

EXTRAPAIR MATING SYSTEM OF AN ASYNCHRONOUSLY BREEDING TROPICAL SONGBIRD: THE MANGROVE SWALLOW

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ABSTRACT.—Variation in the extent of extrapair paternity among avian species could result from ecological differences in breeding synchrony and/or density, or the existence or absence of paternity guards. We studied the extrapair mating system and paternity-assurance behaviors of an asynchronously breeding tropical songbird, the Mangrove Swallow (*Tachycineta albilinea*), and compared this species with the synchronously breeding temperate zone Tree Swallow (*Tachycineta bicolor*). Mangrove Swallows had a moderate level of extrapair paternity (26% of broods, 15% of nestlings), low breeding synchrony (8% of females fertile simultaneously), and low breeding density (average nearest-neighbor distance 313 m). The spatial and temporal distribution of nests with and without extrapair young did not differ significantly. Males did not follow their mates closely during the female's fertile period, and within-pair copulation frequency was low (0.33 copulations/h). Mangrove Swallows had a significantly lower proportion of extrapair young compared with Tree Swallows. Differences in breeding synchrony may explain the difference in extrapair paternity between the two congeners. Received 28 May 1998, accepted 17 February 1999.

THE UNDERLYING ecological and behavioral causes of variation in the frequency of extrapair fertilizations (EPFs) among bird species are not well known (Westneat et al. 1990, Birkhead and Møller 1992, Stutchbury and Morton 1995, Westneat and Sherman 1997). Documenting behaviors and ecological conditions that are correlated with extrapair mating is an important step toward understanding this variation. The majority of parentage studies on socially monogamous birds have focused on temperate-zone breeders (Stutchbury and Morton 1995), however, even though most passerine species occur in the tropics year-round and experience different ecological conditions relative to their temperate-zone counterparts (Ricklefs 1969). Consequently, the need exists for more comparative data from tropical species (Fleischer et al. 1997, Stutchbury et al. 1998). The most obvious difference in breeding biology is the length of the breeding season. Many tropical birds have breeding seasons that last for six to eight months, whereas temperate birds are constrained by climate to breeding seasons of two to three months (Ricklefs 1969). Thus, tropical birds provide an important opportunity for studying how ecology affects the evolution of extrapair mating systems.

Extrapair mating has been well documented in swallows (Møller 1987, Brown and Brown 1988, Morton et al. 1990, Lifjeld and Robertson 1992, Lifjeld et al. 1993, Wagner et al. 1996, Beasley 1996, Magrath and Elgar 1997), but all of this information comes from species nesting in temperate latitudes. Here, we document extrapair paternity, breeding synchrony, nesting density, and paternity-assurance behavior in the tropical Mangrove Swallow (*Tachycineta albilinea*) and compare this species with its well-studied temperate congener, the Tree Swallow (*T. bicolor*). Both species are aerial insectivores that nest in secondary cavities in snags, often over water, and both readily use nest boxes (Robertson et al. 1992, O. R. Moore pers. obs.).

Strong evidence indicates that breeding synchrony is positively correlated with EPF frequency among species (Stutchbury and Morton 1995, Stutchbury 1998). Synchrony may allow females to assess male genetic quality more reliably, and the benefits to females and males of seeking EPFs may be greater. Mangrove Swallows have a long breeding season (five months) and low breeding synchrony. Thus, we predicted they would have a lower EPF frequency than Tree Swallows, which have a short (two month) and synchronous nesting season (Robertson et al. 1992).

We also compared breeding density, amount of mate guarding, frequency of within-pair

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copulations, and testis size between Mangrove and Tree swallows to determine if these factors are associated with EPF frequency. High breeding density may make females more accessible to males as well as increase opportunities for mate assessment and EPFs (Birkhead and Møller 1992). The evolution of paternity guards in many species of birds (Birkhead and Møller 1992) is a testament to the strength of selection that EPFs create on males. Behaviors such as mate guarding and frequent copulation are associated with extrapair mating systems (Birkhead and Møller 1992) and are reflected in relatively large testis size in breeding males (Stutchbury and Morton 1995). Many studies have shown that male paternity guards reduce the frequency of extrapair mating attempts (Björkland et al. 1992, MacDougall-Shackleton et al. 1996); thus, paternity-assurance behaviors could explain the variability in EPF frequency among species.

