration Distance on Reproductive Performance: Variables Standardized by Flyway

For females, migration distance negatively affected the number of young fledged (**Figure 2**). Females migrating the shortest distances within their flyway fledged more young compared to those migrating the farthest distances, suggesting a direct carry-over effect of migration distance on young fledged. In contrast, for males there was no effect of migration distance on clutch size or young fledged, but males that spent longer migrating in the spring arrived later to the breeding site. Breeding arrival date positively influenced first egg dates in females, but males that arrived later had social mates that laid their first clutches earlier. For females, first egg dates did not influence clutch size. Earlier breeding males had social mates that produced larger clutches than later breeding males. For females, clutch size positively affected the number of young fledged, and males mated to females that laid large clutches also fledged more young. Overall, the total effect of migration distance on number of young fledged for females was -0.55 ± 0.33 , resulting in a predicted 1.33 fewer young for every 1,017 km they migrated (**Figure 3**).

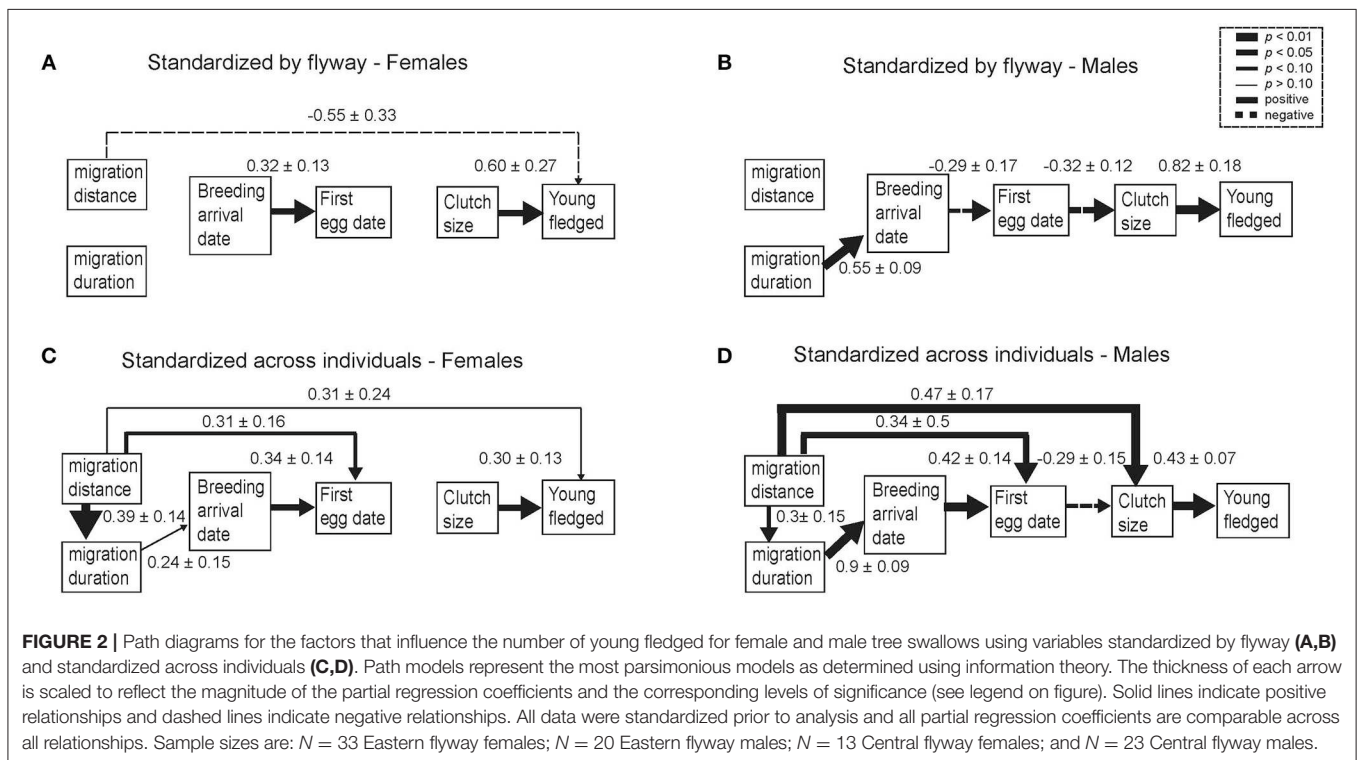
Effect of Migration Distance on Reproductive Performance: Variables Standardized Across All Individuals

