Assessing the benefits of extra-pair mating for female purple martins (*Progne subis*)

Patrick M. Kramer

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ABSTRACT

Approximately 75% of socially monogamous passerines pursue extra-pair mating with the frequency of extra-pair paternity varying among and within taxonomic groups. Despite the ubiquity of extra-pair mating systems, substantial research into the subject has produced mixed results and the benefits to females remain elusive. Two genetic benefits hypotheses, the good genes hypothesis and heterozygosity theory, predict that extra-pair offspring (EPO) should generally be more fit than within-pair offspring (WPO). This study aims to test for genetic-based benefits to extra-pair mating in purple martins (*Progne subis*) by comparing EPO and WPO. Specifically, I compare the first year survival estimates of EPO and WPO and of those offspring that are recruited into the breeding population, I compare the reproductive success of EPO and WPO. I found no differences in first-year survival probability nor did I find any differences in reproductive success between EPO and WPO. I conclude that female purple martins are not benefitting from extra-pair mating through the improved survival or reproductive success of their offspring. Such benefits may be context-dependent or historical contexts in which the benefits of extra-pair mating for females may no longer exist for this semi-domesticated species.

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INTRODUCTION

Approximately 75% of socially monogamous songbird species pursue extra-pair mating

(Griffith *et al*. 2002), with the frequency of extra-pair paternity varying widely among and

within taxonomic groups (Birkhead and Møller 1992, Griffith *et al*. 2002) or among different

populations of the same species (Kempenaers and Schlicht 2010). Extra-pair mating has clear

benefits to males who gain paternity with additional females but benefits are less clear for

females because their fitness does not appear to be tied to the number of males who they

copulate with. The willingness of females in many species to seek out or participate in extra-

pair copulations (Griffith *et al*. 2002) suggests that overall benefits to females outweigh any

potential costs. However, the adaptive significance of extra-pair mating for females has yet to

be convincingly shown (Jennions and Petrie 2000; Simmons 2005; Dunn *et al*. 2009).

There are at least four possible types of costs to females associated with engaging in

extra-pair copulations (Westneat *et al*. 1990, Kempenaers and Schlicht 2010): 1) time and

energetic trade-offs, 2) increased risk of predation or infection with parasites or sexually

transmitted diseases, 3) retribution by the social mate (*e.g*., reduced care, divorce, *etc*.) and 4)

increased competition between half-siblings (*i.e*., reduced kin-selection). Since females produce

the same number of eggs regardless of the number of males they copulate with, the benefits of

extra-pair mating must lie with the quality, rather than quantity, of males. When higher quality

males are already paired, rather than not reproduce at all a female should choose a less

preferable male to obtain the resources he offers (*i.e*., parental care, territory or nest site).

Extra-pair mating may allow a female to choose the best male or males for the genetic fitness

of her offspring when her social mate is of lower quality (Griffith *et al*. 2002). Hypothesized

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benefits to females of EPCs may also include direct benefits from extra-pair partners such as nuptial gifts, or access to resources. Females probably receive a complex suite of various benefits that can vary by individual and species but quantifying such benefits in terms of fitness gains is problematic (Kempenaers and Schlicht 2010).

Numerous sexual selection hypotheses have been suggested to explain extra-pair mating by females (Andersson 1994, Griffith *et al*. 2002, Kempenaers and Schlicht 2010). Females may benefit by ensuring that their eggs become fertilized despite potential infertile social mates (Sheldon 1994), however evidence from studies of socially monogamous species is relatively weak (Kempanaers and Schlicht 2010). Males may be under indirect selection as extra-pair mating behaviour may have a genetic component (Forstmeir *et al*. 2011). Eliassen and Jorgensen (2014) argued that extra-pair mating systems can evolve through cooperative neighborhoods whereby extra-pair copulations may reduce aggression towards offspring that they are not raising themselves.

Two hypotheses predict genetic benefits to females from extra-pair mating: the good genes hypothesis (*i.e.*, additive genetic benefits; see Andersson 1994) and the heterozygosity theory of mate choice (*i.e.*, nonadditive genetic benefits; Brown 1997). The good genes hypothesis states that sexual selection will lead to the improvement of offspring fitness by passing on relatively superior genetic material (Andersson 1994; Griffith *et al*. 2002). The heterozygosity theory predicts that females should mate with males who best complement her genome to produce highly heterozygous offspring, and therefore a given male is not necessarily superior to all other males (Brown 1997; Griffith *et al*. 2002; Kempenaers 2007). Choosing mates that maximally differ from their own genomes (*i.e.*, are less related) will generally

increase the number of loci at which their offspring are heterozygous thus reducing the load of

deleterious or lethal recessive alleles and ultimately resulting in reduced inbreeding depression

in the population (Brown 1997; Kempenaers 2007). Specifically, heterozygotes at the Major

Histocompatibilty Complex (MHC) loci may have an advantage over homozygotes

(overdominance; Brown 1997; Penn and Potts 1999). MHC genes are implicated in immune

function; an individual with a greater diversity of MHC genes should have a more robust

immune response to a greater variety of pathogens (Penn and Potts 1999).

Both the good genes hypothesis and heterozygosity theory both have clear, testable

predictions in the context of extra-pair mating systems (Griffith *et al*. 2002). Both of these

hypotheses assume that females are able to assess the quality of males and predict that

females will choose to mate with those males that will improve offspring fitness (Griffith *et al*.

2002). Comparisons of extra-pair males with the social male have yielded support for the good

genes hypothesis; a meta-analysis by Akçay and Roughgarden (2007) found extra-pair males to

be larger and older than within-pair males. Age is a common factor in the distribution of extra-

pair paternity in birds (Griffifth *et al*. 2002). Davidar and Morton (1993) argued the good genes

hypothesis to explain the general pattern that female purple martins (*Progne subis*) sought

extra-pair matings from older males (Morton *et al.* 1990, Wagner *et al*. 1996, Tarof *et al*. 2012).

When it comes to heterozygosity, female mice can differentiate between males of varying

relatedness at MHC loci and preferentially mate with more dissimilar males (Yamazaki *et al*.

1979; Brown *et al*. 1987; Penn and Potts 1999). Several studies have shown similar mating

preferences in birds using microsatellite loci, however many have failed to find evidence that

females select dissimilar males as extra-pair partners (Kempanaers 2007; Mays *et al*. 2007).

Within the same population of tree swallows (*Tachycineta bicolor*) only one study found support for mate choice based on genetic similarity (Stapleton *et al*. 2007) while another two did not (Kempenaers *et al*. 1999, Barber *et al.* 2005). The importance of mating preferences based on genetic similarity in birds remains uncertain (Andersson and Simmons 2006).

The good genes hypothesis predicts that there should be a small subset of the "best" males and that females mated to poor quality males will seek extra-pair matings with higher quality males. As a result, extra-pair offspring (EPO) should have higher fitness (*e.g.*, survival, reproductive success) than their within-pair half-siblings (WPO) since EPO are sired by males with superior genes. The heterozygosity theory predicts that each female should seek her own "best" males and females with genetically similar social mates should seek EPCs (Griffith *et al*. 2002). The heterozygosity theory predicts that within a nest EPO will be more heterozygous than WPO, and thus will be more fit than their half-siblings. Through different mechanisms, both hypotheses predict that EPO will be more fit than their within-pair half-siblings.

The most unambiguous assessment of potential genetic benefits of extra-pair mating is to compare the fitness of within- and extra-pair offspring from the same brood (Griffith *et al*. 2002). Empirical evidence in support of the good genes hypothesis via offspring fitness is limited to only six of 23 studies reviewed by Akçay and Roughgarden (2007) that tested if EPO differed from WPO in fitness-related traits. In a more recent review of offspring survival by parentage (Sardell *et al.* 2011), only 3 of 8 studies found EPO survived to fledging better than WPO and only 1 of 5 studies found EPO survived better to independence. These studies examined only very short-term fitness differences, in the nest or within several weeks of leaving the nest. However, significant mortality occurs after independence and during the first year of

life (see Tarof *et al*. 2011). It is more difficult to test for survival to recruitment (*i.e.*, the first year), yet 12 studies have made the comparison of WPO and EPO but none found a significant difference in survival over the first year (reviewed in Sardell *et al*. 2011). It is even more difficult to test for longer-term differences in offspring fitness, and only five studies have done so in the context of extra-pair mating; none found significant differences in lifetime survival or return rates between EPO and WPO (Sardell *et al.* 2011, Gerlach *et al* 2012). All five of those studies were conducted on non-migratory species; such a comparison has yet to be attempted with a long-distance migratory species.

This study will examine the benefits of extra-pair mating to female purple martins by testing if extra-pair offspring have a fitness advantage over within-pair offspring as predicted by the good genes hypothesis *and* heterozygosity advantage hypotheses. In this study population, older males ($\geq$ 2 year) sired 83% of offspring in their own nests compared with only 63% for one-year old males, and extra-pair sires were generally older than the males they cuckolded (Appendix A, Tarof *et al*. 2012). This pattern is consistent with female preference for older males as extra-pair sires, but the benefits to females that engage in EPCs have not yet been tested. I hypothesize that female purple martins pursue EPCs to improve the genetic quality of their offspring. I predict that: (1) EPO will have higher first-year survival rates compared with their WPO half-siblings and (2) EPO recruited into the breeding population will have higher reproductive success than WPO. Specifically, first year breeders that were EPO are expected to have higher mating success, earlier nest initiations, more offspring fledged, than first year breeders that were WPO.

This is the first study to test for benefits of EPFs a long distance migratory songbird. Extra-pair fertilization rates tend to be higher for long distance migrants compared with residents (Stutchbury and Morton 1995, 2008; Spottiswoode and Moller, 2004) making the question of how females benefit from EPFs all the more important. However, most studies of migratory species cannot test for first-year survival because almost all young disperse away from the study area, and thus annual first-year survival cannot be estimated. Purple martins in eastern North America migrate ca. 10,000 km to their wintering grounds in Brazil (Appendices B-E, Stutchbury *et al*. 2009b, Fraser *et al*. 2012a, 2012b, 2013) but in my study population natal return rates averaged 22% (1998-2002 cohorts) and long-term mark/resight studies estimated first year survival probability to be 0.27 (Appendix F, Tarof *et al*. 2011). I could therefore test if annual survival, and reproductive success as a first-time breeder, differed between EPO and WPO. My field research during my dissertation made substantial contributions to many publications on which I am a co-author (Appendices A-G) but which are not the subject of my dissertation.

MATERIALS AND METHODS

(Study area, Blood Sampling and Laboratory methods, described below, are published in Tarof *et al*. (2011) but adapted slightly here for the dissertation. Sampling of recruited offspring of known parentage, survival analyses of extra-pair versus within pair young, and genetic sexing methods are unique to this dissertation.)

Study Area

From May to August 2006-2013 I studied purple martins in north-western Pennsylvania for this thesis research on fitness of extra-pair versus within-pair offspring, but also for collaborative studies on juvenile and adult survival (Stutchbury *et al*. 2009a, Tarof *et al*. 2011), age effects on paternity (Tarof *et al* 2012), and migration ecology (Stutchbury *et al*. 2009b, Fraser *et al*. 2012a, 2012b, 2013). Paternity data were collected 2006-2009 at two primary breeding colonies in north-western Pennsylvania, USA that were 19 km apart (Figure 1). The Troyer colony (41.75° N, -80.28° W) averaged 160 pairs/year and was located on the lawn of a home in a rural setting. The Edinboro colony (41.88° N, -80.12° W) averaged 60 pairs/year and was situated on Edinboro Lake in the small town of Edinboro, Pennsylvania. These colonies were part of a long-term banding and re-sight program led by the Purple Martin Conservation Association, Erie PA. All nest houses had predator guards on the poles to prevent climbing nest predators. Exotic bird species (house sparrows, *Passer domesticus*, and European Starlings, *Sturnus vulgaris*) were controlled at both colonies with trapping, shooting or the use of starling-resistant entrance holes. Nest material was replaced if the ectoparasites (feather mites, blowfly larvae and fleas) became severe; usually once per nesting period and rarely after the young reached the age of 20 days.

For survival analyses, I searched for banded individuals from April-August 2006-2012 by visiting all nesting colonies within 40 km from our primary study sites at least once per season to (Table 1A; Figure 1). The two core colonies were searched at least twice a week from April-July. In late July and August, after breeding, purple martins congregate at a pre-migratory roosting site in the western end of Presque Isle Bay (42.11° N, 80.14° W; Tarof *et al.* 2011). Birds attending the roost are known to come from a large area based on band re-sightings; hatch-

year birds from natal colonies over 100 km away are consistently observed at the roost with a few notable dispersal records of over 300 km (PMK, unpublished data). In the evening hours, up to 1500 purple martins at any one time can be attracted to power lines using recordings of purple martin dawn song (Morton 1988) located in a parking area for Beach 11 at Presque Isle State Park (42.16° N, -80.08° W) approximately 7.4 km from the roost site. Each evening from late July-August 2006-2011, I searched for banded individuals among the birds gathered at Beach 11 for 5-6 nights per week from approximately 6:00 pm through sunset. Including re-sightings of birds at the roost substantially improves estimates of survival, because it increases the probability of observing previously banded birds that are alive but whose breeding site is unknown (Stutchbury *et al.* 2009a).

DNA Sampling: Field Methods

Using telescopes, trained field assistants, colleagues and I read alphanumeric color bands of banded birds, identified social pairings and the nest sites occupied by banded birds. Social pairs were confirmed from observations of nest defense, feeding nestlings or fecal sac removal or capture within a cavity. Age is defined with two age classes: Second Year (SY) are 1 year old (but second calendar year of life), and After-Second-Year (ASY) are ≥2 years old. Age class is determined, along with sex, by distinctive plumage characteristics (Pyle 1997, Hill 2002; Tarof and Brown 2013) and when possible, verified by banding records. Of all social parents included in paternity analyses, we had 100 SY males, 82 SY females and 74 older males (2–9 years old) and 44 older females (2-9 years old) of known age (Table 2). We also had another 105 paired males and 151 females for whom minimum age (but not exact age) was known because

they were first banded as an older individual. Across all years, most (66%) first-year females (n = 72) paired to first-year males, whereas older females (n = 225) frequently (82%) paired with older males rather than with first-year males (Tarof *et al*. 2012).

We checked nest contents approximately every five days to determine first egg-laying date and nesting success (clutch size, number of eggs hatched and young fledged). First-year females laid smaller clutches (4.43 ± 0.10 eggs) than older females (4.92 ± 0.06 eggs; Tarof *et al*. 2012). Across all years, older males paired to older females had earlier first egg dates (31 May, 30.8 ± 0.58 days [day 1 = 1 May]) than if paired to a first-year female (5 June, 34.6 ± 1.60 days) and the same was true for first-year males (7 June, 38.5 ± 0.92 days versus 12 June, 42.1 ± 0.85 days; Tarof *et al*. 2012).

In early July, once most eggs hatched, I caught adults at night using a trap that lowered weighted doors over all cavity entrances of a nest house simultaneously. Traps were set in the afternoon with doors open, and were triggered manually after 11 pm. A team of banders returned before dawn to extract adults from compartments for banding and blood sampling. Additional daytime target trapping at individual nest cavities captured birds not caught at night. We banded adults with a U.S. Geological Survey numbered aluminum band and a colour auxiliary band with a unique alphanumeric code. Mass, tarsus, wing chord and tail length were measured for all adults. We also banded 2830 nestlings at 12–20 days old. We collected 10–50 µL blood samples from adults and nestlings and stored samples at 4 °C in 1 mL of Queen's lysis buffer. Unhatched eggs were collected 7-10 days after their expected hatch date (or when siblings reach 7-10 days of age) and dissected; a tissue sample was collected if present. Liver

tissue was collected from any dead nestlings found in nest boxes in lieu of blood samples. Embryo and tissue samples were stored in 1 mL of TE buffer at -20°C.

Blood samples were obtained from nearly all family groups at the Edinboro colony for 3 years. The Troyer colony was sampled partially in 2006 and nearly completely in 2007 but was not blood-sampled in 2008 due to restrictions (landowner request). Fieldwork and blood sampling were conducted under approval of the York University Animal Care Committee.

Reproductive Success of EP versus WPO Recruits

To assess fitness of extra-pair versus within-pair year young, I searched for the nests of returning birds that had been banded and sampled as nestlings for parentage analysis. The search area included all colonies within 25 km of the core colony sites (>70 colonies) and each colony site was visited at least once per breeding season. Purple martins are an ideal species because they have high natal philopatry, are readily observable and aggregate in colonies allowing me locate recruits. The nesting success of these recruiting birds was monitored through nest checks every 4-5 d. In some cases, nest records were obtained from the owners of colonies where recruits were found. The recruit's mate and offspring were banded and blood sampled in order to perform paternity testing and determine the extra-pair mating success as a component of male reproductive success.

Laboratory Methods for Paternity Analysis

Paternity analysis of all samples was performed by myself and Scott A. Tarof (Tarof *et al*. 2012). We used a panel of four hypervariable microsatellite-flanking polymerase chain reaction

(PCR) primer sets (Table 3; Stanley *et al.* 2011) to determine the frequency of extra-pair

fertilizations and assign parentage to 1235 nestlings based on the social parents of 297 families.

Of the offspring sampled, we only included families with known social parents and for which

both attending parents and their offspring were sampled. In addition to family groups, 12

additional males in the population (whose nest sites were unknown) were genotyped as

putative sires of extra-pair offspring (EPO).

Blood samples were stored at 4 °C in 1 mL of Queen's lysis buffer until DNA extraction

by the ethanol method. Genomic DNA was amplified in 10 μL PCR reactions under the following

conditions: initial denaturation at 94 °C for 3 min; 30 cycles consisting of 1 min at 94 °C, 1 min

annealing (Ta: PUMA 19, 55.8 °C; PUMA 49, 50 °C; PUMA 74, 48.2 °C; PUMA 98, 55 °C), 45 s at

72 °C, followed by a final extension at 72 °C for 5 min. Each tube contained 5.7 μl water (PUMA

49, 4.8 μl; PUMA 19, 5.1 μl), 1.0 μl 10x TSG PCR buffer (Bio Basic, Markham, Ontario), 0.8 μl 25

mM MgCl2 (Fermentas, Burlington, Ontario) (PUMA 19 and PUMA 49, 1.2 μl), 0.4 μl 10 mM

deoxyribonucleotide triphosphates (PUMA 19, 0.6 μL; GE Healthcare, Baie d'Urfe, Quebec), 0.2

μl 10 μM fluorescently labeled Beckman Coulter WellRed forward primer (250 nm, HPLC

purification; Integrated DNA Technologies, Coralville, Iowa), 0.2 μl 10 μM reverse primer, 0.2 μl

5 U/μl TSG DNA Polymerase, 1.5 μl undiluted DNA (212.5 ± 5.2 ng/ml) (PUMA 49, 2.0 μl; PUMA

74, 1.0 μl), and 0.5 μl 100% dimethyl sulfoxide (PUMA 74 only; BioShop, Burlington, Ontario).

Products were visualized on 1% agarose gels stained with 5 μl 5 mg/ml ethidium bromide

(BioShop, Burlington, Ontario) to confirm amplification. This protocol yielded dye-labeled

amplicons for fragment analysis. Genotyping was conducted on the Beckman Coulter CEQ 8000.

We genotyped individuals in 3-locus poolplex reactions containing 1.5 μl PCR product mixture

(4.4 μl PUMA 19, 4.3 μl PUMA 49, 1.3 μl PUMA 98) in 38.5 μl of CEQ cocktail (38 μl 99.5%

deionized formamide [Sigma-Aldrich, St. Louis, Missouri] plus 0.5 μl size standard [Beckman

Coulter, Mississauga, Ontario]). We ran 1.0 μl PUMA 74 PCR product separately in 38.5 μl

formamide plus 0.5 μl size standard. Genotypes were scored against a 400-bp size standard

(600 bp for PUMA 74) with phosphoramidite dye mobility calibration and the ''cubic'' algorithm

model (''quartic'' for PUMA 74). Thirty random adults were genotyped twice at all loci to

confirm repeatability; genotypes were 100% repeatable.

We defined within-pair offspring (WPO) as nestlings that matched the genotypes of

their social parents at all loci genotyped (n = 102 in 2006, n = 404 in 2007, n = 219 in 2008) or

that mismatched with the social father at 1 locus and had low probability of resemblance by

chance alone at the other matching loci (Ibarguchi et al. 2004). If mutation rate is high or if

there are genotyping errors, single-locus mismatches can grossly overestimate extra-pair

paternity. Probability of resemblance (P_{Ra}), the likelihood that 2 particular individuals ($e.g.$,

offspring and social father) share at least 1 allele at a specific locus by chance alone, has high-

resolving power for dealing with single-locus mismatches where genotypes for parents and

offspring are known and microsatellite allele frequencies from the sampled population are

available (Ibarguchi et al. 2004). For family groups containing a single-paternal mismatch, we

calculated P_{Ra} using the formula $P_{Ra} = (2p_a-p_a^2)^2$, for a given allele (a) with allele frequency (p_a),

at each locus other than the mismatching locus. The product of these values generated the

cumulative probability of resemblance (P_{RaCum}) for the matching loci. Social males were

considered to be the genetic sires if P_{RaCum} was ≤0.005 (after Ibarguchi et al. 2004). That is,

offspring with a P_{RaCum} meeting this threshold had less than a 0.5% chance of sharing alleles at

the other loci with the social male by chance (n = 91 in 2006, n = 189 in 2007, n = 31 in 2008) and thus were assigned as WPO (mean P_{RaCum} = 0.0005 ± 0.006). The mutation rate (# per meiotic event) of 1 of the loci, HrU10, among 6 species of swallows ranges from 0.6% to 10.8% and is relatively high for our purple martin population (5.6%, Anmarkrud *et al*. 2011). Allele size explained almost all the variance in mutation rate across species and was relatively large (310 bp) in purple martins, which may explain why there were numerous cases of a single-locus mismatch, even though the other microsatellite loci did match the social father.

We identified potential EPO by evaluating genotypes of each offspring in a family against their social parents. EPO were defined as nestlings that mismatched the social male at ≥2 loci (n = 68 in 2006, n = 130 in 2007, n = 42 in 2008) or that had a P_{RaCum} value 0.005 with 1 paternal mismatch (n = 18 in 2006, n = 21 in 2007, n = 1 in 2008; average P_{RaCum} = 0.076 ± 0.013). Next, we used CERVUS 3.0.3 (Kalinowski *et al.* 2007) to identify candidates for true extra-pair sires. Using genotype data, CERVUS calculates allele frequencies, deviations from Hardy–Weinberg equilibrium, polymorphic information content, null allele frequencies, and exclusion probabilities. A likelihood ratio approach determines true parentage of offspring from the pool of candidate sires by evaluating all offspring-sire genotype combinations (given maternal known genotypes). We used allele frequency data from our population in CERVUS' parentage analysis likelihood simulation to generate paternity assignments for individual EPO based on the following criteria. Both social parents needed to genotype at a minimum of 2 loci to be included in parentage analyses. Cases of putative intraspecific brood parasitism (<4.7%) were excluded. We included the putative social male and all other sampled males each year in a colony to identify the most likely and second most likely candidate extra-pair sires. In

simulations, we used 100,000 permutation cycles, 80% (2006), 95% (2007), and 80% (2008) of

candidate sires in our sampled population, a minimum of 2 loci genotyped per individual, 95.6%

of loci genotyped (from allele frequencies), and 1% genotyping error rate. Determination of the

extra-pair sire for EPO was based on delta scores calculated by CERVUS, defined as the

difference in LOD scores between the most likely and second most likely candidate sire, at

either the 80% (n = 68 EPO) or 95% confidence level (n = 64 EPO). Because we sampled 80–95%

of males per colony, we assumed that unassigned offspring were likely sired by males outside

the colony.

We determined the probability of alleles matching the candidate genetic male by

chance alone based on nonexclusion probabilities calculated by CERVUS. Nonexclusion

probability (1-exclusion probability) was the likelihood of not excluding a candidate male that

was unrelated genetically to an offspring. The mean (±SD) nonexclusion probability for EPO

with both social parents known was 0.017 ± 0.002 (median = 0.007). The average for all

offspring (WPO and EPO) was 0.016 ± 0.001 (median = 0.006). Combined exclusion probability

(PE) with both social parents known was 99.998%.

Offspring sex was determined because sex is known to affect apparent annual survival in

this species (Stutchbury *et al*. 2009a, Tarof *et al*. 2011). We determined sex using PCR after

Fridolfsson and Ellegren (1999). Genomic DNA was amplified in 10 μL PCR reactions under the

following conditions: initial denaturation at 94 °C for 2 min; 30 cycles consisting of 30 s at 94 °C,

30 s annealing at 50 °C, 30 s at 72 °C, followed by a final extension at 72 °C for 5 min. Each tube

contained 2.9 μl water, 1.25 μl 10x TSG PCR buffer (Bio Basic, Markham, Ontario), 4.0 μl 20 mM

MgSO4 (Bio Basic, Markham, Ontario), 0.25 μl 10 mM deoxyribonucleotide triphosphates (GE

Healthcare, Baie d'Urfe, Quebec), 0.25 µl 10 µM 2550 forward primer (Integrated DNA

Technologies, Coralville, Iowa), 0.25 µl 10 µM 2718 reverse primer (Integrated DNA

Technologies, Coralville, Iowa), 0.1 µl 5 U/µl TSG DNA Polymerase, and 1.0 µl undiluted DNA

(212.5 ± 5.2 ng/ml). All plates included a known female sample as a positive control and a

negative control with 1.0 µl of water in place of the undiluted DNA. Products were visualized on

1.5% agarose gels stained with 5 µl 5 mg/ml ethidium bromide (BioShop, Burlington, Ontario)

run for 1 hour at 100 constant volts to confirm amplification. Gels were imaged using an

AlphaImager HP (Alpha Innotech, San Leandro, California). Gels were scored manually; samples

showing one band indicate male, two bands indicate female (all females had a band associated

with the CHD1Z intron). Samples that were unclear were rerun. Samples remaining unclear

after two attempts were omitted from the study.

Survival Analyses

My survival analyses included only known-sex nestlings from mixed broods, those

having at least one extra-pair and one within-pair offspring (n=363 nestlings; Table 1B).

Rigorous tests of the good genes and heterozygosity hypotheses for female benefits of EPFs

requires comparison of the fitness of extra-pair and within-pair offspring only from mixed

broods, those having at least one extra-pair and one within-pair offspring (Sardell *et al*. 2011).

This controls for possible maternal effects on offspring fitness, which is especially important for

purple martins because of assortative mating by age (Tarof *et al*. 2012). Furthermore, female

age class affects timing of breeding, clutch size, and the likelihood of females producing extra-

pair offspring (Morton and Derrickson 1990, Tarof *et al*. 2012). The oldest birds arrive to the

colony first, initiate nests earlier and these earlier nests with older parents have fewer extra-pair offspring than the later nests of first year females (Morton *et al*. 1990; Wagner *et al*. 1996, Tarof *et al*. 2012).

I estimated apparent annual survival probabilities using the Program MARK, version 7.1 (White and Burnham 1999, Cooch and White 2008). Program MARK uses maximum likelihood estimation on covariates to impose linear constraints on survival estimates. The first step determining the global model is to determine the best-fit parameters for resighting probability ("p"). This refers to the probability that a bird will be sighted, given that it is known to be alive. It is calculated using at minimum three years of data and estimates probability of seeing birds in year two given that they were subsequently resighted in a future year. To determine my the survival terms of my global model, I compared models with full interactions between age class and time in both survival and encounter probability with additive models that have fewer parameters (Table 4). The model with the best fit allowed survival of young to vary with their age class (juvenile, SY, ASY) and their resighting probability to vary with sex and year (Phi(offspringAgeClass) p(offspringSex+t)); this model fit the data approximately ten times better than the next best basic model.

Using my starting global model Phi(offspringAgeClass) p(offspringSex+t), I constructed an *a priori* set of 14 candidate models to examine the influence of various covariates on apparent juvenile annual survival. All covariates were allowed interact with all age classes. The variables MomMinAge and DadMinAge are the social mother's and social father's minimum known ages, respectively. Hatch date and the number fledged from each offspring's nest were modelled as well because they have been shown to influence offspring survival in this species

(Tarof *et al*. 2011). The hatch dates were available for more nests than was clutch initiation date and they are collinear; incubation periods are extremely consistent in this species (15 days starting from the laying of the penultimate egg; Hill 1999). Offspring sex was included because previous studies have found it important in explaining offspring survival (Sardell *et al*. 2011). Additionally sex explained some variation in adult survival in purple martins (Stutchbury *et al.* 2009a). Parentage was included to address the core predictions of this study. The proportion of extra-pair offspring (PropEPO) was also included in some models since it may reflect the social mother's assessment of the social father and thus have impacts on her egg allocation and parental care.

A priori models were ranked and compared using ΔAIC_c and AIC_c weights (w_i) to compare models (Akaike 1973, Lebreton et al. 1992, Burnham and Anderson 2002). I 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 among 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 $\Delta AICc \leq 2$ were considered equally supported. Maximum-likelihood estimates of apparent survival (ϕ) and encounter probabilities (p) were calculated for models with high AICc weighting.

Statistical Analysis of Reproductive Success of Recruited Offspring of Known Parentage

To explore factors influencing variation in four different parameters of reproductive success of recruited offspring of known parentage (clutch initiation date, clutch size, number of young fledged and fledging success), I fit general linear models with f_1.year,

natal.social.father.min.age, natal.social.mother.min.age, natal.parentage, natal.cid and

natal.fledged as factors using data for all SY-aged f_1 recruits (sexes combined) . In addition to

these factors, the models exploring f_1.prop.EPO, f_1.eggs, f_1.success.rate and f_1.cid also included

f_1.mates.min.age because older individuals are known to have higher reproductive success (Lee

1967, Morton *et al* 1990, Wagner *et al.* 1996, Tarof *et al*. 2012). The model exploring

f_1.prop.EPO included f_1.cid since nests initiated earlier in the season have fewer EPO (Morton

and Derrickson 1990, Wagner *et al.* 1996, Tarof *et al*. 2012).

      Because of the different motivations for each sex, models testing the social and genetic

mating success of first-year breeders were run on males and females separately. I tested

models exploring variation in the minimum known ages of f_1 mates as a measure of social

mating success. To test the genetic mating success, models explored the variation in proportion

of extra-pair offspring in f_1 nests and the number of within-pair and extra-pair offspring.

