

AGE AND SEX INFLUENCE NATAL AND BREEDING DISPERSAL OF PURPLE MARTINS

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ABSTRACT: Dispersal patterns deepen our understanding of population dynamics. Dispersal by all age and sex classes enhances a species' ability to respond to environmental changes, such as in habitat availability, artificial nest sites, and climate. The migration dynamics of the eastern subspecies of the Purple Martin (*Progne subis subis*) are well known, but we know less about its patterns of annual dispersal. We compared the frequency, distance, and direction of dispersal by each age/sex cohort of martins in central Alberta, at the northwestern limit of their breeding range. We used two datasets: (1) adult martins banded in central Alberta as nestlings and encountered during the summers of 2017 and 2018, and (2) records of encounters of banded martins in Canada from 1935 to 2016 from the Canadian Wildlife Service's Bird Banding Office. In Alberta, 36% of birds dispersed from natal sites (by an average distance of 24 km), most commonly to the northeast. Across Canada, 29% of birds dispersed (by an average distance of 183 km), most commonly to the east and northeast. In Alberta, martins at least two years old dispersed less frequently than yearlings since some older martins returned to their natal site after first breeding elsewhere. Dispersal distances of after-second-year martins, which represent natal plus breeding dispersal, were greater than those of second-year birds, which represent natal dispersal alone. Thus some martins continue to disperse after their second year and do not maintain complete fidelity to a breeding site, which is different from our current understanding.

Dispersal refers to the distance and direction an organism moves from where it originated to where it breeds in subsequent years (MacDonald 2003). Dispersal behavior shapes the geographical distribution, population structure, and population dynamics of any species (Walters 2000). There are two major categories of dispersal from one year to the next. Natal dispersal is defined as movement from the site where a bird fledges to where it first breeds, while breeding dispersal is any change in subsequent locations of breeding (Greenwood and Harvey 1982, Colbert et al. 2001). Species in which site fidelity or philopatry are strong return to their place of fledging to breed each year following their seasonal migration (Förschler et al. 2010), so their distances of natal dispersal are low. Dispersal is different from post-fledging wandering by young, in which fledglings or juveniles move from site to site before their first migration (Miller et al. 2001). Dispersal also differs from migration, the regular seasonal movement of animals between their breeding and nonbreeding ranges, in that dispersal does not include the migration route (Winkler et al. 2016). In this paper, we examine the frequency, distance,

and direction of dispersal of the eastern subspecies of the Purple Martin (*Progne subis subis*) in central Alberta and across Canada.

Walters (2000) called for more research on dispersal to help in understanding and modeling population dynamics and structure. Dispersal can vary by sex and age. This variation can be important in analysis of apparent survival rates that are based on capture–mark–recapture studies which, in birds, are typically done by banding individuals and searching for them in subsequent years. If dispersal rates and distances vary by age and sex, apparent survival rates calculated from recaptures or resightings will be skewed (Stutchbury et al. 2009). In addition, a good understanding of dispersal may help in conservation of wildlife populations affected by climate change and human development. For example, dispersal patterns can indicate future range expansions or contractions. Similarly, dispersal among subpopulations can help maintain a metapopulation (Esler 2000), but net dispersal from a subpopulation could contribute to the decline of that subpopulation. Moreover, understanding dispersal patterns can provide insights into the evolution and adaptations of migrants (Rappole 2013). Drivers of dispersal differ both between and within species (Greenwood and Harvey 1982). Ultimately, dispersal is an important life-history characteristic that affects species' persistence and evolution (Colbert et al. 2001).

In many though not all species, younger birds disperse more often than older birds (Greenwood and Harvey 1982). Moreover, Rappole (2013) noted that adults of many species force dispersal of younger birds soon after the young birds arrive at breeding sites. Greenwood and Harvey (1982) showed that among a wide variety of birds, although not some waterfowl, females tend to disperse more than males (Alison 1977). Rappole (2013) suggested that return rates for females are lower than for males because of lower female survivorship and greater female dispersal combined.

The Purple Martin, North America's largest swallow, is a colonial aerial insectivore. Primitively, martins nested primarily in tree cavities, though, over time, they became habituated to nesting in human-made structures (Tautin et al. 2009). Today, the eastern subspecies relies heavily on the provision and maintenance of suitable nest boxes (Brown and Tarof 2013). This article is concerned with dispersal in the eastern subspecies only.

