



SEX AND AGE-SPECIFIC ANNUAL SURVIVAL IN A NEOTROPICAL MIGRATORY SONGBIRD, THE PURPLE MARTIN (*PROGNE SUBIS*)

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ABSTRACT.—We estimated apparent annual survival probability of adult Purple Martins (*Progne subis*) using a 14-year data set from a population in northwestern Pennsylvania. We modeled age, sex, and year effects on adult survival using known-age birds (585 males and 392 females) first banded or resighted as one-year-olds in two core breeding colonies. We resighted banded birds at (1) the two core breeding colonies, (2) other breeding colonies within 50 km of the core colonies, and (3) a large premigratory roost that attracts adult Purple Martins from colonies ≤ 200 km away. Apparent annual survival probability for one-year-olds increased by 0.08 when we included encounters outside the core colonies. Survival probability for older males and females was largely unaffected, a result of their high breeding-site fidelity. The model with age-specific survival (1 year old, 2–4 years old, ≥ 5 years old) and an age*sex interaction had the strongest support when all encounters were included. Apparent annual survival of one-year-old females (0.48 ± 0.03 [SE]) was lower than that of one-year-old males (0.59 ± 0.02), but we detected no sex differences in survival among older birds (2–4 years old: females, 0.64 ± 0.02 ; males, 0.62 ± 0.02). We found evidence of senescence, because birds at least five years old had lower apparent survival (females: 0.51 ± 0.06 ; males: 0.52 ± 0.05). Fully time-dependent models had low support, including those evaluating the relationship between annual variation in prevalence of West Nile virus and the El Niño Southern Oscillation Index, a key climate variable. Received 29 February 2008, accepted 28 October 2008.

Key words: annual survival probability, breeding dispersal, *Progne subis*, Purple Martin, senescence, Southern Oscillation Index, West Nile virus.

Supervivencia Anual Específica por Edad y Sexo en *Progne subis*, un Ave Canora Migratoria Neotropical

RESUMEN.—Estimamos la probabilidad de supervivencia anual aparente de los adultos de *Progne subis* empleando un conjunto de datos tomados a lo largo de 14 años en una población del noroeste de Pensilvania. Modelamos los efectos de la edad, del sexo y del año sobre la supervivencia de los adultos empleando aves de edad conocida (585 machos y 392 hembras) anilladas por primera vez o vistas de nuevo como individuos de un año de edad en dos colonias de cría centrales. Vimos de nuevo a las aves anilladas en (1) las dos colonias de cría centrales, (2) otras colonias de cría a menos de 50 km de las colonias centrales y (3) un gran dormitorio premigratorio que atrae adultos de *P. subis* desde colonias a ≤ 200 km de distancia. La probabilidad de supervivencia anual aparente de los individuos de un año de edad aumentó en 0.08 cuando incluimos los encuentros ocurridos fuera de las colonias centrales. El estimado de la probabilidad de supervivencia de los machos y las hembras más viejos no fue casi afectado debido a la alta fidelidad a los sitios de cría. El modelo que especificaba la supervivencia para cada edad (1 año, 2–4 años, ≥ 5 años) y que consideraba la interacción edad*sexo tuvo el apoyo más fuerte cuando se incluyeron todos los encuentros. La supervivencia anual aparente de las hembras de un año de edad (0.48 ± 0.03 [EE]) fue menor que la de los machos de un año (0.59 ± 0.02), pero no detectamos diferencias en la supervivencia entre las aves más viejas (2–4 años de edad: hembras, 0.64 ± 0.02 ; machos, 0.62 ± 0.02). Encontramos evidencia de senescencia, porque las aves con al menos cinco años de edad presentaron menor supervivencia aparente (hembras: 0.51 ± 0.06 ; machos: 0.52 ± 0.05). Los modelos completamente dependientes del tiempo tuvieron un bajo apoyo, incluyendo aquellos que evaluaron la relación entre la variación anual en la prevalencia del virus del Oeste del Nilo y el Índice de Oscilación del Sur del Niño, una variable climática clave.

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ESTIMATES OF ANNUAL survival are critical for modeling population dynamics and identifying the factors responsible for driving long-term population declines. Neotropical migratory songbirds are a group of particular interest because they are experiencing widespread population declines (Lloyd-Evans and Atwood 2004, Sauer et al. 2006). The ecological and anthropogenic effects on population dynamics are fundamentally different for long-distance migrants than for resident species, because most annual mortality occurs during migration or on the wintering grounds (Sillert and Holmes 2002). Maximum-likelihood estimates of survival from mark-recapture studies (Lebreton et al. 1992) are now available for many Neotropical migratory songbirds (Chase et al. 1997, Powell et al. 2000, Cilimburg et al. 2002, Sillert and Holmes 2002, Gardali et al. 2003), particularly as a result of the continent-wide Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante and Kaschube 2006). However, the difficulty of marking and recapturing large numbers of known-age birds over many years has meant that we still know relatively little about how sex and age influence the annual survival of Neotropical migratory songbirds (Brown and Brown 1996, Sillert et al. 2000). Given the importance of forecasting how introduced diseases, habitat loss, and climate change will affect population dynamics of songbirds (Sillert et al. 2000, Kilpatrick et al. 2007, Wilson et al. 2007), studies of adult survival in migratory songbirds are urgently needed. Our aim in the present study was to investigate how age, sex, and year affect annual adult survival in a long-distance migrant, the Purple Martin (*Progne subis*).