      I used functions in R that use a backwards step procedure (''step'' function; R

Development Core Team 2011) to drop individual explanatory variables one by one, refitting

the model each time, and then used Akaike's Information Criterion (AIC; Akaike 1973, Burnham

and Anderson 2002) to measure model fit and complexity to select the optimal model (Zurr *et*

al. 2009).

RESULTS

Patterns of extra-pair paternity

      DNA samples for 2348 individuals comprising 325 complete family sets were collected

from 2006-2009. Due to severe nestling mortality caused by a weather-related food shortage,

the 2009 samples were excluded leaving a total of 297 complete family groups genotyped. Of

those, 137 broods (46%) contained at least one EPO and 273 of 1235 offspring (22%) were

extra-pair (Tarof *et al.* 2012). Among nests with EPO, the proportion of EPO per brood averaged

0.53 ± 0.03 (Tarof *et al.* 2012). Overall extra-pair paternity rates in my study population by

social father age class were 16.7% of nestlings for ASY males and 33.4% for SY males (Tarof *et

al.* 2012), and is consistent with a population of purple martins in Maryland (4% for ASY and

57% for SY males; Wagner *et al.* 1996).

Annual Survival of EP versus WP Young

Survival analyses were done on 363 known-sex young from mixed broods (*i.e.*, broods

with at least one EPO and one WPO). Resighting probability was modeled with a time effect and

accounted for the sex of the offspring. Search effort varied across years and females are more

difficult to resight than males because they spend more time inside the nesting cavity. Based on

the starting model, phi(AgeClass) p(Sex+t) (see Table 4), resighting probability ranged from

0.36±0.03 for females and 0.72±0.13 for males (Figure 2). Resighting probability declined over

time for both sexes (Figure 2).

Extra-pair offspring did not survive better than within-pair offspring (Table 5). This can

be seen by comparing models that are identical except for the inclusion of parentage (*e.g.*,

models 1 and 3; 10 and 12). If parentage (WP vs EP) of an individual predicts subsequent

survival, then models that include parentage should have a higher ΔAIC_c. However, the models

with parentage had slightly lower AIC_c weighting and did not differ meaningfully in ΔAIC_c scores

(*i.e.*, ΔAIC_c differed by less than 2) than models without parentage. Based on the third best-

fitting model that included parentage, p(AgeClass+MomMinAge+DadMinAge+Sex+Parentage) phi(Sex+t), parentage status did not affect apparent survival estimates, even when controlling for the age and sex of offspring (Figure 3). Apparent survival probability in the first year of life was not higher for young that were the result of extra-pair fertilizations (WP = 0.22 ± 0.041 SE, EP = 0.17 ± 0.040 SE). This was also true for both males (WP = 0.38 ± 0.061 SE, EP = 0.31 ± 0.064 SE) and females (WP= 0.13 ± 0.039 SE, EP=0.10 ± 0.033 SE). Apparent survival probability was far higher in the second year of life for both sexes but EPO did not differ from WPO. Note that the variance of these second year estimates is higher owing to the fact that sample sizes decrease over time due to mortality within cohorts.

Models that include offspring sex explained the re-sighting data far better than the same models without that variable (Table 5). Models 1 and 5 differ only by the inclusion of offspring sex yet model 1 fits over 100 times better than model 5. Model 7 fits the data 43 times better than model 10. Based on the best-fitting model, males had a higher apparent survival probability in their first year than females (females: 0.12±0.03; males: 0.35±0.05; Figure 3).

Survival of young could also be influenced by maternal effects, in that young raised by first-time breeders may be disadvantaged compared to those produced by older females and raised by experienced parents. Models without MomMinAge had no support (*i.e.*, AICc Weights > 0.001; Table 5). For the first year of life, the apparent survival probability for offspring with one year-old mothers was estimated at 0.09±0.03 while the offspring of six year-old mothers was 0.86±0.10 (Figure 4A). This pattern persists in the second year of life however small sample sizes yielded very large 95% confidence intervals (Figure 4B). This maternal effect suggests that

one year-old (SY) birds should prioritize survival over reproduction and may explain why SY

martins arrive in spring 4-6 weeks after ASY birds (Allen and Nice 1952, Morton and Derrickson

1990).

The minimum known age of the social father also appears to improve model fit but only

when modeled with mother's minimum age. Model fit was improved with DadMinAge by a

factor of 8.9 (models 1 and 4) and a factor of 3.2 (models 5 and 6). Comparing models 7 and 8,

which do not include MomMinAge, the model with DadMinAge has a lower weighting but the

ΔAIC_c values indicate the models are not meaningfully different. In contrast with mother age,

the age of the social father has an inverse relationship; apparent survival decreased with father

age (Figure 4C-D).

The variables hatch date and brood size had very poor explanative power for survival

probability. Both hatch date and brood size lowered model fit slightly but the models did not

differ meaningfully from the starting model (Table 5).

Reproductive Success of EP vs WP Young as First-year Breeders

Nesting success was determined for 79 nests belonging to known-parentage offspring

that returned to the study area to breed (f_1 birds), from 2007-2009. Over all years, 40 of these

79 nests belonging to f_1 parents were fully sampled to assess rates of extra-pair paternity

among their own offspring (*i.e.*, f_2 offspring). Most (65 of 79; 88%) recruits were first discovered

breeding as one-year olds with 39 of these nests belonged to f_1 males and 26 to f_1 females

(Table 6). Due to limited sample sizes (n =14), f_1s that were first found nesting at 2 years of age

or older were omitted from subsequent analyses. Furthermore, 11 birds (8 males and 3

females) had their nests sampled in two different years with one male sampled in a third year but these ASY nests were removed to avoid pseudoreplication;

The prediction that females benefit from extra-pair fertilizations by producing offspring that have higher reproductive success was tested using general linear models first on all SY birds (sexes combined). I tested four measures of f_1 reproductive success: clutch initiation date, clutch size, the number of young fledged and fledging success (defined as the number of young fledged divided by the clutch size). To address the predictions of female benefits, the models included natal parentage (EPO vs WPO) and proportion of extra-pair young in the natal nest as predictor variables. Additional variables included f_1 sex, natal clutch initiation date, year, the minimum ages of the social parents and the f_1 mate's minimum age.

An indirect measure of reproductive success is timing of nesting, since this in turn affects key measures of nesting success (Price *et al.* 1988), rates of extra-pair paternity (Morton and Derrickson 1990) and offspring survival (Tarof *et al.* 2011). The best fitting model exploring variation in f_1 clutch initiation dates was significant (Table 7A; $r^2_{Adjusted} = 0.248$, $F_{5,51} = 4.694$, $p = 0.001$). Natal Parentage was included in the best fit model but was not significant (Figure 5A; $t = 1.17$, $p = 0.25$). A strong year effect is present with clutch initiations becoming later over time (model estimate = 3.1934 ± 0.9036, t = 3.534, p = 0.0009).

The best fit model for f_1 clutch sizes explained 34% of the variation in clutch size and was significant (Table 7B). There was a strong year effect for clutch size and later clutch initiation date was associated with smaller clutch size, as expected. Natal parentage was not an important predictor (Figure 5B). Mothers with a higher proportion of extra-pair offspring produced offspring that, when recruited as breeders, had fewer (not more) eggs in their own

nests than the recruits whose mothers had a lower proportion of extra-pair offspring (Table 7B; estimate = -0.099 ± 0.036, t = -2.730, p = 0.009).

Total number of young fledged by f_1 parents was well explained by the best fitting model (Table 7C; $r^2_{Adjusted}$ = 0.4069, $F_{7,49}$ = 6.489, p < 0.0001) with the number of eggs not surprisingly explaining most of the variation in the number of young fledged (t = 5.56, p < 0.0001). Natal parentage of f_1s was included in the best-fit model but was not significant (Figure 5C; t = 1.241, p = 0.22).

Variation in overall fledging success (the number of fledged young divided by the number eggs laid) in f_1 nests was not well explained by the models (Table 7D; $r^2_{Adjusted}$ = 0.051, $F_{5,51}$ = 1.598, p = 0.18). The best fit model included natal parentage but this was not significant (Figure 5D). Year was a significant predictor (t = -2.201, p = 0.032) and in 2009, a weather-related food shortage that caused high nestling mortality (Figure 6).

Social Mating Success of EP vs WP Young as First-year Breeders

One measure of mating success of f_1 birds is the age of their social mate, because this species shows a strong pattern of assortative mating by age class (Wagner *et al.* 1996, Tarof *et al.* 2012), older birds have more eggs in their nests (Allen and Nice 1952, Lee 1967, Finlay 1971, Brown 1978a, Eads 2001, Tarof *et al*. 2012) and older birds initiate nests earlier in the season (Morton and Derrickson 1990, Tarof *et al.* 2012). If a younger male is able to attract an older female, he stands to fledge more offspring than if he had attracted a younger mate. The same applies to females.

Models assessing the ages of f_1 mates were run on males and females separately as I expected the factors relating to mate acquisition would be different for each sex (Table 8). Predictor variables included natal parentage and proportion of extra-pair offspring in f_1's natal nests to assess potential benefits to the mothers of f_1 breeders. Additional variables included year of f_1 nesting attempt, the parents' minimum ages, natal hatch date and natal brood size. For male f_1s, the best fitting model included year of nesting attempt, mother min age and natal hatch date ($r^2_{Adjusted}$ = 0.307, $F_{4,24}$ = 4.101, p = 0.011). F1 males that had had older mothers were more likely to themselves pair with an older female in their first year of breeding. The model failed to explain the variation in f_1 mate's age for females ($r^2_{Adjusted}$ = 0.1964, $F_{3,14}$ = 2.385, p = 0.11). However, the top fitting models for both sexes did not include natal parentage indicating that EP young are not more likely to attract older mates when they begin breeding. Similarly, the proportion of extra-pair young in an f_1's natal nest did not explain variation in f_1 mate's ages the following year.

Genetic Mating Success of EP vs WP Young as First-year Breeders

Females who engage in extra-pair copulations may derive a fitness benefit if their male extra-pair offspring in turn sire more of the offspring in their nests (*i.e.*, are cuckolded less) when they breed for the first time. For both f_1 males and f_1 females, the best fit models were significant (Table 9; male: $r^2_{Adjusted}$ = 0.4601, $F_{3,17}$ = 6.682, p = 0.004; female: $r^2_{Adjusted}$ = 0.5593, $F_{5,7}$ = 4.045, p = 0.048). Natal parentage was not included in the best fit model for males and was not significant for females (t = 1.686, p = 0.14). No difference was found between within-pair and extra-pair f_1s in the proportion of extra-pair offspring in their own nests (Figure 7; t-

test: t = -1.253, df = 12.739, p = 0.23). For males, the clutch initiation dates of the f_1 nesting attempt and the f_1's mother's minimum age best explained the variation in proportion of young that are extra-pair (Table 9). For female f_1s, natal clutch initiation dates, the number fledged from the f_1's natal nest and the f_1's own clutch initiation dates best explained proportion extra-pair (Table 9). F_1s that nested later in the season had proportionately fewer EPO than earlier-nesting f_1s (Figure 8; model estimate -0.04318 ± 0.01099 SE, t = -3.929, p = 0.0005).

Models exploring variation in the number of within-pair and extra-pair offspring in f_1 nests were run on males and females separately as each sex has different motivations for extra-pair mating. All models included natal parentage of f_1s and the proportion of extra-pair offspring in the f_1's natal nest to test for potential benefits extra-mating behavior for the f_0 mothers. Additional variables included year, f_1 mates' minimum known age, clutch initiation date, the minimum known ages of f_0 parents and the clutch initiation date and the number fledged from the f_1's natal nest. Neither of the models for within-pair young and extra-pair young for male f_1s were significant. However, both of the models were highly significant for the females with most of the included variables also significant. For SY-Females, the proportion of extra-pair young in the natal nest was significant within both models and the estimates suggest that a heritability of pursuit of extra-pair mating behavior (Table 10; WPO: estimate = -4.724 ± 1.312 SE, t = -3.60, p = 0.011; EPO: estimate = 3.8147 ± 0.713 SE, t = 5.347, p = 0.006). This relationship was not strong for females (Figure 9; $r^2_{adjusted}$ = 0.1334, $F_{1,12}$ = 3.001, p = 0.11). For both sexes, natal parentage was not included in either of the best fitting models.

DISCUSSION

This is the first study to assess fitness benefits of extra-pair mating to females in a long-distance Neotropical migratory songbird. Contrary to the predictions of genetics benefits hypotheses (*i.e.*, the good genes hypothesis and heterozygosity theory), female purple martins do not appear to be benefitting from extra-pair mating through the improved survival or reproductive success of their extra-pair offspring. Only five other studies, all on resident species, have tested for differences in annual survival or recruitment rates between EPO and WPO and none found significant differences (see Sardell *et al.* 2011, Gerlach *et al.* 2012). With relatively high rates of extra-pair paternity in long-distance migrants, and the greater survival challenges for their offspring, one would expect that fitness benefits would be more evident for migrants than for residents. However, my survival analysis showed no differences in offspring annual survival between within and extra-pair offspring among mixed-broods, even though mortality rates for this species are highest during the first year of life (Tarof *et al*. 2011). Davidar and Morton (1993) argued that purple martins are under intense selection from haemosporidian infections during their first year. Benefits from both good genes and heterozygosity could equip offspring to better survive in face of disease. However, the similar survival probabilities for EPO and WPO, even when controlling for sex and using only mixed broods, provides a strong test that found no support for either hypothesis. Gerlach *et al*. (2012) found that dark-eyed juncos (*Junco hyemalis*) that were EP lived longer than WP individuals. Extra-pair offspring in purple martins may have longer lifespans than within-pair offspring (*i.e.*, enjoy higher survival as adults), but this was not the case for survival from one-year-old to two-years old (Figure 3A). To obtain statistical power to test for differences in survival among the

older age classes (two years of age and older), using only mixed broods, would require a unrealistically large starting sample of nestlings that had been sampled for paternity and happened to come from mixed broods. Cohort attrition due to annual mortality means that only a small proportion of birds survive from their natal year to at least two years of age (*e.g.*, Table 1B).

Dark-eyed juncos (*Junco hyemalis*), who are short distance migrants or even residents, also show higher lifetime reproductive success for EP than WP individuals (Gerlach *et al*. 2012). For migratory species, it is a particular challenge to find the nests of birds that have recruited to their natal region. In this study I sampled about 1,200 nestlings but from these "only" 65 were located as one-year-old breeders throughout the study area. Nevertheless this provides the first study to examine the reproductive fitness of EPO vs WPO in a long-distance migrant species. Among the offspring of known parentage that returned to breed themselves (f_1 birds), there were no differences between EPO and WPO birds in various reproductive success, social mating success or genetic mating success parameters. The predictors of first-year reproductive success were more closely related to environmental variables (year, clutch initiation date). As aerial insectivores, purple martins are highly sensitive to local temperature and rainfall which influences both timing of breeding and nestling survival through food availability. Thus the parentage (EPO vs WPO) of a bird has little influence on its future reproductive success. For instance, in one year of this study (2009) there was 90% nestling mortality due to a period of high rainfall in early July. This suggests that evolutionary benefits of extra-pair mating to females are not derived through improved reproductive output of extra-pair offspring.

In the absence of clear genetic-based benefits of extra-pair mating in this species, it stands to reason that female purple martins are either deriving fitness benefits in more subtle ways than those tested here or they do not benefit from extra-pair mating at all (*i.e.*, EPC is male-driven). Extra-pair mating has clear fitness benefits for males successful in obtaining them (Griffith *et al*. 2002). Forced extra-pair copulations are well documented in this species (Brown 1978b, Morton 1987, Morton *et al*. 1990), but Wagner *et al*. (1996) argued that females solicit extra-pair copulations based on observations of mate guarding by males. It is notable that female-solicited and within-pair copulations are rarely observed in purple martins, unlike many other songbirds. Pairs do not copulate inside, or near, their nest cavity (Tarof *et al*. 2012, JR Hill unpublished data) and so it is presumed that copulations take place while airborne, perhaps during or immediately after so-called sexual chases (Brown 1978b, Wagner *et al*. 1996, ES Morton, personal communication). The only copulations that are readily observable are when females land on the ground to gather nest material; in this instance females can be forcibly mounted by males other than their mate (Brown 1978b, Morton *et al*. 1990). Whether or not this also occurs while airborne, females may have less choice as to whether their offspring are sired by their social mate or some other male. If extra-pair copulations are forced onto females, there are likely costs to the female relating to evasion of forced copulations such as the risk of injury while struggling to break free. Females may therefore accept EPCs to avoid paying these costs (Morton *et al*. 1990) especially since there appear to be no fitness costs to young (this study). Or, females may be unable to prevent EPCs from occurring in the first place if evasion tactics are ineffective. The lack of female benefits shown here suggests a male-driven system in

this species with no apparent benefits to females in terms of the survival or reproductive success of offspring.

Female purple martins may benefit in other ways and alternate hypotheses should be considered. Females may pursue extra-pair copulations for fertility insurance (Sheldon 1994). However, only 26 of 313 nests (8.3%) had 100% EPO so the frequency of complete infertility in social males must be less than this. Another question is whether females who produce EPO bias the sex ratio of their nestlings toward males. Sex ratios appear to be slightly biased toward female (483:558) however this ratio did not differ between EPO and WPO (The sex ratio among EPO was 106:147 and among WPO was 377:411; $\chi^2_{4, 1041}$ = 2.7219, p = 0.099). There is no evidence that females are controlling the sex ratio in the context of extra-pair mating.

Females may also be bet hedging (Yasui 1998, Kempanaers and Schlicht 2010) which can be adaptive in unpredictable environments. Mixed broods should offspring of varying genetic quality whereas broods sired by one male will have minimal variation in genetic quality (Kempanaers and Schlicht 2010). This mating strategy would be beneficial if females were unable to assess the genetic composition of potential mates. Extra-pair mating should enhance the genetic variation in populations that express this behavior and leave them better able to adapt to environmental changes (*e.g.*, global climate change).

The genetic benefits of extra-pair mating may be context-dependent (Schmoll *et al.* 2011) and thus detectable only through long term (> 10 year) studies. Benefits may only be realized under specific environmental situations such as increased selection pressure from inclement weather, disease outbreaks or increased competition for mates. Obligate aerial insectivores such as the purple martin may face starvation during prolonged rainy periods in

the breeding season lasting longer than three to five days (Allen and Nice 1952). Genetic

benefits of extra-pair mating may only be apparent during times of physiological stress. For

aerial insectivores the environmental influence on reproductive success appears to be far

stronger than the genetic (this study) such that EPO offspring are not more likely to have higher

reproductive success.

Benefits of extra-pair paternity to offspring survival may also be context-dependent.

When it comes to survival, it is thought that most annual mortality of migrants occurs during

the trip to, and from, the wintering grounds (Sillett and Holmes 2002). Juvenile survival of

purple martins from fledging to migration departure is high (φ_r = 0.87) with 81% of first year

mortality occurring after the onset of fall migration (Tarof et al. 2011). Migration tracking of

adult purple martins has revealed extensive detail on migration routes and timing and has

identified the highly forested regions of northwestern Brazil as the core over-wintering region

for this subspecies (Stutchbury et $al.$ 2009b, Fraser et $al.$ 2012a, 2012b, 2013), a region where

forest cover has remained stable for centuries. However, limitations in tracking technology do

not yet allow one to detect mortality during migration, where this occurs, or what

environmental factors might influence migration-related mortality. There is high annual

variation in both juvenile and adult survival but it is not known what drives this, or if extra-pair

paternity could influence survival in difficult years. Another alternative is that EPO may no

longer have survival advantages on migration due recent ecological changes along the route

that influence survival. For example, anthropogenic habitat loss in Yucatan Peninsula, a known

key stopover area for this species, is extensive (Fraser et al. 2013). There are no field studies on

purple martin body condition or survival in disturbed versus undisturbed tropical regions and

our understanding of the non-breeding ecology of this species is very limited.

Another possibility is that semi-domestication on the breeding grounds may have

removed the species from the natural selection context in which extra-pair mating behavior

evolved making it difficult to detect fitness benefits to females even if they once existed. Birds

may be genetically constrained to express extra-pair mating behavior even if this behavior is no

longer beneficial (Forstmeier *et al*. 2014). Purple martins east of the Rocky Mountains nest

exclusively in man-made housing and have done so for at least a century (Allen and Nice 1952,

Stutchbury 1991). Purple martin nests are managed extensively often with ectoparasites and

predators controlled or deterred. As recently as 300 years ago, the environmental

circumstances on the breeding grounds were much different for purple martins, notably the

vast primary, deciduous forests and no competition for cavities from invasive house sparrows

(*Passer domesticus*) and European starlings (*Sturnus vulgaris*). Before humans provided nesting

sites for purple martins, they were limited to natural cavities (*i.e.*, abandoned woodpecker

cavities or rock crevices) which would have been 1) far less numerous than martins enjoy today

and 2) far more dispersed compared to modern purple martin housing. Western populations of

purple martins that still nest in natural cavities form loosely aggregated exploded colonies and

martins were not observed nesting closer than 100 meters apart (Stutchbury 1991). Of most

importance, the great concentrations of nesting cavities found in modern martin colonies far

exceeds what would have been available their evolutionary past (Morton *et al*. 1990) and likely

alters competition for mates and nest sites. Based on records dating back to the 1880's through

today, martins appear to be arriving progressively earlier (Rohwer and Niles 1979, Zelt *et al*.

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2012; Arab and Courter 2014), possibly in response to climate change (Zelt *et al*. 2012). It is possible that selection pressures promoting extra-pair mating by females are now either relaxed or totally absent. Future work on benefits of extra-pair mating for female purple martins should sample western subspecies, especially those still nesting in natural contexts (*e.g.*, *P.s. hesperia* and *P. s. arboricola*). Severe anthropogenic impacts have been in place for decades, to the extent that humans may now be the world's greatest evolutionary force (Palumbi 2001). This may explain why so many other studies on female benefits of extra-pair mating have also failed to show any benefit (Dunn *et al*. 2009, Sardell *et al.* 2011).

TABLES AND FIGURES

Table 1: Count data by cohort and year of resightings for all resightings of A) all nestlings of known parentage from years 2006-2008 and B) all nestlings of known sex from mixed broods only. Initial sample sizes for each cohort are indicated by an asterisk.

A) All offspring of known parentage:

		Year of observation							
		2006	2007	2008	2009	2010	2011	2012	2013
Cohort	**2006**	268*	41	17	9	4	0	0	0
	2007	-	711*	78	33	30	9	0	0
	2008	-	-	256*	26	11	3	1	0

B) Only offspring from mixed-broods and with known parentage and sex.

		Year of observation							
		2006	2007	2008	2009	2010	2011	2012	2013
Cohort	**2006**	85*	16	10	7	4	0	0	0
	2007	-	226*	29	9	10	2	0	0
	2008	-	-	52*	6	2	2	0	0

Table 2: Sample sizes of social parents showing both known age birds (actual age is known because bird was first sampled as a nestling or one-year-old breeder) and additional minimum aged birds (age at first banding unknown).

Age	Males		Females	
	Known	Minimum	Known	Minimum
1	100	n/a	82	n/a
2	48	99	28	140
3	7	3	1	9
4	11	1	6	1
5	2	0	1	0
6	2	2	4	1
7	1	0	1	0
8	2	0	0	0
9	1	0	3	0

Table 3: Characterization of the four microsatellite loci used in parentage analysis. This analysis was done with CERVUS 3.0.3. using data from 2007. k=number of alleles, N=number of genotyped individuals, H_{Obs}=observed heterozygosity, H_{Exp}=expected heterozygosity, PIC=polymorphic information content, NE=non-exclusion probability given the genotypes of the nestling and the mother, HW=Hardy-Weinberg equilibrium test, f_{null}=null allele frequency estimate. Combined exclusion probability (PE) with both social parents known was 99.998%. This characterization of microsatellite loci is based on the 2007 cohort of offspring. For the Hardy-Wienberg equilibrium tests, "ND" indicates that the test was unable to be performed by CERVUS.

Locus	k	N	H_{Obs}	H_{Exp}	PIC	NE	HW	f_{Null}
PUMA19	13	1187	0.58	0.86	0.844	0.28	ND	0.1991
PUMA49	5	1187	0.278	0.377	0.343	0.805	ND	0.1416
PUMA98	26	1197	0.846	0.88	0.87	0.234	***	0.0178
PUMA74	152	1131	0.94	0.979	0.978	0.044	ND	0.0202

Table 4: Determing the best-fit basic model from which to build covariate models. The basic

model used in subsequent analysis was Phi(AgeClass) p(Sex+t), Model #1.

Rank	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1	Phi(AgeClass) p(Sex+t)	580.697	0.000	0.502	1.000	9	562.294
2	Phi(AgeClass+t) p(AgeClass+Sex)	581.847	1.149	0.282	0.563	7	567.597
3	Phi(AgeClass+t) p(AgeClass*Sex)	583.919	3.222	0.100	0.200	8	567.597
4	Phi(AgeClass) p(AgeClass+Sex+t)	584.651	3.954	0.069	0.139	11	562.057
5	Phi(AgeClass) p(Sex*t)	586.998	6.301	0.021	0.043	12	562.294
6	Phi(AgeClass+t) p(Sex+t)	588.508	7.811	0.010	0.020	13	561.685
7	Phi(AgeClass) p(AgeClass+Sex*t)	589.774	9.077	0.005	0.011	14	560.822
8	Phi(AgeClass*t) p(Sex+t)	590.547	9.849	0.004	0.007	14	561.594
9	Phi(AgeClass) p(t)	590.600	9.903	0.004	0.007	8	574.278
10	Phi(AgeClass) p(AgeClass)	592.101	11.403	0.002	0.003	6	579.913
11	Phi(AgeClass) p(AgeClass+t)	595.208	14.510	0.000	0.001	10	574.713
12	Phi(t) p(t)	597.197	16.500	0.000	0.000	20	555.266
13	Phi(AgeClass+t) p(AgeClass)	597.938	17.241	0.000	0.000	10	577.444
14	Phi(AgeClass*t) p(t)	598.441	17.744	0.000	0.000	12	573.737
15	Phi(AgeClass) p(AgeClass*t)	598.654	17.957	0.000	0.000	13	571.831

Table 5: Model rankings from Program MARK. The starting model Phi(offspringAge) p(offspringAge+t) is shaded (model #10). All models have the same terms for resighting probability: p(offspringSex+t). Explainations variables included in models: MomMinAge and DadMinAge are the social parents' minimum known ages; Sex is the sex of the offspring; Parentage is the parentage category of the offspring: extra-pair or within-pair; HatchDate is the date that each offspring hatched; Fledged is the total number of young fledged from the nest of each offspring; PropEPO is the proportion of extra-pair in each offspring's nest.

Rank	Model All models include p(sex+t)	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1	Phi(AgeClass+MomMinAge+ DadMinAge+Sex)	552.674	0.000	0.398	1.000	12	527.970
2	Phi(AgeClass+MomMinAge+ DadMinAge+Sex+PropEPO)	553.274	0.600	0.295	0.741	13	526.450
3	Phi(AgeClass+MomMinAge+ DadMinAge+Sex+Parentage)	553.538	0.860	0.258	0.649	13	526.715
4	Phi(AgeClass+MomMinAge+Sex)	557.049	4.370	0.045	0.112	11	534.454
5	Phi(AgeClass+MomMinAge+ DadMinAge)	562.207	9.530	0.003	0.009	11	539.613
6	Phi(AgeClass+MomMinAge)	564.499	11.820	0.001	0.003	10	544.004
7	Phi(AgeClass+Sex)	572.492	19.820	0.000	0.000	10	551.997
8	Phi(AgeClass+DadMinAge+Sex)	574.591	21.920	0.000	0.000	11	551.997
9	Phi(AgeClass+PropEPO)	578.057	25.380	0.000	0.000	10	557.563
10	**Phi(AgeClass)**	**580.697**	**28.020**	**0.000**	**0.000**	**9**	**562.294**

11	Phi(AgeClass+Fledged)	581.689	29.010	0.000	0.000	10	561.194
12	Phi(AgeClass+Parentage)	582.175	29.500	0.000	0.000	10	561.681
13	Phi(AgeClass+HatchDate)	582.702	30.030	0.000	0.000	10	562.208
14	Phi(AgeClass+DadMinAge)	582.743	30.070	0.000	0.000	10	562.249

Table 6: Sample sizes of all second-year f_1s of known parentage that recruited into the breeding population and whose nesting location was known. Sample sizes show breeding attempts for which their mates and the offspring (f_2) were also sampled for parentage analysis. Samples sizes given in parentheses are all f_1 nests for which nesting data are available, regardless of whether the family was sampled for genetic parentage testing. Year is the year in which f1s recruited as breeders (*i.e.*, one year after their natal year).

	2007		2008		2009		Overall	
	EPO	WPO	EPO	WPO	EPO	WPO	EPO	WPO
SY-M	3 (3)	7 (9)	2 (5)	6 (17)	0 (0)	2 (5)	5 (8)	15 (31)
SY-F	3 (3)	3 (4)	1 (3)	7 (15)	0 (0)	0 (1)	4 (6)	10 (20)
All SY	6 (6)	10 (13)	3 (8)	13 (32)	0 (0)	2 (6)	9 (14)	25 (51)

Table 7: Linear model results exploring variation of four reproductive success parameters among all f1 birds that recruited into the breeding population as 1 year olds (sexes combined): A) clutch initiation date (CID), B) clutch sizes, C) the total young fledged and D) fledging success.