Previous studies have found that rates of Purple Martin dispersal are low (Morton and Patterson 1983, Stutchbury et al. 2009, Zelt et al. 2012). The limited dispersal could restrict the species' ability to respond to habitat and climate changes. In a long-term study of a small area in Pennsylvania, the martin's natal fidelity was 84% for females and 87% for males; breeding fidelity was 91% for females and 94% for males (Stutchbury et al. 2009).

Past studies also showed distances of martins' dispersal from both their birth sites and the sites of their successful clutches to be short. Among the few studies, the most common dispersal distances were less than 50 km; distances of 80 km or farther were unusual, and of >300 km were rare (Hill 2003, Ray and Schoenhals 2011). The frequency distribution of dispersal distances is skewed, with many shorter dispersals and few longer dispersals. Hill (2003) reported dispersal distances averaging 13.6 km (range 7–607 km) and that 96% of banded martins bred within 60 km of where they hatched at sites in Pennsylvania, Ohio, and Illinois. In Texas, 86% of banded martins encountered were within 80 km of their natal colony, with the longest dis-

persal distance being 422 km, by a martin of unknown sex and age (Ray and Schoenhals 2011). Other reports of long-distance dispersal are 928 km for a male of unknown age from its original nest to a breeding colony (Houston and Houston 2011), 2060 km for a male of unknown age from its natal site to a nesting site five years later (Chambers 2011), and 2635 km for a bird of unknown sex and age from its natal site to a nesting colony. The longer dispersal distances in band-encounter studies are due, in part, to the larger study area (Greenwood and Harvey 1982).

Results from studies of dispersal directions are mixed, including southward and eastward for martins in Alberta (Finlay 1975) and no trend in Pennsylvania and Ohio (Hill 2003). Ray and Schoenhals (2011) speculated that the availability of nest boxes, particularly in less occupied directions, can aid martins' range expansion, giving them more opportunities to colonize new sites.

Comparisons can be made with studies of other species' dispersal. Dispersal rates range from 50% for adult small passerines to 10% for long-lived species like gulls (Rappole 2013). For the well-studied Tree Swallow (*Tachycineta bicolor*), Hosner and Winkler (2007) found that the percentage of individuals that dispersed less than 13.6 km varied from about 90% in New York to about 50% from band recoveries across the USA. In Saskatchewan, 20% of breeding Tree Swallows studied by Shutler and Clark (2003) had been banded locally as nestlings; thus 80% of breeders had dispersed from elsewhere. In New York, Winkler et al. (2004) found that older female Tree Swallows were less likely to disperse than younger females. More generally, females disperse more frequently than do males in the Barn Swallow (*Hirundo rustica*; Schaub and von Hirschheydt 2009) and Tree Swallow (Shutler and Clark 2003). Female Tree Swallows are more likely to disperse if their nests fail than if they succeed (Hosner and Winkler (2007). With respect to breeding dispersal, Winkler et al. (2004) found that 14% of female Tree Swallows, but only 4% of males, moved between successive breeding sites. In contrast, among Barn Swallows in Spain and Denmark, females are less likely to disperse than are males (Balbontin et al. 2009).

In our study we investigated how Purple Martin dispersal, specifically its frequency, distance, and direction, varies by age/sex cohort in central Alberta and across Canada. We predicted that second-year male martins should disperse farther and more frequently than other age/sex classes because older males arrive and establish nesting territories earlier than do younger males and all females (Brown and Tarof 2013). From the high degree of site fidelity found in previous studies, we predicted that natal dispersal should account for any dispersal patterns of all age/sex classes. Since there is little information on directional preferences for dispersal, we hypothesized that birds should disperse in all directions to promote stability in subpopulations. An alternate hypothesis is that martins should disperse north with warming temperatures brought on by climate change.

METHODS

We used a multi-scale sampling strategy (after Hosner and Winkler 2007) to compare data from a local area with national data. While we expected dispersal distances based on the cross-Canada data to be larger than those

based on the Alberta data, we wanted to determine whether the two scales' patterns for frequency, short/long distances, and directions were consistent.