The basic question of whether adult survival differs between the sexes is poorly understood for migratory songbirds. Female birds are expected to have lower annual survival than males, largely as a result of the higher cost of reproduction in females and a higher risk of predation (reviewed in Breitwisch 1989). For many Neotropical migrants, habitat segregation by sex on the non-breeding grounds in Central America and South America results in females occupying relatively poor-quality habitat, which can reduce body condition and survival (Marra and Holmes 2001). High reproductive effort in females may also delay molt and migration (Evans Ogden and Stutchbury 1996), which has unknown consequences for survival. Apparent annual survival was higher in male than in female Black-throated Blue Warblers (*Dendroica caerulescens*; Sillert and Holmes 2002) and Yellow Warblers (*D. petechia*; Cilimburg et al. 2002), but this was not the case in Wilson's Warblers (*Wilsonia pusilla*; Chase et al. 1997) or Cliff Swallows (*Petrochelidon pyrrhonota*; Brown and Brown 1996). In Europe, males had higher annual survival in migratory Sand Martins (i.e., Bank Swallows [*Riparia riparia*]; Szép 1995) but not in Barn Swallows (*Hirundo rustica*; Møller and Szép 2002).

Senescence is the decline in survival rate or reproduction of older individuals that results from decreased physiological function, increased disease, or both (reviewed in Ricklefs 2000). Short-lived birds are predicted to experience relatively high rates of senescence, given that few individuals live to old age, but few studies of songbirds have examined senescence with formal survival estimates. Annual apparent survival declined steadily with age in Song Sparrows (*Melospiza melodia*; Keller et al. 2008), declined after at least three years of age in Black-capped Chickadees (*Parus atricapillus*; Loery et al. 1987) and Western Bluebirds (*Sialia mexicana*; Keyser et al. 2004), and declined after five years of age

in Great Tits (*Parus major*; McCleery et al. 1996), Willow Tits (*P. montanus*; Orell and Belda 2002), and Barn Swallows (Møller and Szép 2002). In the only study that has examined senescence in a Neotropical migratory songbird, Brown and Brown (1996) found that annual survival probability for Cliff Swallows remained high in individuals three years of age and older.

Annual adult survival in migratory songbirds varies greatly from year to year (e.g., Sillert et al. 2000, Cilimburg et al. 2002), but for most species little is known about the factors that drive these yearly fluctuations. We examined the relationships among annual variation in survival of Purple Martins, the El Niño Southern Oscillation (ENSO), and outbreaks of West Nile virus (WNV). Conditions on the wintering grounds of Neotropical migrants in Central America and South America are affected by the ENSO via changes in global precipitation and temperature patterns. In wintering Black-throated Blue Warblers, ENSO events reduced annual adult survival by causing a decreased insect food supply during the dry conditions that prevail in the Caribbean in El Niño years (Sillert et al. 2000). Similarly, Mazerolle et al. (2005) found that adult survival of breeding Yellow Warblers was lowest during El Niño years and highest during wetter La Niña years. In Bank Swallows, annual adult survival in Europe was related to precipitation on the wintering grounds in Africa (Szép 1995). Precipitation patterns during El Niño events vary greatly throughout Central America and South America (Kiladis and Diaz 1989). In southern Brazil, a major wintering area for Purple Martins, El Niño years result in wetter conditions, whereas La Niña years result in drier conditions. Purple Martins migrate primarily to Brazil and are obligate aerial insectivores, so large-scale fluctuations in precipitation may also affect their annual survival.

The introduction of WNV has been linked to population declines of North American songbirds (LaDeau et al. 2007), and lab experiments have shown a high risk of mortality in some species (Komar et al. 2003). However, the effects of this disease on wild populations of most species remain largely unknown (Kilpatrick et al. 2007). West Nile virus was first detected in northwestern Pennsylvania in 2000, about half-way through our study, which created an opportunity for investigating whether WNV had significant effects on annual adult survival. Many of the species most affected by WNV are common in residential areas where WNV vectors are known to be present (LaDeau et al. 2007). Purple Martins in eastern North America may also be vulnerable to WNV, because they depend on manmade housing that is typically provided in backyard habitat.

We estimated annual survival probability and recapture probability for known-age adult Purple Martins using a 14-year mark-recapture study in northwestern Pennsylvania. We compared different models for the influence of age, sex, and year on apparent survival probability. Our long-term data set (1994–2007) and large sample size of known-age breeding Purple Martins ($n = 977$) also allowed us to examine senescence in both sexes.

METHODS

Study site and species.—Purple Martins in eastern North America breed exclusively in artificial housing (nest-box apartments and gourds) and form breeding colonies of up to several hundred pairs (Brown 1997). For the present study, the Purple Martin

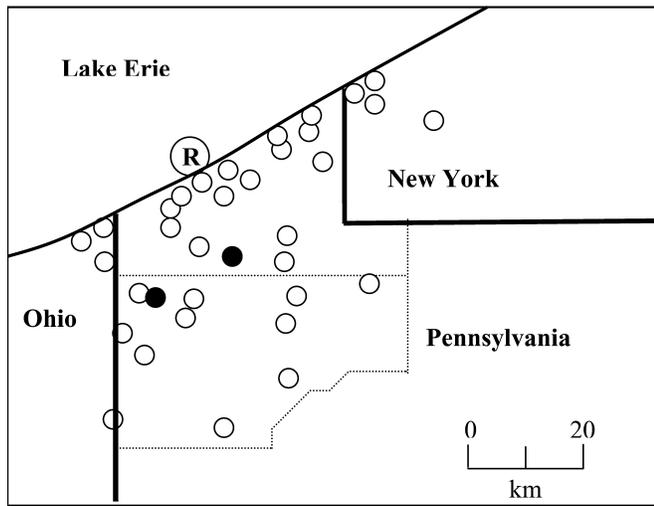


FIG. 1. Map of our study area in northwestern Pennsylvania, showing the locations of the two core breeding colonies (filled circles), the 33 additional breeding colonies that were surveyed annually for banded birds (open circles), and the premigratory roost ("R") at Presque Isle Peninsula on the south shore of Lake Erie. Dotted lines show the boundaries of Erie County (northern) and Crawford County (southern), our main study area.