A) clutch initiation dates ($r^2_{Adjusted}$ = 0.248, $F_{5,51}$ = 4.694, p = 0.0013):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-6371.9937	1814.3806	-3.512	0.000941 ***
natal.parentage	1.3353	1.1412	1.170	0.247418
f_1.sex	1.7375	0.9880	1.759	0.084644 .
f_1.year	3.1934	0.9036	3.534	0.000880 ***
f_1.mates.min.age	-0.7937	0.8426	-0.942	0.350633
natal.social.mother.min.age	-0.6254	0.3863	-1.619	0.111636

B) clutch sizes ($r^2_{Adjusted}$ = 0.3412, $F_{5,52}$ = 6.904, p = 0.0001):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-1.336e+03	5.000e+02	-2.672	0.01005 *
f_1.year	6.696e-01	2.493e-01	2.686	0.00969 **
f_1.cid	-1.178e-01	3.368e-02	-3.498	0.00097 ***
f_1.mates.min.age	1.998e-01	2.111e-01	0.946	0.34832
natal.social.mother.min.age	1.646e-01	9.701e-02	1.697	0.09561 .
natal.prop.EPO	-9.927e-01	3.636e-01	-2.730	0.00863 **

C) Number fledged ($r^2_{Adjusted}$ = 0.4069, $F_{7,49}$ = 6.489, p = 0.00002):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	950.8359	540.4390	1.759	0.0848 .
f1.sex	-0.4180	0.3094	-1.351	0.1830
f1.eggs	0.8143	0.1464	5.560	1.1e-06 ***
f1.year	-0.4735	0.2693	-1.758	0.0850 .
f1.mates.min.age	0.2450	0.2560	0.957	0.3432
natal.parentage	0.4821	0.3884	1.241	0.2204
natal.fledged	0.5881	0.2390	2.461	0.0174 *
natal.success.rate	-3.7536	1.5112	-2.484	0.0165 *

D) Fledging success ($r^2_{Adjusted}$ = 0.05069, $F_{5,51}$ = 1.598, p = 0.1775):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	327.063797	148.222216	2.207	0.0319 *
natal.parentage	0.078199	0.091506	0.855	0.3968
f_1.year	-0.162407	0.073800	-2.201	0.0323 *
f_1.mates.min.age	0.102836	0.068619	1.499	0.1401
natal.social.mother.min.age	-0.039666	0.031739	-1.250	0.2171
natal.cid	-0.010285	0.005566	-1.848	0.0704 .

Table 8: Results from linear models exploring variation in the minimum age of the mates of f_1 birds that recruited as 1-year olds, which is an indicator of social pairing success. The model was run independently on each sex.

Males only ($r^2_{Adjusted}$ = 0.307, $F_{4,24}$ = 4.101, p = 0.0113):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-1.097e+03	4.289e+02	-2.557	0.0173 *
f_1.year	5.461e-01	2.135e-01	2.557	0.0173 *
natal.social.father.min.age	-1.499e-01	8.139e-02	-1.841	0.0780 .
natal.social.mother.min.age	2.209e-01	8.143e-02	2.713	0.0121 *
natal.hd	3.192e-02	1.414e-02	2.258	0.0333 *

Females only ($r^2_{Adjusted}$ = 0.1964, $F_{3,14}$ = 2.385, p = 0.113):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-1.977e+03	9.453e+02	-2.091	0.0552 .
f_1.year	9.847e-01	4.703e-01	2.094	0.0550 .
natal.hd	5.623e-02	3.003e-02	1.873	0.0821 .
natal.fledged	-3.845e-01	1.941e-01	-1.981	0.0676 .

Table 9: Results from general linear models exploring variation in the proportion of extra-pair offspring in f_1 nests for males and females that recruited as one-year olds. Proportion of EPO is defined as the number of EPO divided by total number of offspring.

Males only ($r^2_{Adjusted}$ = 0.4601, $F_{3,17}$ = 6.682, p = 0.0035):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.12218	0.65418	1.715	0.1044
f_1.cid	-0.03270	0.01466	-2.230	0.0395 *
natal.social.mother.min.age	0.09349	0.04402	2.124	0.0486 *
natal.fledged	0.08396	0.05343	1.571	0.1345

Females only ($r^2_{Adjusted}$ = 0.5593, $F_{5,7}$ = 4.045, p = 0.0479):

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	6.39701	1.72543	3.707	0.00758 **
natal.parentage	0.29677	0.17601	1.686	0.13564
f_1.cid	-0.06675	0.01908	-3.499	0.01001 *
natal.social.father.min.age	-0.33543	0.14509	-2.312	0.05404 .
natal.cid	-0.05134	0.01960	-2.620	0.03442 *
natal.fledged	-0.33587	0.12160	-2.762	0.02801 *

Table 10: Results from general linear models on males and females exploring variation in total number of EPO in f_1 nests and the total number of WPO in f_1 nests.

A) *WPO: Males only ($r^2_{Adjusted}$ = 0.3492, $F_{6,14}$ = 2.788, p = 0.0534):*

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	4.12665	3.06121	1.348	0.1991
f_1.mates.min.age	0.61597	0.42823	1.438	0.1723
f_1.cid	0.02840	0.05714	0.497	0.6269
natal.social.mother.min.age	-0.47752	0.18390	-2.597	0.0211 *
natal.cid	-0.05266	0.04573	-1.152	0.2688
natal.fledged	-0.24802	0.22276	-1.113	0.2843
natal.prop.EPO	-1.00864	0.77754	-1.297	0.2155

B) *EPO: Males only ($r^2_{Adjusted}$ = 0.1821, $F_{2,18}$ = 3.227, p = 0.0634):*

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	5.06193	2.24442	2.255	0.0368 *
f_1.cid	-0.12644	0.05524	-2.289	0.0344 *
natal.fledged	0.33097	0.23249	1.424	0.1717

C) *WPO: Females only ($r^2_{Adjusted}$ = 0.8014, $F_{7,6}$ = 8.494, p = 0.0093):*

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-6.668e+03	1.471e+03	-4.534	0.00396 **
f_1.year	3.309e+00	7.309e-01	4.528	0.00398 **
natal.social.father.min.age	2.183e+00	6.000e-01	3.639	0.01085 *
natal.social.mother.min.age	3.463e-01	1.761e-01	1.966	0.09691 .
natal.parentage	2.286e+00	1.194e+00	1.915	0.10398
natal.cid	4.418e-01	8.012e-02	5.514	0.00150 **
natal.fledged	1.922e+00	4.369e-01	4.400	0.00457 **
natal.prop.EPO	-4.724e+00	1.312e+00	-3.600	0.01137 *

D) *EPO: Females only ($r^2_{Adjusted}$ = 0.9374, $F_{8,4}$ = 23.47, p = 0.0042):*

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2772.79684	894.36882	3.100	0.036211 *
f_1.year	-1.36332	0.44501	-3.064	0.037527 *
f_1.mates.min.age	-1.50348	0.27481	-5.471	0.005431 **
f_1.cid	-0.19861	0.03567	-5.568	0.005098 **
natal.social.father.min.age	-1.97995	0.29550	-6.700	0.002582 **
natal.parentage	-2.07460	0.62987	-3.294	0.030111 *
natal.cid	-0.37150	0.04091	-9.081	0.000815 ***
natal.fledged	-2.23489	0.23542	-9.493	0.000687 ***
natal.prop.EPO	3.81468	0.71338	5.347	0.005896 **
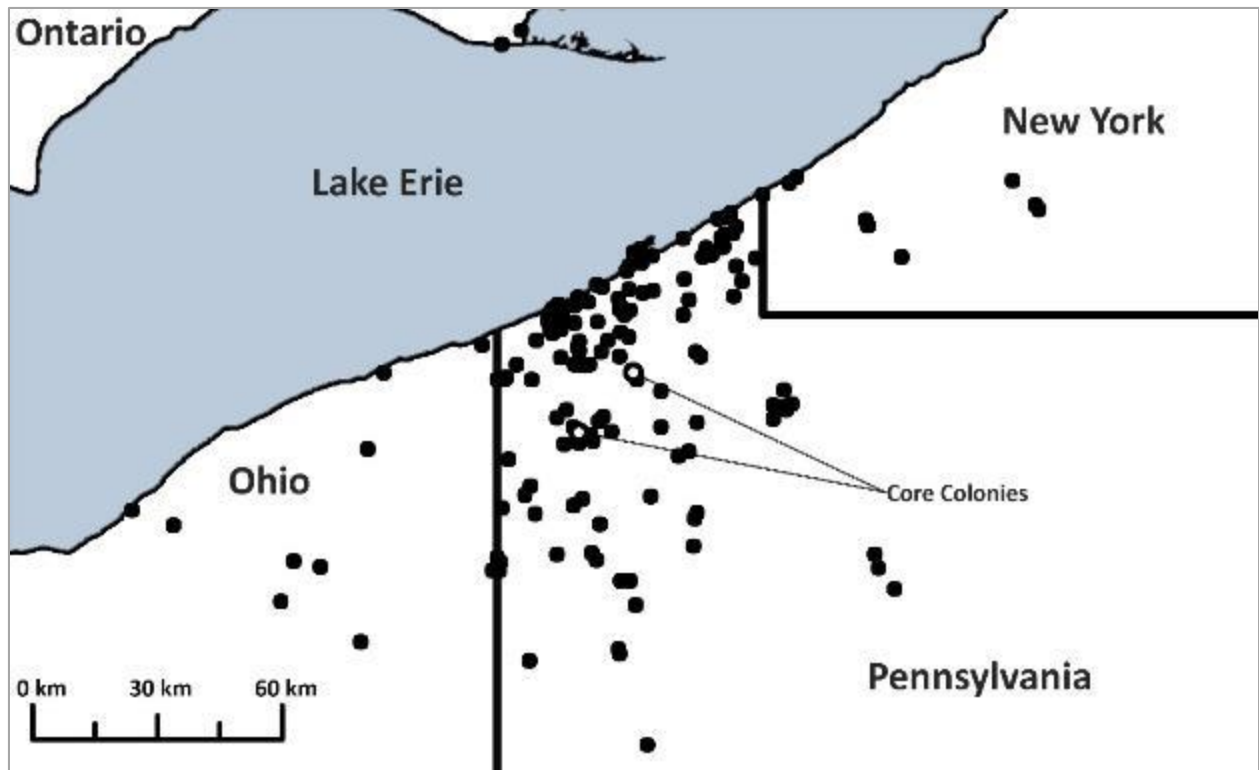
Figure 1: Known purple martin nesting colonies within the study area that were searched for recruited f_1 offspring of known parentage. The core research colonies are indicated by open circles.
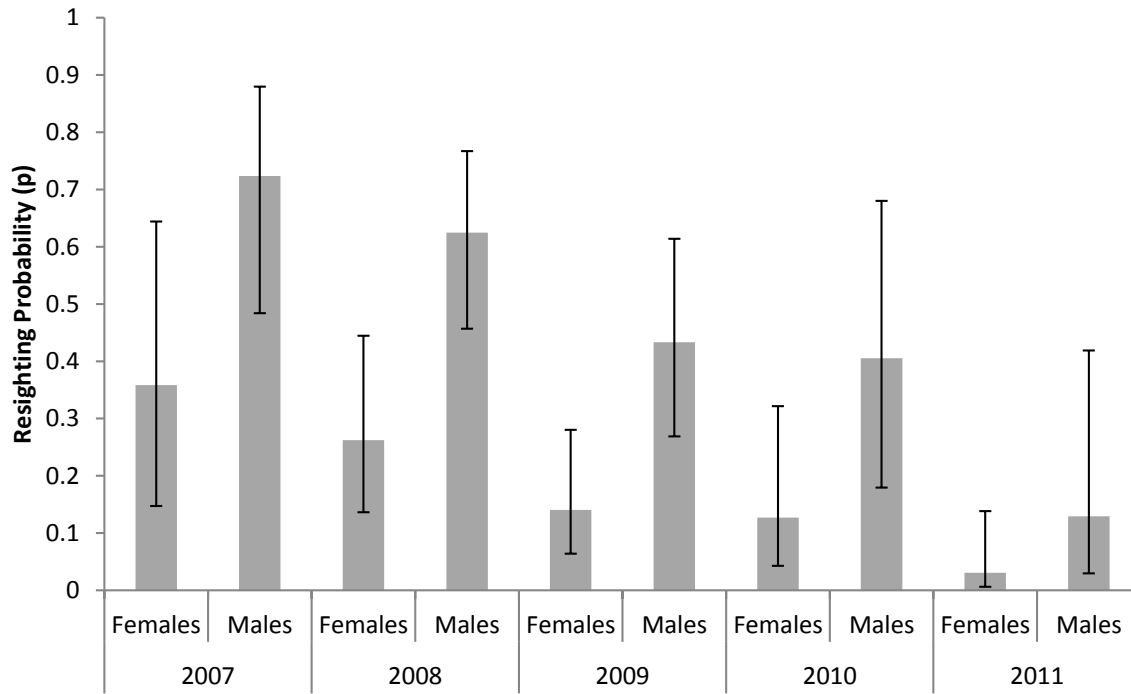
Figure 2: Resighting probability, the probability of resighting a bird given that it was alive, by sex and year. Estimates are based on the starting model: Phi(AgeClass) p(Sex+t). Error bars show 95% confidence interval.
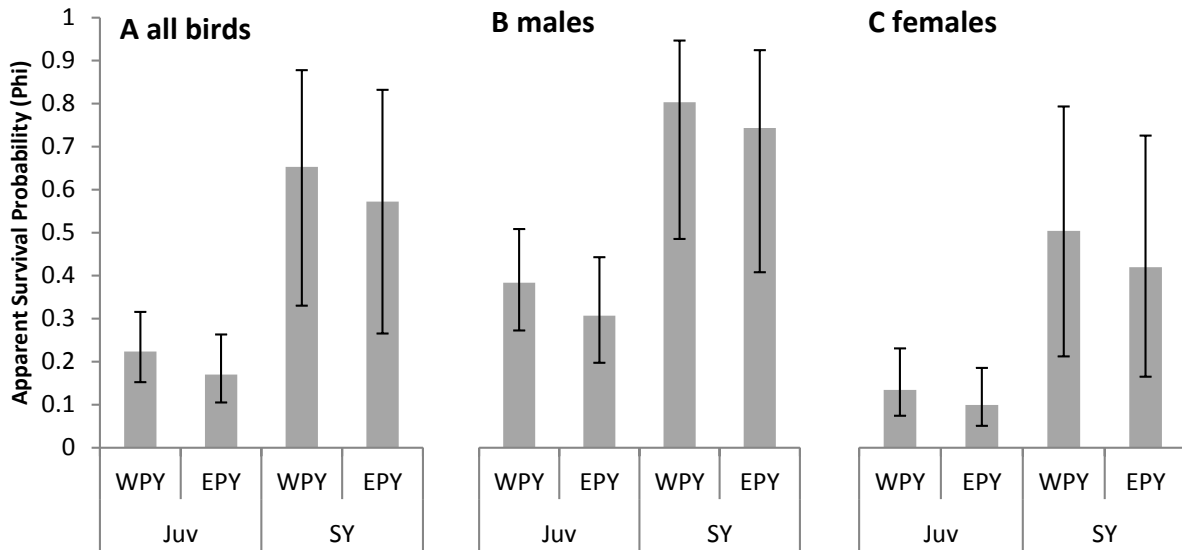
Figure 3: Apparent survival probability of offspring by parentage first year of life (Juv) and the second year of life (SY) for both sexes (A), males only (B) and females only (C). Estimates are based on model 3 in Table 5: Phi(AgeClass+MomMinAge+DadMinAge+Sex+Parentage) p(Sex+t). 95% confidence interval is shown.
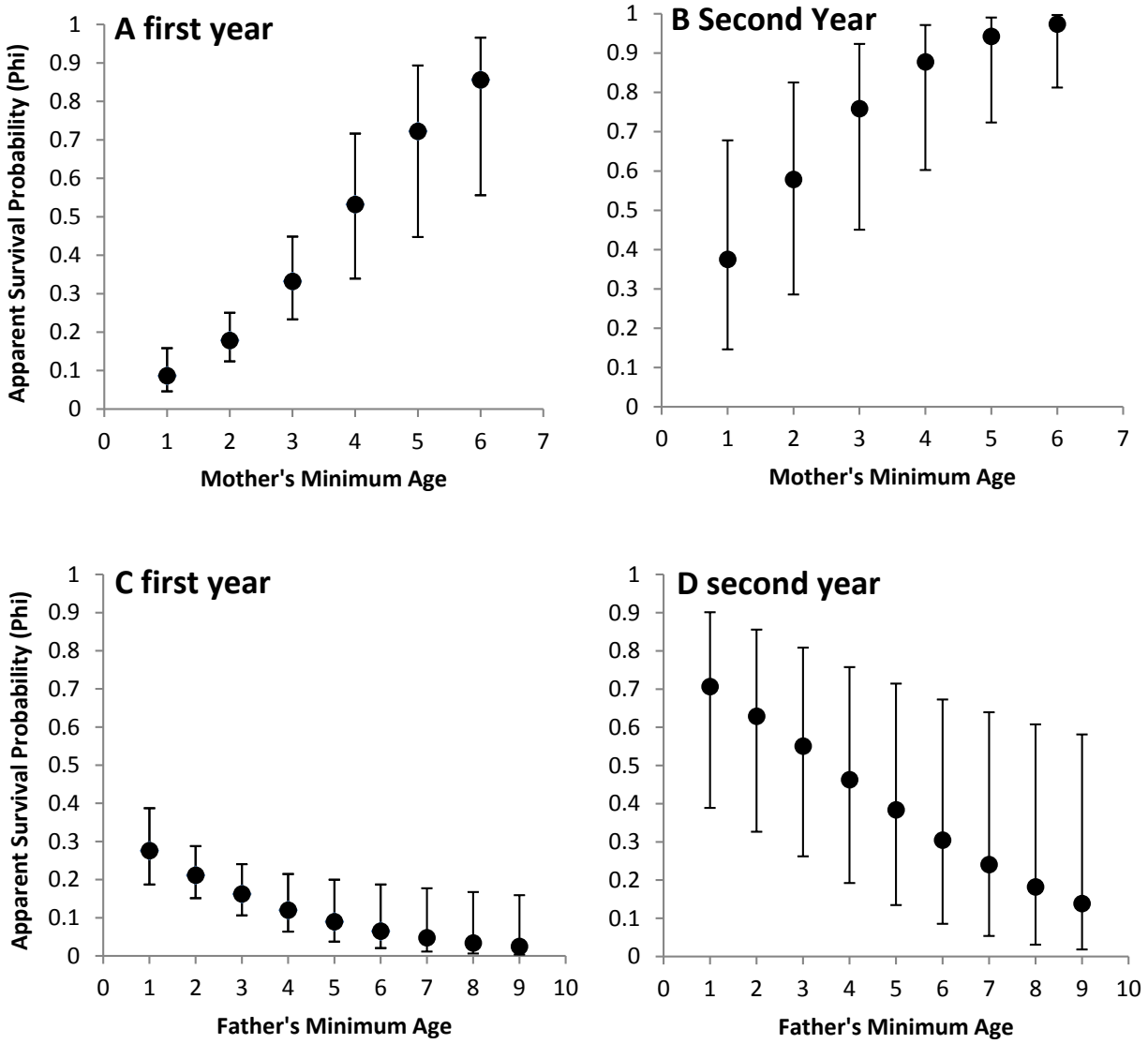
Figure 4: Apparent survival probability of offspring by the social parents' minimum known age for the first two years of life: A) by mother's minimum age for the first year of life, B) by mother's minimum age for the second year of life, C) by father's minimum age in the first year and D) by father's minimum age in the second year of life. 95% confidence intervals are shown. Estimates are based on top-fitting model in Table 5: Phi(AgeClass+MomMinAge+DadMinAge+Sex) p(Sex+t).
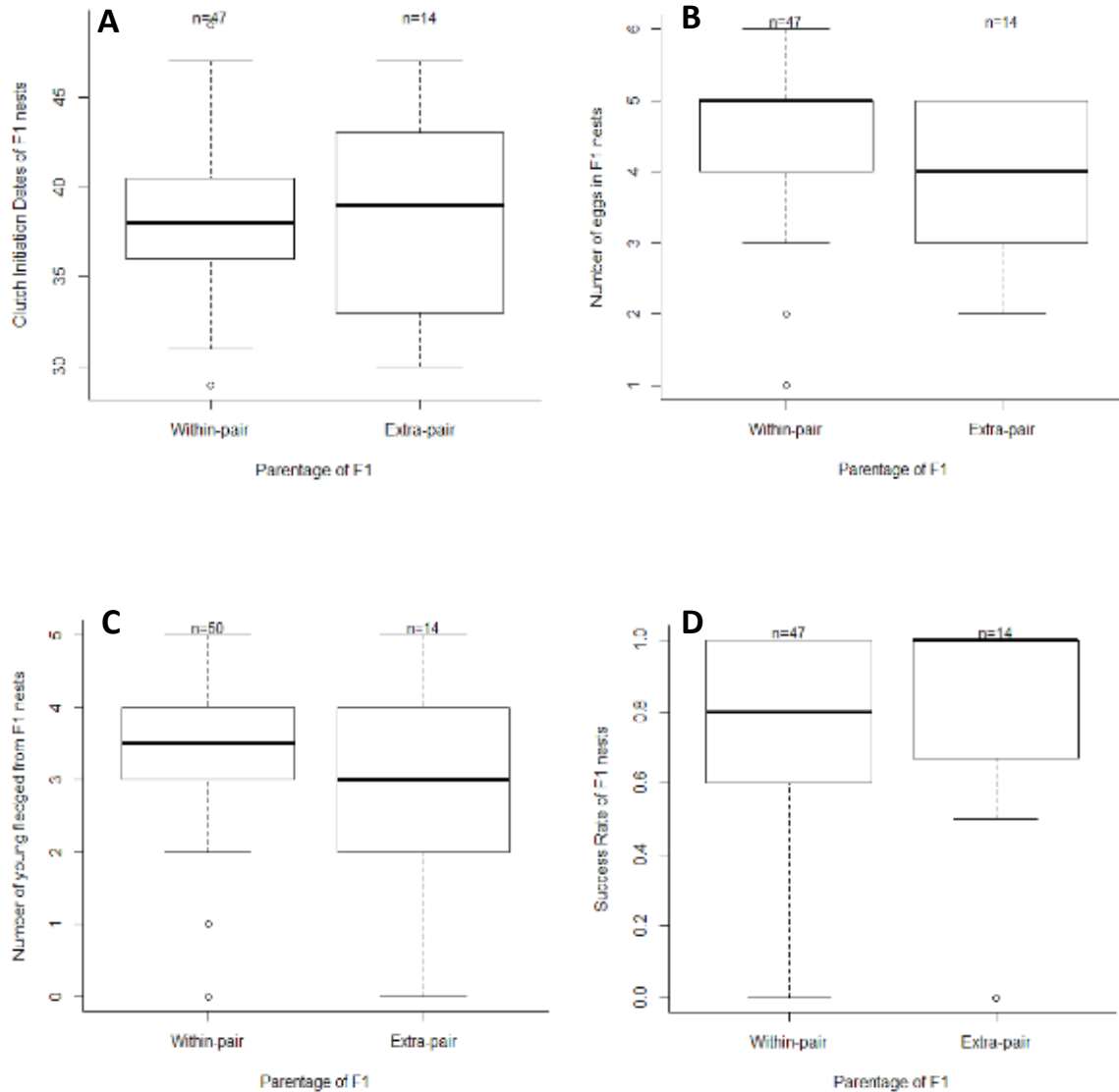
Figure 5: Boxplots exploring determinants of various reproductive success parameters by parentage of f_1 parents for all SYs combined. Bold line is the median, box shows upper and lower quartile, error bars show maximum and minimum values excluding outliers and dots indicate outliers. Sample sizes are shown above. A) the clutch initiation dates of f_1 nests B) the number of eggs in f_1 nests, C) the number of young fledged from f_1 nests and D) the fledging success, defined as the number of young fledged divided by the number eggs laid.
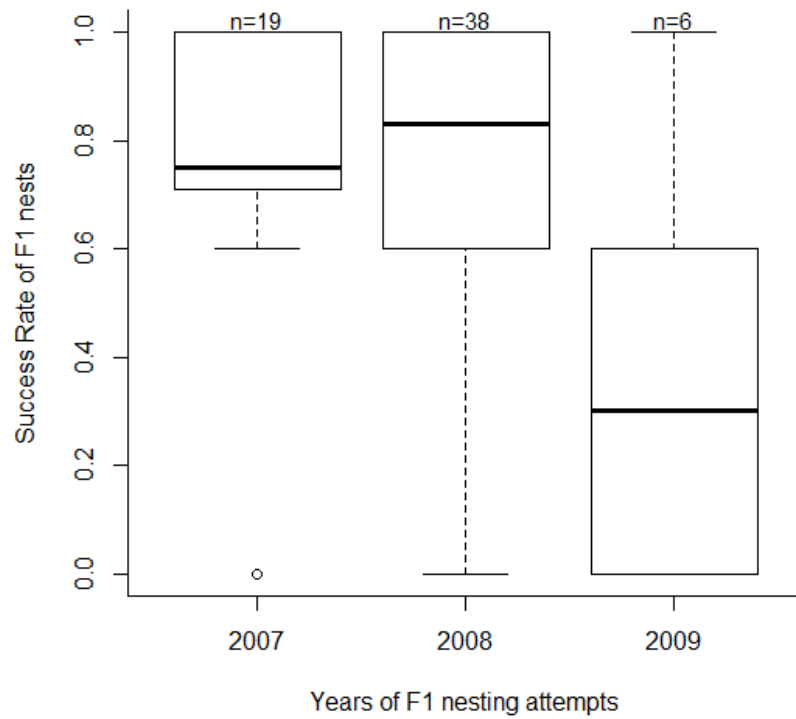
Figure 6: Overall fledging success, defined as total fledged divided by clutch size, by year for all second-year F_1s (sexes combined). In 2009, a prolonged rainy period reduced prey availability causing extreme mortality of nestlings (>90% for all nests monitored).
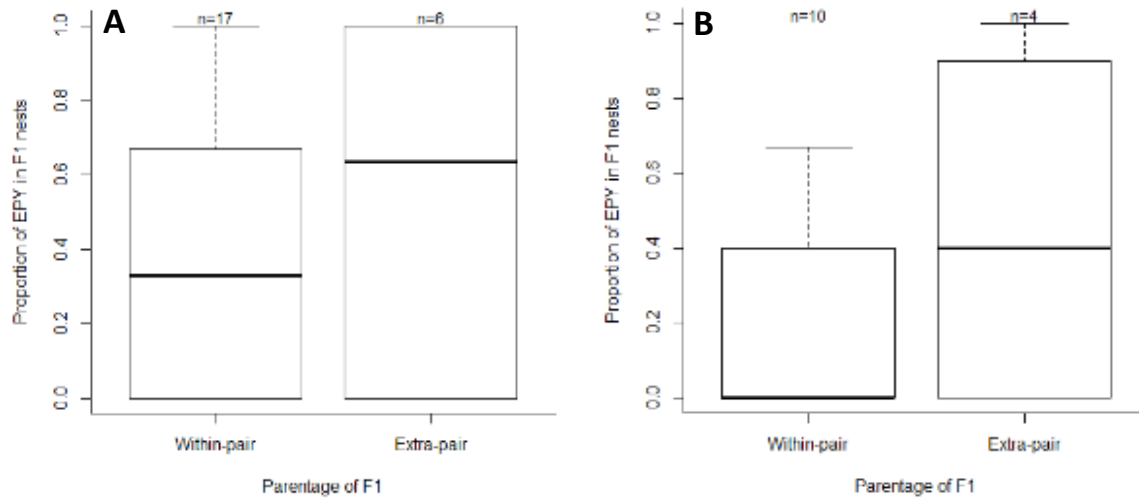
Figure 7: Boxplots exploring proportion of offspring in f_1 nests that are extra-pair (number of EPO/total offspring) by the natal parentage status of f_1s for A) males and B) females. Bold line is the median, box shows upper and lower quartile, error bars show maximum and minimum values excluding outliers and dots indicate outliers.
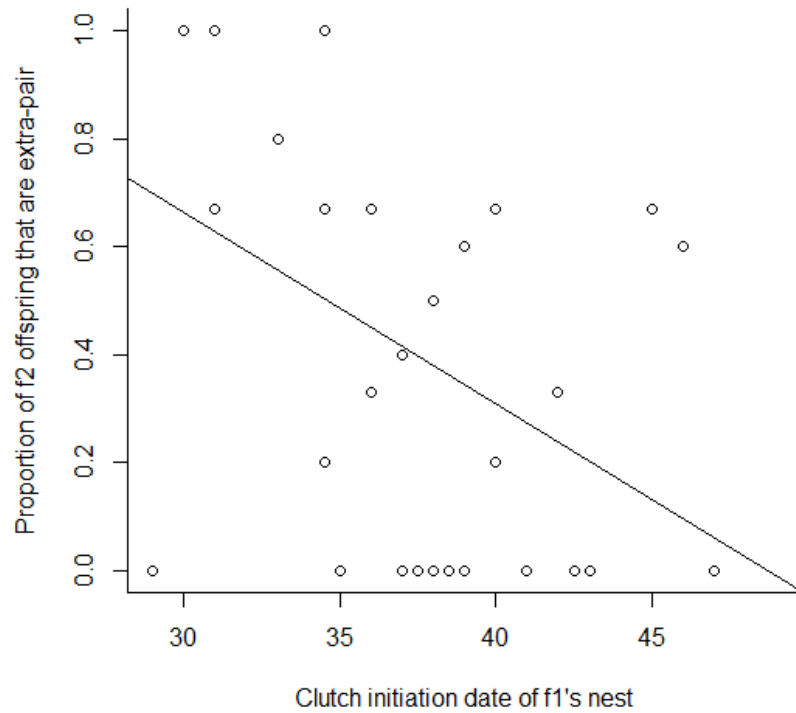
Figure 8: Proportion of f_2 young that are extra-pair by clutch initiation date of f_1 nest. This relationship was included in the best fitting model for all three data sets. These data are all SYs combined ($r^2_{adjusted}$ = 0.1927, $F_{1,32}$ = 8.878, p = 0.006).
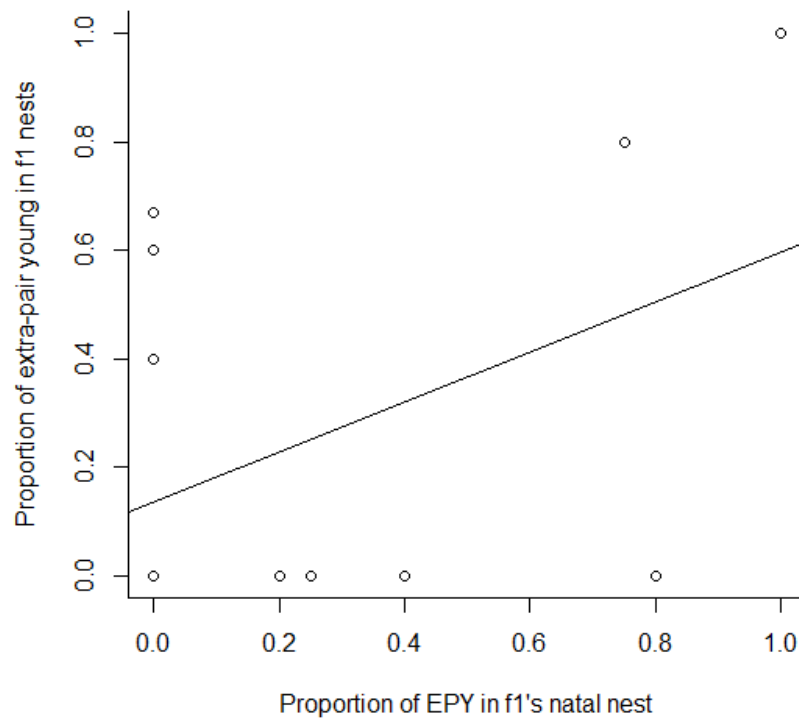
Figure 9: A bivariate plot of the proportion of extra-pair young in f_1s' natal nests and the proportion of extra-pair young in f_1 nesting attempts. These data are SY-Females only ($r^2_{adjusted}$ = 0.1334, $F_{1,12}$ = 3.001, p = 0.11).