Our local 10,000-km² study area in central Alberta extended from the Ellis Bird Farm (52.390° N, 113.611° W) 130 km north to Islet Lake (53.452° N, 112.825° W) and from Daysland (52.865° N, 112.261° W) 80 km west to Wetaskiwin (52.969° N, 113.366° W). We selected eight sites that had a history of housing martin colonies and were the focus of previous banding of nestlings, plus three sites without banding. Banding efforts at or near the former sites increased the likelihood that we could encounter banded birds in later years. For two seasons in early July of 2017 and 2018, our team of four to six people visited each site to search for banded martins.

During the nesting season we captured banded martins in one of two ways. With the first method, we observed all four sides of the square martin houses simultaneously; two observers watched from opposite sides from a distance of 10–15 m for about 30 minutes. We used telescopes and binoculars to identify banded birds entering and exiting compartments and recorded the compartment number, suspected sex, and age of the bird by its plumage. After the target birds had left the house, we lowered it to equip compartments with traps. These traps consisted of a piece of white plastic puck board with two holes drilled into opposite corners, screwed above the existing entrance hole. A washer on either side of the puck board ensured that the puck board would effectively seal the entrance hole after a firm tug of an attached monofilament line tied to the second hole. We strung the line, weighted with a hexagonal nut, through a fencing staple hammered into the wooden compartment to help prevent it from entangling or scaring birds. Once we returned the house to its position at the top of the pole, catchers sat 5–20 m away to wait for the target bird to enter the compartment. At any one time we set up one to four compartment traps. Once the target bird safely entered the compartment, an observer pulled on the fishing line to close the trap door. We lowered the house, carefully removed the bird from the compartment, and transferred it to a cotton bag. For each bird, we recorded its age as second year (SY) or after second year (ASY), sex (visual comparisons with sources such as Stokes et al. 1997), and band number. We tried to capture all banded birds so that the sample was representative of the age/sex cohorts in each colony. After taking other measurements (e.g., weight, wing, tail, and tarsus length), we released the bird.

With the second method, we mass-trapped martins at the Ellis Bird Farm. On the morning of trap day, we attached a white, wooden trap door above the entrance hole of each compartment of each martin house (10 houses with 8–12 compartments per house) with a loose-fitting screw. For each trap, we strung a monofilament line from the top corner of this door down the pole to a central location at the bottom of the pole. We added tension on each line to raise the trap door above the entrance hole. After dusk, at 23:00, when we were confident that most or all of the adult martins were in their compartments to roost for the night, we simultaneously cut the monofilament lines at all of the nesting poles, releasing the trap doors to fall and cover the entrance holes. We banded each captured bird and recorded its age, sex, and band number before returning it to its original compartment. Before local sunrise at 05:00, we removed trap doors so the birds could exit.

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Under both methods, we also recorded the location, house number, compartment number, date, and time of capture. Overall, we captured 161 previously banded birds. The Patuxent Wildlife Research Center's Bird Banding Laboratory provided information about the bird's original banding, including band number, location, and sex. We compared this information with similar details on the bird at the time of recapture.

We also obtained Canadian records of past encounters (1935–2016) with banded martins from the Canadian Wildlife Service's Bird Banding Office. We included only encounters from May to July in years subsequent to the year of banding, i.e., those representing dispersal. We did not include records from our central Alberta study in this analysis of Canada-wide dispersal. Staff at the Ellis Bird Farm also provided records of encounters that were not part of Canada's Bird Banding Office database. We defined an encounter as handling of a live banded bird, recovery of a banded bird found dead, or reading and reporting a band number on a live bird that was not handled (Gustafson et al. 1997). We had no control over the proportion of birds in each age/sex cohort.

For analysis of datasets, we recorded the age of each bird (SY or ASY) by comparing its year of banding to its year of encounter. We recorded its sex as male, female, or unknown, as identified in the original banding records or through visual assessment. From both datasets, we identified a dispersal when the banding location was different from the encounter location. We calculated dispersal distance and direction from the coordinates provided by the banding office, measuring distances (in km) in Google Earth. For dispersal direction, we used the eight cardinal and intercardinal compass directions (N, NE, E, SE, S, SW, W, NW). To account for post-fledging wandering, we excluded any cases of fledglings banded and encountered in the same year.