Conservation Association (PMCA) intensively monitored two large breeding colonies (Troyer and Edinboro) from 1994 to 2007 by banding all nestlings, resighting color-banded adults, and, to a lesser extent, catching breeding adults. These "core" colonies were 19 km apart, and each colony consisted of clusters of 5–10 nest houses and gourd racks. The Troyer colony ($41^{\circ}45'20.01''\text{N}$, $80^{\circ}16'59.75''\text{W}$) had 100–150 pairs year^{-1} and was located on the lawn of a home in a rural setting. The Edinboro colony ($41^{\circ}53'08.50''\text{N}$, $80^{\circ}07'45.80''\text{W}$) consisted of 75–125 pairs year^{-1} and was on the shore of Lake Edinboro in the small town of Edinboro, Pennsylvania. Nest houses had predator guards on the poles to prevent climbing nest predators.

Mark–recapture studies typically cannot distinguish permanent emigration from actual mortality, and this results in underestimates of true survival (e.g., Zimmerman et al. 2007). Because dispersal is often female-biased and more common in young breeders (Greenwood and Harvey 1982), age or sex differences in apparent annual survival are difficult to interpret, in that true survival and permanent emigration are confounded. To reduce this problem, we systematically searched for banded birds over a large study area to document the extent of breeding dispersal and obtain a better estimate of true survival (e.g., Cilimburg et al. 2002, Keyser et al. 2004, Marshall et al. 2004). We analyzed three geographic scales to account for breeding dispersal in Purple Martins. We resighted banded birds at (1) the two intensively studied core breeding colonies, (2) other breeding colonies within 50 km of the core colonies, and (3) a large premigratory roost that is known to attract Purple Martins from ≤ 200 km away (Fig. 1). Monitoring effort at additional colonies varied from year to year and was most intense from 1997 to 2000. Each peripheral colony was visited at least once during the nestling period to read color bands of feeding parents.

From late July to early September, Purple Martins in northwestern Pennsylvania gather in a premigratory roost at the base of Presque Isle Peninsula on the south shore of Lake Erie ($42^{\circ}06'59.6''\text{N}$, $80^{\circ}08'51.92''\text{W}$; Fig. 1). The size of the roost typically peaks at $>50,000$ Purple Martins during mid-August (Hill 2002). Each year, the PMCA searched for banded adults perched on wires at several staging areas in Presque Isle State Park, 5–7.5 km from the roost. We searched these staging areas on five to seven nights each week from the second week of July through the end of August. Up to 100 banded individuals were seen nightly, and adult Purple Martins from breeding colonies ≤ 200 km away used this roost site (J. Hill III unpubl. data). Consequently, birds breeding in the local area but not encountered at a colony could nevertheless be encountered at the roost during the premigratory period.

Field methods.—All nestlings and captured adults were banded with a U.S. Geological Survey numbered band and a color band with a unique alphanumeric code. The identity of adults was determined primarily by using a telescope at close range to read the color-band number while birds were perched on their nest houses or on wires near the colony or roost. Purple Martins are highly conspicuous and perch in the open, which allowed us to read the alphanumeric codes with great accuracy. Observers visited the core breeding colonies several times each week from April through early August and recorded the color-band identification of all visible individuals. In some years, as part of other studies on diet and mating system, breeding adults were also captured while feeding young or sleeping in their houses at night.

During the present study, we banded $>12,000$ nestlings throughout the region, and most ($>90\%$) of the one-year-old breeders in our sample were first banded as nestlings. Purple Martins are strongly sexually dichromatic, and both the males and the females feature a distinct subadult plumage in their first year of breeding (Brown 1997). Thus, we were able to confidently sex all breeders and to classify breeders that had not been banded as nestlings as "one-year-olds," rather than as older. Males that are at least two years old are entirely of a deep, iridescent, dark blue hue, whereas females that are at least two years old have brownish-blue backs and white undersides washed with brown. One-year-old males are female-like in appearance but typically have variable amounts of deep blue feathers in a mottled pattern on the throat, belly, under-tail coverts, and back. One-year-old females have less blue on the back than older females and whiter under-tail coverts.

For the survival analysis, we used known-age birds first banded or encountered as one-year-olds in a core colony ($n = 595$ males, 392 females). Purple Martins are single-brooded at our study site, and we restricted encounters at breeding colonies to birds seen during the peak nesting period, between 15 May and 31 July. This reduced the bias attributable to early arrival and sighting of older birds (≥ 2 years) in late April and early May and the possibility of transients early in the spring. Individuals in our sample were occasionally found dead near colonies or inside their nesting compartments ($n = 16$) and were removed from the sample after their last encounter. These known-fate encounters represented only 1.6% of our birds and included both sexes (5 males and 11 females) and multiple age classes (6 one-year-olds and 10 older birds).