Migration distance in females directly and positively affected migration duration, first egg dates, and young fledged (**Figure 2**). Given the later first egg dates and higher number of young fledged in the Central flyway than the Eastern flyway (**Table 2**), results from the path analysis showed that females migrating the farthest distances (most birds in the Central flyway) fledged

TABLE 2 | Summary of the means, standard deviations (s.d.) and range (minimum and maximum) of migration distance and duration, timing (breeding arrival date, first egg date) events, and reproductive variables (clutch size and number of young fledged) for females and males within each flyway.

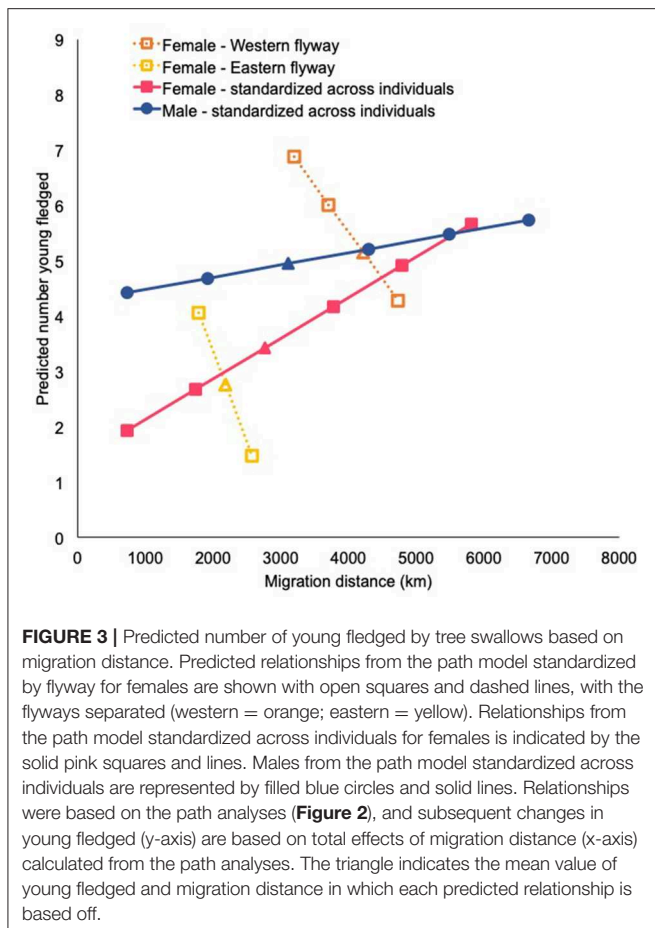
Flyway	Timing or reproductive variable	Females			Males		
		Mean	s.d.	Range (min-max)	Mean	s.d.	Range (min-max)
Eastern							
	Migration duration (days)	27	18	3–77	31	27	3–95
	Migration distance (km)	2,187	394	1,601–3,207	1,930	314	1,496–2,800
	Breeding arrival date	115	11	93–143	106	14	82–146
	First egg date	139	9	130–169	136	9	128–169
	Clutch size	5.48	0.79	3–7	5.55	0.89	3–7
	Number young fledged	2.78	2.36	0–6	4.10	1.77	0–7
Central							
	Migration duration (days)	42	19	12–77	44	21	11–90
	Migration distance (km)	4,218	509	3,291–4,811	4,137	485	3,157–4,879
	Breeding arrival date	120	14	89–136	121	8	109–135
	First egg date	147	4.5	137–156	149	7	142–177
	Clutch size	5.46	1.45	2–7	6.50	0.94	4–8
	Number young fledged	5.15	1.57	2–7	5.70	1.11	4–8

