



## BROOD SIZE AND LATE BREEDING ARE NEGATIVELY RELATED TO JUVENILE SURVIVAL IN A NEOTROPICAL MIGRATORY SONGBIRD

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**ABSTRACT.**—Widespread decline of Neotropical migrant songbirds requires better understanding of the mechanisms driving juvenile mortality. We used mark–resight encounter histories of 3,990 banded fledglings (1998–2002) to test whether late breeding or large brood size negatively affected apparent annual and migration–wintering survival probability of juvenile Purple Martins (*Progne subis*). We estimated apparent annual juvenile survival ( $\phi_a$ , fledging to 1 year old) by resighting individuals as adults at regional breeding colonies and at a premigratory roost. We tested for carryover effects of fledge week and brood size on migration–wintering survival ( $\phi_m$ , premigratory roost to 1 year old) using two encounter occasions per season (pre migratory roost, breeding colony) to partition annual survival into premigration versus migration–wintering survival. Annual survival ( $\pm$  SE) was  $0.27 \pm 0.027$  and the best model (model weight = 0.93) included week of fledging and brood size, with survival probability decreasing with increasing fledge date and brood size. Apparent fledgling survival probability to premigratory roosts ( $\phi_r$ ) was  $0.87 \pm 0.03$  and migration–wintering juvenile survival ( $\phi_m$ ) averaged  $0.32 \pm 0.04$  (range: 0.25–0.46 among years). The best model included an effect of fledging week (model weight = 0.99) on migration–wintering survival but little support for brood size effects. Late-fledged young that survive to begin migration may incur higher subsequent mortality because of less foraging time and experience before migration. Telemetry of 15 fledglings in 2007 also revealed high premigration survival to the premigratory roost (0.73). Most (81%) juvenile mortality occurred after the onset of migration. Juvenile recruitment and population dynamics are likely closely linked to migration and wintering ground threats. Received 19 April 2011, accepted 23 August 2011.

Key words: carryover effects, dispersal movements, juvenile survival, migration survival, *Progne subis*, Purple Martin, recruitment.

### El Tamaño de la Parvada y la Reproducción Tardía se Relacionan Negativamente con la Supervivencia de Individuos Jóvenes en un Ave Canora Migratoria Neotropical

**RESUMEN.**—La disminución generalizada de las poblaciones de aves canoras migratorias neotropicales requiere una mejor comprensión de los mecanismos que afectan la mortalidad juvenil. Utilizamos datos históricos de marcado y reavistamiento de 3990 polluelos anillados (1998–2002) para comprobar si la reproducción tardía o el tamaño de parvada grande afectaron negativamente la probabilidad de supervivencia aparente anual de invernada y la migración de aves jóvenes de la especie *Progne subis*. Estimamos la supervivencia aparente anual de las aves jóvenes ( $\phi_a$ , desde volantones hasta 1 año de edad) a partir de los individuos reavistados como adultos en las colonias de cría regional y en un sitio de descanso premigratorio. Pusimos a prueba los efectos de la semana de emplumamiento y el tamaño de la parvada sobre la supervivencia durante el período migración–invernada ( $\phi_m$ , descanso premigratorio a 1 año de edad), utilizando dos ocasiones encuentro por temporada (descanso premigratorio y colonias de cría) para separar la supervivencia anual en la supervivencia antes de la migración y la supervivencia migración–invernada. La supervivencia anual ( $\pm$  DE) fue de  $0.27 \pm 0.027$  y el mejor modelo (peso del modelo = 0.93) incluyó la semana de emplumamiento y el tamaño de la parvada, y una disminución de la probabilidad de supervivencia con el aumento de la fecha y el tamaño de la parvada. La probabilidad de supervivencia aparente hasta el descanso premigratorio ( $\phi_r$ ) fue de  $0.87 \pm 0.03$  y la supervivencia de los jóvenes durante el período migración–invernada ( $\phi_m$ ) fue en promedio de  $0.32 \pm 0.04$  (rango: 0.25–0.46 entre los años). El mejor modelo incluyó un efecto de la semana de emplumamiento (peso del modelo = 0.99) sobre la supervivencia migración–invernada, pero muy poco apoyo para un efecto del tamaño de la parvada. Las aves jóvenes que emplumaron tardíamente y que sobrevivieron hasta comenzar la migración pueden incurrir en una mayor mortalidad posterior por tener menos tiempo de forrajeo y experiencia antes de la migración. El seguimiento por telemetría de 15 polluelos en el año 2007 también reveló una supervivencia alta durante el período previo a la migración hasta el descanso premigratorio (0.73). Gran parte (81%) de la mortalidad de las aves jóvenes se produjo después del inicio de la migración. La dinámica del reclutamiento de aves jóvenes y de la población están probablemente estrechamente vinculadas con las amenazas en las áreas de migración y de invernada.

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IN ANIMAL POPULATIONS, factors that influence survival and recruitment as a first-time breeder are quintessential to fitness and the evolution of life history strategies (Clutton-Brock 1988, Low and Pärt 2009, Grorud-Colvert and Sponaugle 2011; reviewed by Doligez and Pärt 2008). In birds, mechanisms that drive classic reproductive tradeoffs between clutch size and offspring recruitment probability have been studied intensively (Newton 1989, Magrath 1991, Morton et al. 2004). Variation in survival and recruitment of fledglings or juveniles (reviewed by Müller et al. 2005) may be explained by (1) timing of breeding (Verboven and Visser 1998, Naef-Daenzer et al. 2001, Wheelwright et al. 2003, Dolan et al. 2009) or (2) parental care (Naef-Daenzer and Keller 1999, Schiegg et al. 2002, Schwagmeyer and Mock 2008). Late breeding is hypothesized to affect individual fitness by reducing fledgling or juvenile survival because of seasonal decline in food availability to young in the nest (Verboven and Visser 1998, Wheelwright et al. 2003; but see Monrós et al. 2002), although provisioning larger prey items can ameliorate this seasonal trend (Schwagmeyer and Mock 2008). The fledgling stage, when young have left the nest but still receive parental care, is a period of high mortality risk for many passerines, especially during the first week after fledging (Kershner et al. 2004, Rush and Stutchbury 2008, Low and Pärt 2009), and temporal variation in fledgling predation risk may favor early nesting (Naef-Daenzer et al. 2001, Götmark 2002). Other possible mechanisms underpinning the timing of breeding hypothesis include resource competition between early- versus late-fledged young (Verboven and Visser 1998) and variation in social dominance of young birds that differ in age (Heg and van der Velde 2001). Although many studies have shown low juvenile recruitment among offspring of late breeders, the underlying mechanism causing mortality often remains unknown (Shutler et al. 2006). In addition to breeding effects on fledgling and juvenile survival, overwinter survival can also depend on winter habitat quality (Angelier et al. 2009) and likelihood of recruitment can be strongly influenced by sex (Greenwood and Harvey 1982).