Southern Oscillation Index (SOI) values, which indicate sea-level pressure in the South Pacific Ocean, were obtained from the

TABLE 1. Model-selection results to assess effects of sex, age, year, and colony on apparent survival probability (ϕ) and encounter probability (p) for known-age adult Purple Martins in northwestern Pennsylvania, 1994–2007. All individuals in the sample ($n = 977$) were first banded or encountered as one-year-olds at a core breeding colony. We show results for individuals encountered at (1) only a core colony, (2) a core or peripheral breeding colonies, and (3) any breeding colony or the premigratory roost. Columns give model notation, number of estimable parameters (K), second-order Akaike's information criterion (ΔAIC_c) values and AIC_c weights (w_i). Recapture probability was modeled with a year*colony effect for all models. Subscripts describe parametrization of ϕ with three age-specific models ($\phi_{1,2^+}$; $\phi_{1,2-4,5^+}$; $\phi_{1,2,3,4,5^+}$) modeled alone and with a full interaction (age*sex) versus additive (age + sex) effect. We tested two models for full year effects ($\phi_{1,2^+*time}$; $\phi_{1,2^+*sex*time}$) and specific year effects of West Nile virus ($\phi_{1,2^+*sex*WNV}$) prevalence and the Southern Oscillation Index ($\phi_{1,2^+*sex*SOI}$). The full model set included 13 *a-priori* models, but only models with $w_i > 0$ are shown.

Model	K	Core colonies		All breeding colonies		Colonies or roost	
		ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
$\phi_{1,2^+*sex}$	30	0.00	0.376	0.00	0.271	4.63	0.042
$\phi_{1,2-4,5^+*sex}$	32	0.87	0.245	0.20	0.246	0.00	0.423
$\phi_{1,2,3,4,5^+*sex}$	36	1.64	0.167	1.01	0.164	3.98	0.058
$\phi_{1,2,3,4,5^+*sex}$	32	3.60	0.063	1.28	0.143	1.93	0.161
$\phi_{1,2,3,4,5^+}$	31	4.32	0.049	3.43	0.049	3.52	0.073
$\phi_{1,2-4,5^+*sex}$	30	4.97	0.032	3.27	0.053	2.06	0.151
$\phi_{1,2^+*sex}$	29	5.45	0.024	4.86	0.024	8.45	0.006
$\phi_{1,2-4,5^+}$	29	5.72	0.022	5.46	0.018	3.69	0.067
$\phi_{1,2^+}$	28	6.24	0.017	7.04	0.008	10.05	0.003
$\phi_{1,2^+*sex*WNV}$	32	8.94	0.004	4.82	0.024	6.53	0.016

National Oceanic and Atmospheric Administration (see Acknowledgments). We used annual mean monthly values of the standardized SOI for each calendar year (Silleet et al. 2000). El Niño years correspond with low negative SOI values, whereas La Niña years correspond with high positive SOI values.

For an index of WNV prevalence, we obtained data from the Pennsylvania West Nile Virus Surveillance Program (see Acknowledgments) on the percentage of dead birds sampled in a given year that tested positive for WNV. These birds, representing a wide range of species, had been reported dead and were subsequently tested. The number of birds tested each year ranged from 181 to 2,449 (average = 948 birds year⁻¹).

Statistical methods.—We estimated apparent annual survival probabilities using the program MARK, version 4.3 (White and Burnham 1999, Cooch and White 2008). We constructed an *a-priori* set of 13 candidate models (see below) to examine the influences of age, sex, and year on adult survival. We used Akaike's information criterion adjusted for small sample sizes (AIC_c ; Akaike 1973, Lebreton et al. 1992, Burnham and Anderson 2002) to compare models. When modeling mark–recapture data, a critical initial step requires testing the fit of the global model by calculating the variance inflation factor (\hat{c}) and then adjusting for any lack of fit if $\hat{c} > 1$. To assess goodness-of-fit (Lebreton et al. 1992, Burnham and Anderson 2002), we used MARK to calculate median \hat{c} for the global model for each of the three data sets (core only, all colonies, colonies and roost).

A-priori models were ranked and compared using ΔAIC_c and AIC_c weights (w_i). We used ΔAIC_c to estimate the relative difference between the top-ranked model and each other model, and w_i (normalized to sum to 1) to assess a model's relative probability of being the best in the set of candidates. The model with the lowest AIC_c (and highest w_i) is the model that best explains the

data. Models with $\Delta AIC_c \leq 2$ were considered equally parsimonious. Maximum-likelihood estimates of apparent survival (ϕ) and encounter probabilities (p) were calculated for models with high AIC_c weighting.

Our candidate model set was constructed to examine the influences of sex, age, and year on annual apparent survival of adults (Table 1). First, we ran three different age models, with and without an interaction with sex (age*sex), and then with an additive model of age and sex (age+sex). The first age model considered only two age classes (1 year old vs. ≥ 2 years old; $\phi_{1,2^+}$), because studies based on return rates at a colony in Maryland found that one-year-olds had a lower return rate (31%) than older individuals (56%; Davidar and Morton 2006). We examined senescence in survival using two models for age-specific survival among older birds. One model ($\phi_{1,2-4,5^+}$) lumped birds aged two to four years because studies of senescence in other short-lived passerines have found (1) no difference in survival of middle-aged birds and (2) a decrease in survival beginning at five years (McCleery et al. 1996, Møller and de Lope 1999, Orell and Belda 2002). A second model ($\phi_{1,2,3,4,5^+}$) allowed age-specific survival for each age (Keller et al. 2008) and pooled birds five years of age and older because of sample-size considerations.