Sample sizes are: $N = 33$ Eastern flyway females; $N = 20$ Eastern flyway males; $N = 13$ Central flyway females; and $N = 23$ Central flyway males.



more young and also began breeding later than females migrating shorter distances (most birds in the Eastern flyway). For males, migration distance had a positive direct effect on migration duration, and the male's social mate's first egg date and clutch size. Furthermore, males traveling the farthest distances (typically in the Central flyway) began breeding later and their social mate had larger clutches than those migrating shorter distances (typically

the Eastern flyway). But the negative relationship between first egg date and clutch size suggested that males with social mates that began breeding later had smaller clutches. Overall, the total effect of migration distance on young fledged for females was 0.31, which implied that females fledged 0.74 more young for every 1,017 km farther they migrated. For males, the total effect of migration distance on young fledged was 0.16, which implied



that males fledged 0.26 more young for every 1,186 km farther they migrated (Figure 3).

DISCUSSION

Collectively, previous research suggests that non-lethal effects of migration distance on reproduction might be species or context specific (Hötter, 2002; Bregnballe et al., 2006; Gunnarsson et al., 2006; Alves et al., 2012; Lok et al., 2016; Kentie et al., 2017), but if migration distance is energetically costly then individuals that migrate farther distances may experience carry-over effects into stationary periods of the annual cycle (Harrison et al., 2011 but see Conklin et al., 2017). Our results suggest that variation in migration distance within a flyway with individuals breeding at similar latitudes, had a negative effect on the number of young fledged for females. For males, there were no effects of migration distance when data were standardized by flyway, but males that migrated faster arrived earlier, and were mated to females that began breeding later. This suggests males migrating at faster paces may experience a cost in their ability to acquire an early breeding mate, even though they arrived early to the breeding site. In contrast, when data were standardized across all individuals, we show that overall migration distance is positively associated with fledging success, and thus, may be representing broader life-history differences.

It is possible that the negative relationship between migration distance on young fledged in females was the result of location-specific life history variation rather than a carry-over effect. However, we argue that this is unlikely for several reasons. First, breeding sites within the Central and Eastern Flyways varied little in latitude within their flyways (i.e., 1.68°N in the Central flyway and 3.05°N in Eastern flyway), suggesting any such effects of migration distance were likely unrelated to latitudinal variation in the breeding location. Second, within breeding sites there was often large variation in migration distance (Table 1). This was especially true of birds in the Central flyway as individuals migrated to Mexico, the Gulf of Mexico, and in some cases, Florida resulting in migration distances within sites that varied by over 1,000 km (Figure 1). Thus, by standardizing within flyways we were able to separate the potential effects of breeding location from migration on reproductive variables. However, future research that includes additional sites and individuals within a migratory network would likely provide a clearer picture of the effect of migration distance on reproduction.

In contrast, when standardizing across all individuals, males and females that migrated the farthest distances fledged the most young. We argue that this result was likely driven by broader life-history differences related to breeding latitude (Ricklefs, 1980; Dunn et al., 2000; Jetz et al., 2008) rather than migration distance, *per se*. Tree swallows wintered within a narrow band ranging ~11° of latitude whereas their breeding range covers ~34° of latitude (Winkler et al., 2011), leading to spring migration distance, when examined across the entire network, being positively correlated with breeding latitude (see also Gow et al., 2019). Previously, we provided evidence that tree swallows breeding at higher latitudes arrived later and began breeding later (Gow et al., 2019), similar to the positive effects of migration distance we observed on first egg date of males and females in this study when we standardized across individuals.