The parental care hypothesis states that fledgling or juvenile survival may depend on food delivery by parents and parental attributes of quality such as age or physiological condition (Schiegg et al. 2002). Young with older social parents or parents in superior condition should be more likely to survive to reproduction because they receive higher-quality care. This hypothesis can also operate through parental provisioning rate and brood size variation (Naef-Daenzer and Keller 1999). Brood size manipulations have shown adverse effects on nestling body mass and growth for individuals from enlarged broods (Siefferman and Hill 2007). If food is limited, offspring growth may be compromised in larger broods, which in turn could affect offspring survival once birds leave the nest (van Noordwijk et al. 1995, Naef-Daenzer and Keller 1999). In their study on parental foraging effects on nestling growth Naef-Daenzer and Keller (1999) noted that a brood size effect on nestling growth might carry over to also reduce overwintering survival of juveniles (see also Reid et al. 2003). Yet Shutler et al. (2006) found that although nestling body mass was lower in enlarged Tree Swallow (*Tachycineta bicolor*) broods, recruitment of juveniles was not affected significantly by brood size.

Carryover effects of breeding season events on juvenile survival may be particularly strong in long-distance migrants because of high survival costs of migration (Silleet and Holmes 2002). Consequently, accurate estimates of fledgling and juvenile survival are required to better understand how this vulnerable

period affects avian life history tradeoffs, but obtaining these metrics is problematic in migratory birds for several reasons. Survival to first reproduction is difficult to estimate given high natal dispersal and low philopatry in many species. Resighting juveniles as adults requires extensive surveys on the breeding grounds (Winkler et al. 2005, Balbontin et al. 2009). Furthermore, studies rarely distinguish between fitness costs to fledgling versus juvenile survival because newly fledged birds are often difficult to observe without radiotelemetry and fledglings disperse off their natal territory prior to migration (Vega Rivera et al. 1998, Imlay et al. 2010).

Here, we used mark-resight encounter histories for almost 4,000 fledglings banded from 1998 to 2002 and resighted up to 2007 to test whether timing of breeding or brood size predicted juvenile survival in the Purple Martin (*Progne subis*), a colonial swallow that migrates to South America for the non-breeding season (Stutchbury et al. 2009b). Our study provides a unique opportunity to quantify offspring survival in a long-distance Neotropical migrant because we resighted 22% of fledglings as adults in subsequent years by conducting intensive surveys of local breeding colonies and a premigratory roost (hereafter "roost"). Tens of thousands of Purple Martins in our study area gather at a large roost from late July through early September, which allowed us to resight adults whose breeding colony was unknown. We also resighted fledglings at the roost many weeks after they left their natal colony and thus could partition annual juvenile survival into premigration versus migration-wintering survival.

Using maximum likelihood estimation and model fitting in Program MARK we evaluated the effects of fledging date and brood size on apparent annual juvenile ( $\phi_a$ , fledging to 1 year old or second year [SY]). First we tested whether fledgling Purple Martins from earlier nests or smaller broods exhibit higher apparent survival compared with those reared in later nests or larger broods. Previous tests of these hypotheses have not made explicit predictions about when in the annual cycle survival costs are incurred (e.g., van Noordwijk et al. 1995). Resightings at the roost allowed us to partition annual survival into that from fledging to the roost ( $\phi_r$ ) versus migration-wintering survival ( $\phi_m$ , premigratory juvenile to 1 year old). If low survival is a consequence of fledgling predation risk we predicted a strong time of season effect on apparent annual survival but not migration-wintering survival. If low survival is a result of an ontological handicap from poor provisioning or resource competition we predicted timing of breeding effects to carry over into migration-wintering survival because of high energetic costs of migration (Stutchbury et al. 2011). We estimated premigration survival of fledglings to the roost ( $\phi_r$ ) via band resightings at the roost (1998–2007) and by radiotracking newly fledged young in 2007. We show that timing of fledging but not brood size is associated with low migration-wintering survival and conclude that most first-year mortality of Purple Martins occurs after the onset of migration.

## METHODS

*Study area and species.*—Purple Martins are North American breeding swallows that nest in colonies of  $\leq 300$  pairs and, in eastern North America, breed exclusively in artificial housing (Brown 1997). In our study area adults ( $\geq 2$  years old or after second year [ASY]) arrive in late April and SY 1-year-olds are first seen at breeding colonies in mid-May. Purple Martins are single brooded

and forage on aerial insects. Juveniles are independent from parental care 7–10 days after fledging (Brown 1978) and in late summer they aggregate with adults in roosts (Allen and Nice 1952, Morton and Patterson 1983, present study).

Our study area (Fig. 1) comprised two “core” breeding colonies, 19 km apart, south of Erie, Pennsylvania (42°08′N, 80°18′W), two dozen smaller peripheral colonies, and a roost at the base of Presque Isle State Park on the south shore of Lake Erie (42°06′59.6″N, 80°08′51.92″W) that have been monitored by the Purple Martin Conservation Association (PMCA) since 1994 (Stutchbury et al. 2009a). The Indianhead colony (41°53′08.50″N, 80°07′45.80″W), located on Edinboro Lake, consisted of 75–125 pairs year<sup>-1</sup> breeding in three wooden houses and several dozen natural and plastic gourds. The Troyer colony (41°45′20.01″N, 80°16′59.75″W) in Conneautville had 100–150 pairs year<sup>-1</sup> that bred in nine wooden or plastic houses and several dozen nest gourds. Nests were initiated from late April through mid-July and checked approximately every 5 days to monitor nesting success. All nestlings were banded with a federal band and a color band with a unique alphanumeric code. Young fledged from the nest 26–30 days posthatch. Parental age class (SY or ASY based on plumage color) was available for only 50% of nests so this variable was not included in survival analyses.