STUDY AREA AND METHODS

The Mangrove Swallow is a socially monogamous species that occurs throughout lowland areas of Mexico and Central America. Pair formation and nest-site defense begin in early January, often many weeks prior to egg laying.

Our study was conducted from January to July 1996 at the Smithsonian Tropical Research Institute in the waters surrounding Barro Colorado Island Biological Reserve on Lake Gatun, Panama (09°10'N, 79°51'W). Mangrove Swallows nested in boxes (26 × 13 × 13 cm; 4.4-cm diameter entrance hole) placed on snags 1 to 1.5 m above the water level. About 70 nest boxes were erected on 17 January 1996, and 20 older boxes had been present for several years previously. Mangrove Swallows occupied 37% (33 of 90) of the nest boxes over the breeding season, whereas other species (Gray-breasted Martin [*Progne chalybea*], wasps, bees, snakes, and bats) occupied another 33% of the boxes. The spatial distribution of nest boxes was determined using a Trimble Scout 2000 global positioning system and Map Info geographical information system (version 4.0).

We captured adults at their nest boxes using a simple trap described by Stutchbury and Robertson (1986). Adults were marked with unique combinations of colored leg bands and small streaks of acrylic paint on the wings, tail, and breast feathers. Females were identified by the presence of an incubation patch and by copulation behavior. Blood samples were collected from the brachial vein of adults and 12-day-old nestlings and stored in PBS/EDTA. We checked nest boxes every three days to estimate first-egg dates and to determine nesting success.

Behavioral observations were conducted at nest boxes with marked pairs. We made 1-h observations at nest sites from 0700 to 1530 EST, with an average of 6 h of observation per pair. We recorded the number of copulation attempts and whether cloacal contact occurred. We analyzed mate guarding by recording male and female following behavior (i.e. flying within 15 s of each other) to and from the nest and the amount of time individual pairs spent together, and compared these during the pre-fertile and fertile periods. The fertile period was defined as six days before the first egg was laid until the penultimate egg was laid, which represents the period when copulations are thought to have the highest probability of fertilization (Birkhead et al. 1989). Observations during the pre-fertile period took place one to four weeks prior to egg laying. We calculated a synchrony index (Kempnaers 1993) for each nest by determining the proportion of females that were fertile on the same days that a given female was fertile.

Relative testis mass (testis mass/body mass) was determined by laparoscopy on males in the pre-laying and nestling stages ($n = 3$). Males were immobilized and a 1.5-mm incision was made dorsally between the first and second ribs. Length and width measurements were converted to testis mass using the corrected formula from Møller (1991).

Nonparametric statistical analysis was performed using Statistica (version 5), and parentage analysis was performed using Cervus (version 1). Means are presented \pm SE, and all tests are two-tailed.

Molecular analysis.—Blood samples were diluted in a total volume of 3.5 mL of 1× lysis buffer and incubated overnight on a rotating wheel. The following day we added 80 units of proteinase K and incubated the samples overnight under the same conditions. The next day we washed each sample twice with an equal volume (4 mL) of phenol:chloroform:water (40:40:20) and once with chloroform (100%). DNA was precipitated by adding 0.1 volume of 3 M sodium acetate and two volumes 95% ethanol followed by gentle mixing. DNA was washed in 70% ethanol, air-dried, and resuspended in 1× TNE₂ (10mM Tris-Cl, 10 mM NaCl, 2 mM EDTA, pH 8.0) overnight on a rotating wheel at 37°C.