In addition to age and sex effects, we also examined two specific factors (SOI and WNV) that could explain annual variation in apparent survival of one-year-olds as compared with older birds. Our model set included a fully time-dependent model for each age class ($\phi_{1,2^+*time}$) and a global model with a sex interaction effect ($\phi_{1,2^+*sex*time}$). We then assessed the fit of models that constrained estimates of survival as a linear function of the local prevalence of WNV ($\phi_{1,2^+*sex*WNV}$) and SOI ($\phi_{1,2^+*sex*SOI}$).

Resighting effort varied among years and between the two core colonies, so we modeled encounter probabilities as a function

TABLE 2. Between-year dispersal by one- and two-year-old Purple Martins encountered at a core colony as a one-year-old, showing the number that were encountered the next year at a core colony, a peripheral breeding colony or were sighted only at the roost (i.e., breeding colony unknown). Birds first encountered in the final two years of the study (2006–2007) were excluded because their return history was not yet complete.

Known age (year)	Sex	Location of encounter the following year		
		Core colony	Peripheral colony	Roost
1	F	107 (84.2%)	11 (8.7%)	9 (7.1%)
1	M	213 (87.4%)	17 (7.3%)	13 (5.3%)
2	F	50 (90.9%)	2 (3.6%)	3 (5.5%)
2	M	111 (94.0%)	5 (4.3%)	2 (1.7%)

of the interaction between year and colony ($p_{\text{year} \times \text{colony}}$). Preliminary analyses had confirmed that models with a year*colony interaction always had higher AIC weighting than the same model with only a year-dependent encounter probability. There was no reason, *a priori*, to expect that encounter probability varied by sex or age, given that all breeders at a colony are highly visible, so we omitted these factors from consideration.

RESULTS

Colony site-fidelity was high among one-year-olds that bred at a core colony; 84% of females and 87% of males that were encountered the next year returned to a core colony (Table 2). Site-fidelity was even higher among two-year-olds that bred in a core colony in both their first and second year; 91% of those females and 94% of the males were subsequently encountered at a core colony in their third year. We anticipated, therefore, that between-year breeding dispersal would have an important influence on apparent survival estimates for one-year-olds, but not for older individuals. A small percentage of individuals were sighted at the premigratory roost but not at a breeding colony (Table 2). This may have resulted from incomplete sampling of breeding colonies, from individuals breeding outside our study region, or from the individuals in question being nonterritorial floaters.

The global model ($\phi_{1,2+ \text{sex} \times \text{time}} p_{\text{year} \times \text{colony}}$) for adults encountered at core colonies fit the data well ($P = 0.32$), and there was no evidence of overdispersion (median $\hat{c} = 0.99$). This global model also fit the data for encounters at any breeding colony ($P = 0.28$, median $\hat{c} = 1.0$) and for all encounters, including the premigratory

roost ($P = 0.24$, median $\hat{c} = 0.99$). Therefore, we did not adjust for overdispersion and used AIC_c as a criterion to evaluate the relative plausibility of each model in our set.

We found that apparent adult survival was strongly related to both age class and sex but that the best-fitting age-class model depended on whether we accounted for local breeding dispersal. Using the data set for encounters only at core colonies (Table 1), the encounter probability ranged from 0.49 to 1.0 among years and averaged 0.81 for the Troyer colony and 0.79 for the Edinboro colony. The top three models ($\phi_{1,2+ \text{sex}}$, $\phi_{1,2-4,5+ \text{sex}}$, and $\phi_{1,2,3,4,5+ \text{sex}}$) had AIC_c values that differed by <2.0, which indicates that they were equally parsimonious (Burnham and Anderson 2002). Models that include two age classes ($\phi_{1,2+}$) had stronger support (total $w_i = 42\%$) than three-age-class models ($\phi_{1,2-4,5+}$; total $w_i = 29.9\%$) and five-age-class models ($\phi_{1,2,3,4,5+}$; total $w_i = 27.9\%$). Models that included an interaction effect between age and sex ($\phi_{1,2+ \text{sex}}$, $\phi_{1,2-4,5+ \text{sex}}$, and $\phi_{1,2,3,4,5+ \text{sex}}$) had total $w_i = 79\%$ and had 6× the support of models with an additive age and sex effect (11.9%).

When encounters at all breeding colonies were included, the same three models ($\phi_{1,2+ \text{sex}}$, $\phi_{1,2-4,5+ \text{sex}}$, and $\phi_{1,2,3,4,5+ \text{sex}}$) had the strongest support and were equally parsimonious (Table 1). For encounters including the premigratory roost, however, the model with three age classes ($\phi_{1,2-4,5+ \text{sex}}$) fit the data far better than any other model ($\Delta\text{AIC}_c > 3.98$), and models with three age classes (combined $w_i = 64\%$) fit the data twice as well as models with five age classes ($\phi_{1,2,3,4,5+}$; $w_i = 29\%$).

Using the model with three age classes ($\phi_{1,2-4,5+ \text{sex}}$), the apparent survival estimate for one-year-olds increased by 0.08 when we included all encounters outside the core colonies (Table 3). Apparent annual survival probability for one-year-old females (0.48 ± 0.03) was lower than that for one-year-old males (0.59 ± 0.02) and older females (0.64 ± 0.03), even when local breeding dispersal were taken into account (Fig. 2). Apparent survival probability of birds that are at least two years old did not differ between females and males (Fig. 2). Using resightings at the core colonies only, survival probability for one-year-old males was 0.09 lower than that for males two to four years of age, but this difference diminished to 0.03 when all encounters were included (Table 1). There was strong evidence of senescence in Purple Martins, in that apparent survival probability dropped by 0.10–0.13 for individuals at least five years of age (Fig. 2).