Mark–recapture studies typically cannot distinguish permanent emigration from actual mortality (Low and Pärt 2009), thus resulting in underestimates of true survival (Cilimburg et al. 2002, Keyser et al. 2004, Marshall et al. 2004). To obtain a more robust estimate of true annual survival we searched systematically for banded birds at the two intensively studied core breeding colonies, at all other breeding colonies within 50 km of the core colonies,

and at the roost (Fig. 1; Stutchbury et al. 2009a). Identity of juveniles and adults was determined primarily by using a telescope at close range to read color bands when birds were perched on their nest houses or wires. Observers visited the core breeding colonies several times each week from April through early August and each peripheral colony was visited at least once during the nestling period to identify feeding parents. Breeding adults were sometimes captured when feeding young or sleeping in their houses at night, but encounter histories were composed almost entirely (>95%) of resightings. We restricted our analyses to nestlings banded between 1998 and 2002 because our resighting efforts at the peripheral colonies and the roost were most intensive during those years. Overall, 22% (range: 15–33% year<sup>-1</sup>) of all fledglings ( $n = 3,990$ ) were seen in the study area as adults.

The roost in this region attracts >50,000 Purple Martins each night, peaking in mid-August, and is attended by individuals from ≤200 km away (Hill 2002). The PMCA searched intensively for banded Purple Martins perched on wires at several staging areas in Presque Isle State Park near the roost (5–7.5 km). These staging areas were searched 5–7 nights per week from mid-July to the end of August, and as many as 150 banded individuals were seen nightly. Bands were read at these staging areas before banded birds entered the roost for the night. Of the thousands of birds attending the roost on a given night, only a fraction visited the staging area. The average date of sighting a banded juvenile at the roost was 13 August and 26% (range: 22–32% year<sup>-1</sup>) of fledglings were resighted as juveniles at the roost ( $n = 1,138$ ).

**Statistical analysis of survival.**—We estimated survival probabilities using the general methods of Lebreton et al. (1992) and Burnham and Anderson (2002). We assessed the parsimony of different models to the data using Program MARK, version 6.0 (White and Burnham 1999), evaluated the support of different hypotheses, and generated maximum likelihood estimates of survival and recapture probabilities. We identified *a priori* a set of survival and encounter probability models that were fit to the data. We first analyzed apparent annual juvenile survival ( $\phi_a$ , fledging to 1 year old) using encounter histories of fledglings (banded 1998–2002,  $n = 3,990$ ) resighted as adults up to 2007. Our global starting model ( $\phi_{\text{age} \times \text{year}} p_{\text{age} \times \text{year}}$ ) was a Cormack–Jolly–Seber model that was age class (juvenile, adult) and time (year) structured for survival ( $\phi$ ) and encounter probability ( $p$ ). When modeling mark–resight data a critical initial step requires testing global model support by calculating the variance inflation factor ( $\hat{c}$ ) in MARK to adjust the  $AIC_c$  through quasi-likelihood if  $\hat{c} > 1$ , resulting in a QAIC<sub>c</sub>. To assess goodness-of-fit (Lebreton et al. 1992, Burnham and Anderson 2002) we calculated median  $\hat{c}$  for the global model and corrected for overdispersion. The global model supported the data adequately for modeling apparent annual juvenile survival (median  $\hat{c} = 1.3$ ).

We used linear models to constrain apparent survival as a logit function of week of fledging and brood size, starting with an additive model for age and year effects ( $\phi_{\text{age} + \text{year}} p_{\text{age} + \text{year}}$ ). This model fit better than the general model ( $\phi_{\text{age} \times \text{year}} p_{\text{age} \times \text{year}}$ ) in which effect of age on survival was allowed to vary with year. Linear models included an interaction effect between age and each covariate because we expected these factors to affect juvenile but not adult survival, and year was included as an additive effect. We assessed whether survival varied as a function of fledge week and brood size by evaluating the support of survival models with these

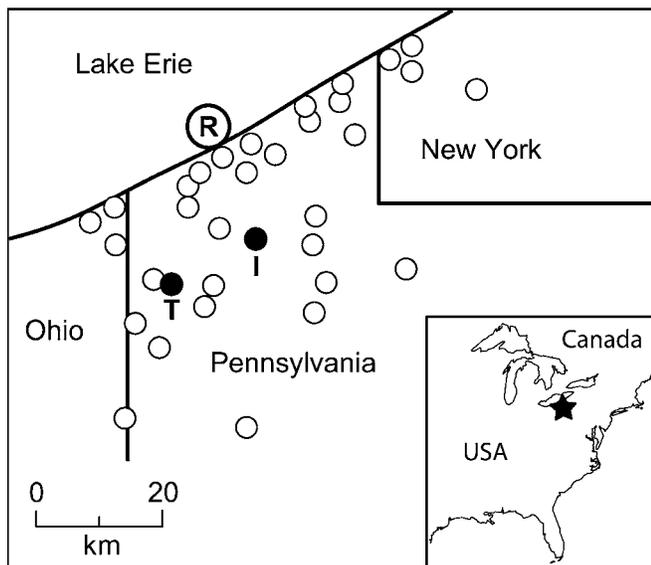


FIG. 1. Location of study area in North America (inset) and of the two core Purple Martin breeding colonies in northwestern Pennsylvania where nestlings were banded and resighted (black circles; Indianhead, Troyer). Peripheral colonies (white circles) surveyed annually to resight juveniles that dispersed from their natal colony and the roost (“R”) on the south shore of Lake Erie, where Purple Martins in the region gathered before migration, also shown.

covariates ( $\phi_{\text{age}+\text{week}+\text{year}}$ ;  $\phi_{\text{age}+\text{brood}+\text{year}}$ ). We also included a model with interaction between week of fledging and year ( $\phi_{\text{age}*\text{week}*\text{year}}$ ) because the relationship between survival and week of fledging could vary annually because of population-level differences in timing of breeding. Finally, we included a model with both week of fledging and brood-size effects ( $\phi_{\text{age}+\text{week}+\text{brood}+\text{year}}$ ). For each analysis, we ranked models using QAIC<sub>c</sub> values corrected for small sample sizes (Burnham and Anderson 2002) and compared models on the basis of the difference between the most supported model and all others ( $\Delta\text{QAIC}_c$ ). We used the Akaike weight ( $w_i$ ) as a measure of the model's relative probability of being the best model for the data compared with other models tested (Akaike 1973).