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Appendix A: Tarof SA, PM Kramer, J Tautin and BJM Stutchbury. 2012. Effects of Known Age on

Male Paternity in a Migratory Songbird. *Behavioral Ecology*, 23(1): 313-321.

        I collaborated on fieldwork, lab work and analysis for this project. This paper

used the same samples and dataset included in this dissertation.

Original article

Effects of known age on male paternity in a migratory songbird

Scott A. Tarof,[a] Patrick M. Kramer,[a] John Tautin,[b] and Bridget J. M. Stutchbury[a]
[a]Department of Biology, York University, 4700 Keele Street, Toronto, Ontario, Canada M3J 1P3 and
[b]Purple Martin Conservation Association, 301 Peninsula Drive, Suite 6, Erie, PA 16505, USA

Many avian studies have shown that reproductive performance improves with age, but little is known about how key components of male fitness, extrapair and within pair paternity, vary across life spans. We tested for age effects on male paternity in purple martins (*Progne subis*) using cross-sectional analyses of known-aged males (1–9 years old) and longitudinal analyses of individuals sampled in 2 successive years. Microsatellite analyses found that 137 of 297 (46%) nests contained extrapair offspring and 273 of 1235 (22%) offspring were extrapair. Using a subsample of unique known-aged males ($n = 160$), we found significant linear and nonlinear effects of male age on the number of within pair offspring and, to a lesser extent, on the number of extrapair offspring sired. Male genetic reproductive success increased with age to 3 years and then leveled off. In longitudinal comparisons of known age males sampled in successive years ($n = 41$), within pair offspring increased with age, even for males ≥2 years old. Paired comparisons ($n = 74$) found that extrapair sires were older than the males they cuckolded, and that first-year males were significantly underrepresented as extrapair sires given the known age distribution in the population. Poor genetic reproductive performance in younger males is likely constrained through male–male competition during mate guarding and female choice for older males. *Key words:* age-related, extrapair paternity, genetic reproductive success, known age, life history strategies, sexual selection. *[Behav Ecol]*

INTRODUCTION

Numerous studies on birds have shown that measures of individual reproductive performance (e.g., laying date, clutch size, egg volume, number of offspring produced, nesting success) improve with age (Robertson and Rendell 2001; van de Pol and Verhulst 2006; Brommer et al. 2007). Reproductive performance may also stabilize at mid-age and then decline in old individuals as a result of senescence (Bouwhuis et al. 2009; Ricklefs 2010). 3 main hypotheses explain why reproductive performance increases with age (reviewed in Forslund and Pärt 1995). 1) The selection hypothesis proposes that progressive mortality of lower quality individuals results in a population-level, but not individual-level, increase in performance among the remaining older birds (Perrins and Moss 1974). 2) The restraint hypothesis suggests that young birds face life-history trade-offs and withhold reproductive effort to improve future survival (Hamann and Cooke 1987; Lessels and Krebs 1989). 3) The constraint hypothesis suggests that young birds perform poorly due to lack of experience, lower foraging success, and/or lower competitive ability (Lack 1968).

Where females copulate with multiple partners a "hidden" component of male reproductive performance could include increased or decreased genetic reproductive success among older males. High fertilization success in older males could result from female choice (Morton et al. 1990) if females can use male age as a proxy for genetic quality (Kokko 1998, but see Beck and Promislow 2007). Low paternity by young males as a result of female choice would be a form of constraint on

performance. Age-related mating success could also occur via constraint if older males are more effective in male–male competition for females due to experience or larger size (Johnsen et al. 2003; Wagner et al. 1996). The oldest males may experience senescence in genetic reproductive success via reduced sperm competition (Raveh et al. 2010) or decline in male dominance and social status that limits mate access (Mainguy et al. 2009; Raveh et al. 2010). Older male feral fowl (*Gallus gallus domesticus*) experienced senescence in social dominance during intense male–male competition and older males were far less effective in sperm competition and fertilization (Dean et al. 2010). Many birds feature intense male–male competition for copulations via extrapair paternity in socially monogamous species (Westneat and Stewart 2003) but little is known about whether extrapair or within pair paternity varies with age among older males (Table 1).

Age class effects are common in avian paternity studies, with first-year males typically siring fewer within pair offspring (WPO) in their own nest (Griffith et al. 2002) or fewer extrapair offspring (EPO) in other nests compared with older males (Johnsen et al. 2001). Age class comparisons do not fully test for age effects in paternity because first-year versus older males may differ greatly in many other characteristics (e.g., experience, size, coloration) and one would expect age effects to continue beyond the second year. Few paternity studies have tested how components of genetic reproductive success vary among older males (Table 1) and most include individuals for whom only minimum age was known which may obscure subtle age effects. Some studies have found significant age effects among older males, but others have not and none have found that age affects both within pair and extrapair paternity.

Here, we investigate effects of known age on male paternity in purple martins (*Progne subis*), a short-lived migratory passerine for which age class has been previously shown to be

Table 1

DNA fingerprinting and microsatellite paternity studies on short-lived socially monogamous passerines that test for age effects among older males

Species	Age effect among older males?			Proposed mechanism	Reference
	WPO	EPO	Total		
Pied flycatcher *Ficedula hypoleuca*	Yes	—	—	Territory defense	Moreno et al. (2010)[1]
Blue tit *Cyanistes caeruleus*	No	—	—	—	Kempenaers et al. (1997)[1]
Coal tit *Periparus ater*	No	Yes	No	Unknown	Schmoll et al. (2007)[2]
Purple martin *Progne subis*	Yes	Yes	Yes	Mate guarding, female choice	This study[2]
American redstart *Setophaga ruticilla*	Yes	—	—	Male experience	Perreault et al. (1997)[1]
Hooded warbler *Wilsonia citrina*	No	No	—	—	Stutchbury et al. (1997)[1]
Red-winged blackbird *Agelaius phoeniceus*	No	Yes	No	Male experience, female choice	Weatherhead and Boag (1995)[1]

In all cases, significant effects were positive. Variables not tested indicated by '—'. Studies are based on minimum or known age birds (superscript 1 or 2, respectively, after reference) and report data for age effects among older males.

a powerful predictor of male genetic success (Morton et al. 1990; Wagner et al. 1996). Male age class is readily discernible in purple martins due to delayed plumage maturation; first-year males have dull female-like subadult plumage in contrast to the iridescent steel-blue coloration of older males (Brown 1997). We collaborated with the Purple Martin Conservation Association who has banded over 14 000 nestlings in north-western Pennsylvania since 1994 resulting in known age martins up to 9 years old. Natal recruitment is relatively high in this region (26%, Tarof et al. 2011). We tested whether genetic reproductive success increased with age using 1) a cross-sectional analysis of known age males and 2) a longitudinal analysis of known age individuals sampled in 2 consecutive years. We also tested whether known age extrapair sires were older than the males whom they cuckolded using paired comparisons, and if first-year males were significantly underrepresented as extrapair sires given the known age distribution in the population. We demonstrate significant linear and nonlinear effects of known age on genetic reproductive success in purple martins.

MATERIALS AND METHODS

Study species and general field methods

Purple martins nest colonially in nest boxes in eastern North America and migrate to South America in winter (Brown 1997). From May to August 2006–2008, we studied purple martins at 2 breeding colonies in northwestern Pennsylvania, USA (42°08′N, 80°18′W) that were 19 km apart. The Edinboro colony averaged 60 pairs/year; Troyer colony 160 pairs/year. We visited colonies several times weekly and, using telescopes, read alphanumeric color bands of returning banded birds and identified social pairings. Social pairs were confirmed from observations of nest defense and nestling feeding. Males and females were assigned to age class (first-year versus older, i.e., ≥2 years old) using distinctive plumage characteristics (Brown 1997) and/or band records. Across all years, more first-year females paired to first-year males ($n = 48$) compared with older males ($n = 24$), whereas most older females paired with older males ($n = 184$) rather than with first-year males ($n = 41$).

We checked nest contents approximately every 5 days to determine first egg-laying date and nesting success. In a generalized linear model (GLM) involving unique females and taking year into account, first-year females laid smaller clutches (4.43 ± 0.10 eggs) than older females (4.92 ± 0.06 eggs) (whole model: $\chi^2_3 = 25.54$, $n = 262$, $P < 0.0001$; female age class: $\chi^2 =$ 16.92, $P < 0.0001$; year: $\chi^2 = 8.04$, $P = 0.02$). Martins are single-brooded in our population and females rarely lay a replacement clutch following early nest failure. Across all years, older males paired to older females had earlier first egg dates (31 May, 30.86 ± 0.58 days [day 1 = 1 May]) than if paired to a first-year female (5 June, 34.69 ± 1.60 days; $F_{1,208} = 5.06$, $P = 0.03$). The same was true for first-year males (7 June, 38.58 ± 0.92 days versus 12 June, 42.11 ± 0.85 days; $F_{1,89} = 8.65$, $P = 0.004$).

In early July, once most eggs hatched, we caught adults at night using a trap that lowered doors simultaneously over all cavity entrances of a nest house. We returned before dawn to extract adults from compartments for banding and blood sampling. Daytime target trapping captured individuals not caught at night. We banded adults with a USGS numbered aluminum band and color auxiliary band with a unique alphanumeric code. We banded 2830 nestlings at 10–20 days old. Edinboro colony was blood sampled nearly completely in all 3 years of this study. Troyer colony was sampled partially in 2006 and nearly completely in 2007 but was not sampled in 2008 due to restrictions on access. Fieldwork and blood sampling were conducted under approval of the York University Animal Care Committee.

Known male age

Of all paired birds observed at the 2 breeding colonies, we had 89 first-year males and 71 older males (2–9 years old) of known age. We also had 137 other paired males for whom minimum age was known because they were first banded as an older individual. These males were included in general paternity patterns and age class comparisons but were excluded from paternity analyses involving known age birds.

Paternity methods

We used a panel of 4 hypervariable microsatellite-flanking polymerase chain reaction (PCR) primer sets (Stanley et al. 2011) to determine the frequency of extrapair fertilizations and assign parentage to 1235 nestlings based on the social parents of 297 families. Of the offspring sampled, 957 (77.5%) genotyped at 4 loci, 226 (18.3%) genotyped at 3 loci, 26 (2.1%) genotyped at 2 loci, and 26 (2.1%) genotyped at 1 locus. Offspring genotyped at less than 2 loci were excluded from further analysis. We only included families with known social parents and for which both attending parents and their offspring were sampled. In addition to family groups, 12 males were genotyped

as putative sires of EPO. In 2007, 37 males (14%) were also sampled in 2006 but only 1 paired with the same female both years. In 2008, 14 males (25%) were sampled in a previous year but all paired with different females.

We collected 10–50 µl blood samples from adults and nestlings and stored samples at 4 °C in 1 ml of Queen's lysis buffer until DNA extraction. Genomic DNA was amplified in 10 µl PCR reactions under the following conditions: initial denaturation at 94 °C for 3 min; 30 cycles consisting of 1 min at 94 °C, 1 min annealing (T_a: PUMA 19, 55.8 °C; PUMA 49, 50 °C; PUMA 74, 48.2 °C; PUMA 98, 55 °C), 45 s at 72 °C, followed by a final extension at 72 °C for 5 min. Each tube contained 5.7 µl water (PUMA 49, 4.8 µl; PUMA 19, 5.1 µl), 1.0 µl 10× TSG PCR buffer (Bio Basic, Markham, Canada), 0.8 µl 25 mM $MgCl_2$ (Fermentas, Burlington, Canada) (PUMA 19 and PUMA 49, 1.2 µl), 0.4 µl 10 mM deoxyribonucleotide triphosphates (PUMA 19, 0.6 µL; GE Healthcare, Baie d'Urfe, Quebec), 0.2 µl 10 µM fluorescently labeled Beckman Coulter WellRed forward primer (250 nm, HPLC purification; Integrated DNA Technologies, Coralville, Iowa), 0.2 µl 10 µM reverse primer, 0.2 µl 5 U/µl TSG DNA Polymerase, 1.5 µl undiluted DNA (212.5 ± 5.2 ng/ml) (PUMA 49, 2.0 µl; PUMA 74, 1.0 µl), and 0.5 µl 100% dimethyl sulfoxide (PUMA 74 only; BioShop, Burlington, Canada). Products were visualized on 1% agarose gels stained with 5 µl 5 mg/ml ethidium bromide (BioShop, Burlington, Canada) to confirm amplification. This protocol yielded dye-labeled amplicons for fragment analysis. Genotyping was conducted on the Beckman Coulter CEQ 8000. We genotyped individuals in 3-locus poolplex reactions containing 1.5 µl PCR product mixture (4.4 µl PUMA 19, 4.3 µl PUMA 49, 1.3 µl PUMA 98) in 38.5 µl of CEQ cocktail (38 µl 99.5% deionized formamide [Sigma-Aldrich, St. Louis, MO] plus 0.5 µl size standard [Beckman Coulter, Mississauga, Canada]). We ran 1.0 µl PUMA 74 PCR product separately in 38.5 µl formamide plus 0.5 µl size standard. Genotypes were scored against a 400-bp size standard (600 bp for PUMA 74) with phosphoramidite dye mobility calibration and the "cubic" algorithm model ("quartic" for PUMA 74). Thirty random adults were genotyped twice at all loci to confirm repeatability; genotypes were 100% repeatable.

We defined WPO as nestlings that matched the genotypes of their social parents at all loci genotyped ($n = 102$ in 2006, $n = 404$ in 2007, $n = 219$ in 2008) or that mismatched with the social father at 1 locus and had low probability of resemblance by chance alone at the other matching loci (Ibarguchi et al. 2004). If mutation rate is high, single-locus mismatches can grossly overestimate extrapair paternity. Probability of resemblance (P_{Ra}), the likelihood that 2 particular individuals (e.g., offspring and social father) share at least 1 allele at a specific locus by chance alone, has high-resolving power for dealing with single-locus mismatches where genotypes for parents and offspring are known and microsatellite allele frequencies from the sampled population are available (Ibarguchi et al. 2004). For family groups containing a single-paternal mismatch, we calculated P_{Ra} using the formula $P_{Ra} = \left(2p_a - p_a^2\right)^2$, for a given allele (a) with allele frequency (p_a), at each locus other than the mismatching locus. The product of these values generated the cumulative probability of resemblance (P_{RaCum}) for the matching loci. Social males were considered to be the genetic sires if P_{RaCum} was ≤0.005 (after Ibarguchi et al. 2004). That is, offspring with a P_{RaCum} meeting this threshold had less than a 0.5% chance of sharing alleles at the other loci with the social male by chance ($n = 91$ in 2006, $n = 189$ in 2007, $n = 31$ in 2008) and thus were assigned as WPO (mean $P_{RaCum} = 0.0005 ± 0.006$). The mutation rate (# per meiotic event) of 1 of the loci, HrU10, among 6 species of swallows ranges from 0.6% to 10.8% and is relatively high for our purple martin population (5.6%, Anmarkrud et al. 2011). Allele size explained almost all the variance in mutation rate across species

and was relatively large (310 bp) in purple martins, which may explain why there were numerous cases of a single-locus mismatch, whereas the other microsatellite loci did match the social father.

We identified potential EPO by evaluating genotypes of each offspring in a family against their social parents. EPO were defined as nestlings that mismatched the social male at ≥2 loci ($n = 68$ in 2006, $n = 130$ in 2007, $n = 42$ in 2008) or that had a P_{RaCum} value >0.005 with 1 paternal mismatch ($n = 18$ in 2006, $n = 21$ in 2007, $n = 1$ in 2008; average $P_{RaCum} = 0.076 ± 0.013$). Next, we used CERVUS 3.0.3 (Kalinowski et al. 2007) to identify candidates for true extrapair sires. Using genotype data, CERVUS calculates allele frequencies, deviations from Hardy–Weinberg equilibrium, polymorphic information content, null allele frequencies, and exclusion probabilities. A likelihood ratio approach determines true parentage of offspring from the pool of candidate sires by evaluating all offspring-sire genotype combinations (maternal genotype known). We used allele frequency data from our population in CERVUS' parentage analysis likelihood simulation to generate paternity assignments for individual EPO based on the following criteria. Both social parents needed to genotype at a minimum of 2 loci to be included in parentage analyses. Cases of putative intraspecific brood parasitism (<4.7%) were excluded. We included the putative social male and all other sampled males each year in a colony to identify the most likely and second most likely candidate extrapair sires. In simulations, we used 100 000 permutation cycles, 80% (2006), 95% (2007), and 80% (2008) of candidate sires in our sampled population, a minimum of 2 loci genotyped per individual, 95.6% of loci genotyped (from allele frequencies), and 1% genotyping error rate. Determination of the extrapair sire for EPO was based on delta scores calculated by CERVUS, defined as the difference in LOD scores between the most likely and second most likely candidate sire, at either the 80% ($n = 68$ EPO) or 95% confidence level ($n = 64$ EPO). Because we sampled 80–95% of males per colony, we assumed that unassigned offspring were likely sired by males outside the colony.

We determined the probability of alleles matching the candidate genetic male by chance alone based on nonexclusion probabilities calculated by CERVUS. Nonexclusion probability (1-exclusion probability) was the likelihood of not excluding a candidate male that was unrelated genetically to an offspring. The mean (±standard deviation) nonexclusion probability for EPO with both social parents known was 0.017 ± 0.002 (median = 0.007). The average for all offspring (WPO and EPO) was 0.016 ± 0.001 (median = 0.006). Combined exclusion probability (P_E) with both social parents known was 99.998%.

Statistical analysis

Analyses were performed using JMP 9.0.2 for Macintosh. We verified parametric assumptions and evaluated outliers using Cook's D Influence tests and Mahalanobis plots. Equal variance–covariance between groups was tested using Bartlett's test (all Bartlett's $F < 0.87$, all $P > 0.35$). Pearson chi-square Goodness-of-fit analysis tested whether the distribution of EPO in nests was random among brood sizes. Unless otherwise indicated, we used the proportion of WPO instead of the number of WPO in analyses to control for variation in brood size. Means are presented ± standard error of the mean (SEM) and significance level was set at 0.05.

We used maximum likelihood (χ^2) GLMs to test for population-level (e.g., cross-sectional analysis) effects of male known age on genetic reproductive success (McCullagh and Nelder 1989). We ran GLMs on 160 independent males

of known age (1–9 years old). In the 41 cases where we sampled the same individual in multiple years, we used only the latest year. Response variables (WPO, EPO, total number of offspring) were nontransformed. Independent variables used to examine age-related patterns of male success included known age (fixed continuous effect), female age class, and year (fixed categorical effects). We included the quadratic age^2 term because male success could vary nonlinearly with age, and quadratic curves were fit onto model-generated GLM estimates (Schmoll et al. 2007; Mainguy et al. 2009; Raveh et al. 2010). For the number of WPO, we used a binomial distribution with logit links. Clutch size was set as the binomial denominator to account for variation in within pair paternity due to older females laying larger clutches. We used the Poisson distribution function with log links for number of EPO and total number of offspring sired (Everitt 2010).

We used paired t-tests to examine longitudinal variation in genetic reproductive success within unique repeat-sampled individuals as they aged (year x, $x + 1$; $n = 41$) (Schmoll et al. 2007). Longitudinal analysis over the full range of ages was not possible as this was a 3-year study and only 12 males were sampled in 3 consecutive years. We compared the known age of each cuckolded male with the age of the identified extrapair sire using a Wilcoxon paired test. Because old birds are less prevalent in the population, we also tested whether the overall known age distribution of extrapair sires differed significantly from the population distribution of known age males using a heterogeneity chi-square test.

We used a GLM with Poisson distribution and log links to investigate if clutch size (response) differed for first-year versus older females. Female age class and year were fixed effects. To investigate possible correlates of known age among older males (other than genetic reproductive success) while controlling for multicollinearity, we performed a partial correlation analysis. Variables included male body mass, wing chord length, tarsus length, and tail length. Finally, to determine if first egg date was related to the known age of older males, we performed a GLM with a Poisson distribution and log links. In this analysis, we set Julian first egg date as the response and male age and year as fixed effects.

RESULTS

Extrapair paternity

For the 297 families genotyped from 2006 to 2008 (minimum and known age males combined), 137 nests (46%) contained EPO and 273 of 1235 offspring (22%) were extrapair. Brood size averaged 4.24 ± 0.07 offspring per brood, and for nests containing at least 1 EPO, the proportion of EPO per brood averaged 0.53 ± 0.03 ($n = 137$ nests). We identified extrapair sires for 132 of 273 (48%) EPO and for nests containing ≥ 2 EPO, 46% (32 of 70) had multiple extrapair sires.

Older males sired 83% of offspring in their own nests and produced a total (WPO + EPO) of 4.0 offspring annually compared with only 63% WPO and 2.5 offspring for first-year males. Because purple martins feature strong assortative mating by age class, we examined if the age class of a male's mate influences paternity. For both first-year and older males, the proportion of WPO in males' nests was similar irrespective of the age class of their social mates (Figure 1a), whereas individuals paired to older females tended to sire more EPO compared with males paired to first-year females (Figure 1b). An overall effect of female age class was observed in the total number of offspring sired for older ($F_{1,208} = 4.06$, $P = 0.045$) but not first-year males ($F_{1,89} = 0.61$, $P = 0.44$) (Figure 1c).

First-year males who sired EPO had higher total genetic reproductive success compared with other first-year males who
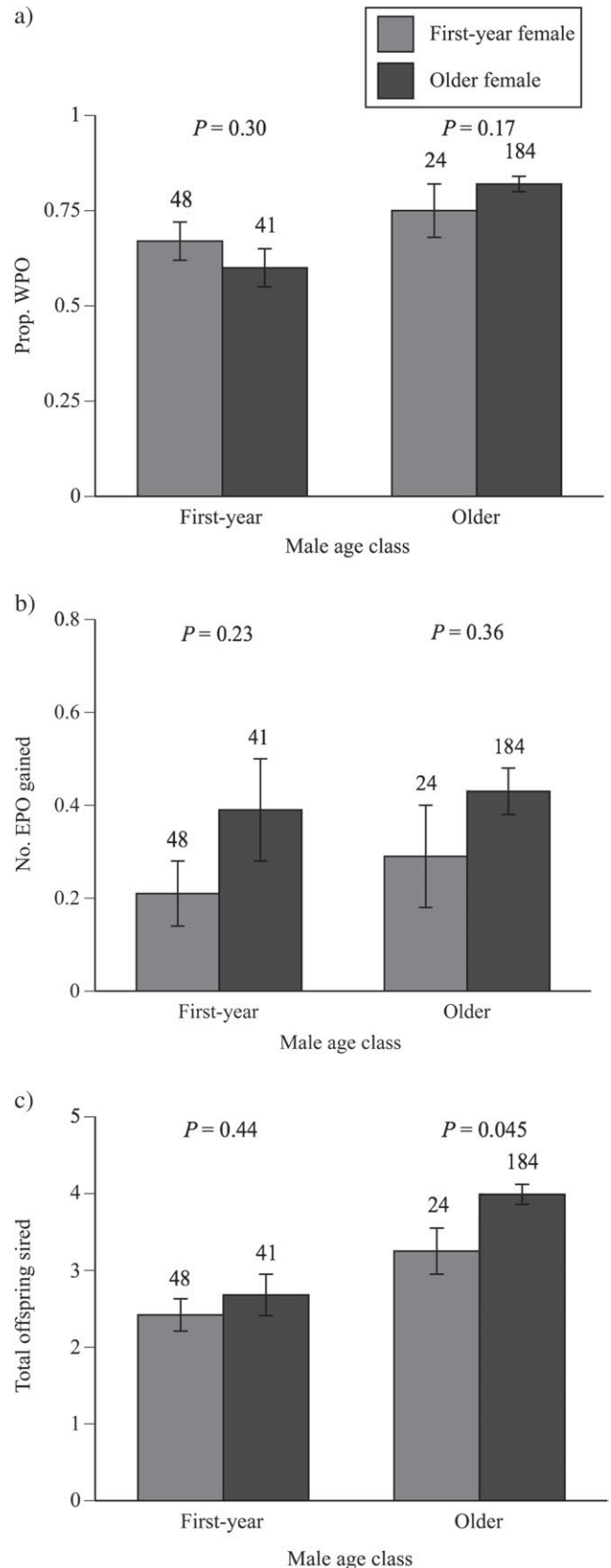

Figure 1
Genetic reproductive success of first-year and older males paired to first-year versus older females in terms of the (a) proportion of WPO, (b) number of EPO gained, and (c) total number of offspring sired. Values are mean $\pm$ SEM with sample sizes above bars.

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Table 2
GLM models testing the effects of male age, male age^2, female age class, and year on the number of WPO, number of EPO gained, and total number of offspring sired for unique known age purple martins ($n = 160$) breeding in Pennsylvania

	Est. ± SEM	Lower, upper	χ_5^2	P
No. of WPO				
Male age	0.47 ± 0.24	$0.004, 0.93$	3.80	0.05
Male age^2	-0.04 ± 0.03	$-0.09, 0.02$	1.44	0.23
Female age class	0.03 ± 0.12	$-0.21, 0.27$	0.06	0.81
Year	-0.39 ± 0.19	$-0.76, -0.03$	11.07	0.004
No. of EPO				
Male age	-0.08 ± 0.32	$-0.72, 0.57$	0	1.00
Male age^2	0.01 ± 0.04	$-0.07, 0.08$	0	1.00
Female age class	0.26 ± 0.19	$-0.09, 0.66$	2.15	0.14
Year	0.29 ± 0.22	$-0.14, 0.74$	2.04	0.36
Total RS				
Male age	0.22 ± 0.08	$0.06, 0.38$	7.28	0.007
Male age^2	-0.02 ± 0.01	$-0.04, 0.003$	3.07	0.08
Female age class	0.06 ± 0.05	$-0.03, 0.15$	1.61	0.20
Year	-0.17 ± 0.08	$-0.32, -0.02$	7.74	0.02

Functions based on a binomial distribution (binomial denominator = clutch size) with logit links (WPO) and Poisson distributions with log links (number of EPO, total number of offspring). Parameter estimates (Est.) with SEMs, lower and upper confidence intervals, maximum-likelihood χ^2 values, and P-values reported. See text for whole model statistics.

did not gain extrapair fertilizations (gained EPO: 3.39 ± 0.37, $n = 18$; no EPO: 2.32 ± 0.18, $n = 71$; analysis of variance (ANOVA), $F_{1,89} = 6.75$, $P = 0.01$). We found a similar pattern among older males as individuals who gained EPO produced 39% more offspring annually than older males who sired no EPO (gained EPO: 4.79 ± 0.19, $n = 72$; no EPO: 3.44 ± 0.14, $n = 136$; ANOVA, $F_{1,208} = 33.79$, $P < 0.0001$).

Genetic reproductive success and male known age

For unique males of known age, we found significant effects of male age on the number of WPO in a male's own nest (GLM, whole model: $\chi_5^2 = 23.74$, $n = 160$, $P = 0.0002$, Table 2). There was also a significant effect of year ($P = 0.004$) but not of female age class ($P = 0.81$) (Table 2). Male within pair reproductive success increased up to 3 years old and then leveled off (Figure 2a). The influence of male age on within pair reproductive success was captured by the linear (age) and quadratic (age^2) variables (age: $r^2 = 0.41$, $n = 160$, $P < 0.0001$, $\beta = 0.34 \pm 0.03$; age^2: $r^2 = 0.53$, $n = 160$, $P < 0.0001$, $\beta = -0.07 \pm 0.01$; Figure 2a, Table 2). Modeling variation in the number of EPO sired by males in relation to male age, male age^2, age class of the social mate, and year revealed a non-significant whole model fit (GLM, $\chi_5^2 = 4.26$, $n = 160$, $P = 0.51$; Table 2). Number of EPO increased from 1 to 2 years of age but remained relatively constant among older males (age: $r^2 = 0.10$, $n = 160$, $P < 0.0001$, $\beta = 0.02 \pm 0.004$; age^2: $r^2 = 0.10$, $n = 160$, $P < 0.0001$, $\beta = -0.003 \pm 0.002$; Figure 2b, Table 2). In a GLM analysis of the total number of offspring sired (WPO + EPO), male age and year were significant ($\chi_5^2 = 34.31$, $n = 160$, $P < 0.0001$, Table 2). Total number of offspring sired annually increased between 1 and 3 years old, but did not continue to increase after 3 years of age (age: $r^2 = 0.58$, $n = 160$, $P < 0.0001$, $\beta = 0.37 \pm 0.02$; age^2: $r^2 = 0.73$, $n = 160$, $P < 0.0001$, $\beta = -0.08 \pm 0.008$; Figure 2c, Table 2). Quadratic effects for the 3 measures of genetic reproductive success had shallow negative slopes and were driven primarily by unavoidably small sample sizes for the oldest males.
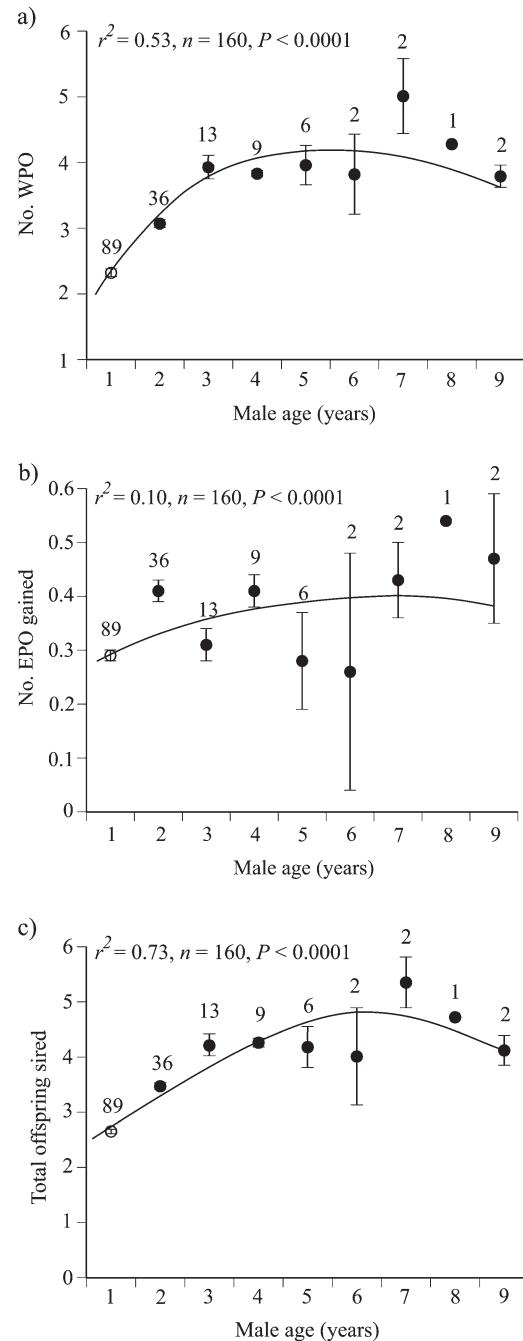
Figure 2
Quadratic curve fits of male known age (1–9 years old) versus the (a) number of WPO, (b) number of EPO, and (c) total number of offspring sired. Values are mean ± SEM GLM estimates from Table 2. See text for complete regression results.