In the central Alberta dataset, we excluded any cases where the bird's sex was unknown, leaving 153 records for further analyses (25 SY males, 27 SY females, 52 ASY males, and 49 ASY females). Using SPSS 25.0 (IBM, Armonk, NY), we conducted a one-way ANOVA test to look for differences of dispersal distance in relation to age/sex cohorts. Post hoc Tukey's honestly significant difference (HSD) was used to identify differences among age/sex cohorts. We used chi-squared tests to evaluate differences in frequencies and direction of dispersal by age/sex cohort.

In the cross-Canada dataset, after excluding records of birds banded and encountered west of the Rocky Mountains in British Columbia, we ended up with a total of 397 records. The majority of these records were incomplete, as 90% lacked a verified sex, thus reducing our dataset to 38 records with known sex (2 SY males, 1 SY female, 10 ASY males, and 25 ASY females). The higher rate of unknown sex was probably due to the birds' deteriorated condition—most encounters in this sample were of martins found dead—and the lack of general public knowledge of plumages. Because the sample size was small, we used a Mann–Whitney nonparametric test to evaluate differences between age/sex cohorts in dispersal distance. We used this test rather than a Kruskal–Wallis nonparametric test because essentially only two cohorts, ASY males and ASY females, were represented in the cross-Canada dataset. Again we used chi-squared tests to assess differences in frequencies and direction of dispersal by age/sex cohort.

In both datasets, we based descriptive tests of average distance and

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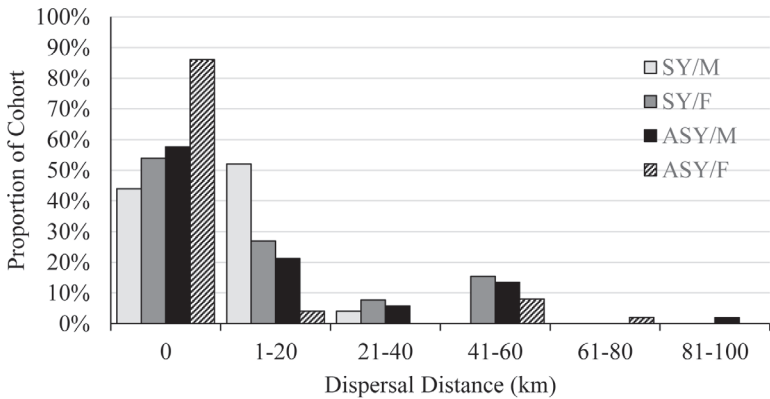


FIGURE 1. Proportion of encounters of banded Purple Martins of each age/sex cohort by distance of dispersal (km) from their natal colonies in central Alberta ($n = 153$).

direction of dispersal exclusively on dispersing birds. We set the significance thresholds at $P < 0.05$. We report the statistical details only for tests yielding differences that were significant.

RESULTS

Within our central Alberta dataset ($n = 153$), 33% of the encountered martins were one-year-old birds and 67% were older; the mean age was 2.0 years (range 1–8); 50% were male and 50% were female. Overall, 36% of the birds dispersed from the sites where they were banded originally. Among these dispersers ($n = 55$), the mean dispersal distance was 23.7 km (range 4–82 km; Figure 1) and the most common dispersal direction was northeast (51%; Figure 2). For each sex, we can describe the characteristics of natal dispersal

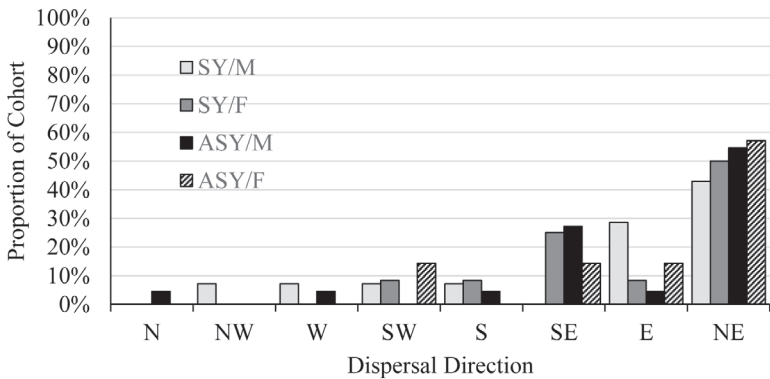


FIGURE 2. Proportion of encounters of banded Purple Martins of each age/sex cohort by direction of dispersal from colonies in central Alberta ($n = 55$).