In a second analysis, we partitioned annual juvenile survival into premigration survival to the roost ( $\phi_r$ ) versus migration-wintering survival ( $\phi_m$ ) by constructing encounter histories using two resighting occasions per year (roost and breeding colony; total of 20 encounter occasions 1998–2007) for each individual. For the full model survival probability was modeled with four age classes (survival from fledgling at colony to fledgling at roost, from fledgling at roost to adult at breeding colony in first breeding season, from adult at colony to adult at roost, and from adult at roost to adult at breeding colony the following year). Because our focus was on juvenile survival, year effects on survival were included only for the first two age classes. For encounter probability we used three age classes: probability of detecting a fledgling at the roost (with year effects), probability of detecting an adult at a colony (whether 1 year old or older), and probability of detecting an adult at a roost. This global model supported the data adequately (median  $\hat{c} = 1.34$ ). Preliminary analyses indicated that late-fledged young who returned to breed were less likely to have been observed at the roost the previous year than early-fledged young (see below) and, therefore, encounter probability was subsequently modeled with week of fledging. To compare monthly survival rate between the two periods we ran the model set with interval lengths as 1 month for fledging to roost attendance and 11 months from roost to the first breeding season. Means are presented  $\pm$  SE.

**Radiotelemetry.**—To obtain a second and independent estimate of fledgling survival we deployed radiotransmitters (1.1 g; Holohil Systems, Carp, Ontario) on 15 nestlings ( $\leq 2$  per nest, average age 23 days old posthatch) in 2007 at the Indianhead colony. Transmitters were attached dorsally using a figure 8 leg-loop harness (Rappole and Tipton 1991) made of triple braided, soft Kevlar thread. Transmitters weighed  $< 3\%$  of body mass at time of deployment. In Barn Swallows (*Hirundo rustica*) radiotagged young showed no adverse survival effects from transmitters (Gruebler and Naef-Daenzer 2008). We attempted to locate birds daily (0900–1300 hours EST) within several kilometers of the breeding colony from 10 July to 22 August and after sunset at the roost, from the closest shoreline position, from 28 July to 29 August. We monitored radiotagged young using a handheld 3-element Yagi antenna and R-1000 programmable scanning receiver (Communications Specialists, Orange, California). Maximum detection range on the ground was 2–3 km, depending on the landscape. We obtained Universal Transverse Mercator coordinates (datum NAD 1983 zone 17) for individuals using a Garmin Global Positioning Systems 72 data logger equipped with real-time correction and 3 m accuracy. An individual was recorded as “dead” if we found its carcass, if the radio signal was stationary for 2 consecutive days, or if the bird disappeared within 1 week of fledging.

Approximately 2 weeks after fledging we conducted 4 h of aerial telemetry to search for individuals that could no longer be detected from the ground. We equipped each wing of a fixed-wing Cessna aircraft with a Yagi antenna strut-mounted at  $\sim 45^\circ$  and connected to separate R-1000 receivers programmed for repeat scanning of transmitter frequencies. Signals could be detected  $\leq 10$  km away. Upon signal detection we adopted a multiple-pass search pattern to triangulate the bird's location. We returned to each location later the same day by car to confirm fledgling status.

## RESULTS

**Apparent annual, fledgling, and migration-wintering survival.**—Models for annual juvenile survival that did not include week of fledging had no support (Table 1) and the best-fitting model ( $\phi_{\text{age}+\text{week}+\text{brood}+\text{year}}$ ) included linear effects of week of fledging and brood size (model weight,  $w_i = 0.93$ ). This model had 13 $\times$  more support than the model with no brood size effect ( $\phi_{\text{age}*\text{week}+\text{year}}$ ;  $w_i = 0.07$ ). The model with a week\*year interaction term had far less support ( $\Delta\text{QAIC}_c = 18.4$ ) than the additive model (week+year,  $\Delta\text{QAIC}_c = 5.2$ ). Using the best-fitting model, apparent annual juvenile survival probability ( $\phi_a$ ) was  $0.27 \pm 0.03$  (range: 0.21–0.36 among years) and, as expected, was much lower than annual adult survival (0.52  $\pm$  0.02). Resighting probability ranged from 0.51 to 0.79 among years (average 0.69  $\pm$  0.05). Annual juvenile survival decreased strongly with fledging date ( $B_{\text{age}*\text{week}} = -0.20 \pm 0.06$ , 95% confidence interval [CI]:  $-0.32$  to  $-0.07$ ) and late-fledged young had a 50% reduction in apparent survival probability compared with early-fledged young (Fig. 2A). Apparent annual survival of juveniles also decreased with brood size ( $B_{\text{age}*\text{brood}} = -0.18 \pm 0.07$ , 95% CI:  $-0.31$  to  $-0.04$ ; Fig. 2B).

In each year we searched for juveniles at the roost to partition annual survival into the premigration versus migration-wintering survival periods. The postfledge age of juveniles when first detected at the roost averaged  $21 \pm 0.3$  days (range: 2–61 days)

TABLE 1. Models used to evaluate the influence of timing of fledging and brood size on apparent annual survival ( $\phi_a$ ; fledglings resighted in subsequent years) of Purple Martins banded as nestlings in Pennsylvania from 1998 to 2002 ( $n = 3,990$ ) and encountered as adults up to 2007. The model set included a general time dependent model ( $\phi_{\text{age}*\text{year}} P_{\text{age}*\text{year}}$ ) that fit the data adequately. Starting with the model for an additive effect of age class (juvenile vs. adult) and year ( $\phi_{\text{age}+\text{year}} P_{\text{age}+\text{year}}$ ), linear constraints were used to test for linear effects of week of fledging (week) and brood size (brood) on survival (see text). The model with the lowest QAIC<sub>c</sub> score is considered to best fit the data.  $K$  is the number of parameters in each model,  $\Delta\text{QAIC}_c$  is the difference between the current model and that of best fit, and  $w_i$  is model weight.