Models with time dependence in adult survival had no support (Table 1 and Fig. 3). Prevalence of WNV increased dramatically in Pennsylvania in 2001; if this had caused widespread mortality among Purple Martins, we would expect to see a sudden drop in apparent annual survival beginning that year. However, there was little support for the linear model including WNV

TABLE 3. Estimates of apparent annual survival (\pm SE) for three age classes of males and females ($\phi_{1,2-4,5+ \text{sex}}$). Survival estimates are shown for encounters at core colonies only, encounters at all breeding colonies, and encounters at any colony or the premigratory roost.

Encounter location	1 year old		2–4 years old		≥ 5 years old	
	Female	Male	Female	Male	Female	Male
Core colony	0.40 \pm 0.03	0.51 \pm 0.02	0.64 \pm 0.03	0.60 \pm 0.02	0.52 \pm 0.07	0.54 \pm 0.05
All colonies	0.44 \pm 0.03	0.56 \pm 0.02	0.64 \pm 0.03	0.61 \pm 0.02	0.52 \pm 0.07	0.53 \pm 0.05
Colonies or roost	0.48 \pm 0.03	0.59 \pm 0.02	0.64 \pm 0.03	0.62 \pm 0.02	0.51 \pm 0.07	0.52 \pm 0.05

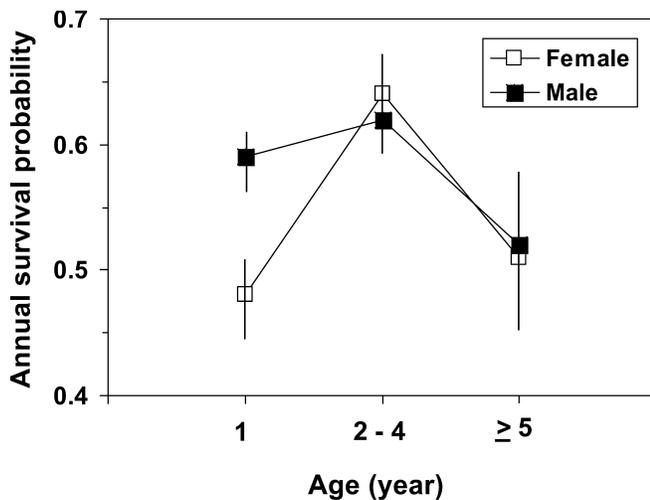


FIG. 2. Apparent annual survival probability (\pm SE) of age classes of male and female Purple Martins ($\phi_{1,2-4,5}^{+sex}$; Table 1), based on individuals breeding in the core colonies as one-year-olds (585 males and 392 females) and encountered in future years at any colony or the premigratory roost, 1994–2007. Ages 5–9 were pooled.

prevalence ($\phi_{1,2-4,5}^{+sex} \cdot W_{NV}$; $w_i < 2\%$). Similarly, the SOI varied from -1.23 to 0.76 from 1994 to 2005, but the linear model including the SOI had no support ($w_i = 0\%$).

DISCUSSION

Age and sex differences in apparent survival of passerines could reflect local breeding dispersal rather than true survival, but few studies have systematically quantified local breeding dispersal to evaluate its effect on apparent survival (e.g., Cilimburg et al. 2002). We found strong age- and sex-specific patterns in apparent annual survival probability for Purple Martins, even after taking local breeding dispersal into account (Fig. 2). Apparent annual survival probability for one-year-olds increased by 0.08 when encounters away from the core breeding colonies were included, but this had little effect on survival estimates for older birds because of their high site-fidelity (Tables 2 and 3). For all spatial scales of encounters, apparent annual survival probability for one-year-old females was lower than that for either yearling males or older females. There were no sex differences in apparent survival probability for birds at least two years old, and we found evidence of senescence in both sexes after five years of age (Fig. 2).

Transients do not likely explain the lower apparent survival of one-year-olds, because floaters are far less common in Purple Martins than in other obligate cavity-nesting swallows, owing to the apartment-style housing that allows most yearlings to claim unused nesting cavities (Stutchbury and Robertson 1985, Stutchbury 1991). High visibility of banded birds and our ability to identify individuals without capturing them typically resulted in multiple encounters with individuals during each breeding season at the core colonies. Despite our systematic search for banded birds away from the core breeding colonies, we cannot rule out the possibility of permanent emigration from our study region, but it

is unlikely that individuals in our older age classes, in which colony fidelity is high (Table 2), permanently emigrated.

Swallows have been the focus of many demographic studies, in part because adults can be captured in large numbers because many species breed in colonies and artificial housing. Most survival studies of swallows have searched nearby colonies for banded birds (Szép 1995, Brown and Brown 1996, Møller and Szép 2002), so estimates of apparent annual survival account for local breeding dispersal to some extent, which facilitates interspecific comparisons. In Cliff Swallows, no sex difference in survival was detected and survival of older birds was relatively high (Brown and Brown 1996). In European Barn Swallows, there were also no sex differences in survival, but senescence occurred in older birds (Møller and de Lope 1999, Møller and Szép 2002).