For microsatellite DNA fingerprinting, 10 primer sets cloned from Barn Swallows (*Hirundo rustica*; Primmer et al. 1995) and Tree Swallows (Crossman 1996) were screened for variability on Mangrove Swallows. Six primer sets amplified variable products; however, two primer sets, HrU6 and HrU4 (Primmer et al. 1995), were di-allelic and were dropped from the analysis. The four primer sets used in this microsatellite analysis were HrU3, HrU5 (Primmer et al. 1995) 2-7, and 3-13 (Crossman 1996). All 10- μ L PCR reactions were performed on a PTC-100 thermal cycler using 0.25U *Taq* polymerase, 200- μ M dNTP, and a final buffer concentration of 10 mM Tris-HCl pH 8.3, 50 mM KCl, 1.5 to 2.0 mM MgCl₂,

TABLE 1. Composition of four microsatellite loci used for parentage analysis in Mangrove Swallows. Shown are number of alleles per locus, number of heterozygotes and homozygotes among the 54 adults analyzed, expected heterozygosity, and probability of exclusion for each locus. The mean probability of exclusion for all loci combined was 0.977.

Locus	No. of alleles	No. of heterozygotes	No. of homozygotes	Expected heterozygosity	Probability of exclusion
2-7	40	53	1	0.969	0.850
3-13	10	46	8	0.753	0.357
HrU5	12	45	9	0.865	0.551
HrU6	16	40	14	0.817	0.470

and 0.0001% gelatin. Two pmol of each primer (one being end-labeled with ^{32}P dATP) and 50 ng of genomic DNA were included in each reaction. The general PCR profile consisted of one cycle of 94°C for 3 min, 55°C for 1 min, and 72°C for 1 min followed by 30 cycles of 94°C for 30 s, 55°C for 30 s, and 72°C for 40 s. Samples were loaded into a 6% acrylamide gel, run at 1,600 V, 45 W, and 50 A, and viewed by autoradiograph and phosphorimaging.

Germ-line mutations were suspected at locus 2-7 because (1) the genotypes of four offspring (from four different broods) did not match the putative mother, (2) exclusions were expansions ($n = 5$) or reductions ($n = 2$) of one penta-nucleotide repeat with that of a parental allele, (3) excluded offspring were matched at the other three loci with their putative parents, and (4) locus 2-7 was extremely variable in Mangrove Swallows (Table 1). Thus, all exclusions based solely on locus 2-7 ($n = 7$) were subsequently verified with multilocus fingerprinting.

For multilocus fingerprinting on these seven nestlings and their parents, DNA was digested with *Hae* III according to the manufacturers directions (BRL). Five μg of digested DNA was run through a 30-cm 0.8% agarose gel in 1 \times TBE buffer (90 mM Tris, 90 mM boric acid, 2 mM EDTA, pH 8.0) at 1.3 V/cm for approximately 48 h. The gel was then depurinated by treatment with 0.25 M HCL for 10 min, denatured with 0.4 M NaOH and 0.6 M NaCl for 60 min, and neutralized in 0.5 M Tris-Cl and 1.5 M NaCl for 30 min before it was Southern blotted into Immobilon transfer membranes in 10 \times SSC (1.5 M NaCl, 0.15 M sodium citrate). Membranes were dried and baked and then placed in 12 mL of prehybridization mix (Westneat et al. 1988) in a sealed plastic bag for 3 to 8 h at 65°C. Jeffreys 33.15 minisatellite probe (Jeffreys et al. 1986) was labeled with alpha ^{32}P -dCTP by primer extension to specific activities greater than 4.5×10^8 cpm/ μg . The labeled probe was added to the prehybridization solution, and prehybridization proceeded at 65°C overnight with constant shaking. Membranes were washed four times with 2 \times SSC and 0.1% SDS solution, twice at room temperature for 15 min and once at 65°C for 30 min. Autoradiography was carried out for four to seven days at 20°C, using Kodak film and one intensifying screen.

Band-sharing calculations were done according to Wetton et al. (1987).

RESULTS

Genetic mating system.—Eight of 31 broods (26%) contained extrapair young (EPY), and 15 of 97 young (15%) were the result of EPFs. Of 97 offspring from 31 broods, 93 offspring had a complete allelic match with the putative mother at all four microsatellite loci, and four were unmatched at locus 2-7 but were verified with multilocus fingerprinting to be mutations (see below). Therefore, we concluded that all offspring were descendent from the putative mother. For 79 offspring the non-maternal alleles at all four loci matched those of the putative father, and an additional three offspring that were excluded solely by locus 2-7 were verified to be mutations.