Model	$K$	QAIC <sub>c</sub>	$\Delta\text{QAIC}_c$	$w_i$
$\phi_{\text{age}+\text{week}+\text{brood}+\text{year}} P_{\text{age}+\text{year}}$	24	5,965.9	0	0.93
$\phi_{\text{age}+\text{week}+\text{year}} P_{\text{age}+\text{year}}$	22	5,971.1	5.2	0.07
$\phi_{\text{age}*\text{week}*\text{year}} P_{\text{age}+\text{year}}$	30	5,984.3	18.4	0
$\phi_{\text{age}+\text{year}} P_{\text{age}+\text{year}}$	20	5,995.9	30.0	0
$\phi_{\text{age}+\text{brood}+\text{year}} P_{\text{age}+\text{year}}$	22	5,997.5	31.6	0
$\phi_{\text{age}*\text{year}} P_{\text{age}*\text{year}}$	34	6,017.4	51.5	0
$\phi_{\text{age}} P_{\text{age}}$	4	6,097.9	132.0	0

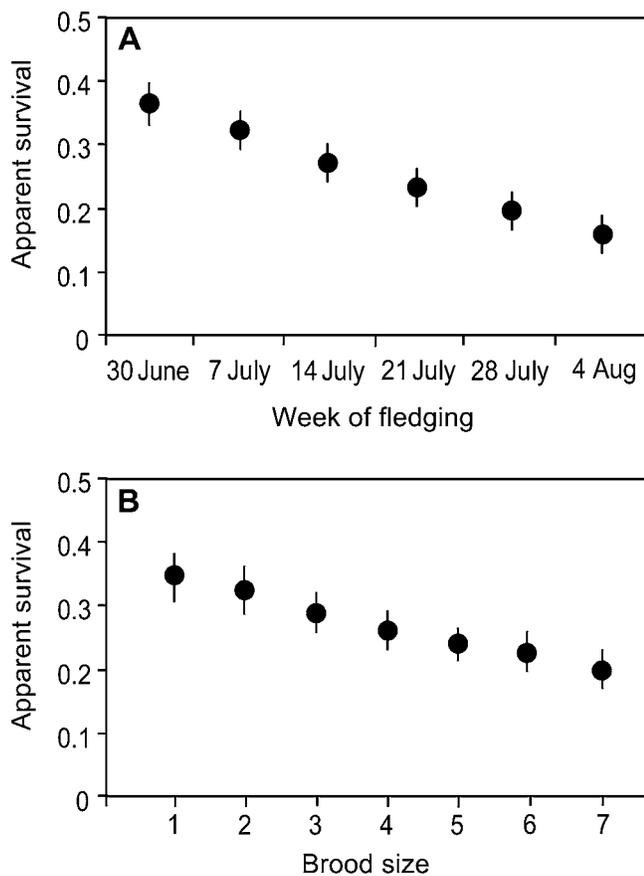


FIG. 2. Mean ( $\pm$  SE) apparent annual juvenile survival  $\phi_a$  of Purple Martins from Pennsylvania versus (A) week of fledging, given the average brood size of 4.2, and (B) brood size, given the average week of fledging of 3.3.

and declined significantly with week of fledging (analysis of variance [ANOVA]:  $F = 33.9$ ,  $df = 5$  and  $1,052$ ,  $P < 0.001$ ). Young fledged in late June and early July ( $n = 502$ ) were first seen at the roost 24 days after fledging, compared with young fledged in late July or early August ( $n = 48$ ) that were, on average, 15 days old postfledge when first seen at the roost. Thirty-two percent of fledglings were sighted at the roost more than once before their first migration and the duration between first and last sighting averaged  $9.4 \pm 0.4$  days ( $n = 337$ ).

For estimating and modeling fledgling survival to the roost versus migration–wintering survival the model that included fledge week in the probability of encountering fledglings at the roost ( $\phi_{\text{fldg}^* \text{year}^* \text{juv}}; P_{\text{fldg}^* \text{year}^* \text{week}}$ ) had far more support than the global model ( $\phi_{\text{fldg}^* \text{year}^* \text{juv}^* \text{year}}; P_{\text{fldg}^* \text{year}}$ ; Table 2) and was used for all subsequent models. Comparing models with no covariates of week or brood in survival probability, the model with year effects only on juvenile migration–wintering survival ( $\phi_{\text{fldg}^* \text{juv}^* \text{year}}; P_{\text{fldg}^* \text{year}^* \text{week}}$ ) had stronger support ( $\Delta AIC > 2$ ) than models with year effects on only fledgling survival. Adult survival was held year-independent in all models. Next we compared models with an additive effect of week of fledging on fledgling survival versus juvenile migration–wintering survival and included a year effect

TABLE 2. Models used to evaluate the influence of timing of fledging and brood size on fledgling Purple Martin survival to the roost ( $\phi_r$ ; fledglings resighted at the roost prior to their first migration) versus migration–wintering survival of juveniles by using two encounter occasions per year (roost, breeding colony). Individuals were banded as nestlings in Pennsylvania from 1998 to 2002 ( $n = 3,990$ ). The model set included a global model with year effects on fledgling survival to the roost and juvenile migration–wintering survival as well as fledgling encounter probability at the roost ( $\phi_{\text{fldg}^* \text{year}}; \text{juv}^* \text{year}; P_{\text{fldg}^* \text{year}}$ ; see text) that fit the data adequately. Encounter probability of fledglings at the roost was then modeled with week of fledging before using linear constraints to test for linear effects of week of fledging and brood size on survival. The model with the lowest QAIC<sub>c</sub> score is considered to best fit to the data.  $K$  is the number of parameters in each model,  $\Delta \text{QAIC}_c$  is the difference between the current model and that of best fit, and  $w_i$  is model weight.

Model	$K$	QAIC <sub>c</sub>	$\Delta \text{QAIC}_c$	$w_i$
$\phi_{\text{fldg}}(\text{juv}^* \text{year}^* \text{week}); P_{\text{fldg}^* \text{year}^* \text{week}}$	19	11,494.6	0	0.99
$\phi_{\text{fldg}^* \text{week}^* \text{juv}^* \text{year}}; P_{\text{fldg}^* \text{year}^* \text{week}}$	19	11,504.3	9.7	0.01
$\phi_{\text{fldg}^* \text{brood}^* \text{juv}^* \text{year}}; P_{\text{fldg}^* \text{year}^* \text{week}}$	19	11,516.2	21.5	0
$\phi_{\text{fldg}} \text{juv}^* \text{year}; P_{\text{fldg}^* \text{year}^* \text{week}}$	17	11,523.4	28.7	0
$\phi_{\text{fldg}}(\text{juv}^* \text{year}^* \text{brood}); P_{\text{fldg}^* \text{year}^* \text{week}}$	19	11,526.5	31.9	0
$\phi_{\text{fldg}^* \text{year}^* \text{juv}^* \text{year}}; P_{\text{fldg}^* \text{year}^* \text{week}}$	21	11,528.1	33.5	0
$\phi_{\text{fldg}^* \text{year}^* \text{juv}}; P_{\text{fldg}^* \text{year}^* \text{week}}$	17	11,548.8	54.2	0
$\phi_{\text{fldg}} \text{juv}; P_{\text{fldg}^* \text{year}^* \text{week}}$	13	11,576.5	81.8	0
$\phi_{\text{fldg}^* \text{year}^* \text{juv}^* \text{year}}; P_{\text{fldg}^* \text{year}}$	20	11,733.1	238.5	0