Adult survival in migratory songbirds could be influenced by vulnerability to blood parasites, resulting in higher mortality of one-year-olds. Most species of Neotropical migratory songbirds are infected with blood parasites, and, during spring migration, individuals are most likely to be infected with the hematozoan *Haemoproteus* (Garvin et al. 2006). Transmission of *Haemoproteus* likely occurs during fall migration or on the wintering grounds, and the initial acute infection, which results in high mortality, typically occurs before the first breeding season (Davidar and Morton 1993, Hasselquist et al. 2007). There is evidence, however, that blood parasites may also affect the survival of one-year-old Purple Martins after their first breeding season. At a colony in Maryland, 17% of one-year-old Purple Martins were infected with a filarial nematode, and 17% were infected with *Haemoproteus prognei* (Davidar and Morton 1993, 2006). The return rate of one-year-olds infected with *Haemoproteus* was high (41%), but individuals infected with filaria had very low return rates (9%), as did those cross-infected with both parasites (18%). None of the two-year-old Purple Martins sampled at the breeding colony was cross-infected, which further suggests high mortality of co-infected one-year-olds (Davidar and Morton 2006). If infection by, and resistance to, blood parasites is a major determinant of overwinter survival in Purple Martins, then heterozygosity, particularly at major histocompatibility complex (MHC) genes, should be related to an individual's infection prevalence and subsequent survival (Davidar and Morton 1993, Westerdahl et al. 2005).

High female mortality in other species of migratory songbirds has been attributed to low-quality wintering habitat occupied by females (Marra and Holmes 2001), but this is unlikely for Purple Martins, which are not territorial in the nonbreeding season. Males and females appear to mix freely in wintering roosts in Brazil (B. Stutchbury and J. Hill III pers. obs.), and the sex ratio of captured birds was equal during blanket mist netting at several roosts (Davidar and Morton 1993). Spring arrival times of two-year-old male and of female Purple Martins differed by only five days, on average (Morton and Derrickson 1990), which suggests that inclement spring weather during migration and soon after arrival at the breeding colony (Brown 1997) would present a similar mortality risk for both sexes.

The pronounced low apparent survival probability for one-year-old female Purple Martins could instead reflect a high cost of reproduction in their first breeding season. Only females incubate eggs, and virtually all females obtain territories and

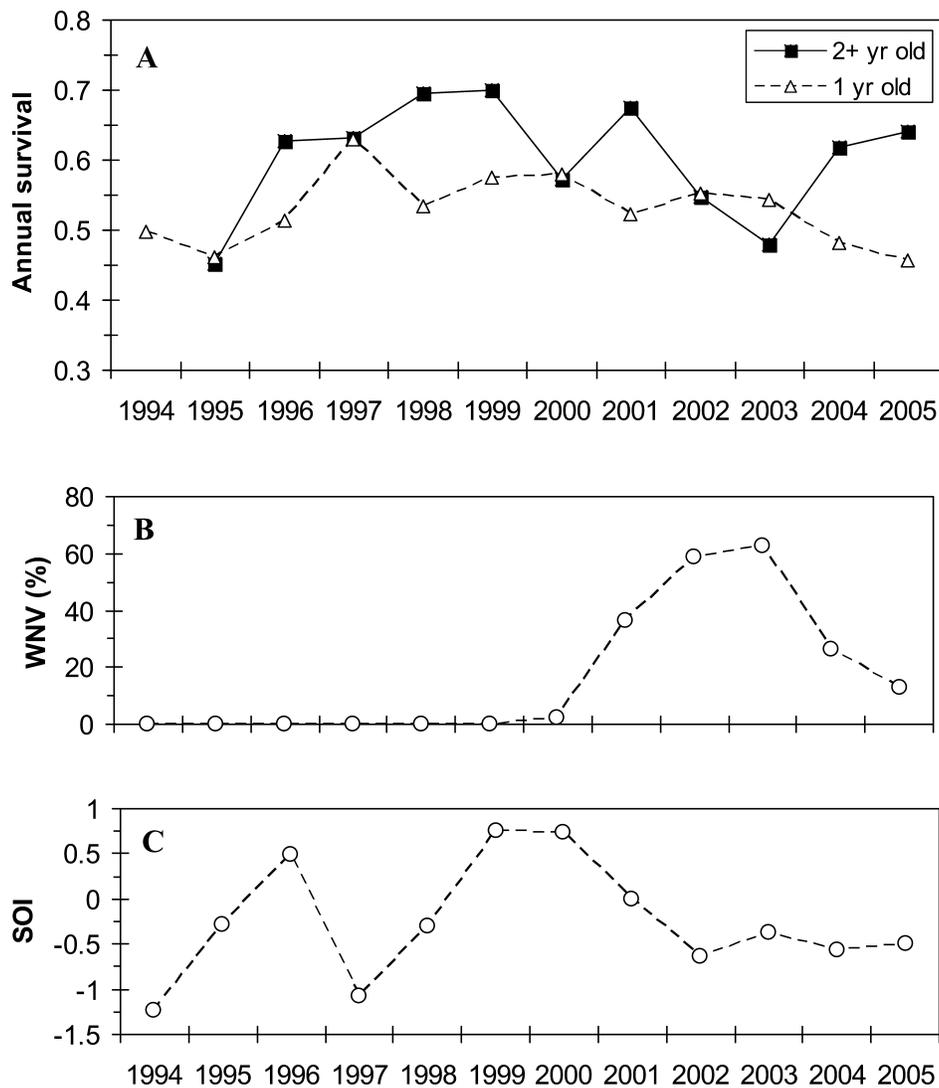


FIG. 3. Annual variation in (A) apparent annual survival (Table 1: $\phi_{1,2+\text{time}}$) of two age classes of Purple Martins breeding in the core colonies as one-year-olds ($n = 977$) and encountered in future years at any colony or the migratory roost, (B) percentage of dead birds of various species sampled in Pennsylvania that tested positive for West Nile virus (WNV), and (C) the standardized Southern Oscillation Index (SOI). "Year" refers to the beginning of the interval over which survival was estimated.