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TABLE 1 Numbers of Encounters of Banded Purple Martins with Respect to Dispersal and Age/Sex Cohort^a

Dispersal and age	Central Alberta dataset		Cross-Canada dataset	
	Male	Female	Male	Female
Dispersed				
SY	14 (09.0)	12 (09.7)	0 (0.6)	0 (00.3)
ASY	22 (18.7)	7 (17.6)	6 (2.9)	5 (07.2)
At natal colony (no dispersal)				
SY	11 (16.0)	15 (17.3)	2 (1.4)	1 (00.7)
ASY	30 (33.3)	42 (31.4)	4 (7.1)	20 (17.8)

^aValues in brackets indicate values expected from a chi-squared crosstabs test.

for SY birds, but because of the limited sample size we can describe only the characteristics of natal and breeding dispersal combined for ASY birds.

Of the dispersing martins ($n = 55$), 47% were SY with males ($n = 14$) and females ($n = 12$) represented similarly. Older martins constituted 53% of the sample; ASY males ($n = 22$) outnumbering females ($n = 7$). Frequencies of dispersal of the age/sex cohorts differed significantly ($\chi^2 = 16.112$, $df = 3$, $P = 0.001$, Table 1). Of the birds recaptured where banded ($n = 98$), SY birds (26%) were less frequent than ASY birds (74%), and males (42%) were less frequent than females (58%; Table 1).

The average distance of natal dispersal for SY birds (sexes combined) was 16.8 km (range 4–56 km), whereas for ASY birds (sexes combined) it was 29.9 km (range 5–82 km). For both age cohorts, females' average dispersal distance was greater than males' (Table 2). The bird that dispersed farthest was an ASY male displaced 82 km to the northeast.

Dispersal distance of age/sex cohorts differed significantly (one-way ANOVA, $P = 0.006$, $F = 4.699$, $df = 3$). Post hoc Tukey's HSD test revealed that the significance was between the means of SY males and ASY females. We found no significance between age/sex cohorts in direction of dispersal (Figure 2).

In our cross-Canada dataset ($n = 38$), 8% of the banded birds encountered were SY and 92% were ASY; regarding sex, 32% were male, 26% were female, and 42% were of unknown sex. All dispersing martins ($n = 11$) in this sample

TABLE 2 Averages and Ranges of Distances of Dispersal (km) from Natal Sites of Purple Martins by Age/Sex Cohort

Age	Central Alberta dataset ($n = 55$)		Cross-Canada dataset ($n = 11$)	
	Male	Female	Male	Female
SY	10.1 (4–23) ^a	24.6 (4–56) ^{a, b}	0 (0)	0 (0)
ASY	26.7 (5–82) ^{a, b}	39.8 (8–69) ^b	145.2 (11–544)	228.7 (3–1023)

^{a, b}Cases with different letters indicate differences significant according to Tukey's HSD post hoc test.

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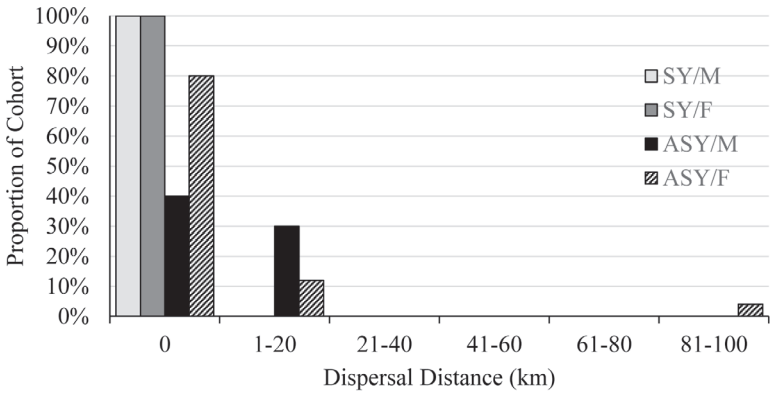


FIGURE 3. Proportion of encounters of banded Purple Martins of each age/sex cohort by distance of dispersal (km) from colonies in the cross-Canada dataset ($n = 38$).