for juvenile survival. We made the same comparison with brood size. The model that included week of fledging on migration–wintering survival ( $\phi_{\text{fldg}}(\text{juv}^* \text{year}^* \text{week}); P_{\text{fldg}^* \text{year}^* \text{week}}$ ) had almost full support ( $w_i = 0.99$ ;  $B_{\text{juv}^* \text{week}} = -0.23 \pm 0.04$ , 95% CI:  $-0.31$  to  $-0.15$ ) and outcompeted the model with a week of fledging effect on fledgling survival to the roost. There was little support for brood size effects on juvenile migration–wintering survival.

Apparent fledgling survival probability ( $\phi_r$ ) to the roost using the best-fitting model was  $0.87 \pm 0.03$  and migration–wintering survival of juveniles ( $\phi_m$ ) averaged  $0.32 \pm 0.04$  (range: 0.25–0.46 among years). Encounter probability was  $0.31 \pm 0.05$  for fledglings at the roost,  $0.27 \pm 0.01$  for adults at the roost, and  $0.50 \pm 0.01$  for adults at a breeding colony. To obtain monthly estimates of survival rather than season-long estimates we reran our best-supported model and specified a time interval length of 1 month for fledgling survival to the roost and 11 months for survival from the roost to the next breeding season. Monthly juvenile survival probability during migration–wintering averaged  $0.90 \pm 0.01$  (range: 0.88–0.94 among years) compared with  $0.87 \pm 0.03$  for fledgling survival to the roost. Monthly migration–wintering survival probability for adults was  $0.94 \pm 0.002$ .

**Reproductive parameters.**—For all years combined, 1-year-old females nested later (mean fledge date 17 July  $\pm$  0.8 days) than older females (13 July  $\pm$  0.5 days) (Welch's ANOVA,  $F = 22.69$ ,  $df = 1$  and 338,  $P < 0.0001$ ; Bartlett's  $F = 8.27$ ,  $P = 0.004$ ). For all nests (1998–2002) clutch size averaged  $4.61 \pm 0.04$  eggs (range: 1–8;  $n = 995$ ), brood size was  $4.17 \pm 0.05$  nestlings (range: 1–7;  $n = 905$ ), and number of young fledged was  $3.65 \pm 0.05$  (range: 0–7;  $n = 905$ ). Average fledge date was 15 July  $\pm$  0.30 days (range: 29 June–29 July;  $n = 881$  nests) and was independent of brood size ( $r = -0.03$ ,  $P = 0.26$ ,  $n = 881$ ).

*Survival and movements of radiotagged fledglings.*—Radiotagged young fledged at an average age of  $29 \pm 0.5$  days posthatch (range: 25–32 days). All 15 radiotagged young in 2007 survived the first week after fledging ( $\phi_f = 1.0$ ). An owl killed two birds near their natal colony 11 and 14 days after fledging as determined by owl pellets that contained functional transmitters and leg bands. The average distance from the colony at which fledglings were detected on the day they fledged was  $939 \pm 234$  m (Fig. 3A) and most fledglings (80–100%) were detected within 2 km of the colony area on a daily basis until day 13 (Fig. 3B). Nine individuals were detected during the aerial flight on 1 August 2007, at 13–18 days postfledging, an average of  $6 \pm 2.4$  km from their natal colony. Individuals were first detected at the roost 11–16 days after fledging and 11 of 15 fledglings (73%) were detected at the roost. Six to 11 radiotagged fledglings occupied the roost on a given night and individuals used the roost for an average of  $14.7 \pm 2.3$  nights each (range: 2–24 nights).

We estimated daily survival rate using a nest survival model in Program MARK (e.g., Dinsmore et al. 2002) based on the 14-day period after fledging. We assumed that for the first 2 weeks after fledging birds that were alive would be detectable within the survey region via ground telemetry at the colony and roost or via the

single aerial telemetry search. Given the high mobility of newly fledged Purple Martins (Fig. 3) it is possible that birds that disappeared prior to 14 days postfledging had dispersed outside of the search region. Daily survival probability of fledglings was  $0.979 \pm 0.01$  with a cumulative survival probability over 2 weeks postfledging of 0.74 (95% CI: 0.59–0.89). We compared the support of models in which survival was constant, time dependent (age since fledging), or sex dependent. The model that included age since fledging had very high support (AIC weight = 0.98), reflecting the fact that all 15 fledglings survived the first 10 days after fledging.

## DISCUSSION

*Timing of breeding and brood size effects.*—Our results provide strong evidence for the timing of breeding and parental care hypotheses for variation in survival probability of juvenile Purple Martins. Apparent annual juvenile survival declined sharply for young that fledged late in the season and from large broods. Support for the timing of breeding hypothesis has been found in other passerines, including Great Tits (*Parus major*; Verboven and Visser 1998), Savannah Sparrows (*Passerculus sandwichensis*; Wheelwright et al. 2003), and Red-backed Shrikes (*Lanius collurio*; Müller et al. 2005). Gruebler and Naef-Daenzer (2008) manipulated timing of breeding while controlling for inherent variation in parental provisioning in Barn Swallows by exchanging similar-sized second brood clutches such that pairs that laid early clutches were given eggs from nests of late-laying parents and vice versa. Their experiment revealed a reduction in fledgling survival with date of fledging that seemed independent of brood manipulation but linked to inter-annual variation in food supply for this aerial insectivore (Gruebler and Naef-Daenzer 2008). In Cliff Swallows (*Petrochelidon pyrrhonota*) annual juvenile survival was highest for early nesters in most years (Brown and Brown 1999) but only for fumigated nests, indicating that nest parasites are directly or indirectly associated with first year mortality. Wheelwright et al. (2003) found that greater body mass at fledging in Savannah Sparrows tended to improve juvenile survivorship (see also Naef-Daenzer et al. 2001, Monrós et al. 2002, Low and Pärt 2009). Our study is the first that we are aware of that specifically examined carryover effects of fledge week on juvenile migration–wintering survival in a migratory songbird. After the onset of migration the probability that a juvenile survived migration–winter was independent of brood size but declined with week of fledging.