Of the 15 EPY, one had a complete match of the non-maternal haplotype to a neighboring male located 580 m away. The other 14 EPY could not be matched with any sampled males, including neighbors, despite sampling 73% (24 of 33) of the resident males. We could not sample males nesting in natural cavities, and we knew of fewer than 10 such nests in the study area. We assigned paternity to a given male for 83 offspring. The mean exclusionary power for the four microsatellite loci used was 0.98 (Table 1), and the probability that the combination of paternal alleles found in an offspring of an assigned father could occur purely by chance was 0.0034 (range 0.13 to 0.0001).

Seven exclusions that were based solely on locus 2-7 (four with putative mothers, three with putative fathers) had multilocus band profiles that completely matched the profiles of the two putative parents. The proportion of bands shared between the offspring and the parent excluded based on locus 2-7 varied between

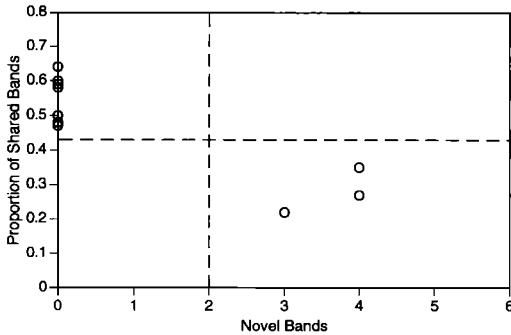


FIG. 1. Multilocus analysis of seven Mangrove Swallow nestlings excluded based solely on locus 2-7, plus three other nestlings known to be extrapair young based on other microsatellite loci. The proportion of bands shared with the nestling represents bands from the parent in which the mutation occurred (three males, four females); for the known extrapair young, nestlings were compared with their putative fathers.

0.48 to 0.63. Based on multilocus fingerprinting, the proportion of bands shared between the offspring and putative father for a nest with three confirmed EPFs varied between 0.23 to 0.36, with three to four novel bands (Fig. 1); the proportion of bands shared with the putative mother was 0.44 to 0.56. Thus, we concluded that locus 2-7 exhibited germ-line mutations at a rate of 3.6% per meiotic event (7 mutations in 97 offspring). Although this rate is very high, a similar rate has been observed in Barn Swallows for a tetranucleotide repeat (Primmer et al. 1996).

Breeding synchrony and density.—First-egg dates ranged from 31 January to 28 May, with no sharp peak in laying at any time during the breeding season (Fig. 2); the average synchrony was 7.7% (Table 2). Nearest-neighbor distances ranged from 50 to 1,300 m (\bar{x} = 313 m; Table 2). Neither breeding synchrony (Mann-Whitney U -test, Z = 0.95, P = 0.34) nor nesting density (Z = 0.83, P = 0.40) differed significantly between nests with and without EPY. One nest that contained EPY had no neighbors within a 1.3-km radius. Nearest-neighbor distances typically exceeded 200 m, but unoccupied nest boxes often were much closer (1 to 50 m away).

Paternity-assurance behaviors.—Evidence for paternity-assurance behaviors would include (1) males following fertile females more often than females followed males, (2) males following more closely or more often during the fertile period, and (3) intrapair copulations occurring at high frequency. Males often followed females (31 to 35% of trips; Fig. 3) and did so significantly more often than females followed males (Wilcoxon matched-pairs test, T = 2.00, P < 0.01). Following behavior by males, however, did not vary significantly between the prefertile and fertile periods (Mann-Whitney U -test, Z = 0.90, P = 0.37). There was also no difference between the prefertile and fertile periods in the amount of time pairs spent together at their nest site (Z = 1.42, P = 0.16; Fig. 4).

No copulations (with cloacal contact) or attempted copulations were observed during the prefertile period (n = 8 pairs, 30 h observation).