were ASY; of these, 6 were males and 5 were females (Table 1). Of the 35 ASY birds, 11 individuals (31%) dispersed and 23 (69%) did not disperse. Of the nondispersing birds ($n = 27$), many more were ASY (89%) than SY (11%) and females (78%) predominated over males (22%; Table 1). The average dispersal distance for ASY birds (males and females combined) was 183.1 km ($n = 11$, range 3–1023 km, Figure 3). Of the ASY birds, females had the greater average dispersal distance and dispersal range (Table 2). The most common directions of dispersal were east and northeast (Figure 4). Of all encounters, the bird that dispersed the farthest was an ASY female displaced 1023 km to the southeast. Because of the incompleteness of the cross-Canada dataset and small sample sizes, we did not use statistics to compare the age/sex categories in relation to distance and direction of dispersal.

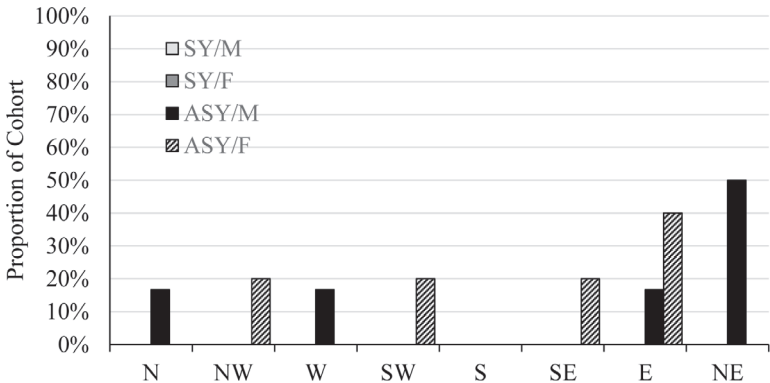


FIGURE 4. Proportion of encounters of banded Purple Martins of each age/sex cohort by direction of dispersal from colonies in the cross-Canada dataset ($n = 11$).

DISCUSSION

Overall, the rates of dispersal of the Purple Martin in our samples (36% for central Alberta and 29% for all of Canada east of the Rocky Mountains) were in the mid-range of the rates reported for the Tree Swallow (Hosner and Winkler 2007, Shutler and Clark (2003) and in Rappole's (2013) review. Dispersal patterns vary considerably among and within bird species (Sutherland et al. 2000, Rappole 2013). Some studies of martins have not distinguished natal and breeding dispersal. All ages combined, 36% of the martins in our Alberta study area dispersed from their natal site where they were banded. This is slightly more than the 24% reported in a subsample of martins in west Texas, based on breeding within a 30-mile and 50-mile radius of their natal site (Ray and Schoenhals 2001).

Differences in rates of dispersal of each age and sex class in our Alberta study indicate that fidelity has a pattern more complex than previously described for this species. Our results gave only weak support for our prediction that SY male martins should disperse at frequencies greater than other age/sex classes; the frequency of dispersal of SY males, SY females, and ASY males was greater than that of ASY females.

In agreement with our prediction that natal dispersal should account for any patterns of dispersal by age/sex class, 50% of SY martins of both sexes in our study dispersed from their natal colony, but only 29% of ASY martins had dispersed from their natal colony in their second or subsequent breeding season. Provided that conditions in the Alberta study were similar from year to year, these numbers indicate that about 20% of martins return to their natal colony in their second season after spending their first season elsewhere. This difference is most pronounced in females, of which only 14% of those older than one year are not at their natal colony. For male ASY martins, 40% continued to nest away from their natal colony. Some of those martins that dispersed as yearlings continue to disperse, since the distances of dispersal of ASY martins are greater than those of SY martins. In summary, 50% of martins dispersed in their first year, but in year two and subsequently, the sum of natal and breeding dispersal is less than natal dispersal alone. Thus some martins return to their natal site in their second and subsequent breeding seasons.