In longitudinal analyses of individuals sampled in 2 successive years, the proportion of WPO and total number of offspring sired increased from 1 to 2 years old (Table 3). This pattern was also true for older males between year x and $x + 1$. Most (19/22) older males in this analysis were <5 years old when first sampled.

An alternative approach for assessing the effect of known age on extrapair mating is to compare directly the ages of the extrapair sire and cuckolded male for EPO where both male identities are known. Extrapair males were significantly older

Table 3

Longitudinal comparisons of genetic reproductive success for male purple martins sampled in successive years

	Year x Mean ± SEM	Year $x + 1$ Mean ± SEM	t	P
1- to 2-year-old males				
Proportion of WPO	0.63 ± 0.09	0.82 ± 0.06	1.67	0.056
No. of EPO gained	0.29 ± 0.10	0.35 ± 0.11	0.44	0.33
Total offspring sired	2.48 ± 0.31	3.85 ± 0.38	2.79	0.01
Older males				
Proportion of WPO	0.74 ± 0.06	0.86 ± 0.05	2.19	0.02
No. of EPO gained	0.48 ± 0.13	0.42 ± 0.15	−0.54	0.70
Total offspring sired	3.45 ± 0.32	4.45 ± 0.36	2.37	0.01

Analyses (paired t-tests) based on within-individual success for males at 1 year old versus 2 years old ($n = 19$) and for older males sampled in 2 consecutive breeding seasons ($n = 22$).

than males they cuckolded (Wilcoxon, $W = -179.5$, $n = 74$, $P = 0.02$, Figure 3a). Only 5 of 15 2-year-old males and 3 of 18 males ≥ 3 years old were cuckolded by a first-year extrapair male, despite the fact that 55% of known age males in the population were first-year. Most (59%, 24 of 41) first-year males were cuckolded by older extrapair males rather than by other first-year extrapair males. If extrapair success is random with respect to male age then the age distribution of extrapair sires should not be significantly different from the age distribution of all known-aged males in the population. The age distribution of extrapair sires that cuckolded first-year (heterogeneity chi-square test, $\chi^2_4 = 11.78$, $n = 41$, $P < 0.05$) and older males ($\chi^2_4 = 10.15$, $n = 33$, $P < 0.05$) differed from that expected under random mating (Figure 3b). First-year males were underrepresented as extrapair sires, whereas males ≥ 3 years old were extrapair sires more often than expected by chance. Distributions of ages of extrapair sires that cuckolded first-year versus older social males did not differ from each other ($\chi^2_{4\text{hetero}} = 2.97$, $P > 0.05$).

Known age and male size, fertility, and timing of breeding

To explore factors that might contribute to higher paternity by older males, we looked for other correlates of age among known age older males. In a multivariate analysis age (2–9 years) was not correlated with body mass, wing chord length, tarsus length, or tail length (partial correlation: $-0.11 < r < 0.18$, $n = 68$, all $P > 0.05$). The proportion of infertile eggs was also not correlated with male age ($r = -0.12$, $n = 71$, $P = 0.30$). In a GLM analysis examining the relationship between first egg date and male age, we found that older males tended to have earlier first egg dates (whole model: $\chi^2_3 = 23.73$, $n = 71$, $P < 0.0001$; age: $\chi^2 = 3.05$, $n = 71$, $P = 0.08$; year: $\chi^2 = 20.62$, $n = 71$, $P < 0.0001$) after controlling for year. Older pairs also tended to mate assortatively by known age (2–9 years old; $r = 0.25$, $n = 49$, $P = 0.087$).

DISCUSSION

4 main results emerged from our analysis of age-related patterns of paternity in purple martins. 1) First-year males experienced lower within pair paternity and were underrepresented as extrapair sires. 2) There were significant linear and nonlinear effects of known age on the number of WPO and total reproductive success of males, with paternity increasing to 3 years of age and then leveling off. 3) For individual males, the number of WPO increased between successive years both for 1- to 2-year-old comparisons and for males ≥ 2 years old. 4) In paired tests, extrapair sires were older than the males they cuckolded.
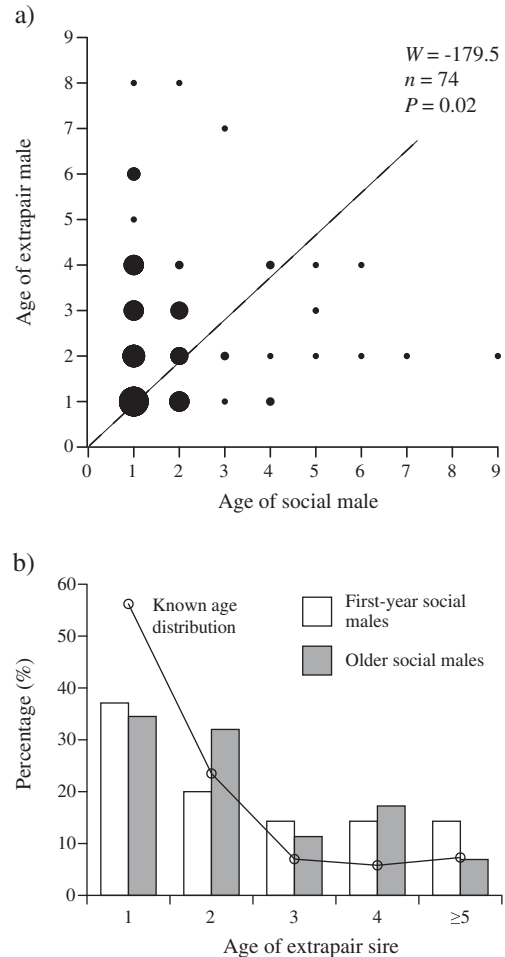
Figure 3
(a) Paired comparison of the age of the identified extrapair sire versus the social male that lost paternity ($n = 74$ EPO). In cases where multiple EPO in a social male's nest had the same extrapair sire, only 1 was included in the analysis. Diagonal is the line of equality. Dot size reflects the number of entries with equal value (range = 1–13). (b) Age distribution of extrapair sires of offspring in nests of first-year ($n = 41$, white bars) and older ($n = 33$, gray bars) social males in relation to the population distribution of all known age males ($n = 160$, solid line with open symbols).

Older males sired 83% of offspring in their own nests compared with only 63% WPO for first-year males, similar to a different population of purple martins (96% and 57%, respectively; Wagner et al. 1996). We also showed that within pair mating success increased among older males (Figure 2) in both cross-sectional and longitudinal comparisons. In pied flycatchers (*Ficedula hypoleuca*), within pair fertilization success increased with age among older males and was greater for males that exhibited more aggressive territorial defense (Moreno et al. 2010). In American redstarts (*Setophaga ruticilla*), within pair success increased among older males, and Perreault et al. (1997) suggested that experience allows males to better prevent extrapair copulations from occurring through more effective territory defense. Purple martins defend nesting compartments rather than large feeding territories and copulations (within pair or extrapair) do not occur at the nest site. Nevertheless, male defense of the mate while females are away from the colony could determine within pair paternity and drive age-related patterns. Wagner et al. (1996) found that first-year males guard their fertile mates more intensely than older males

suggesting that restraint in time or energy invested in mate defense does not explain the poor performance of young males. Despite high guarding effort, first-year males may be constrained to be less effective in mate guarding as a result of inexperience or smaller size (Wagner et al. 1996; Johnsen et al. 2003). It is not known how mate guarding effectiveness or effort varies among older male martins.

Older males may have an advantage in gaining access to extrapair partners due to age-dependent spring arrival schedules in purple martins. First-year males arrive several weeks after older males, and their mates lay eggs a week or more later than do the social mates of older males (Morton and Derrickson 1990; Wagner et al. 1996). Older males are therefore emancipated from guarding their own mate at the same time as most first-year females are egg laying, giving older males a competitive edge in terms of the time and energy available to pursue extrapair matings. Similarly, among older males, there was a strong negative trend between first egg date and age which could explain why 3-year-old males performed better in siring young in their own nest than did 2-year-old males. Extrapair success may be also be driven by timing of breeding and create pronounced variation among males in opportunity to seek extrapair matings, similar to the "mating opportunity" hypothesis for protandrous emergence in insects (Wiklund and Fagerström 1977).

Morton et al. (1990) proposed that extrapair choice of female martins is based on male age because older males have "good genes" or greater heterozygosity as a result of differential mortality of poor quality males at a younger age (Davidar and Morton 1993). If male paternity is strongly influenced by female choice, and females use male age as a proxy for male genetic quality, then 1) older males should gain more EPO as well as lose less WPO and 2) females would be expected to have an open-ended mating preference resulting in the oldest males having the highest genetic reproductive success (Johnsen et al. 2001; Schmoll et al. 2007). In coal tits (*Periparus ater*), Schmoll et al. (2007) found that EPO but not WPO increased among older males, up to 3 years of age. In purple martins, WPO increased up to 3 years of age, but there was not as strong an age effect on EPO, which increased from 1 to 2 years of age and remained relatively constant among older males. In a paired comparison, extrapair sires were significantly older than the males they cuckolded (Figure 3a) and fewer first-year males achieved EPO than expected by chance, similar to several other age-related studies (Weatherhead and Boag 1995; Schmoll et al. 2007). The oldest males in our population were extrapair sires surprisingly often. Although only 12% of known age males in our sample were ≥4 years old, these males sired approximately 30% of EPO in nests of first-year males and 23% of EPO in the nests of older males (Figure 3b). These results are consistent with female preference for the oldest males; however, we caution that we do not demonstrate female choice. Direct observation of female choice for particular males (e.g., Chiver et al. 2008) is difficult to obtain for purple martins because they travel far from their nest on a daily basis and within pair copulations are rarely observed at the colony (Tarof SA, personal observation).

If females prefer the oldest males as extrapair mates, it remains unclear how females might discern age among older males and whether females assess age directly or indirectly (Brooks and Kemp 2001). Male age is often correlated with body size, competitive ability, ornament size, color, display, or song making it difficult to separate age effects from age-trait relationships (Freeman-Gallant et al. 2009). Several studies have shown that age, rather than color ornaments, predict paternity among older males despite the presence of a correlation between age and ornament (Weatherhead and Boag 1995; Moreno et al. 2010). In our study, body size was independent of known age among older males, leaving ornament size, color, or song and other behaviors as potential phenotypic mechanisms for females to assess male age. Annual survival probability in our study population is relatively high (0.48–0.62, Stutchbury et al. 2009) and older pairs tended to mate assortatively by age, making individual recognition of males by returning females another possible mechanism.

We found a low assignment rate (48%) for EPO despite sampling 80–95% of the candidate sires in our population. First-year males spend from several days up to several weeks "floating" while they compete with older males for nesting sites (Stutchbury 1991). Consequently, it is possible that some unassigned extrapair sires were non-territorial floaters that gained extrapair copulations before obtaining a nest site in a different colony. We cannot distinguish between floaters siring EPO versus females leaving the colony to mate with breeding males at other colonies. In purple martins, adults often leave the breeding colony for extended periods of time during the day and therefore have opportunities to mate with distant individuals. Similarly, in tree swallows, most extrapair sires originate from outside the immediate population (Kempenaers et al. 2001) and breeding females travel far from their nest site when fertile (Dunn and Whittingham 2005).

Interpreting patterns of female choice based on male fertilization success may fail to detect age effects if older males are less fertile due to senescence (Hansen and Price 1995; Brooks and Kemp 2001; Dean et al. 2010). Male reproductive senescence could generate sexual conflict in age-structured populations if older males are more likely to achieve extrapair copulations with females but have low fertility, resulting in lower than expected female reproductive success (Gasparini et al. 2009; Dean et al. 2010). Passerines are expected to exhibit senescence in male genetic mating success because they typically have a "fast" life-history strategy (Jones et al. 2008). Senescence is best tested longitudinally by examining genetic mating success over an individual's lifetime, but for paternity studies, this is logistically difficult. In purple martins, we found no correlation between egg infertility and age among older males, implying that the lack of increase in total fertilization success among males ≥3 years old was not simply a result of low fertility. A robust test of the hypothesis that females choose older males in order to benefit by producing higher genetic quality EPO could compare fitness-related traits of half-siblings and differences in offspring quality should correspond to the age difference of the cuckolded versus extrapair male (Schmoll et al. 2007).

Predicting and interpreting age-related patterns in paternity among species (Table 1) are difficult because the underlying behavioral mechanisms that determine paternity are often not well understood. In hooded warblers (*Wilsonia citrina*), for example, paternity is not male age-related (Stutchbury et al. 1997) and their extrapair behavior, studied via radiotelemetry, provides insights as to why. Males make little attempt to mate guard (Fedy et al. 2002) because females make frequent off-territory forays to neighbouring males and most intrusions onto the territory by neighbouring males go undetected (Stutchbury 1998). Extrapair paternity is determined primarily via female choice. Females made more frequent off-territory forays if their social mates had a low song rate, and in paired comparisons extrapair sires sang more than the males whom they cuckolded (Chiver et al. 2008).

For species where mate guarding and territory defense are effective for increasing within pair paternity, age effects on within pair success would be expected if older males are competitively superior as a result of aggression (Moreno et al. 2010), earlier breeding (Wagner et al. 1996, this study), or experience in territory defense (Perreault et al. 1997). Similar traits may also influence extrapair paternity depending on the mating system. In some species, neighboring females

eavesdrop on male–male territorial disputes to assess male quality for extrapair matings (Mennill et al. 2002). Weatherhead and Boag (1995) suggested that older male Red-winged blackbirds (*Agelaius phoeniceus*) may be more successful in gaining extrapair fertilizations due to experience, but it is not known whether there are age-related differences in male off-territory foray frequency, duration, or strategy.

If paternity is determined primarily by female choice, then within pair and extrapair fertilization success should be the result of a male's intrinsic quality, as assessed indirectly by females, and preferred males should both gain WPO and EPO. In purple martins, we found evidence for age-related increases in WPO and, to a lesser extent, EPO. 2 other studies found that males gained more EPO but not more WPO as they aged (Weatherhead and Boag 1995; Schmoll et al. 2007) but it is not clear why. Extrapair copulations occur in the context of a complex social environment of male–male competition during defense and acquisition of mates, as well as female choice of extrapair mates. Although patterns of age class effects on paternity are well documented (Griffith et al. 2002), we suggest that the subtle age effects among older males will be far more variable as a result of the details of how and why extrapair copulations are achieved.

CONCLUSIONS

Our results, along with studies of other species (Table 1), are consistent with the constraint hypothesis for age-related male performance (reviewed in Forslund and Pärt 1995). WPO increased for male martins sampled in consecutive years, suggesting that the cross-sectional age-related patterns were not simply a result of mortality of lower quality individuals (see also Weatherhead and Boag 1995; Perreault et al. 1997; Schmoll et al. 2007). Young martins have lower competitive ability in mate guarding (Wagner et al. 1996), later initiation of egg-laying by their mates (Morton et al. 1990, this study), and are disadvantaged as a result of female preference for older males (Wagner et al. 1996). In purple martins, the relatively high level of mate guarding shown by first-year males (Wagner et al. 1996) is not consistent with the restraint hypothesis. Furthermore, first-year males who sired EPO had 46% higher total genetic reproductive success compared with first-year males who did not gain extrapair fertilizations. Among older males, individuals who gained EPO produced 39% more offspring. Even given the comparatively short life span of this species (Stutchbury et al. 2009), the high fitness gains of extrapair fertilizations would presumably be sufficient to offset life-history trade-offs. If so, the survival probability of males who sired EPO should be similar to same-aged males that did not sire EPO. Studies of other species showing age effects among older males (Table 1) also suggest that poor paternity performance in younger males is constrained via male–male competition and female choice.

FUNDING

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Appendix B: Stutchbury BJM, SA Tarof, T Done, E Gow, PM Kramer, J Tautin, JW Fox and V Afanasyev. 2009. Tracking Long-Distance Songbird Migration Using Geolocators. *Science*, 323: 896.

I was involved in the planning and implementation of fieldwork portion of this project for deployments and retrievals on purple martins. I trapped adult purple martins, measured, banded and blood sampled them prior to them receiving a geolocator. Conducted most of the visual searching for tagged individuals as they returned each spring and trapped any purple martins carrying a geolocator.

Tracking Long-Distance Songbird Migration by Using Geolocators

Bridget J. M. Stutchbury,[1]* Scott A. Tarof,[1] Tyler Done,[1] Elizabeth Gow,[1] Patrick M. Kramer,[1] John Tautin,[2] James W. Fox,[3] Vsevolod Afanasyev[3]

Until now it has been impossible to track migratory songbirds to their tropical wintering grounds. Songbirds are far too small for satellite tracking, and our current understanding of individual movements comes from brief snapshots of the journey via radar images, opportunistic recaptures of banded individuals, studies of migrants on the ground refueling, and an exceptional study that followed radio-tagged songbirds by airplane (1–4). We tracked songbird migration by mounting light-level geolocators (5, 6) on 14 wood thrushes (Hylocichla mustelina) and 20 purple martins (Progne subis) breeding in northern Pennsylvania during 2007. The next summer we retrieved geolocators from five wood thrushes and two purple martins and analyzed sunrise and sunset times to reconstruct migration routes and estimate wintering locations (±300 km).

Rapid long-distance movement occurred in both species, and prolonged stopovers were common during fall migration (Fig. 1). Both purple martins flew south 2500 km to the Yucatan Peninsula in 5 days (500 km/day) and, on the basis of longitude estimates, then had a stopover of 3 to 4 weeks in the region (fig. S1). Four wood thrushes spent 1 to 2 weeks in the southeastern United States in late October before crossing the Gulf of Mexico (Fig. 1C), and two individuals stopped on the Yucatan Peninsula for 2 to 4 weeks before continuing migration (Fig. 1D).

Wood thrushes overwintered in a narrow band from 83.7° to 85.0°W (±1.4°) in Honduras or Nicaragua (Fig. 1), suggesting a level of connectivity not previously documented for migratory songbirds. Stable isotope analysis of black-throated blue warbler (Dendroica carulescens) feathers, for instance, showed that individuals wintering on western Caribbean islands originate from the northern portion of the breeding range, whereas those on easterly islands are from southern breeding areas (7).

Overall migration rate was 2 to 6 times more rapid in spring than in fall (table S1). One female martin (Fig. 1A) left the Amazon basin after the night of 12 April and flew about 7500 km in 13 days (577 km/day). Nine days involved migration flights, and 4 days were spent on stopover. Most wood thrushes returned to their breeding territory in only 13 to 15 days (233 to 271 km/day). One wood thrush did not cross the Gulf of Mexico on spring migration and took 29 days to complete the 4600-km overland route (Fig. 1D). Previous studies appear to greatly underestimate the true flight performance of migrating songbirds (4) because spring migration speed has typically been estimated at under 150 km/day.

Alarming long-term declines of migratory songbird species in North America and elsewhere heighten the urgency of mapping migration routes and wintering locations with far greater accuracy than is currently possible with stable isotope analysis (8). Tracking individuals to their wintering areas is essential for predicting the impact of tropical habitat loss and climate change (7, 9). Survival estimates can now be obtained from regions where individuals from a specific breeding population overwinter, improving our understanding of how wintering versus breeding threats drive population fluctuations of migratory songbirds.

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Fig. 1. Interpolated geolocation tracks of individual purple martins (**A** and **B**) and wood thrushes (**C** and **D**) that bred in northern Pennsylvania, USA (42°N, 80°W). Blue, fall migration; yellow, winter range movements; and red, spring migration. Dotted lines link locations when latitude could not be determined. Inset shows winter territory locations of wood thrush and species winter range (shaded); the standard deviation for one individual is shown.

[1]Department of Biology, York University, Toronto, Ontario M3J 1P3, Canada. [2]Purple Martin Conservation Association, Tom Ridge Environmental Center, 301 Peninsula Drive, Erie, PA 16505, USA. [3]British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK.

*To whom correspondence should be addressed. E-mail: bstutch@yorku.ca

Appendix C: Fraser KC, CA Silverio, PM Kramer, N Mickle, R Aeppli and BJM Stutchbury. 2012a.

A Trans-Hemispheric Migratory Songbird Does Not Advance Spring Schedules or Increase

Migration Rate in Response to Record-Setting Temperatures at Breeding Sites. *PLoS ONE*, 8(5):

e64587.

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project for deployments and retrievals on purple martins. I trapped adult purple

martins, measured, banded and blood sampled them prior to them receiving a

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returned each spring and trapped any purple martins carrying a geolocator.

A Trans-Hemispheric Migratory Songbird Does Not Advance Spring Schedules or Increase Migration Rate in Response to Record-Setting Temperatures at Breeding Sites

Kevin C. Fraser[1]*, Cassandra Silverio[1], Patrick Kramer[1], Nanette Mickle[2], Robert Aeppli[3], Bridget J. M. Stutchbury[1]

1 Department of Biology, York University, Toronto, Ontario, Canada, 2 Woodbridge, Virginia, United States of America, 3 Purple Martin Conservation Association, Erie, Pennsylvania, United States of America

Abstract

The decline of long distance migratory songbirds has been linked to an increasing mismatch between spring arrival date and timing of food availability caused by climate change. It is unclear to what extent individuals can adjust migration timing or en route rate in response to annual variation in temperature at breeding sites. We tracked the ca. 7300 km spring migration of 52 purple martins *Progne subis* from the Amazon basin to two breeding sites in eastern North America. Spring 2012 was the warmest on record in eastern North America, but contrary to predictions, this did not result in earlier departure, faster migration, or earlier arrival at breeding areas compared with earlier years. Temperatures and rainfall in the Amazon basin at the time of departure were not higher in 2012, and conditions along migration routes did not give consistent signals of a warmer spring at the breeding site. Once in North America, individuals likely had limited opportunity to speed up their migration because this final portion of the journey was already very rapid (570 km/d; 4–5 d in duration). Migration timing over the entire journey was best predicted by breeding latitude and sex and was not sensitive to ecological cues (temperature and rainfall amount) at departure from South American overwintering sites or en route, in contrast to recent studies of other songbirds. Our results provide the first direct evidence for a mismatch between higher spring temperatures at breeding sites and departure schedules of individual songbirds, and suggest phenotypic responses to short-term climatic warming may be limited for some species. Further direct-tracking data with greater geographic and temporal scope is needed to test for individual plasticity in response to temperature and rainfall along migratory routes for this, and other, species.

Introduction

Many animals have shown long-term advancement in spring phenology in response to climate change [1]. The failure of some long-distance migratory songbirds to sufficiently shift arrival date at breeding areas in response to warmer spring temperatures can result in severe population declines [2]. The cause of this inability to shift arrival schedules is much debated [3], and may be driven by constraints on departure date from distant tropical 'wintering' areas, and/or by varying conditions and environmental constraints along migratory routes [4]. For long-distance migrants it is unclear if suitable temperature cues are available at tropical wintering sites or if individuals are able to make short-term phenotypic adjustments in departure timing or rate in response to changes in temperature [3]. The amount of rainfall, either at tropical overwintering sites or along migratory routes, may also influence migratory timing of songbirds through its effect on food availability [5,6,7]. Recently it has become possible to determine start-to-

finish migration timing and rate of small songbirds through direct tracking [8], allowing an unprecedented opportunity to assess phenotypic responses to temperature and rainfall all along migratory routes.

We examined migratory schedules of purple martin *Progne subis*, a declining [9], trans-hemispheric migrant that travels between the Amazon basin and breeding colonies in North America. In 2012, eastern North America experienced the warmest spring since record-keeping began in 1895 [10]. Several studies have shown the existence of large-scale climate and behavioural connectivity between temperate breeding and tropical overwintering sites [11,12,13]. Migrants in the tropics may receive signals of anomalous weather events at breeding areas, even while thousands of kilometres away [11]. Weather conditions in 2012 allowed a unique opportunity to examine the extent to which migration schedules and rate are flexible from year to year. Our objectives were to 1) determine if, near the time of departure from tropical

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non-breeding sites and at passage through key points en route, birds received temperature or rainfall cues of advanced spring and record-setting temperatures at breeding sites in North America, 2) if birds had earlier migration timing (departure, en route, arrival) and faster rate in the warmest spring on record, and, 3) determine if rainfall amount, at departure or en route, was a significant predictor of migration timing and rate.

Materials and Methods

This study was conducted in accordance with the recommendations of the Ornithological Council 'Guidelines to the Use of Wild Birds in Research' and was approved by the York University Animal Care Committee (Animal Care Protocol Number: 2009-2 W (R1)).

Geolocator Deployment and Analysis of Light Data

Purple martins were fitted with geolocators (British Antarctic Survey, models MK10, MK12, MK14, MK20) during the nesting period (2007–2011, n = 228) at two eastern breeding locations (Pennsylvania, Virginia; Table S1). Geolocators were retrieved (n = 73; 52 with spring migration data) in the year following deployment. Purple martins fitted with geolocators did not have a lower return rate than those not carrying geolocators [14]. Raw light data were corrected for clock drift using BASTrak and analyzed using TransEdit (British Antarctic Survey). We manually verified a sharp transition at each sunrise and sunset and deleted obvious shading events during the daytime. We used a light-level threshold of 32 (MK14, MK10) or 5 (MK12, MK20) to define sunrise and sunset transitions, and used live calibration data from birds after nesting but prior to migration to determine the average sun elevation that corresponded with this light threshold level at the breeding site. Sun elevation values were averaged across individuals within each year to better represent average conditions for migrating birds at unknown locations. Latitude was not determined for 15 days before and after the spring equinox when day length is similar everywhere. During this period, positions were estimated using longitude [8]. This is appropriate for spring migration in this species, as migratory routes have a large longitudinal component [15]. Latitude and longitude coordinates were calculated with Locator software (British Antarctic Survey) using midnight locations because purple martins are primarily diurnal migrants. Movements away from tropical roosts consistent with spring migration, and from one stopover location to another (>200 km latitude, >100 km longitude), were defined as migration. Arrival at breeding sites was considered to have occurred when the latitude and longitude ceased to shift in a direction consistent with spring migration and fluctuated around a narrow range of values (less than 2 degrees longitude), consistent with a stationary bird, and frequent shading events indicated use of nesting boxes. To estimate geolocator accuracy we calculated location for two weeks after nesting but prior to migration and compared that with the known roost or breeding colony location. Average geolocator accuracy at breeding sites prior to migration, ranged from 20–60 km for latitude, and 20–75 km for longitude [14].

Temperature Data

We compared average maximum daily temperatures at two breeding areas in 2012 versus prior years (2008–2011 PA; 2011 VA) during the main departure period from Brazil (March 15 to April 15). We also compared spring warmth sum (sum of maximum daily temperatures [16]) over the same period to provide a cumulative estimate of differences between years. The average daily maximum temperature 10 days before and after the median passage date [4] of each population in 2012 was compared using t-tests to prior years at the core wintering area (Manaus Brazil), and at three points en route: 1) Panama (Panama City); 2) Yucatan Peninsula (Merida, Mexico), 94% of birds crossed the Yucatan Peninsula; and 3) Along the U.S. Gulf coast (PA population: Mobile, Alabama; VA: Panama City, Florida). Total rainfall amount was determined for the month (30 d) prior to median migration passage date at each of the 4 locations above because rainfall in the month leading up to migration is expected to have the greatest influence on migration timing via effects on food supply [5]. Temperature and rainfall data are from the National Oceanic and Atmospheric Administration [17].

Statistical Tests of Migration Timing and Rate

First, we used univariate tests to compare migration timing (t-test) and rate (ANOVA) between 2012 and earlier years, for each breeding population. Next, we used linear mixed-effects models fit by REML to assess the influence of temperature and rainfall on migration timing and rate at the core wintering and stopover locations. We examined timing at four locations (Brazil, Panama, Yucatan, and breeding site) and rate in three migration zones (South, Central and North America). We fit a separate timing and rate model for each location and zone. For arrival date at stopover sites and migration rate in each zone, we used temperature and rainfall amounts at the preceding site as factors, reasoning that timing and rate would be most influenced by conditions prior to arrival (i.e. at the previous site). The full models included fixed factors of population (PA or VA), sex, rainfall and temperature with a random effect of year. We dropped individual explanatory variables one by one, then used Akaike's Information Criterion weights to select the best-fit model. To assess the significance of each variable, we removed them one by one from the full model, then compared each reduced model to the full model using a likelihood ratio test. All analyses were conducted using R [18].

Results

In 2012, maximum daily spring temperature was significantly higher at breeding sites for both populations (Fig. 1a–b; PA: $t = -3.42$, $df = 49.38$, $P = 0.001$, VA: $t = -3.09$, $df = 54.51$, $P = 0.003$) and spring warmth sum was 46% (PA) and 25% (VA) higher than previous years. However, in 2012 birds departed significantly later, not earlier, from wintering sites (PA: $t = 2.29$, $df = 30.06$, $P = 0.03$; VA: $t = 2.99$, $df = 15.35$, $P = 0.008$) and there was no difference between years in the timing of crossing the Gulf of Mexico (23.4°N) or arrival at breeding sites (Fig. 2a–b). The Virginia population, as expected, had earlier departure, passage, and arrival dates than the more northern Pennsylvania population.