Naef-Daenzer et al. (2001) concluded that the seasonal decline in survival of fledgling Great and Coal tits (*P. ater*) was likely due to an increase in predation risk. Götmark (2002) identified Sparrowhawk (*Accipiter nisus*) predation as the best explanation for seasonal decline in fledgling survival for tits in Sweden. Seasonal patterns in survival of fledglings or juveniles may vary within a species from year to year as a result of fluctuations in predator abundance. For example, Monrós et al. (2002) reported evidence for higher annual survival of earlier-fledged Great Tits in 3 of 8 years but higher survival in late nests during 2 years and an initial increase followed by a reduction in survival in the remaining 3 years. Two radiotagged juveniles were killed by owls, but further radiotracking of juvenile Purple Martins would be necessary to identify explicitly key predators in our study area and how causes of juvenile mortality prior to migration vary seasonally.

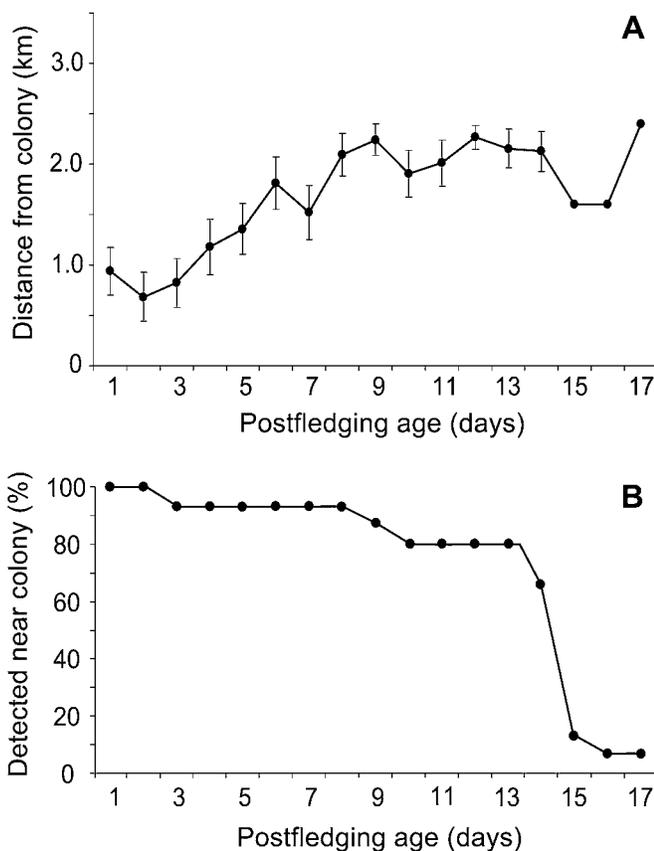


FIG. 3. (A) Mean ( $\pm$  SE) distance that the 15 radiotagged fledgling Purple Martins in 2007 were detected from the natal colony and (B) percentage of birds (alive at that age) detected within 2–3 km of the colony versus postfledging age. On days when multiple locations were recorded for a bird the maximum distance was used.

Although much is known about how timing of breeding affects fledgling or annual juvenile survival, it is typically not known whether time of fledging affects fledgling survival and migration–wintering survival of juveniles. We found strong evidence for a carryover effect of fledge week on migration–wintering survival. Despite our systematic search for banded birds over a large area we cannot rule out the possibility of permanent emigration outside of our study region or that late-fledged young were more likely to exhibit natal dispersal out of our study area. In Tree Swallows, however, dispersal distance was not related to date of fledging (Winkler et al. 2005). Late fledging may disadvantage juveniles in surviving migration if late-fledged young depart on migration at a similar time as early-fledged young (presumably in late August) and are therefore several weeks younger at the time of their first migration. Adult Purple Martins from our population fly rapidly to the southern Gulf Coast and cross the Gulf of Mexico on their way south (Stutchbury et al. 2009b), traveling  $\leq 2,500$  km in the first week. It is not known whether juveniles also do this or how timing of fledging affects timing of migration, migratory routes, or survival. The difference in age at migratory departure could also mean that earlier-fledged birds were more experienced and better at food acquisition or predator avoidance early in migration.

Brood size had an effect on apparent annual juvenile survival but not migration–wintering survival, which implies that individuals from large broods experience relatively low fledgling survival. Brood-size manipulation studies often show adverse effects on nestling body mass and growth of individuals from enlarged broods (Shutler et al. 2006, Siefferman and Hill 2007). If food is limiting then offspring growth may be lower in larger broods, which in turn could affect offspring survival once birds leave the nest (van Noordwijk et al. 1995, Naef-Daenzer and Keller 1999). However, Reid et al. (2003) found that juveniles from larger broods had higher survival probability and were more likely to recruit locally into the breeding population in Red-billed Choughs (*Pyrrhocorax pyrrhocorax*) (see also Müller et al. 2005). Wagner et al. (1996) found evidence for food competition within broods of Purple Martins because there was a negative relationship between brood size and feeding rate per nestling and at least one nestling starved in 20% of nests. Nonetheless, our results suggest that young from larger broods that survive the fledgling period are not disadvantaged during migration.

In Purple Martins ASY breeders arrive earlier in the spring and initiate nesting about 2 weeks before SY breeders (Morton and Derrickson 1990). Thus, time of breeding and female age class are closely related such that young fledged from the first nests of the year typically have older mothers whereas most late-fledged young have young mothers. Maternal effects associated with parental experience or reduced parental care by young parents may explain some seasonal variation in apparent juvenile survival. Disentangling these effects would require manipulation of fledge date by swapping eggs between SY and ASY females.

*Juvenile survival before and after onset of migration.*—Our study allowed us to partition annual mortality of juveniles into different portions of the annual cycle (Fig. 4). Radiotracking of a small number of fledglings found very high survival during the first week postfledging (1.0) and to the roost (0.73), and survival analysis of band resighting at the roost and colonies also estimated

high survival to onset of migration ( $\phi_r = 0.87$ ). On the basis of observations of family groups near the colony, Brown (1978) also reported high fledgling survival of Purple Martins in the first few days after fledging.