This pattern of fidelity could be explained by the age/sex-specific timing of the martins' return to nest sites. The sequence of the return to breeding colonies is that martins >3 years old arrive first and those 1 year old arrive last, with males arriving before females (Morton and Derrickson 1990, Tarof et al. 2011). Therefore, SY martins are less likely to find suitable nest sites available and are forced to disperse to vacant sites elsewhere, as has been shown in other species (Greenwood and Harvey 1982). However, we found that 20–35% of martins return to their natal sites in later years and secure nest sites at their natal colony, which they were not able to do as yearlings. The pattern was not included in the analysis of the martin's annual survival by Stutchbury et al. (2009) but will affect estimates of survival.

In both our central Alberta and Canada-wide datasets, encounters of ASY martins exceed those of SY martins. This pattern is not surprising since the category SY represents only a one-year cohort while ASY includes the

remaining annual cohorts. The central Alberta dataset had an even balance of encounters between the sexes, while the Canada-wide dataset had more encounters of females than of males. While the Alberta data were from live-trapped martins, the Canada-wide data were mostly from martins found dead by the public, presumably at nesting sites. Hill (2003) and Stutchbury et al. (2009) found that because of the high energy expenditures and stresses of laying eggs, female martins tend to have shorter life spans. In particular, SY females have an apparent probability of survival lower than that of SY males (Stutchbury et al. 2009), which could lead to more females found dead in the Canada-wide sample at breeding sites. The difference in recovery rates between our Alberta sample and the Canada-wide encounters implies that females are more likely than males to die during the breeding season.

We found that male Purple Martins (both age cohorts combined) were more likely to disperse than were females, as have other studies (Hill 2003, Ray and Schoenhals 2011). Hill (2003) reported that female martins tend to prefer experienced males, which can result in SY males not mating at their natal sites and choosing to disperse. A possible explanation for fewer females dispersing than males is the “martin hog theory,” the concept that some large colonies attract more SY females than they produce (Morton and Stutchbury 1997, Hill 2003). This pattern reduces the dispersal of SY females to unoccupied sites and is an example of conspecific cueing. Conspecific cueing is an individual assessing habitat quality by the presence of other individuals (Nordell and Valone 2017). The pattern of male martins dispersing more than females (Hill 2003, Ray and Schoenhals 2011) may result from competition for mates. If females are the limiting factor (by choosing to stay close by in hopes of attracting an older male), then younger males would need to disperse to find available breeding females.

Contrary to our prediction that SY male martins should disperse farther than other age/sex classes, we found that the mean distance of dispersal of ASY females was greater than that of SY males, as in the Tree Swallow (Winkler et al. 2005).

Of course, the distances of dispersal we recorded varied with the size of the study area. Our cross-Canada dataset included encounters from all of southern Canada east of the Rocky Mountains, but our Alberta dataset limited the maximum distance to 148 km, the longest diagonal in our rectangular study area. Estimates of dispersal distances will affect analysis of annual survival, such as that of Stutchbury et al. (2009), the radius of whose study area was only 50 km. In the Tree Swallow, Shutler and Clark (2003) found that breeding dispersal of females averaged farther than that of males, but distance of natal dispersal did not vary by sex. Hosner and Winkler (2007) reported that one-year-old Tree Swallows dispersed farther than older adults, but distances of natal dispersal did not differ by sex.

Contrary to our initial prediction that martins should disperse in all directions equally, the dominant directions in both datasets were east and northeast. Our alternate hypothesis that martins should disperse north with warming temperatures was partially supported. Ray and Schoenhals (2011) suggested that the martin's dispersal can be directed to previously unoccupied areas by providing nesting structures. This strategy could support martins

dispersing northward into new habitats that become available through climate change and are suitable with regard to other requirements such as food.

Some limitations of our study should be considered. First, as in any study of dispersal, our local central Alberta study area was limited in extent. We were not able to encounter banded birds outside of the study area, and we were not able to measure mortality in successive seasons (Greenwood and Harvey 1982). Second, given the privacy concerns of some bird banders (who did not report exact locations of banding to us), some banding locations are expressed only as the coordinates of the center of blocks measuring 10 minutes on a side (<https://www.pwrc.usgs.gov/BBL/MANUAL/loc.cfm>); thus in central Alberta the exact location can vary by 5 km (<https://stevemorse.org/nearest/distance.php>). Third, since the effort at banding across our study area varied from year to year, rates of subsequent encounters likely varied as well. Last, we did not record data on other variables that can influence sex-biased dispersal, such as colony size, social behavior, density (Shutler and Clark 2003, Förschler et al. 2010, Steifetten and Dale 2012), plumage color, body size (Sutherland et al. 2000), ectoparasite load (Brown and Brown 1992, Saino et al. 2014), feeding guild (Sutherland et al. 2000), and breeding success (Greenwood and Harvey 1982, Shutler and Clark 2003, Winkler et al. 2004, Schaub and von Hirschheydt 2009).