Rate of spring migration varied significantly (PA: $F_{1,96} = 30.52$, $P < 0.0001$; VA: $F_{1,39} = 25.61$, $P < 0.0001$) during passage through South America (PA: 310 km/d ±30; VA: 289 km/d ±28), Central America (PA: 333 km/d ±25; VA: 370 km/d ±37) and North America (PA: 538 km/d ±35; VA: 649 km/d ±75). Migration rate was not significantly faster in 2012 versus prior years (Fig. 2c–d) for any stage of migration (PA: $F_{1,96} = 1.75$, $P = 0.19$; VA: $F_{1,39} = 0.05$, $P = 0.83$). Migration duration from the Yucatan Peninsula to the breeding colony was only 4–5 days on average (PA: 5±0.35; VA: 4±0.55).

Temperatures at the core overwintering area [14] in northern Brazil were not significantly warmer in 2012 (Table 1; Fig. 1). Temperatures were generally similar between years along migratory routes, during the peak passage period specific to each population. However, there were warmer temperatures in
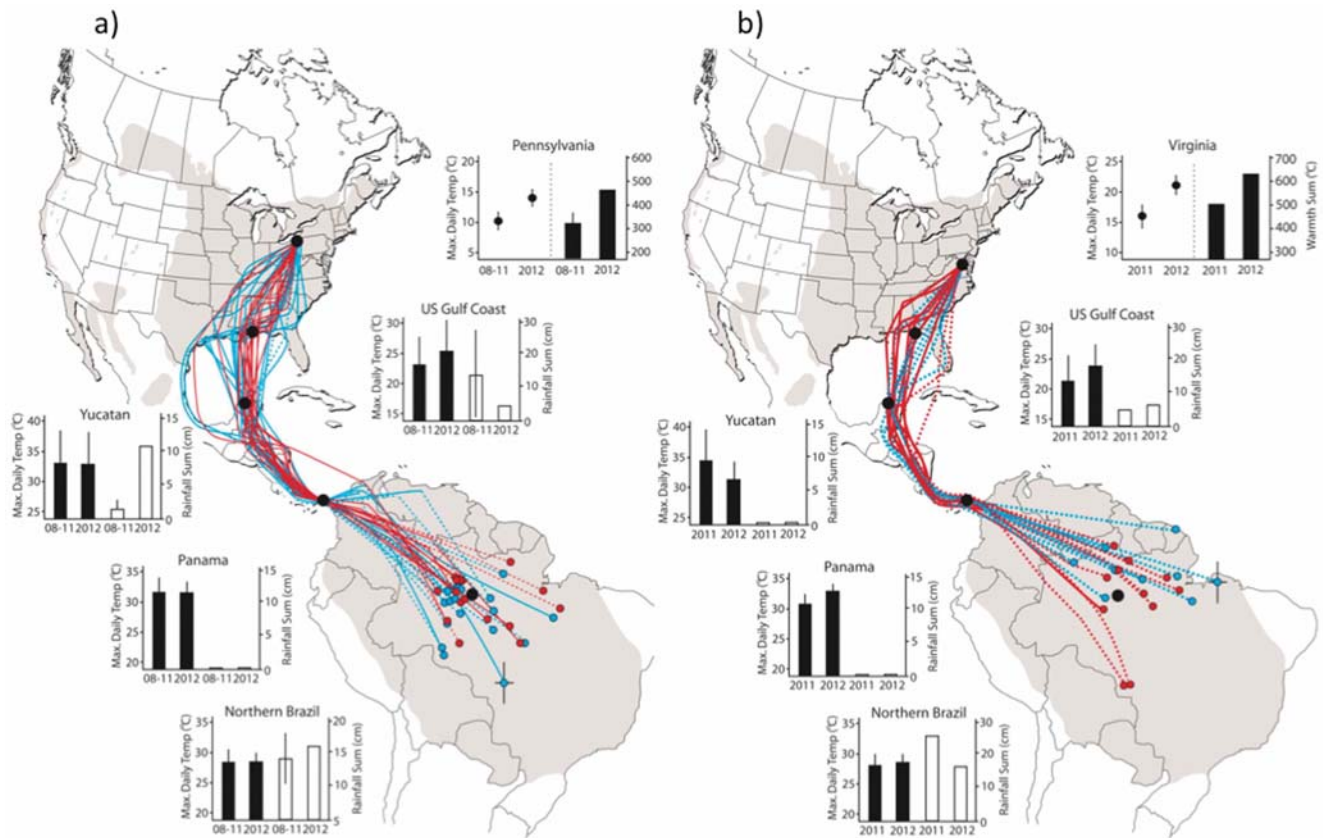
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Figure 1. Spring migration routes and en route temperatures and rainfall for purple martins. Birds were tracked from two breeding populations a) Pennsylvania (41.8°N, 79.9°W) and b) Virginia (38.61°N, 77.26°W). Spring routes shown in red (2012) and blue lines (2008-11 PA; 2011 VA). Dashed lines show estimated route based on longitude when latitude was uncertain due to equinox. Black circles show locations of en route temperature and rainfall measurements and correspond to adjacent graphs showing mean ± SD temperature during passage (10 d pre-and post-median passage date) and rainfall sum (30 d pre-median departure/passage date; ± SD where multiple years). Breeding site graphs (Pennsylvania and Virginia) show maximum daily temperature and spring warmth sum at breeding sites March 15– April 15 (circles show mean, bars standard deviation). Last winter roost locations in South America before spring migration are shown by red and blue circles. Error bars, shown for one bird on each map, are typical standard deviation in latitude and longitude for estimated winter locations.
doi:10.1371/journal.pone.0064587.g001

2012 at Panama for birds from the Virginia breeding population and a trend for higher temperatures in 2012 for both populations once birds reached the U.S. Gulf Coast (Table 1; Fig. 1). Rainfall at wintering and passage sites was not consistently higher in 2012.

Based on our model results, neither rainfall amount or temperature were significant factors predicting departure date from South American overwintering sites in the Amazon Basin. Our best-fit models of migration departure date included only sex and breeding location (PA or VA) and both were significant in the model (sex: $r^2 = 4.71$, df = 1; breeding location: $r^2 = 16.27$, df = 1, P<0.0001). On average, males left 5 days earlier than females and individuals breeding at the more southerly Virginia colony departed 14 days earlier than birds breeding in Pennsylvania. We had similar results for migration timing en route at Panama, Yucatan and breeding arrival where best-models included only sex and breeding location. Both factors were significant in the models except for sex at the Yucatan ($r^2 = 3.77$, df = 1, P<0.052). None of the factors in our models of migration rate during each of the three stages of migration (SA, CA, NA) were significant, illustrating that birds did not differ their rate in response to temperature or rainfall en route and that rate did not differ by breeding location or sex.

Discussion

We found no evidence that purple martins advanced their departure date from South America, or increased their migration rate, during the warmest spring on record at breeding sites in eastern North America. Consistent temperature and rainfall cues were not present in South or Central America, and these weather variables were not significant predictors of departure date and en route migration timing and rate. These results, based on direct-tracking of purple martin, are surprising and contrast recent papers that show that some species may be able to increase rate in response to conditions en route [19,20,21] or in general enact a strong phenotypic response to changing weather and environmental conditions [5,6,7,22,23].

Spring departure date from tropical overwintering sites of a forest songbird was highly repeatable between years, suggesting limited phenotypic plasticity in some species [24]. Inflexible departure schedules in warm springs could be a result of mostly endogenous control of migration timing [25,26,27] but may also reflect limited environmental cues available to long-distance migrants about conditions at the breeding grounds [11,12,13]. Purple martins apparently received limited or conflicting environmental cues of an early spring at breeding sites while still at wintering sites and en route. Once en route, birds received no (PA

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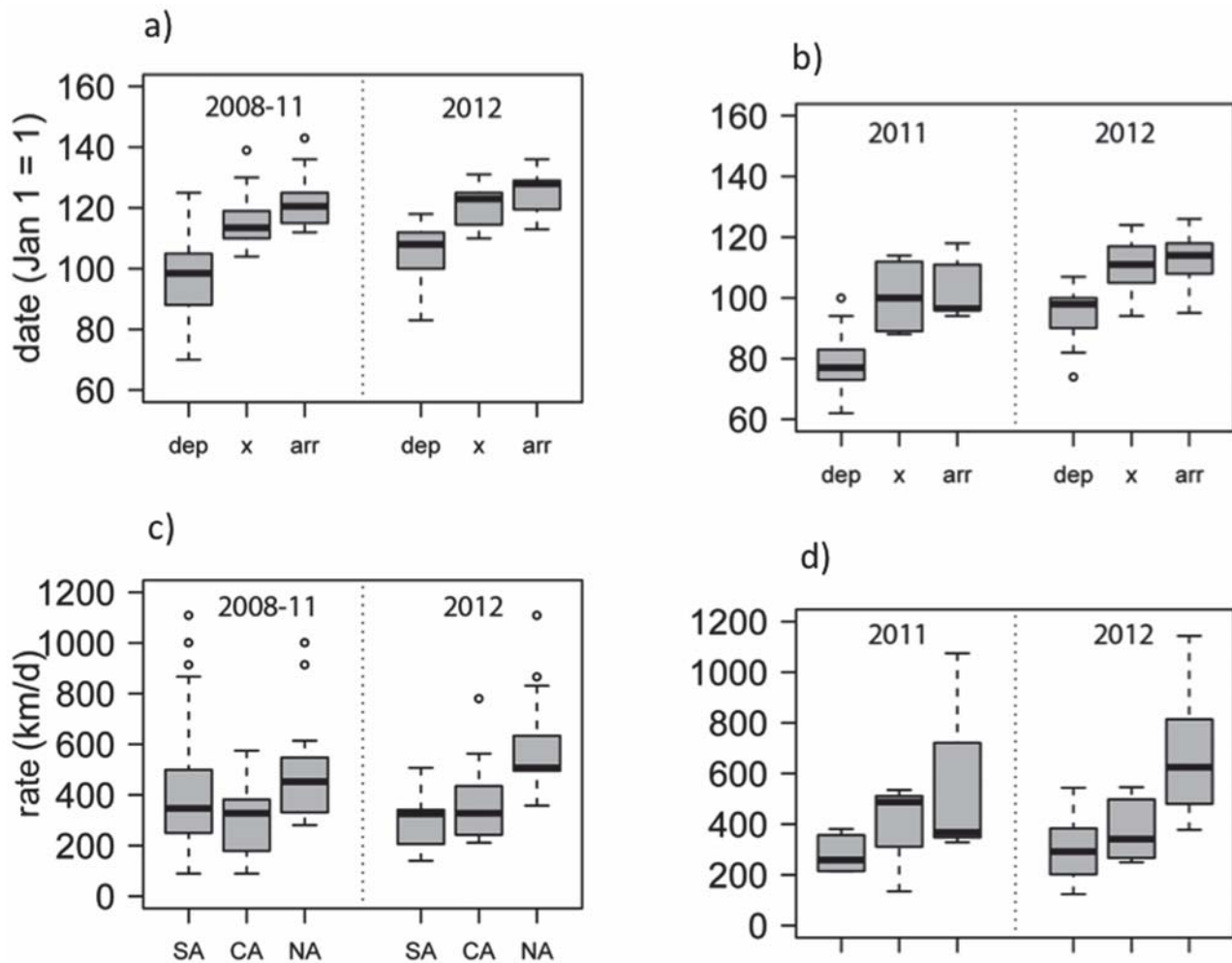
Figure 2. Migration rate of purple martins in record warm year 2012 versus prior year(s). Timing of spring migration at departure (dep), date crossing 23.4°N (x), breeding arrival date (arr) for breeding populations from a) Pennsylvania and b) Virginia. Spring migration rate during three stages en route (South America, SA; Central America, CA; North America, NA), c) Pennsylvania (2008-11, n = 18; 2012, n = 15) and d) Virginia (2011, SA n = 9, CA n = 6, NA n = 8; 2012, n = 10).
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Table 1. Temperatures experienced by purple martins during peak passage times along migratory routes.

En route location and breeding population tracked	pre-2012	2012	t	P
U.S. Gulf Coast				
Pennsylvania	23.1±4.7	25.2±4.9	−1.72	0.097
Virginia	21.8±3.9	24.1±3.6	−1.95	0.059
Yucatan Peninsula				
Pennsylvania	33.2±5.3	32.9±5.8	−0.21	0.84
Virginia	34.3±5.4	31.0±3.2	2.34	0.03
Panama City				
Pennsylvania	31.8±1.9	32.0±1.9	−0.45	0.65
Virginia	31.0±1.9	32.7±1.0	−3.59	0.001
Manaus, Brazil				
Pennsylvania	28.0±2.1	28.1±1.9	−0.03	0.98
Virginia	27.9±2.0	28.2±1.8	−0.50	0.62

Mean (± SD) maximum daily temperature 10 days before and after median departure date from Brazil, and at passage through Panama, the Yucatan Peninsula, and the U.S. Gulf Coast for birds tracked from two breeding populations (Pennsylvania, n = 33; Virginia, n = 19). Statistics reported from t-tests.
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population) or inconsistent (VA population) temperature cues of the warm spring until they reach the U.S. Gulf coast. However, most martins travelled more than 400 km/d during their final 4–5 day spring passage to their breeding sites, supporting the hypothesis that long-distance migrants have little opportunity to advance their rate of migration in response to temperature cues at the final stage of their journey [4]. Our model results suggest that migration timing and rate in purple martin is not highly sensitive to short-term variation in temperature and rainfall. We suggest that multiple years of increasing spring temperatures may be required to generate an adaptive response of earlier breeding arrival timing of purple martins, via selection for earlier departing individuals. Further direct-tracking data with greater geographic and temporal scope, and repeat tracking of individual birds, is needed to better understand individual plasticity in response to temperature and rainfall along migratory routes.

Aerial insectivores, particularly species migrating longer distances and populations breeding in the north, are experiencing strong population declines [9]. We suggest that this could be driven by constraints on spring departure date, the absence of strong and consistent temperature cues, and low opportunity for rate adjustments during migration leading to a mismatch between arrival date and optimal breeding conditions. Recent direct tracking of other species has shown a strong correlation between departure and arrival date as well as rapid spring migration [28], suggesting many long-distance migrants may have limited opportunities to respond to short-term climatic warming.

Supporting Information

Table S1 Geolocator deployment locations, year, type, number of units deployed, geolocators retrieved (does not include birds who lost tags) and total sample size for spring migration (excludes tags that failed prior to spring migration). Most (75%) geolocators were 1.1 g with a <10 mm stalk (MK10S, British Antarctic Survey) and were mounted using a leg-loop backpack harness [1,2].
(DOCX)

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Appendix D: Fraser KC, BJM Stutchbury, CA Silverio, PM Kramer, J Barrow, D Newstead, N

Mickle, BF Cousens, JC Lee, DM Morrison, T Shaheen, P Mammenga, K Applegate and J Tautin.

2012b. Continent-Wide Tracking to Determine Migratory Connectivity and Tropical Habitat

Associations of a Declining Aerial Insectivore. *Proceedings of the Royal Society Series B*, 279:

4901-4906.

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returned each spring and trapped any purple martins carrying a geolocator.

Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore

Kevin C. Fraser[1],*, Bridget J. M. Stutchbury[1], Cassandra Silverio[1], Patrick M. Kramer[1], John Barrow[2], David Newstead[3], Nanette Mickle[4], Bruce F. Cousens[5], J. Charlene Lee[5], Danielle M. Morrison[5], Tim Shaheen[6], Paul Mammenga[7], Kelly Applegate[8] and John Tautin[9]

[1]*Department of Biology, York University, 4700 Keele St., Toronto, ON, Canada M3J 1P3*
[2]*4146 Congressional Dr., Corpus Christi, TX 78413, USA*
[3]*Coastal Bend Audubon Society, 645 Sharon Drive, Corpus Christi, TX 78412, USA*
[4]*1501 Spoonbill Court, Woodbridge, VA 22191, USA*
[5]*Georgia Basin Ecological Assessment and Restoration Society, #4-1150 N. Terminal Ave, Nanaimo, BC, Canada V9S 5L6*
[6]*15 Wigwam Road, Locust, NJ 07760, USA*
[7]*12345 396th Ave., Columbia, SD 57433, USA*
[8]*Mille Lacs Band of Ojibwe Department of Natural Resources, 43408 Oodena Drive, Onamia, MN 56359, USA*
[9]*Purple Martin Conservation Association, Tom Ridge Environmental Center, 301 Peninsula Dr., Ste. 6, Erie, PA 16505, USA*

North American birds that feed on flying insects are experiencing steep population declines, particularly long-distance migratory populations in the northern breeding range. We determine, for the first time, the level of migratory connectivity across the range of a songbird using direct tracking of individuals, and test whether declining northern populations have higher exposure to agricultural landscapes at their non-breeding grounds in South America. We used light-level geolocators to track purple martins, *Progne subis*, originating from North American breeding populations, coast-to-coast ($n = 95$ individuals). We show that breeding populations of the eastern subspecies, *P. s. subis*, that are separated by *ca.* 2000 km, nevertheless have almost completely overlapping non-breeding ranges in Brazil. Most (76%) *P. s. subis* overwintered in northern Brazil near the Amazon River, not in the agricultural landscape of southern Brazil. Individual non-breeding sites had an average of 91 per cent forest and only 4 per cent agricultural ground cover within a 50 km radius, and birds originating from declining northern breeding populations were not more exposed to agricultural landscapes than stable southern breeding populations. Our results show that differences in wintering location and habitat do not explain recent trends in breeding population declines in this species, and instead northern populations may be constrained in their ability to respond to climate change.

Keywords: geolocator; songbird; South America

1. INTRODUCTION

Population dynamics of neotropical migratory songbirds are driven by the interaction of productivity on the breeding grounds and mortality, which occurs primarily during migration and the non-breeding season in the tropics [1–3]. Migratory birds are predicted to be more vulnerable to habitat disturbance and environmental change at their wintering grounds if they exhibit strong migratory connectivity, in which most members of a given breeding population migrate to the same region within the non-breeding range [4,5]. In contrast, species with weak migratory connectivity are buffered from habitat disturbance in specific non-breeding regions because reduced survival of individuals is spread diffusely across the breeding range [6]. However, understanding the population dynamics of long-distance migratory songbirds has been hampered by the difficulty in determining migratory connectivity [2,6] because until recently it was not possible to track migration of songbirds [7].

Connectivity patterns between breeding and wintering sites thousands of kilometres apart have been determined for migratory songbirds using large-scale band-recovery efforts [8–10], but for many species recovery records

linking breeding and tropical 'wintering' sites are too infrequent. Stable isotope values of feathers, and to a lesser extent genetic markers, have been used to document migratory connectivity in several songbirds, but precision is generally restricted to large geographic regions [11–14]. Songbirds can exhibit coarse patterns of east–west parallel connectivity at a continental [10,12,14,15] or subcontinental [8,16] scale. Less common are patterns of leapfrog migration, where northern breeding populations have relatively southern non-breeding destinations [17], and crossover connectivity, in which western populations are connected to eastern non-breeding regions [18].

Many aerial insectivores in North America, particularly long-distance migrants, have experienced steep population declines since the mid-1980s [19,20]. There is a strong geographic pattern in declines, which are more prevalent towards the northeast of North America. One explanation for this pattern is that north-eastern regions receive relatively high levels of atmospheric pollutants, including acid precipitation, which in turn has negative effects on insect abundance and thus productivity of aerial insectivores [20]. Climate change is also expected to disproportionately affect populations in more seasonal habitats due to a phenological mismatch between food availability and timing of breeding in long-distance migrants [21]. Agricultural pesticide use may also influence aerial insectivore populations, through broad changes in their prey base [22]. Nebel *et al.* [20] suggested that northern populations may face higher mortality on the wintering grounds due to agricultural pesticides in South America, either through direct mortality or indirectly via reduction in food availability [23]. Associations with agricultural landscapes in the winter quarters could increase exposure to pesticides and their effects, potentially influencing year-round population dynamics of long-distance migratory birds. If this latter hypothesis is correct, then migratory connectivity should be strong in aerial insectivores and northern populations are predicted to have stronger associations with agricultural landscapes in the non-breeding season.

For the first time, using light-level geolocators, we tracked individual ($n = 95$) songbirds that originated from coast-to-coast breeding populations in North America and travelled to wintering sites in South America. Purple martins, *Progne subis*, are declining throughout much of their northern range [19,20] and their non-breeding range extends from the relatively undisturbed upper Amazon basin down to southern Brazil where the landscape has been converted almost entirely to agricultural use. Our primary objectives were to (i) measure the range-wide degree of migratory connectivity between breeding and non-breeding populations of purple martin and (ii) determine whether northern populations of this declining aerial insectivore may face distinct threats through greater association with agricultural habitat at their non-breeding grounds in South America.

2. METHODS

(a) *Geolocator deployment*
Purple martins were captured and fitted with geolocators during the breeding season by trapping birds in nest boxes at eight breeding locations across the range ($n = 421$, electronic supplementary material, table S1). Geolocators (≤ 1.6 g; MK10s/12/12s/14s/20, British Antarctic Survey) were mounted using a leg-loop backpack harness [7,24] constructed with Teflon ribbon or, in some cases, polypropylene thread. Geolocators were retrieved ($n = 120$) at the same breeding sites in the year following deployment. Geolocator battery failure prior to arrival and residency at winter roosts reduced sample size to 95. At the Pennsylvania breeding site (2009–2011), the return rate of birds wearing geolocators was not lower than that of banded birds without geolocators (see the electronic supplementary material, table S2). Harness failure occurred for 10 per cent of birds when using a thread harness but only 3 per cent of birds using a Teflon harness.

(b) *Analysis of light data from geolocators*
Geolocators measured the intensity of visible light every 1 min and recorded the maximum reading within each 10 min interval (MK16, MK10) or each 2 min interval (MK12, MK20). Raw light data were corrected for clock drift (1–3 min lost during 10-month deployment) using BASTrak and analysed using TransEdit (British Antarctic Survey). We manually verified a sharp transition at each sunrise and sunset and ignored obvious shading events during the daytime. We used a light threshold level of 32 (MK16, MK10) or 5 (MK12, MK20) to define sunrise and sunset transitions, and used live calibration data (see below) from birds prior to migration to determine the average sun elevation that corresponded with this light threshold level at the breeding site. Transitions with light peaks or non-linear transitions before sunrise or after sunset were rejected from further analysis. Latitude was not determined for 15 days before and after the fall equinox when day length is similar everywhere.

Latitude and longitude coordinates were calculated with Locator software (British Antarctic Survey) using midnight locations because purple martins are diurnal migrants, and therefore midnight locations should be more accurate because birds are stationary during the night. No compensation for longitudinal movement was made when estimating latitude because birds were assumed to be stationary from sunset to sunrise. Locations that were clearly anomalous (i.e. >1000 km from previous location) were rejected as outliers.

All geolocators received a static pre-deployment and post-deployment calibration for 1 week in open habitat with a clear view of the horizon, to assess light sensitivity of units. Light sensitivity was virtually identical among units of similar model and was similar before and after deployment. Analysis of live locations for birds prior to migration was used to determine the average sun elevation (BASTrak, British Antarctic Survey) that corresponds to the light level (32 or 5, depending on geolocator model) that was used to define sunrise and sunset transitions. The sun elevation, in turn, is used in Locator (British Antarctic Survey) to determine location given the sun's position on a given date and time. Sun elevation was calculated separately for different geolocator models, after birds finished nesting but before migration, and averaged across individuals within each year to better represent average conditions for migrating birds at unknown locations.

(c) *Estimating geolocator error*
Geolocation accuracy was estimated for birds at each of the eastern breeding populations by averaging locations of individuals in late July and early August, prior to autumn migration. Average geolocator estimates closely matched breeding sites (see the electronic supplementary material,

table S3), and geolocator positions for individuals mismatched breeding sites by an average of 49–60 km in latitude (range: 0–210 km) and 38–48 km in longitude (0–196 km). Differences in geolocation accuracy among individuals reflect individual pre-migration habitat at dawn and dusk and differing weather conditions at the time of live calibration. During the pre-migration period, the standard error of latitude for an individual ranged from 0.15 to 1.0 (avg. 0.3) and for longitude ranged from 0.06 to 0.36 (avg. 0.2).

Arrival at the wintering ground was considered to have occurred when the latitude and longitude ceased to shift in a direction consistent with autumn migration, fluctuated around a narrow range of values (less than 2° longitude), consistent with a stationary bird, and fluctuated around a similar value for at least 10 days within the winter range. During stationary periods at the wintering grounds, location was determined by calculating average latitude and longitude during the period. Most (63 of 95) martins shifted roost locations while at the wintering grounds, averaging *ca*. 700 km between sites.

(d) Band recovery data for connectivity

Band recovery data can be used to independently assess migratory connectivity, and to supplement geolocator tracking data [8]. Analysis of North American band recovery data (1921–2010) for purple martins banded at breeding sites ($n = 2884$ recoveries) identified 12 birds that were recovered in South America after autumn migration and before spring migration (see the electronic supplementary material, figure S1). However, 11 of 12 birds were banded as a nestling and therefore their first breeding site was unknown. Band recovery data were therefore not included in our analyses.

(e) GIS data and analysis

Northern breeding populations of purple martins (*P. s. subis*) are declining more severely than central or southern populations (figure 2*a*). For all roost sites in South America occupied for ≥ 30 days, we used kernel density analysis to test whether the core wintering region of northern breeding populations was associated with more extensive agricultural land use than breeding populations from central and southern regions. We measured winter roost density of northern (SD, MN, PA, NJ, $n = 59$ individuals, 97 roosts) versus southern and central (VA, OK, TX, $n = 30$ individuals, 55 roosts) breeding populations based on points of 1–3 roosts per individual bird using fixed kernel densities in the program ArcGIS 10 [25]. We determined kernel densities at 20, 40, 60 and 80 per cent of the total density using a sample radius of 50 km (or 0.45 decimal degrees) and a cell size of 1 km². We derived land-cover data for the purple martin wintering range in South America from Eva *et al.* [26]. We calculated per cent of agricultural land-cover versus forest and other vegetated, non-agricultural cover (hereafter called forest) within a 50 km radius (which corresponds to longitudinal geolocator error) around each winter roost and compared roosts of northern versus south-central breeding birds using a *t*-test.

3. RESULTS

Migratory connectivity was very weak, and there was extensive overlap in non-breeding sites within South America for martins originating from across eastern North America (figure 1). Individuals from breeding

sites up to 2000 km apart in both latitude and longitude were often mapped to within 100 km of each other in South America, the limit of geolocator accuracy. Birds from the western subspecies, *P. s. arboricola* ($n = 6$), appear to have a distinct wintering region in southeastern Brazil, whose core area is *ca*. 3000 km from the core wintering region of the eastern subspecies.

Most individuals (76%; 68 of 89) of the eastern subspecies roosted for the longest period in northern Brazil (*ca*. 6° S to 1° N) from the Rio Negro region eastward to the mouth of the Amazon River (64° to 47° W). Many individuals had multiple roost sites that they occupied for at least 30 days (1 roost: 26%; 2 roosts: 61%; 3 roosts: 11%). Individuals moved an average of 700 km between roost sites (up to 1400 km in some cases), but all these additional roosts were within the same geographic region as defined by the longest occupied roosts. The average occupancy of the longest roost (124 days) was more than double that of other roost sites (2nd longest roost: 55 days, 3rd longest: 43 days). For the longest occupied roosts, there was no significant correlation between breeding and wintering latitude ($r_s = -0.12$, $p = 0.80$, $n = 89$), or between breeding and wintering longitude ($r_s = -0.04$, $p = 0.77$, $n = 89$) (see the electronic supplementary material, figure S2) and sex was not a significant factor in winter roost location ($t = -1.46$, df = 90, $p = 0.15$).

Individuals from a discrete breeding population had a broad distribution at the wintering grounds. For the Pennsylvania population, for instance, the average distance between individuals, for the longest occupied roost sites, was 903 km (±23 km SE, $n = 34$ individuals, 561 comparisons) with an average nearest neighbour distance of 140 ± 20 km and average farthest neighbour distance of 1787 ± 336 km.

Birds originating from northern and south-central North American breeding populations shared a similar and mostly overlapping over-wintering area centred in northern Brazil near the Amazon River (figure 2*b*). The distance between the centre of northern (lat. $-2.51°$, long. $-62.19°$) and south-central (lat. $-1.34°$, long. $-61.6°$) wintering ranges was just 144 km, within a region dominated by relatively undisturbed evergreen tropical forest (figure 2*b*). Ground cover within 50 km of overwintering roosts was mostly forest (average for all birds $91\% \pm 1$ forest and $4\% \pm 0.8$ agriculture). Northern breeding birds did not have greater per cent agricultural ground cover at winter roosts than birds from southern and central breeding sites ($t = -0.59$, df = 109, $p = 0.55$).