One reason we observed a negative effect of migration distance on young fledged in females but not males (when data were standardized within flyways) may be related to how the sexes differ in their sensitivity to the energetic or physiological costs of migration distance. Under the reproductive stress hypothesis, the sex with the higher reproductive demands will be more sensitive to their energetic or physiological state when investing in reproduction (Nagy et al., 2007; Gow et al., 2013; Gow and Wiebe, 2014). In tree swallows, females invest in reproduction through nest building, egg laying, incubation, feeding young and intense female-female competition. Males only engage in feeding young, but also invest in male-male competition, pursuit of extra-pair fertilizations, and securing and defending nest sites (Winkler et al., 2011). Thus, female tree swallows are the sex investing more heavily in the production of young. Experimental studies manipulating female quality or timing of breeding (Winkler and Allen, 1995; Dawson, 2008; Harriman et al., 2016) suggest a female's quality may affect her ability to produce and care for offspring. In this way, it is possible that migration distance influenced the number of young fledged by affecting female condition, but did not affect whether a male was capable of mating with a female that produced more young.

Male tree swallows that migrated faster relative to other individuals in their flyway arrived earlier to the breeding site. However, arriving earlier to the breeding grounds may not necessarily be beneficial if it leaves an individual in a poorer condition (e.g., González-Prieto and Hobson, 2013), unless they acquired larger reserves prior to migration (Bayly et al., 2016). Arriving to the breeding grounds in a poor physiological state may be particularly detrimental for male tree swallows given their reliance on aerial insects. Interestingly, male tree swallows that arrived early to the breeding grounds (when standardizing by flyway) seemed to be mated to females that began breeding relatively late. One reason for this negative relationship may be related to how breeding tree swallows are impacted by poor weather (Weegman et al., 2017; Cox et al., 2019) and low insect abundances (McCarty and Winkler, 1999; Imlay et al., 2017). Both poor weather and low insect abundances may impair reproductive performance via their effects on the timing of breeding (Dawson, 2008; Harriman et al., 2016), and female body condition (Winkler and Allen, 1995; Paquette et al., 2014). These factors may also differ among flyways. Populations in the Central and Western flyways appear to be more strongly affected by timing of breeding and insect abundances during egg laying (Dawson, 2008; Harriman et al., 2016), while those in the Eastern flyway may experience more negative effects from poor weather conditions (Weegman et al., 2017; Cox et al., 2019) rather than variation in insect abundance (McCarty and Winkler, 1999; Imlay et al., 2017). This difference may explain why when we did not standardize by flyway and instead standardized across all individuals faster arriving males arrived earlier (similar to within flyway standardization). These early arriving males mated with females whom also began breeding earlier, demonstrating an overall positive benefit to migrating faster and arriving early across the range.

Our findings provide valuable insight into how migration distance may influence current and future population declines of tree swallows, as well as other species. Many tree swallow populations in the northeastern parts of their range have experienced declines over the past couple of decades (Shutler et al., 2012). The cause(s) of these declines are unclear, but one possibility is that deterioration of overwintering habitat quality influences survival and carries over to influence reproductive performance. Another mechanism for population declines in this species, and potentially others, may occur if individuals are forced to migrate farther. Individuals may migrate farther distances if there is a reduction in habitat quality, which may reduce the carry-capacity of those sites (e.g., Stutchbury et al., 2016), forcing individuals to seek alternative roosting sites farther south. For swallows breeding in the Western or Central flyways, this may mean either crossing the Gulf of Mexico or moving to areas farther south in Central America, whereas those breeding in the Eastern flyway may be forced to seek habitat on Caribbean Islands or travel even farther distances to Mexico. Alternatively, with the globally rising temperatures, suitable habitat for tree swallows may be available farther north. The geographic differences among flyways may affect the potential distances some individual migrate, which in turn may affect the number of young fledged, and contribute to population declines.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the manuscript/**Supplementary Files**.

ETHICS STATEMENT

This study was carried out in accordance with the principles of Animal Utilization Protocols or Animal Care Protocols and was approved by each University of the primary researcher for each field site.

AUTHOR CONTRIBUTIONS

EG and DN designed the research and wrote the manuscript. EG analyzed these data. SK processed the geolocator data. All other authors conducted fieldwork and helped with manuscript revisions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00380/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer, MH, declared past collaborations with several of the authors, DN, DW, CT, and EB, to the handling editor.

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