Our survival estimates for fledgling (1.0) and premigratory (0.73, 0.87) juvenile Purple Martins were higher than those reported for many other Neotropical migratory songbirds. For example, only 19% of fledgling Hooded Warblers (*Wilsonia citrina*) survived 4 weeks (Rush and Stutchbury 2008) and 53% of fledgling Ovenbirds (*Seiurus aurocapilla*) survived 5 weeks (King et al. 2006). Small passerine nestlings typically fledge at a relatively young age (<2 weeks posthatch) and survival probability is lowest during the first week after fledging (Dickcissels [*Spiza americana*], Berkeley et al. 2007; Western Bluebirds [*Sialia mexicana*], Wightman 2009; Rose-breasted Grosbeaks [*Pheucticus ludovicianus*], Moore et al. 2010). Fledglings at this age cannot fly well and travel relatively short distances (<500 m; Kershner et al. 2004, Rush and Stutchbury 2008). In Purple Martins young fledge at 4 weeks posthatch and can fly well, so they are presumably far less vulnerable to ground predators. We found radiotagged fledglings an average of 1 km from their natal colony on the first day and the two documented cases of predation were attributed to owls. Gruebler and Naef-Daenzer (2008) found that in Barn Swallows

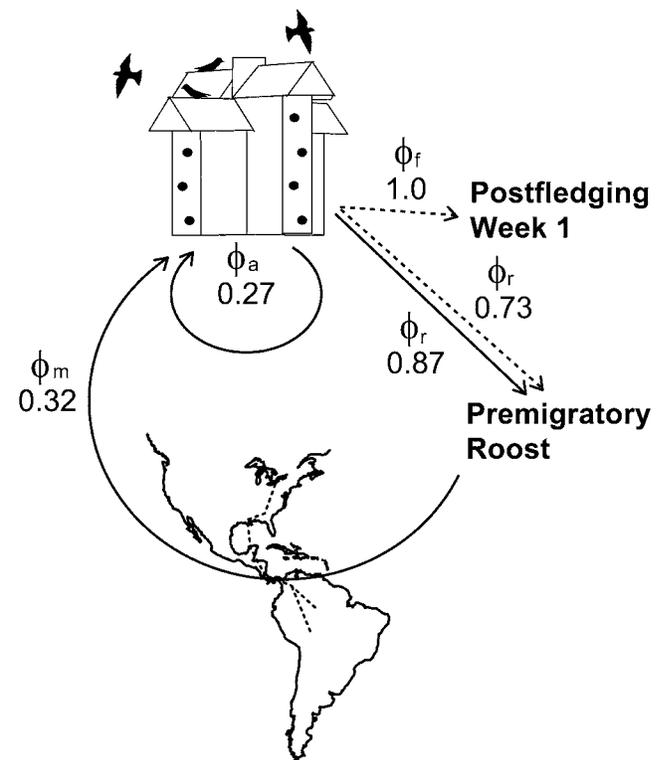


FIG. 4. Apparent survival probability of juvenile Purple Martins at different stages in their annual life cycle ( $\phi_f$ : survival during the first week postfledging;  $\phi_r$ : fledgling survival to the roost;  $\phi_m$ : juvenile survival after onset of migration to South America and back to the breeding colony;  $\phi_a$ : annual juvenile survival). Data based on radiotelemetry (2007; dashed lines) and mark-recapture data (1998–2002; solid lines).

fledgling survival probability to 3 weeks was 0.61, which suggests that pre-migratory survival may be generally high in swallows.

Fledgling Purple Martins were highly mobile, consistent with other studies on this species (Brown 1978, Morton and Patterson 1983). Most radiotagged individuals were detected daily near the colony for the first 2 weeks after fledging, often returning to the colony at night, but were rarely detected at the colony at older ages. Sleeping at the colony could benefit fledglings directly by extending the period of parental care, reducing nocturnal predation risk, and improving site familiarity. Juveniles may also visit active colonies prior to migration to gain information on reproductive success of adults and use these assessments of colony site quality for future choice of breeding site (Danchin et al. 1998, 2004; Miller et al. 2001; Sergio and Penteriani 2005). We did not systematically search for radiotagged juveniles at other colonies prior to migration, but auto-loggers could be used to monitor visits to non-natal colonies remotely and then relate search patterns to subsequent recruitment.

On the basis of apparent fledgling survival to the roost ( $\phi_r = 0.87$ ) and seasonal migration–winter survival ( $\phi_m = 0.32$ ) we estimate that 81% of all annual juvenile mortality in Purple Martins occurred after fall migration began. Juvenile mortality after the onset of migration could be caused in part by parasitic infections by *Haemoproteus*, filaria parasites (larval nematodes detected in blood smears), or both in naive birds. In migratory birds *Haemoproteus* parasite transmission likely occurs during fall migration or on the wintering grounds, with infection contributing to high levels of mortality before young birds return in the spring (Davidar and Morton 1993, Hasselquist et al. 2007). Furthermore, return rates of Purple Martins infected with just filaria or both filaria and *Haemoproteus* were  $\leq 32\%$  lower than birds of the same age infected by *Haemoproteus* alone (Davidar and Morton 1993, 2006). To our knowledge survival estimates after the onset of migration are not available for other juvenile migratory songbirds. However, in Black-throated Blue Warblers (*Setophaga caeruleascens*) comparison of within-season versus annual survival indicated that  $>85\%$  of annual adult mortality occurred during migration rather than on the breeding or wintering grounds (Sillert and Holmes 2002). Purple Martins from our breeding population overwinter in the Amazon basin of northern Brazil (Stutchbury et al. 2009b) but mark–recapture studies at wintering roosts to assess survival on the wintering grounds versus migration would not be practical given the large number of roosts in the region and individual movements between roosts.

Many aerial insectivore species (e.g., Common Nighthawks [*Chordeiles minor*], Chimney Swifts [*Chaetura pelagica*], and Barn Swallows) are experiencing population declines (Sauer et al. 2008, Nebel et al. 2010), and for migratory species conservation efforts should include identification of threats during migration and on the wintering grounds (Dionne et al. 2008). Data are needed that evaluate how breeding season disturbances to food supply through habitat loss, pesticides, climate change, and parental provisioning may affect nestling development components of survival (Fig. 4). Most annual mortality of juvenile Purple Martins occurred after, rather than before, the onset of fall migration, so survival during migration, on the wintering grounds, or both likely plays an important role in juvenile recruitment and population demography. Studies examining timing of migration,

migratory routes, and destination (Stutchbury et al. 2009b) will be important for understanding geographic patterns of juvenile survival and population differences in demographic trends.

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