4. DISCUSSION

For the first time, we determined the degree of range-wide migratory connectivity between northern breeding populations and corresponding non-breeding areas in the tropics using direct tracking of individual songbirds. We show that seven breeding populations of the eastern subspecies of purple martin (*Progne s. subis*) exhibit very weak connectivity, and share a broad, overlapping non-breeding region along the Amazon River in northern Brazil. This is remarkable, considering that breeding populations were separated by up to 2000 km, and other songbird species have exhibited sub-continental patterns of connectivity [8,16]. This shared core area
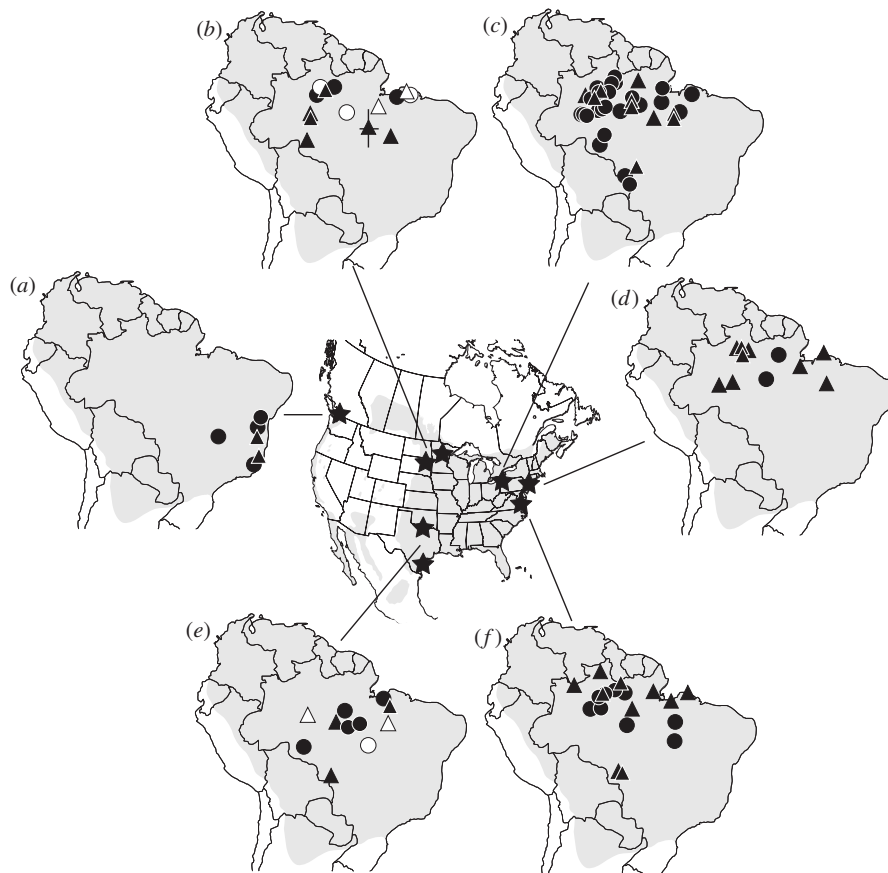
Figure 1. Migratory connectivity of purple martin breeding populations tracked with geolocators to South America; range shown with grey shading. The site with the longest winter residency (124 ± 5.4 days, $n = 95$) is shown for each individual (triangles are males, circles are females) from (*a*) British Columbia ($n = 6$), (*b*) Minnesota (white, $n = 5$) and South Dakota (black, $n = 9$), (*c*) Pennsylvania ($n = 34$), (*d*) New Jersey ($n = 11$), (*e*) Oklahoma (white, $n = 3$) and Texas (black, $n = 8$), and (*f*) Virginia ($n = 19$). British Columbia birds are *Progne subis arboricola* and all other populations are *P. s. subis*. Error bars for roost location in (*b*) shows typical standard deviation in latitude and longitude for estimated winter locations. Map of North America shows the breeding range in grey and stars indicate the location of geolocator deployments.

encompasses only about 20 per cent of the entire wintering distribution of the species, yet supports an estimated 80 per cent of the eastern subspecies. Threats to the core overwintering areas in the upper Amazon could therefore influence population dynamics across the eastern breeding range of purple martin.

Long-distance migratory songbirds that feed on aerial insects, as a group, show strong breeding population declines, with steeper declines in more northern populations of several species [20]. Direct tracking of individual Swainson's hawk (*Buteo swainsonii*) using satellite tags revealed that breeding population declines in North America were likely a result of intensive spraying of organophosphate insecticides and associated mortality (approx. 1% of global population) at wintering sites in South America [23,27]. Similarly, range-wide declines in dickcissel (*Spiza americana*) were attributed to associations with intensive agriculture and persecution at their South American wintering sites [28]. The use of agricultural habitats in the non-breeding season could expose purple martins to pesticides, causing either direct mortality or reduced food availability with subsequent fitness costs, potentially contributing to declines observed at breeding areas [20]. However, we found no significant difference between declining and stable breeding populations in the use of agricultural non-breeding habitat. The core 'wintering' region for the eastern subspecies of purple martin, including declining northern breeding populations, is dominated by largely undisturbed tropical rainforest (figure 2*b*). Our kernel density analyses show that the centre of the core over-wintering area of northern and south-central birds was only 144 km apart. Owing to this overlap, eastern breeding populations likely experience similar conditions at their overwintering sites in South America, and wintering ground events are unlikely to be the cause of differential population declines in breeding populations. Thus we conclude that exposure to agricultural landscapes does not appear to be the cause of declines of northern breeding populations.

Proposed alternative explanations for population declines of purple martins (and other aerial insectivores) include the effects of acid rain on prey abundance at breeding sites, which is greatest in the northeast, and climate change [20]. For the latter, constrained migratory schedules can limit adaptive responses to climate change, and can result in severe population declines of long-distance migratory songbirds [21,29,30], and these patterns are expected to be stronger for birds in more seasonal habitats [21], such as more northern breeding sites of purple martin.
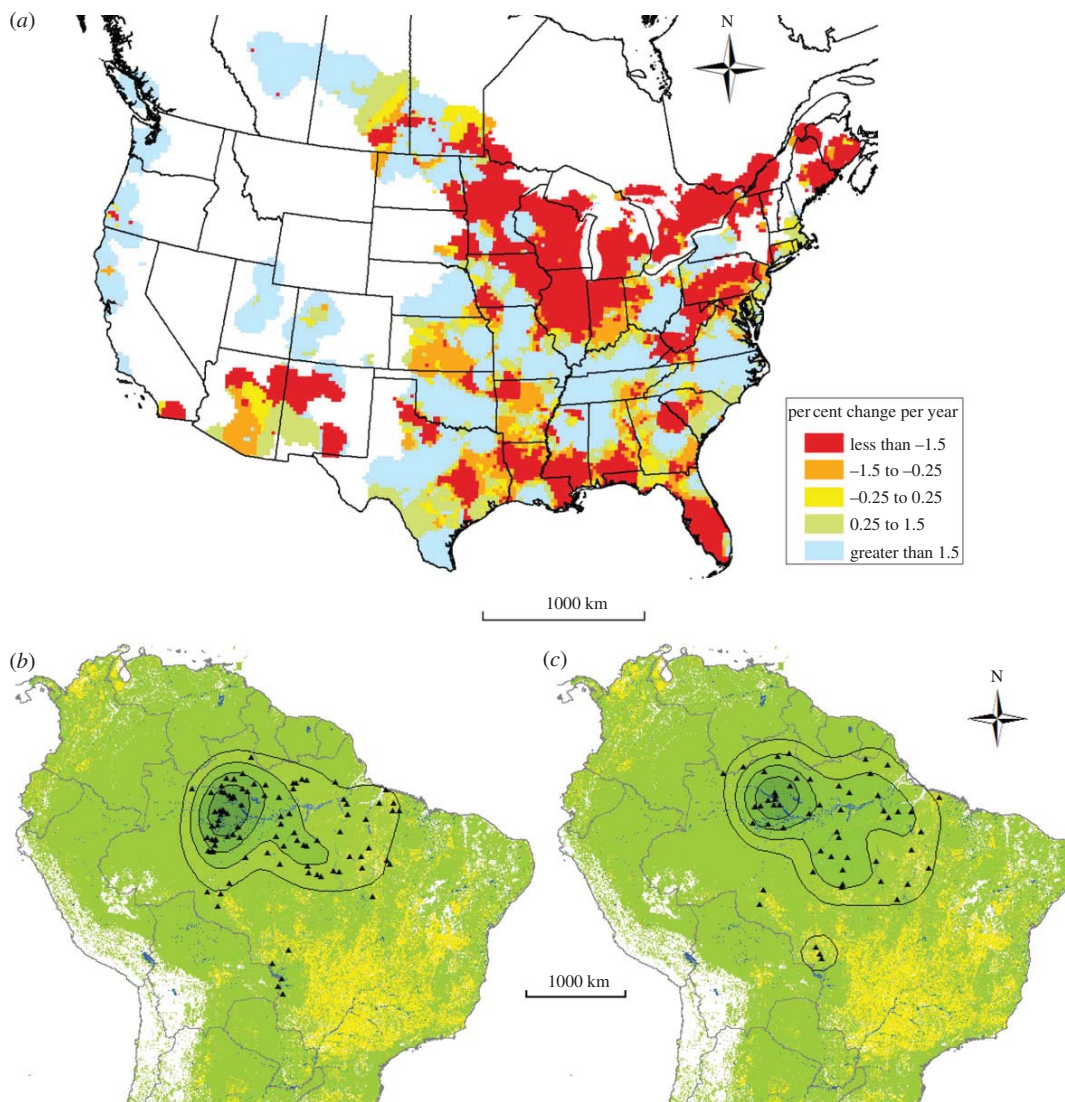
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Figure 2. (*a*) Population trends based on the BBS data (1966–2010). Kernel density of all winter roost locations occupied for ≥30 days by martins (*P. s. subis*) from (*b*) northern breeding populations (Minnesota, South Dakota, Pennsylvania, New Jersey; $n = 59$ individuals, 97 roosts) and (*c*) central/southern breeding populations (Oklahoma, Texas, Virginia; $n = 30$ individuals, 55 roosts). Maps show kernels of 20, 40, 60 and 80% of the total density. Green shading represents forest and non-agricultural vegetated cover; yellow shading represents agricultural lands.

Populations of long-distance migratory birds may be most limited during the overwintering and migratory period, thus it is important to determine connections between different periods of the annual cycle in order to better understand, and mitigate, population declines [2]. Determining continent-wide connectivity using direct tracking provided the surprising result that breeding populations separated by up to 2000 km share a broad overwintering region in South America, suggesting that future habitat disturbance in this region would have a broad influence on population dynamics across the range. We also quantified habitat use thousands of kilometres away from breeding sites to show that the patterns of population decline in this long-distance migratory aerial insectivore are not associated with different threats on the wintering grounds. The dramatic increase in direct tracking of songbirds will soon establish the levels of migratory connectivity in a wide range of

species, allowing for better conservation and management of declining songbirds.

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Appendix E: Fraser KC, BJM Stutchbury, PM Kramer, CA Silverio, J Barrow, D Newstead, N Mickle, T Shaheen, P Mammenga, K Applegate, E Bridge and J Tautin. 2013. Consistent Range-Wide Pattern in Fall Migration Strategy of Purple Martin (*Progne subis*), Despite Different Migration Routes at the Gulf of Mexico. *The Auk*, 130(2): 291-296.

I was involved in the planning and implementation of fieldwork portion of this project for deployments and retrievals on purple martins. I trapped adult purple martins, measured, banded and blood sampled them prior to them receiving a geolocator. Conducted most of the visual searching for tagged individuals as they returned each spring and trapped any purple martins carrying a geolocator.

CONSISTENT RANGE-WIDE PATTERN IN FALL MIGRATION STRATEGY OF PURPLE MARTIN (*PROGNE SUBIS*), DESPITE DIFFERENT MIGRATION ROUTES AT THE GULF OF MEXICO

Kevin C. Fraser,[1,10] Bridget J. M. Stutchbury,[1] Patrick Kramer,[1] Cassandra Silverio,[1]
John Barrow,[2] David Newstead,[3] Nanette Mickle,[4] Tim Shaheen,[5] Paul Mammenga,[6]
Kelly Applegate,[7] Eli Bridge,[8] and John Tautin[9]

[1]*Department of Biology, York University, Toronto M3J 1P3, Canada;*
[2]*4146 Congressional Drive, Corpus Christi, Texas 78413, USA;*
[3]*Coastal Bend Audubon Society, Corpus Christi, Texas 78401, USA;*
[4]*1501 Spoonbill Court, Woodbridge, Virginia 22191, USA;*
[5]*15 Wigwam Road, Locust, New Jersey 07760, USA;*
[6]*South Dakota Department of Game, Fish and Parks, Aberdeen, South Dakota 57401, USA;*
[7]*Mille Lacs Band of Ojibwe Department of Natural Resources, Onamia, Minnesota 56359, USA;*
[8]*Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, Oklahoma 73019, USA; and*
[9]*Purple Martin Conservation Association, Erie, Pennsylvania 16505, USA*

Abstract.—The migration rate of Nearctic–Neotropic songbirds is expected to be influenced by whether the route is around or across migration barriers such as the Gulf of Mexico. To examine factors that influence fall migration strategies, we used light-level geolocators to track the journeys of 91 Purple Martins (*Progne subis*) originating from breeding colonies across the eastern range of the species. We expected individuals that crossed the Gulf of Mexico to have slower migration rates, and more stopover days in Central America to refuel after the crossing, than birds that took routes around the gulf. Owing to expected variability in conditions experienced by individuals en route, we anticipated that departure date would be a poor predictor of arrival date within and among populations. Despite widely separated breeding origins, one-way journeys of >7,000 km, and high variability in departure dates and routes, individuals showed a strikingly similar fall migration strategy. Fall migration featured a rapid (450 km day^{-1}) initial migration covering ≥2,000 km, followed by prolonged stopovers and a slower rate of travel before the birds continued to South America. Contrary to predictions, route explained little of the variation in the overall migration rate or the rate to Central America. Stopover duration in Central America was unrelated to whether birds crossed or circumnavigated the Gulf of Mexico. As expected, breeding location (primarily longitude) was the strongest predictor of the routes that birds took at this barrier. Within-breeding-region departure date alone predicted much of the variation in arrival date at the first winter roost, but route was not a significant factor. Our results reveal a consistent range-wide pattern in fall migration strategy, with route and migration timing predicting little of the variation in rate or stopover duration. *Received 1 December 2012, accepted 19 March 2013.*

Key words: autumn migration, geologger, migration rate, migration schedule, *Progne subis*, Purple Martin, songbird, South America, stopover.

Patrones Consistentes en las Estrategias de Migración de Otoño de *Progne subis* en Toda su Distribución a Pesar de Presentar Rutas Migratorias Diferentes en el Golfo de México.

Resumen.—Se espera que la tasa de migración de aves canoras entre el Neártico y el Neotrópico se vea influenciada por si la ruta migratoria se da alrededor o a través de barreras para la migración como el golfo de México. Para examinar los factores que influyen en las estrategias de migración de otoño, usamos geolocalizadores basados en niveles de luz para seguir el viaje de 91 individuos de la especie *Progne subis* desde colonias reproductivas distribuidas en el sector oriental de la distribución de la especie. Esperábamos que los individuos que cruzaban el golfo de México presentaran tasas de migración más lentas, y más días de parada en Centro América para reabastecerse después del cruce en comparación con las aves que tomaban rutas rodeando el golfo. Debido a la variabilidad esperada en las condiciones experimentadas por cada individuo en la ruta, anticipamos que la fecha de salida sería un predictor pobre de la fecha de llegada dentro de poblaciones y entre poblaciones. A pesar de que los sitios originales de reproducción estaban ampliamente separados, de los viajes de más de 7000 km y de la alta variabilidad en las fechas y rutas

[10]E-mail: fraserkev@gmail.com

de salida, todos los individuos mostraron una estrategia de migración de otoño sorprendentemente similar. La migración de otoño consistió de una migración inicial rápida (450 km día^{-1}) de más de 2000 km, seguida por paradas prolongadas y una tasa más lenta de viaje antes de que las aves continuaran hacia Sur América. De modo contrario a nuestras predicciones, la ruta explicó poco de la variación en la tasa migratoria general o en la tasa de llegada a Centro América. La duración de las paradas en Centro América no estuvo relacionada con el hecho de que las aves hubiesen cruzado o circunnavegado el golfo de México. Como se esperaba, la localidad de reproducción (principalmente la longitud) fue el predictor más fuerte de las rutas que tomaron las aves al encontrarse con esta barrera. La fecha de salida estimada dentro de las regiones reproductivas predijo por sí sola mucha de la variación en la fecha de llegada al primer sitio de descanso de invierno, pero la ruta no fue un factor significativo. Nuestros resultados revelan un patrón consistente a través de la distribución geográfica de *P. subis* en la estrategia migratoria de otoño, y que muy poca de la variación en la tasa de migración o en la duración de las paradas fue explicada por la ruta y el momento en que tiene lugar la migración.

Route selection and migration rates of birds may be shaped by selection pressure to avoid risk and arrive optimally at both stopover locations and final destinations (Alerstam 2003, Newton 2008). Large open-water crossings, such as the Gulf of Mexico, may serve as migration barriers and influence migration rates if birds require greater refueling time before or after crossing (Newton 2008). Factors that affect individual decisions to either cross or circumnavigate large barriers, and subsequent effects of that decision on migration rate and arrival date at wintering sites, are poorly understood. For passerines, other factors such as departure date and migration distance may also affect migration rate. Birds that depart breeding sites later in the year may be able to accumulate larger fat stores prior to migration that support a faster migration rate and effectively allow them to "catch up" to birds that departed earlier (Fransson 1995, Newton 2008). Birds with longer overall migration distances may also travel at a faster rate; passerines traveling through Europe to destinations 1,000 km away traveled at about half the rate of those with journeys of 5,000–6,000 km (Alerstam 2003). Owing to variability in migration speed, stopover duration, and routes, departure date alone is expected to be a poor predictor of arrival date at the destination (Newton 2008, Both 2010).

Previous estimates of fall migration strategy (here referring to rate, departure date, arrival date, and stopover duration or timing) have been based largely on band recovery data, providing only a snapshot of behavior. Direct tracking using geolocators allows an examination of migration strategies for many individuals over the whole of the migratory journey. We tracked the transhemispheric migration of individual Purple Martins (*Progne subis*) that originated from seven breeding populations spanning the eastern part of the species' North American breeding range. We expected, given the wide spread in latitude and longitude between breeding populations, that the fall migration route would differ among populations, particularly at the Gulf of Mexico. We predicted greater stopover duration and a slower rate of travel in Central America for individuals crossing the Gulf of Mexico (800–1,000 km) because birds presumably require more refueling time after a nonstop flight across a large open-water barrier than after they follow an overland route around the barrier (Newton 2008). Because en route factors experienced by individual birds are expected to uncouple the relationship between departure and arrival date within and among populations (Newton 2008, Both 2010), we predicted that departure dates in fall would explain little of the variation in arrival dates at winter roosts in South America.

Methods

Geolocator deployment.—Purple Martins were captured and fitted with geolocators over several years during the breeding season in seven regions across the eastern range of the species: Pennsylvania (2007–2011; 41°53′08″N, 80°07′46″W), Texas (2009–2010; 27°41′N, 97°24′W), Virginia (2010–2011; 38°36′47″N, 77°15′46″W), South Dakota (2011; 45°36′00″N, 96°42′00″W and 45°36′59″N, 98°17′59″W), Minnesota (2011; 45°23′59″N, 94°12′00″W; 46°08′59″N, 93°43′11″W; 45°15′36″N, 92°57′22″W; and 45°16′43″N, 92°59′6″W), New Jersey (2011; 40°23′59″N, 74°00′00″W), and Oklahoma (2011; 33°52′51″N, 96°48′1″W). All birds tracked on fall migration were at least 1 year old. See Fraser et al. (2012) for details regarding geolocator type and mounting procedures by population and year. Geolocators were retrieved at the same breeding sites in the year after deployment, and battery failure prior to completion of fall migration reduced the sample size to 91, with lower sample sizes for some variables owing to the equinox (when day length is similar across latitudes) or poor-quality sunrise–sunset transitions because of shading or light pollution.

Analysis of light data from geolocators.—Raw light data were corrected for clock drift using BASTRAK and analyzed using TRANSEDIT (British Antarctic Survey). We manually verified a sharp transition at each sunrise and sunset and ignored obvious shading events during the daytime. Transitions with light peaks or nonlinear transitions before sunrise or after sunset were rejected from further analysis. We used a light-level threshold of 32 (MK16, MK10) or 5 (MK12, MK20) to define sunrise and sunset transitions and used live calibration data from birds prior to migration to determine the average sun elevation that corresponded with this threshold at the breeding site (for additional methods specific to Oklahoma geolocators, see Fraser et al. 2012). Latitude was not determined for 15 days before and after the fall equinox, when day length is similar everywhere. Latitude and longitude coordinates were calculated with LOCATOR software (British Antarctic Survey), using midnight locations because Purple Martins are diurnal migrants. Locations that were clearly anomalous (i.e., >1,000 km from previous location) were rejected as outliers. Sun elevation was calculated separately for different geolocator models, after birds finished nesting but before migration, and averaged across individuals within each year to better represent average conditions for migrating birds at unknown locations. Average geolocator accuracy at each breeding location was assessed prior to fall migration. Average accuracy ranged from 49 to 60 km in latitude (range: 0–210 km) and from 38 to 48 km in longitude (range: 0–196 km) for different breeding sites; see additional details and return rates of birds with and without geolocators in Fraser et al. (2012). Movements of >200 km in latitude and >100 km in longitude away from the breeding site, and from one stopover location to another, were defined as migratory movements. Movements during the fall equinox, when latitude could not be determined, were based on longitude alone. Locations that remained consistent for ≥2 days and were within the location error of stationary birds were defined as stopover locations.

Arrival at the wintering ground was considered to have occurred when the latitude and longitude were consistent with a stationary bird; that is, latitude and longitude (1) ceased to shift in a direction consistent with fall migration, (2) fluctuated around a narrow range of values (<2° longitude), and (3) fluctuated around a similar value for ≥10 days. To explore migration rate and stopover duration in the vicinity of the Gulf of Mexico, we analyzed the migration rate within each breeding population separately for three stages of fall migration: breeding site to the tropics (Gulf of Mexico, ~23.5°N), travel within Central America, and entry into South America to first night at the winter roost. Migration rate is defined as the number of kilometers traveled divided by the total number of days traveled, including stopover days. Migration distance was calculated as the straight-line distance between breeding sites, stopover locations, and winter sites.

Statistical analyses.—To test predictors of circum- versus trans-Gulf crossing, we fit general linear models (GLMs) with breeding latitude, breeding longitude, fall departure date, and sex as factors. Using hypothesis-testing procedures, we dropped the least significant explanatory variables one-by-one on the basis of t and P values to arrive at an optimal model (Zuur et al. 2009). We used similar methods to explore factors that influenced the overall fall migration rate (km day^{-1}) and the rate on the first leg of the journey (between the breeding site and arrival in Central America), with route at Gulf of Mexico (across, east route around, or west route around), departure date, distance (overall and between breeding site and Central America), and sex as factors. We expected the migration rate (overall and first leg) to be faster for birds that traveled a greater distance (Alerstam 2003) and departed later from breeding colonies (Newton 2008). We expected a slower rate of travel for birds that made a direct crossing of the Gulf, owing to greater stopover duration for fueling before and after crossing. We also examined variation in stopover duration (days) in Central America, the ratio of days spent in flight to days spent at stopover, and the arrival date at first winter roost in South America. Because of the presumed greater stopover time needed to fuel before and after a crossing of the Gulf of Mexico, we expected birds taking this route to have a longer stopover in Central America, a lower ratio of flight to stopover nights, and later arrival at winter roosts. To compare variation in migration rate by stage of migration (breeding site to tropics, through Central America, to South America) and breeding region, we fit general linear mixed-effects models with region and stage as fixed factors and individual as a random factor. We grouped breeding regions by longitudinal proximity because we expected longitude to predict route and migration rate. Because of large latitudinal differences between Texas–Oklahoma and South Dakota–Minnesota that might also influence migration strategy, these colonies were grouped separately despite longitudinal similarity. Some migration variables were not available for all birds because of equinox, missing days, and battery failure. All analyses were conducted using R (R Development Core Team 2011). Results are presented as means ± SE unless otherwise noted.

RESULTS

As expected, once birds reached the Gulf of Mexico, the fall migration route varied widely among populations across the breeding range (Fig. 1) and, in some cases, also varied within populations. However, migration routes of Purple Martins at the Gulf
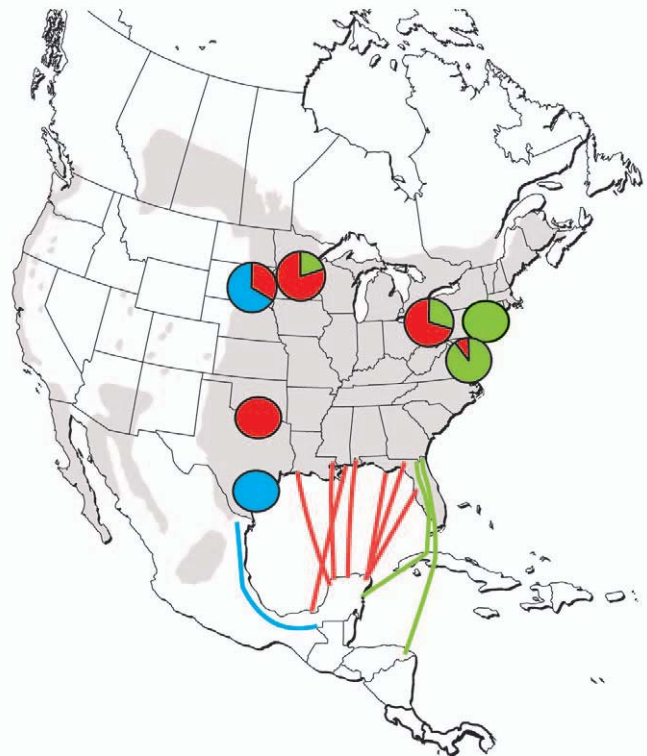

FIG. 1. Breeding sites and fall migration routes at the Gulf of Mexico of birds originating from seven breeding colonies (South Dakota, $n = 9$; Minnesota, $n = 5$; Pennsylvania, $n = 34$; New Jersey, $n = 11$; Virginia, $n = 20$; Oklahoma, $n = 3$; and Texas, $n = 8$). Pie charts show the percentage of birds from each breeding colony that used one of three major routes at the Gulf of Mexico (blue = western route around the gulf, red = direct crossing of the gulf, and green = eastern route around the gulf). Lines illustrate tracks taken by individuals for each of the three major routes.

of Mexico were predicted reasonably well by breeding longitude. Birds from more western breeding populations (South Dakota, Texas) were much more likely to take a western route around the gulf, whereas those from breeding populations nearer to the Atlantic coast (New Jersey, Virginia) took a mostly overland route eastward around the gulf, traversing the Florida panhandle and crossing a shorter open-water distance to Cuba, followed by a flight to either the Yucatan Peninsula or Central America. Birds that bred directly north of the Gulf of Mexico (Pennsylvania) were the most likely to make a direct gulf crossing to the Yucatan Peninsula. In the GLM fitted to describe the route taken at the Gulf of Mexico, only breeding latitude (model estimate = −0.065 ± 0.021) and longitude (model estimate = 0.079 ± 0.012) were retained in the top model ($F = 37.3$, df = 2 and 88, $r^2 = 0.46$, $P < 0.0001$), illustrating that departure time and sex did not predict whether birds crossed or went around the gulf.

Despite different breeding origins and migration routes across or around the gulf (Fig. 1), individuals from widely separated populations (≤2,500 km) and with different migration routes showed a strikingly similar fall migration strategy (Fig. 2). The migration rate was very rapid for the first 2,000 km for all populations (mean breeding population rate = 360–473 km day^{-1}), after which individuals had a slower overall migration rate during the
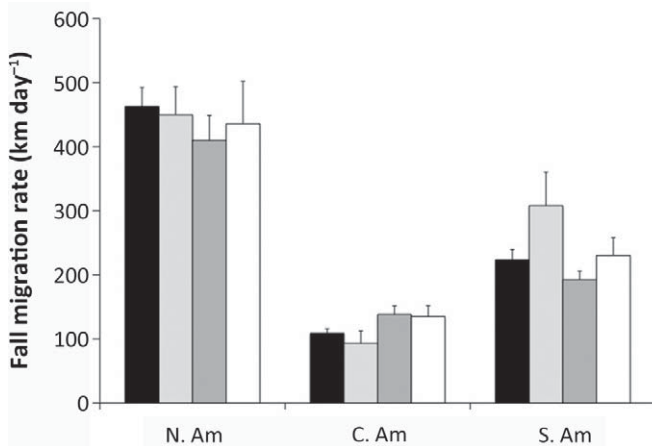
Fig. 2. Mean (± SE) fall migration rate by zone (North America, Central America, and South America) and grouped by breeding region (black bars = Pennsylvania, n = 31; light gray = Oklahoma and Texas, n = 11; dark gray = New Jersey and Virginia, n = 27; and white = South Dakota and Minnesota, n = 14).

second leg of their journey (68–157 km day^{-1}) owing to long stopovers (average [± SD] stopover duration = 16 ± 9; n = 84) in the Yucatan peninsula, Cuba–Caribbean, and Central America before reaching Panama. The migration rate then increased across northern South America (180–361 km day^{-1}) to the first wintering site (Fig. 2). The migration rate varied significantly with stage of migration (North, Central, and South America; t = −8.39, df = 163, P < 0.0001), but breeding region was not a significant predictor of rate (t = −0.34, df = 86, P = 0.73). The route taken at the Gulf of Mexico (across, east route around, or west route around) did not influence the migration rate from the breeding site to the first night at the roost in South America; migration rate was also independent of distance from the breeding colony, departure date from the breeding grounds, and sex (F = 0.43, df = 4 and 83, R^2 = 0.03, P < 0.82). For the first rapid leg of the journey between the breeding site and arrival in the tropics, migration route did not influence rate. Fall departure date and distance were retained as significant factors in the top model but, overall, were poor predictors of migration rate because they explained just 13% of the variation in migration rate (km day^{-1}) between the breeding site and Central America (F = 4.03, df = 3 and 78, R^2 = 0.13, P < 0.01). Fall departure date and migration rate over the entire route were positively correlated (model estimate = 5.95 ± 2.3, t = 2.6, P < 0.01), as were distance from the breeding colony and rate (model estimate = 0.18 ± 0.06, t = 2.97, P < 0.004).

Birds that crossed the Gulf of Mexico were expected to have a greater stopover duration in Central America; however, our GLM results showed that stopover duration was independent of route at Gulf of Mexico, rate and distance from breeding site to Mexico, and sex, in that none of these factors examined to explore variation in stopover duration (days) was significant. Route also did not account for variation in the ratio of flight to stopover days over the whole journey, showing that birds crossing the Gulf did not take a proportionally greater number of stopover days to compensate for the long open-water crossing.

Departure date from the breeding colony alone predicted much of the variation in arrival date at the first winter roosts in South America (Fig. 3). The GLM analysis of arrival date on the winter grounds

included departure date from the breeding ground, route at Gulf of Mexico, overall migration distance, and sex, but only fall departure date (model estimate = 0.881 ± 0.0991) and distance (model estimate = 0.0061 ± 0.0017) were retained in the top model, which explained 56% of the variation (F = 54.42, df = 2 and 86, r^2 = 0.56, P < 0.0001).