In the future, researchers can use new technologies, such as the Motus Wildlife Tracking System (<https://motus.org>), geolocators, and geotags, to examine patterns of dispersal throughout the breeding season before and after migration, rather than at only two points in time. For example, a dense array of Motus stations could allow an investigation of pre-breeding movements between colonies of martins of all ages and sexes (i.e., scouting of future nest sites). Future research could also investigate other factors affecting patterns of dispersal, including juvenile survivorship (Miller et al. 2001, Tarof et al. 2011), arrival times after migration (Nordell and Valone 2017), breeding success (Shutler and Clark 2003, Winkler et al. 2004), and post-fledging wandering (Morton and Patterson 1983, Miller et al. 2001, Hill 2003, Stutchbury et al. 2009). Last, future research should investigate the benefits and costs of dispersal (e.g., reproductive success and lifespan) over the lifetimes of individual martins (Balbontin et al. 2009, Schaub and von Hirschheydt 2009). Such investigations are relevant to many other species that could be affected by climate change and have a largely “eastern” distribution, but with ranges extending into the West.

CONCLUSIONS

The continued dispersal of martins ≥ 2 years old should facilitate range expansion as needed because of climate change or other factors. Since nesting success is typically higher for these older birds, in general and in martins in particular (Stutchbury et al. 2009), we should expect that their chance of dispersing successfully and establishing new colonies is greater. Future estimates of annual survival should include the frequency of birds returning to breed in their natal colony at an age of ≥ 2 years, and studies of dispersal should encompass larger areas to account for dispersal over longer distances.

The frequency and distances of martin dispersal we recorded are greater

than those reported in other studies of eastern populations of the species. Why? Dispersal is likely tied to the degree of stability in the breeding habitats. Prior to European contact, martins nested in natural cavities in trees and cliffs as well as in gourds provided by Indigenous Peoples (Bent 1942, Taverner 1945). While the cliff sites should have offered stability from year to year, the tree sites are in large, typically dead trees that remain standing for a limited time. Thus martins should be adapted to seek new nest sites when needed.

External factors could be key to the Purple Martin's future. First, with climate change forcing temperature patterns northward, we should expect range expansions in a similar direction. Patterns of dispersal can be an indication of range expansions (Duckworth and Badyaev 2007). We found most dispersals toward the northeast and east, with north being consistent with climate change in Alberta and Canada (Romero-Lankao et al. 2014). Changing prey availability in response to climate change is a concern for martin conservation since martins do not adjust their migration schedule in response to increased temperatures (Fraser et al. 2013).

Second, landlords (people who manage martin nest boxes) play a critical role in the success of martin colonies. If human-made nest boxes are a limiting factor, then the direction, proximity, and management of these nest boxes might influence dispersal patterns and subsequent range expansion or recolonization. Nest boxes provided to the northeast and east within 80 km of existing colonies at the edge of the species' breeding range may aid in changing the direction of dispersal over time. Landlords' efforts to manage martin colonies can affect nest-box occupancy (Anderson and Hvenegaard 2021) and the number of birds that survive to disperse in later years (Raleigh et al. 2019). Such conservation efforts are important because according to the results of the Breeding Bird Survey, 1996–2019, Purple Martin numbers are declining across North America (<https://www.mbr-pwrc.usgs.gov/>) and the eastern population relies almost completely on human-provided nest boxes.

Third, the declines in aerial insectivores in general, and the Purple Martin in particular, are concentrated in the northeastern part of their ranges (Nebel et al. 2010). Our results suggest that these declines are not directly affected by dispersal but by other factors (Spiller and Dettmers 2019). However, since all age classes of the Purple Martin disperse, the species retains the capability of adapting to changing environments and new opportunities for nesting. It is important to continue to monitor patterns of dispersal in bird populations to account for changes in movement ecology and provide better scientific support for conservation programs.

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