breed. In one population, for instance, 13% of yearling males but <1% of females were unmated, even though both defended nesting compartments (Wagner et al. 1996). Young females may experience a greater overlap with the energetically expensive activities of molt and migration than older females (Evans Ogden and Stutchbury 1996, Norris et al. 2004). In our study population, one-year-olds arrive, nest, and fledge young two to three weeks later than older birds. Late breeding may impose higher physiological and energetic costs that, in turn, decrease overwinter survival. In Cliff Swallows, for instance, an individual's corticosterone level at the end of the breeding season was strongly related to annual survival (Brown et al. 2005). If a high cost of reproduction explains low annual survival of first-time breeders, timing of egg laying and brood size should be related to apparent annual survival.

The cost of reproduction in young males includes male–male competition for social mates and extrapair mates. Purple Martins have an extrapair mating system in which most extrapair young occur in nests of one-year-old males and extrapair sires are males that are at least two years old (Morton et al. 1990, Wagner et al. 1996). Young males who guard their mates intensively (by following the mate to the ground when gathering nest material) achieve high paternity (Wagner et al. 1996). It is unknown whether this intense competition early in the breeding season affects annual survival.

In Purple Martins, we found strong evidence of senescence at five years of age (Table 3 and Fig. 2). During mark–recapture studies, the average age of the sample population will increase over time as the number of older, marked individuals increases. Thus, apparent senescent decline could occur as a result

of environmental deterioration over the duration of the study, rather than because older individuals have lower survival (Nisbet 2001). No such deterioration was detectable in our study in terms of weather conditions, nesting success, or annual survival of younger age classes.

Senescence has not been widely studied in short-lived passerines (Orell and Belda 2002), but most studies have found declines in adult survival probability either continuously with age (Keller et al. 2008) or after a threshold age at three to five years (Loery et al. 1987, McCleery et al. 1996, Orell and Belda 2002, Keyser et al. 2004). The only other study of a Neotropical migratory songbird found no evidence of strong senescence in Cliff Swallows (Brown and Brown 1996). Possible causes of senescence include the expression of late-acting deleterious alleles in older individuals as a result of mutation accumulation, delayed negative pleiotropic effects of alleles that are beneficial at a young age, or both (Partridge and Barton 1993). In a resident population of Song Sparrows, inbreeding depression reduced male survival and increased with age, which indicates that late-acting deleterious alleles may be a factor (Keller et al. 2008). In our population of Purple Martins, the probability of juvenile survival and recruitment to a core breeding colony is relatively high (0.13; B. Stutchbury et al. unpubl. data), so inbreeding depression could occur, especially given that Purple Martins have an extrapair mating system (Morton et al. 1990). The other primary cause of senescence is the long-term cost of high reproductive effort early in life, and several studies have shown that in short-lived birds, individuals that delay the onset of reproduction or do not breed have slower senescence (McCleery et al. 1996, Sanz and Moreno 2000, Orell and Belda 2002). This could be tested in Purple Martins by experimentally manipulating reproductive effort of one-year-olds (e.g., Gustafsson and Pärt 1990).

Apparent annual survival probability varied with time (Fig. 3), but models including general year effects were not well supported by our data (Table 1). Models that included the specific effect of WNV prevalence each year had little or no support (Table 1). Survival probability of birds at least two years of age was particularly low in 2002 and 2003 (Fig. 3), but no such effect was seen in one-year-old birds even though young birds are typically more susceptible to WNV than older birds (Kilpatrick et al. 2007). LaDeau et al. (2007) found a significant decline, following the introduction of WNV, in numbers of individuals per Breeding Bird Survey (BBS) route of several species predicted to be affected by this virus. Long-term BBS trends for Purple Martins in the Great Lakes Plains region show a significant decrease (-5.2% year $^{-1}$) since 1966 but an increasing trend ($+2.2\%$ year $^{-1}$) for the larger northeastern U.S. region (U.S. Fish and Wildlife Service [USFWS] Region 5; Sauer et al. 2006). There is no sharp drop in Purple Martin numbers associated with the spread of WNV into the region in either case.

Determining the influence of ENSO on annual survival of Neotropical migratory songbirds is important because increases in global surface temperatures are predicted to increase the frequency of El Niño events (Kerr 1999, Timmermann et al. 1999; but see Collins 2005). Two studies have found a strong link between ENSO and adult survival of Neotropical migrants (Sillert et al. 2000, Mazerolle et al. 2005). However, for Purple Martins, we found no evidence that ENSO influences adult survival (Table 3

and Fig. 3). The winter range of Purple Martins extends from northeastern South America to southern Brazil (Brown 1997), encompassing regions that are dry and wet, respectively, during El Niño years. Thus, the influence of ENSO depends on where a particular breeding population overwinters and the degree of migratory connectivity. A study conducted by the USFWS marked Purple Martins in several wintering roosts in southern Brazil with fluorescent micro-dots and asked owners of martin houses throughout eastern North America to collect feathers during the breeding season (Coulson 1985, Klimkiewicz and Knittle 1985). Purple Martins that had occupied a single large roost in Brazil were subsequently found in widely scattered breeding colonies from Texas to Maryland, which indicates low migratory connectivity. The effects of global climate change on the survival of Neotropical migratory songbirds are difficult to predict, because for most species we know little about the connectivity of breeding and wintering populations or how weather on the wintering grounds affects survival.

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