Discussion

Purple Martins have been described as leisurely diurnal migrants that forage while migrating (Brown 1997), but our results show that individuals that originated from breeding populations across eastern North America had very rapid migration (440 ± 188 [SD] km day^{-1}) during the first days of fall migration, followed by a prolonged stopover in Central America. It is not known how food supply (aerial insects) varies along the journey or affects stopover duration, or whether stopover sites used in Central America are locations with regionally abundant food resources. Purple Martins do not exhibit the expected stop–refuel–resume strategy thought to be typical of migrating songbirds (Hedenström and Alerstam 1997). Instead, Purple Martins gather at premigratory roosts near their breeding sites for 4–6 weeks prior to fall migration, then travel ~2,000 km in less than 1 week. The prolonged Central American stopover could also be a staging site for subsequent rapid migration to Brazil.

Within species, migration rate is generally predicted to be highly flexible and influenced by the availability of fueling resources at stopover sites, migration routes, migration barriers, distance of migration, weather, molt strategies, and distance to the final destination (Newton 2008). Contrary to predictions, our results reveal that fall route at Gulf of Mexico, departure date, and migration distance were not significant predictors of Purple Martins' start-to-finish migration rate and explained little of the variation in the migration rate to Central America. Whether birds crossed or took an overland route around the Gulf of Mexico also did not influence stopover duration in Central America, which suggests that "barrier" crossing did not require greater time to refuel after an extended migratory flight. It is surprising that our data reveal similar migration rates among widely separated breeding populations and that the overall migration rate is largely independent of breeding origin, timing, route, and distance.

We speculate that the subsequent stopover by many individuals in the Yucatan Peninsula, which includes birds breeding in Texas that made a detour to this region (Fig. 1), is a staging area to refuel for the longer migration to the Amazon basin and/or serves as a location to continue their annual molt. Purple Martins may begin flight feather molt in premigratory roosts that form throughout eastern North America in late summer and early fall (Russell et al. 1998), but museum records suggest that this molt is interrupted during migration (Niles 1972). In some western songbirds, long stopovers in coastal western Mexico are associated with molt (Rohwer et al. 2005, 2009) during the seasonal flush in food resources with monsoon rains. The Yucatan Peninsula may serve Purple Martins in a similar manner; it remains to be determined whether a seasonal abundance of aerial insects there might support the nutritional and energetic costs of molt.

That winter arrival dates in the Amazon basin can be predicted largely from departure dates from breeding sites >6,000 km away is surprising, especially given the different migration routes across (or around) the Gulf of Mexico and long stopovers during
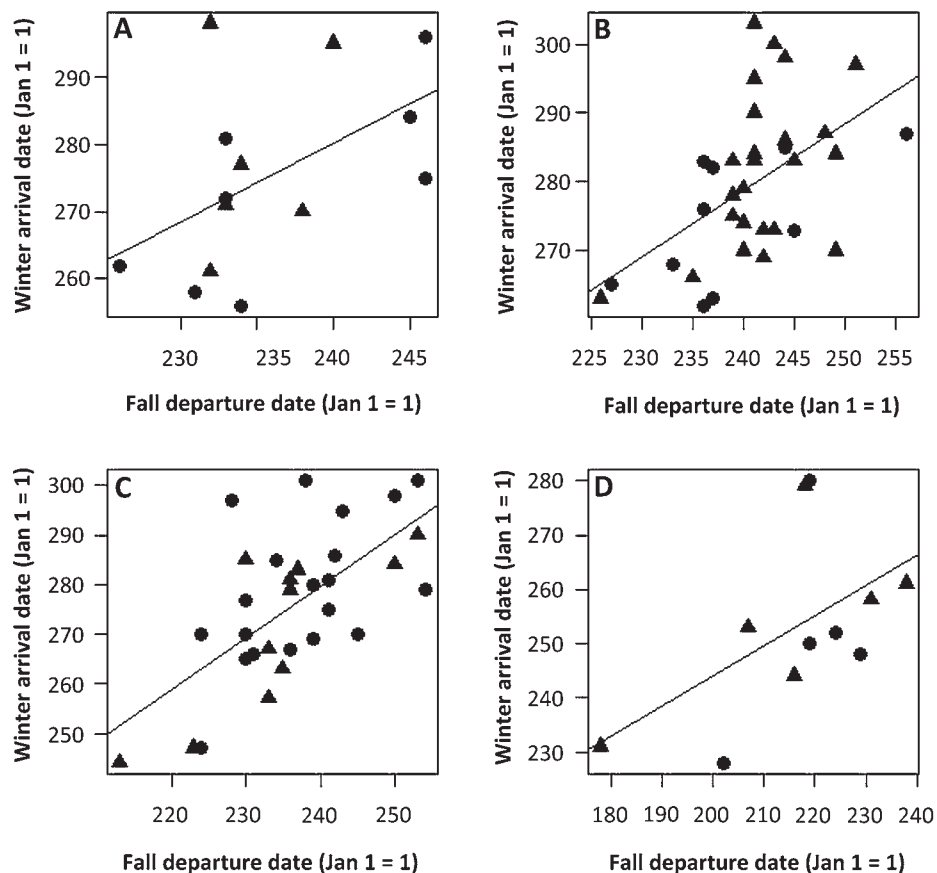
FIG. 3. Within-population patterns of fall departure versus winter arrival date for birds of four breeding regions: (A) South Dakota and Minnesota ($n = 14$, $r^2 = 0.27$, $P = 0.06$), (B) Pennsylvania ($n = 34$, $r^2 = 0.28$, $P = 0.001$), (C) New Jersey and Virginia ($n = 31$, $r^2 = 0.43$, $P < 0.0001$), and (D) Oklahoma and Texas ($n = 11$, $r^2 = 0.30$, $P = 0.08$) (triangles = males; circles = females).

autumn migration (Tøttrup et al. 2012). Even within populations, departure date was a strong predictor of arrival date. A predictable trans-hemispheric migration schedule that includes long stationary periods en route has been described for shorebirds (Hedenström and Alerstam 1997, Conklin et al. 2010) but has not been previously documented in songbirds. We suggest that the range-wide migration strategy described here is more similar to shorebird migration, in which individuals have prolonged staging periods to refuel, followed by rapid migration to the next refueling site (Newton 2008). As in shorebirds and waterbirds (Baker et al. 2004), the convergence of widely separated breeding populations on predictable staging areas during migration increases vulnerability to localized reduction in food resources due to habitat loss or climate change.

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Appendix F: Tarof SA, PM Kramer, JR Hill, J Tautin and BJM Stutchbury. 2011. Brood Size and Late Breeding are Negatively Related to Juvenile Survival in a Neotropical Migratory Songbird. *The Auk*, 128(4): 716-725.

I compiled and digitized 15 years of written banding data from numerous sources into a modern database making this study possible. Starting in 2001, I also contributed thousands of my own observations of marked individuals and banded approximately 1200 nestlings and 200 adults annually. I also conducted the radio-tracking field work including deployment of tags on nestlings and most of the radio-telemetry work.

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

Scott A. Tarof,[1,3] Patrick M. Kramer,[1] James R. Hill III,[2] John Tautin,[2] and
Bridget J. M. Stutchbury[1]

[1]*Present address: Department of Biology, York University, 4700 Keele Street, Toronto, Ontario M3J 1P3, Canada; and
[2]Purple Martin Conservation Association, 301 Peninsula Drive, Suite 6, Erie, Pennsylvania 16505, USA*

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 (φ_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 (φ_m, premigratory roost to 1 year old) using two encounter occasions per season (premigratory roost, breeding colony) to partition annual survival into premigration versus migration–wintering survival. Annual survival (± SE) was 0.27 ± 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 (φ_r) was 0.87 ± 0.03 and migration–wintering juvenile survival (φ_m) averaged 0.32 ± 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 (φ_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 (φ_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 (± DE) fue de 0.27 ± 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 (φr) fue de 0.87 ± 0.03 y la supervivencia de los jóvenes durante el período migración - invernada (φm) fue en promedio de 0.32 ± 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.

[3]E-mail starof@yorku.ca

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 (Sillett 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, Balbontín 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 (φ_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 (φ_r) versus migration–wintering survival (φ_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 (φ_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 ≤300 pairs and, in eastern North America, breed exclusively in artificial housing (Brown 1997). In our study area adults (≥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^{-1} 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^{-1} 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,

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.

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^{-1}) 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^{-1}) 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 (φ_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 ($\varphi_{age*year} p_{age*year}$) was a Cormack-Jolly-Seber model that was age class (juvenile, adult) and time (year) structured for survival (φ) 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$_c$. 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 ($\varphi_{age+year} p_{age+year}$). This model fit better than the general model ($\varphi_{age*year} p_{age*year}$) 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
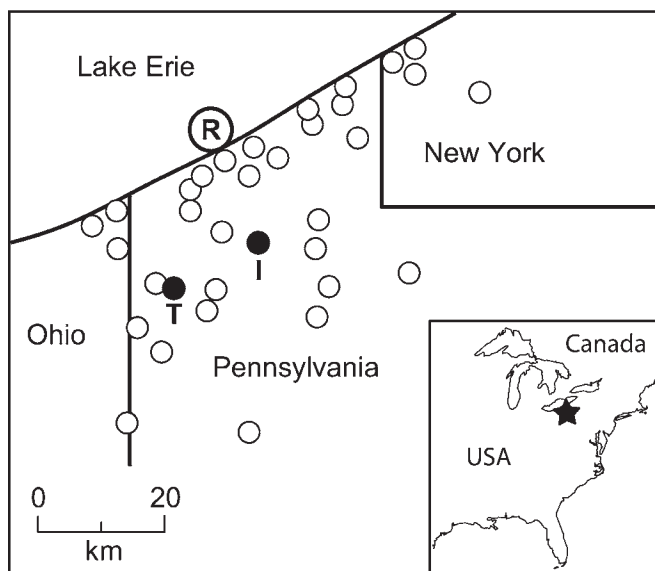
covariates ($\varphi_{age+week+year}$; $\varphi_{age+brood+year}$). We also included a model with interaction between week of fledging and year ($\varphi_{age*week*year}$) because the relationship between survival and week of fledging could vary annually because of population-level differences in timing of breeding. Finally, we included a model with both week of fledging and brood-size effects ($\varphi_{age+week+brood+year}$). For each analysis, we ranked models using QAIC$_c$ 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 (ΔQAIC$_c$). 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 (φ_r) versus migration–wintering survival (φ_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 ± 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 (≤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 (Grüebler 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 ~45° and connected to separate R-1000 receivers programmed for repeat scanning of transmitter frequencies. Signals could be detected ≤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 ($\varphi_{age+week+brood+year}$) included linear effects of week of fledging and brood size (model weight, w_i = 0.93). This model had 13× more support than the model with no brood size effect ($\varphi_{age*week+year}$, w_i = 0.07). The model with a week*year interaction term had far less support (ΔQAIC$_c$ = 18.4) than the additive model (week+year, ΔQAIC$_c$ = 5.2). Using the best-fitting model, apparent annual juvenile survival probability (φ_a) was 0.27 ± 0.03 (range: 0.21–0.36 among years) and, as expected, was much lower than annual adult survival (0.52 ± 0.02). Resighting probability ranged from 0.51 to 0.79 among years (average 0.69 ± 0.05). Annual juvenile survival decreased strongly with fledging date ($B_{age*week}$ = −0.20 ± 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 ($B_{age*brood}$ = −0.18 ± 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 ± 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 (φ_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 ($\varphi_{age*year}$ $p_{age*year}$) that fit the data adequately. Starting with the model for an additive effect of age class (juvenile vs. adult) and year ($\varphi_{age+year}$ $p_{age+year}$), 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$_c$ score is considered to best fit the data. K is the number of parameters in each model, ΔQAIC$_c$ is the difference between the current model and that of best fit, and w_i is model weight.

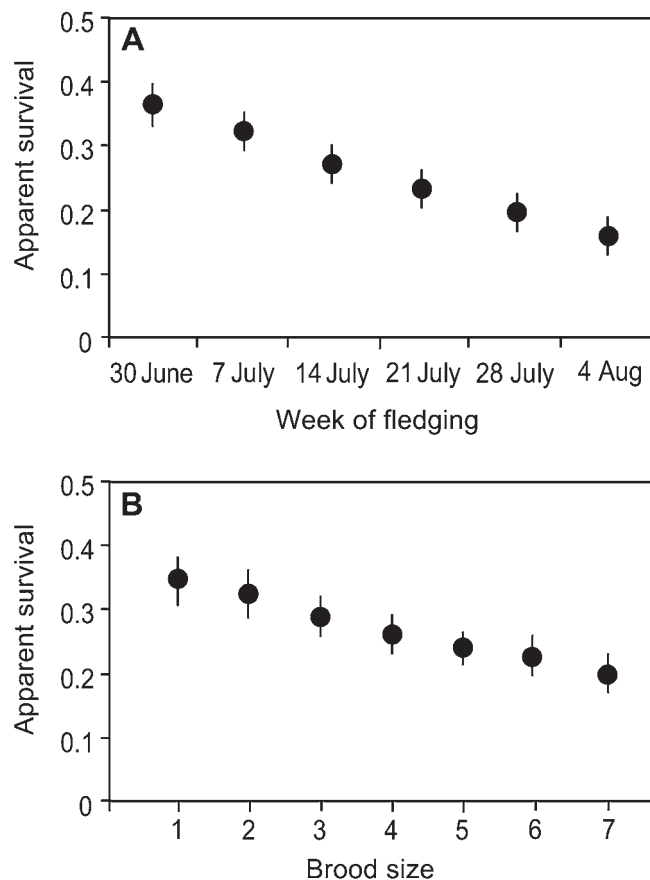| Model	K	QAIC$_c$	ΔQAIC$_c$	w_i
$\varphi_{age+week+brood+year}$ $p_{age+year}$	24	5,965.9	0	0.93
$\varphi_{age+week+year}$ $p_{age+year}$	22	5,971.1	5.2	0.07
$\varphi_{age*week*year}$ $p_{age+year}$	30	5,984.3	18.4	0
$\varphi_{age+year}$ $p_{age+year}$	20	5,995.9	30.0	0
$\varphi_{age+brood+year}$ $p_{age+year}$	22	5,997.5	31.6	0
$\varphi_{age*year}$ $p_{age*year}$	34	6,017.4	51.5	0
φ_{age} p_{age}	4	6,097.9	132.0	0

Fig. 2. Mean (± SE) apparent annual juvenile survival φ_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 ± 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 ($\varphi_{\text{fldg*year juv}}$; $p_{\text{fldg*year+week}}$) had far more support than the global model ($\varphi_{\text{fldg*year juv*year}}$; $p_{\text{fldg*year}}$; 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 ($\varphi_{\text{fldg juv*year}}$; $p_{\text{fldg*year+week}}$) 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 (φ_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 ($\varphi_{\text{fldg*year , juv*year}}$; $p_{\text{fldg*year}}$; 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 $QAIC_c$ score is considered to best fit to the data. K is the number of parameters in each model, $\Delta QAIC_c$ is the difference between the current model and that of best fit, and w_i is model weight.

Model	K	$QAIC_c$	$\Delta QAIC_c$	w_i
$\varphi_{\text{fldg (juv*year+week)}}$; $p_{\text{fldg*year+week}}$	19	11,494.6	0	0.99
$\varphi_{\text{fldg+week juv*year}}$; $p_{\text{fldg*year+week}}$	19	11,504.3	9.7	0.01
$\varphi_{\text{fldg+brood juv*year}}$; $p_{\text{fldg*year+week}}$	19	11,516.2	21.5	0
$\varphi_{\text{fldg juv*year}}$; $p_{\text{fldg*year+week}}$	17	11,523.4	28.7	0
$\varphi_{\text{fldg (juv*year+brood)}}$; $p_{\text{fldg*year+week}}$	19	11,526.5	31.9	0
$\varphi_{\text{fldg*year juv*year}}$; $p_{\text{fldg*year+week}}$	21	11,528.1	33.5	0
$\varphi_{\text{fldg*year juv}}$; $p_{\text{fldg*year+week}}$	17	11,548.8	54.2	0
$\varphi_{\text{fldg juv}}$; $p_{\text{fldg*year+week}}$	13	11,576.5	81.8	0
$\varphi_{\text{fldg*year juv*year}}$; $p_{\text{fldg*year}}$	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 ($\varphi_{\text{fldg (juv*year+week)}}$; $p_{\text{fldg*year+week}}$) had almost full support (w_i = 0.99; $B_{\text{juv*week}}$ = −0.23 ± 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 (φ_r) to the roost using the best-fitting model was 0.87 ± 0.03 and migration–wintering survival of juveniles (φ_m) averaged 0.32 ± 0.04 (range: 0.25–0.46 among years). Encounter probability was 0.31 ± 0.05 for fledglings at the roost, 0.27 ± 0.01 for adults at the roost, and 0.50 ± 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 ± 0.01 (range: 0.88–0.94 among years) compared with 0.87 ± 0.03 for fledgling survival to the roost. Monthly migration–wintering survival probability for adults was 0.94 ± 0.002.

Reproductive parameters.—For all years combined, 1-year-old females nested later (mean fledge date 17 July ± 0.8 days) than older females (13 July ± 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 ± 0.04 eggs (range: 1–8; n = 995), brood size was 4.17 ± 0.05 nestlings (range: 1–7; n = 905), and number of young fledged was 3.65 ± 0.05 (range: 0–7; n = 905). Average fledge date was 15 July ± 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 ± 0.5 days posthatch (range: 25–32 days). All 15 radiotagged young in 2007 survived the first week after fledging ($\varphi_f = 1.0$). 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 ± 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 ± 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 ± 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 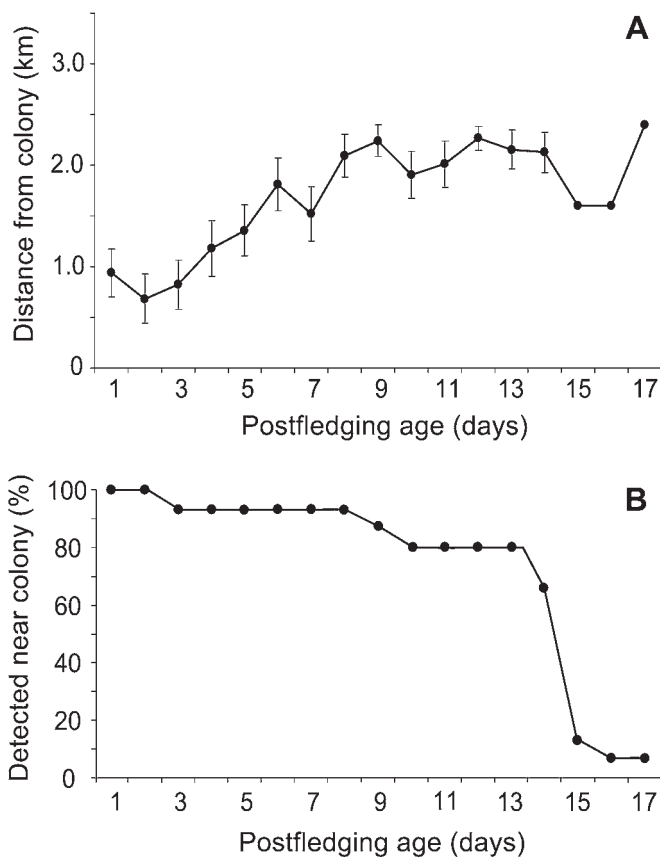at the colony and roost or via the single aerial telemetry search. Given the high mobility of newly fledged Purple Martins (Fig. 3) it is possible that birds that disappeared prior to 14 days postfledging had dispersed outside of the search region. Daily survival probability of fledglings was 0.979 ± 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). Grüebler 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 (Grüebler 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 (± 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 ≤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 (φ_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. Grüebler and Naef-Daenzer (2008) found that in Barn Swallows
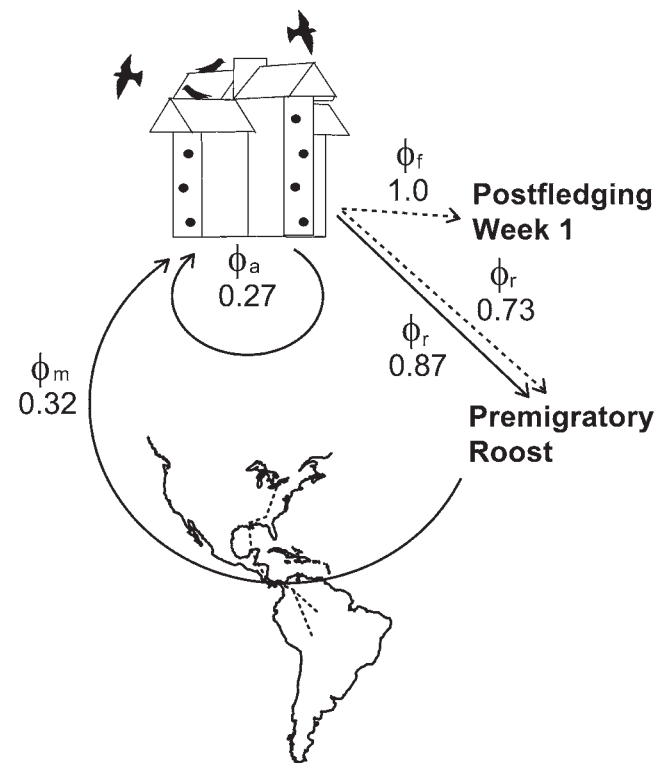
Fig. 4. Apparent survival probability of juvenile Purple Martins at different stages in their annual life cycle (φ_f: survival during the first week postfledging; φ_r: fledgling survival to the roost; φ_m: juvenile survival after onset of migration to South America and back to the breeding colony; φ_a: 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 premigratory 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 ($\varphi_r = 0.87$) and seasonal migration–winter survival ($\varphi_m = 0.32$) 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 ≤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 caerulescens*) 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 (Sillett 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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Appendix G: Stutchbury BJM, JR Hill, PM Kramer, SA Rush and SA Tarof. 2009. Sex and Age-specific Annual Survival in a Neotropical Migratory Songbird, the Purple Martin (*Progne subis*). *The Auk*, 126(2): 278-287.

I compiled and digitized 15 years of written banding data from numerous sources into a modern database making this study possible. Starting in 2001, I also contributed thousands of my own observations of marked individuals and banded approximately 1200 nestlings and 200 adults annually.

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

Bridget J. M. Stutchbury,[1,4] James R. Hill III,[2] Patrick M. Kramer,[1,2]
Scott A. Rush,[3] and Scott A. Tarof[1]

[1]*Department of Biology, York University, Toronto, Ontario M3J 1P3, Canada;*
[2]*Purple Martin Conservation Association, Tom Ridge Environmental Center, 301 Peninsula Drive, Suite 6, Erie, Pennsylvania 16505, USA; and*
[3]*Daniel B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia 30602, USA*

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 *Proge 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 dormidero 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.

[4]E-mail: bstutch@yorku.ca

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 (Sillett 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, Sillett 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, Sillett et al. 2000). Given the importance of forecasting how introduced diseases, habitat loss, and climate change will affect population dynamics of songbirds (Sillett 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*; Sillett 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 (*Poecile 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., Sillett 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 (Sillett 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
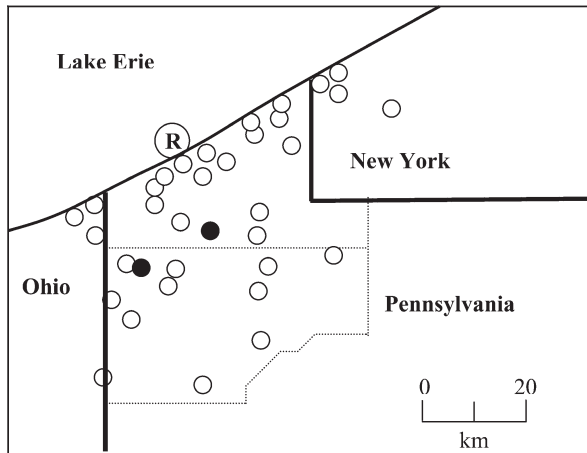
Fig. 1. Map of our study area in northwestern Pennsylvania, showing the locations of the two core breeding colonies (filled circles), the 33 additional breeding colonies that were surveyed annually for banded birds (open circles), and the premigratory roost ("R") at Presque Isle Peninsula on the south 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°45′20.01″N, 80°16′59.75″W) had 100–150 pairs year^{-1} and was located on the lawn of a home in a rural setting. The Edinboro colony (41°53′08.50″N, 80°07′45.80″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°06′59.6″N, 80°08′51.92″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

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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 (AIC$_c$) values and AIC$_c$ weights (w_i). Recapture probability was modeled with a year*colony effect for all models. Subscripts describe parametization 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 (Sillett 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 ΔAIC$_c \leq 2$ 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 ($p_{year*colony}$). 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 ($\phi_{1,2^{+}*sex*time} \, p_{year*colony}$) 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 ($\phi_{1,2^{+}*sex}$, $\phi_{1,2-4,5^{+}*sex}$, and $\phi_{1,2,3,4,5^{+}*sex}$) 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 ($\phi_{1,2^{+}*sex}$, $\phi_{1,2-4,5^{+}*sex}$, and $\phi_{1,2,3,4,5^{+}*sex}$) 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 ($\phi_{1,2^{+}*sex}$, $\phi_{1,2-4,5^{+}*sex}$, and $\phi_{1,2,3,4,5^{+}*sex}$) had the strongest support and were equally parsimonious (Table 1). For encounters including the premigratory roost, however, the model with three age classes ($\phi_{1,2-4,5^{+}*sex}$) fit the data far better than any other model ($\Delta AIC_c > 3.98$), 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 ($\phi_{1,2-4,5^{+}*sex}$), 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 (± SE) for three age classes of males and females ($\phi_{1,2-4,5^{+}*sex}$). Survival estimates are shown for encounters at core colonies only, encounters at all breeding colonies, and encounters at any colony or the premigratory roost.

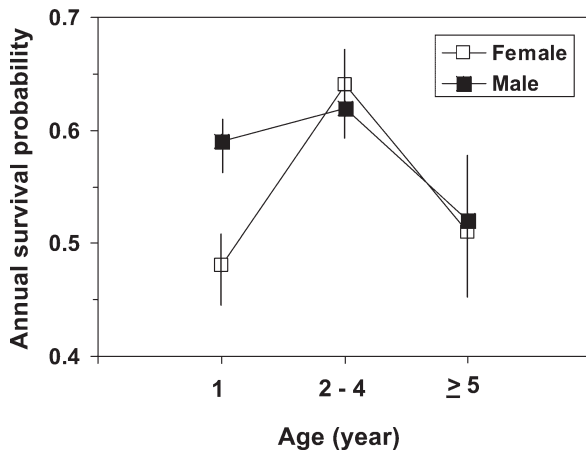| Encounter location | 1 year old | | 2–4 years old | | ≥5 years old | |
	Female	Male	Female	Male	Female	Male
Core colony	0.40 ± 0.03	0.51 ± 0.02	0.64 ± 0.03	0.60 ± 0.02	0.52 ± 0.07	0.54 ± 0.05
All colonies	0.44 ± 0.03	0.56 ± 0.02	0.64 ± 0.03	0.61 ± 0.02	0.52 ± 0.07	0.53 ± 0.05
Colonies or roost	0.48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

Fig. 2. Apparent annual survival probability (± 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 ($\phi_{1,2}{}^{+*sex*WNV}$; $w_i < 2\%$). 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
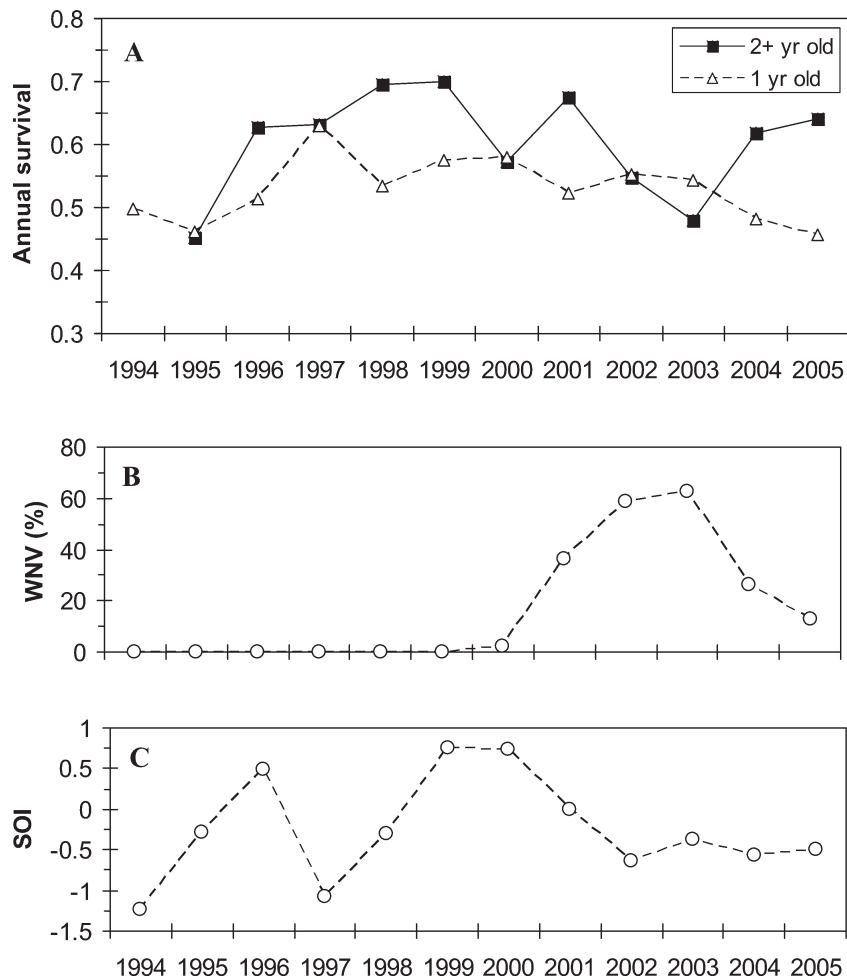
Fig. 3. Annual variation in (A) apparent annual survival (Table 1: $\phi_{1,2^{+}*time}$) of two age classes of Purple Martins breeding in the core colonies as one-year-olds ($n = 977$) and encountered in future years at any colony or the premigratory roost, (B) percentage of dead birds of various species 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 (Sillett 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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