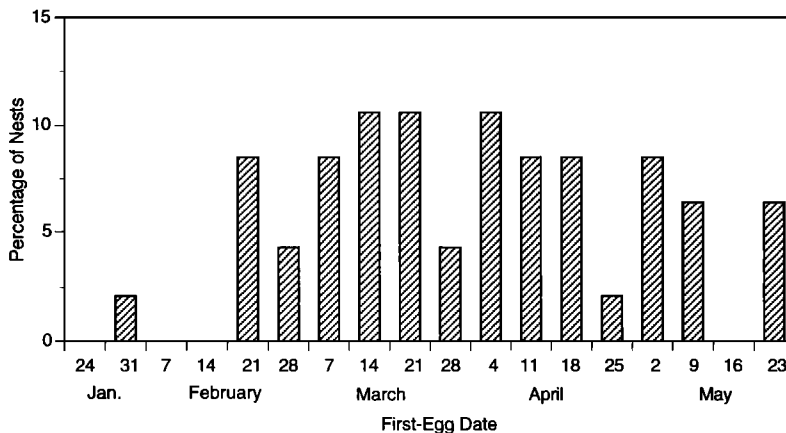


FIG. 2. Distribution of first-egg dates of female Mangrove Swallows (n = 48) by one-week intervals over the entire breeding season.

TABLE 2. Breeding-synchrony index (SI) and nearest-neighbor distance (NND) for all Mangrove Swallow nests, nests with extrapair young (EPY), and nests with no EPY. Values are $\bar{x} \pm SE$, with n in parentheses.

Variable	All nests	EPY nests	Non-EPY nests
SI (%)	7.7 \pm 0.5 (48)	9.3 \pm 1.21 (8)	7.6 \pm 0.83 (23)
NND (m)	313 \pm 51.8 (33)	434 \pm 135.6 (8)	342 \pm 73.6 (23)

The copulation rate during the fertile period averaged 0.33 ± 0.12 copulations per h ($n = 6$ pairs, 18 h observation). Every copulation attempt at this stage resulted in cloacal contact, and only one copulation occurred per bout. We observed no extrapair copulations. We estimated mean testis mass to be 0.031 ± 0.002 g ($n = 3$ males). Given an average body mass of 15 g for Mangrove Swallows, the mean relative testis mass was 0.002 ± 0.0004 g.

DISCUSSION

Breeding synchrony and density.—DNA fingerprinting of Mangrove Swallows in Panama revealed that 15% of the young resulted from EPFs, and 26% of the broods contained EPY. Although this EPF rate is moderate, it is significantly lower than that commonly observed in a temperate zone congener, the Tree Swallow (Table 3). The relatively low frequency of EPFs in Mangrove Swallows was expected based on their low level of breeding synchrony (8%), in contrast to Tree Swallows that have a high rate of EPF and high breeding synchrony (Table 3). Breeding synchrony is correlated with frequency of EPF across species (Stutchbury and Morton 1995, Stutchbury 1998), and the few socially monogamous tropical passerines that have

been studied via DNA fingerprinting exhibit low breeding synchrony and few or no EPFs (Fleischer et al. 1994, Fleischer et al. 1997). The exception is the Clay-colored Robin (*Turdus grayi*), which breeds relatively synchronously during the dry season and has a high frequency of EPF (Stutchbury et al. 1998). This supports the idea that breeding synchrony, rather than latitude per se, influences the evolution of extrapair mating systems.

In Mangrove Swallows, nests with EPY did not have higher breeding synchrony or density than nests without EPY. Although synchrony is correlated with EPF frequency in some species (Gowaty and Bridges 1991, Stutchbury et al. 1997), within-population variation in EPF frequency is not always explained by breeding synchrony (Weatherhead 1997). For example, Tree Swallow populations that differed moderately in breeding synchrony did not differ significantly in EPF frequency (Dunn et al. 1994b).

Breeding density is the other major ecological factor suggested to explain between-species differences in EPF frequency (Westneat et al. 1990, Birkhead and Møller 1992). However, Westneat and Sherman (1997) showed that breeding density is not correlated with frequency of EPFs among species. Similarly, in-

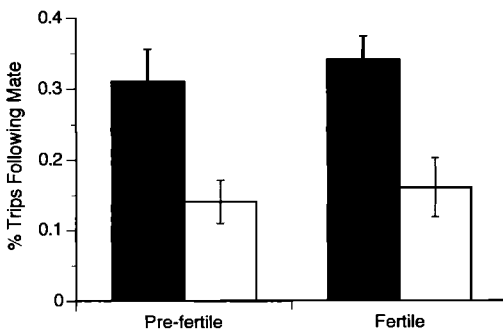


FIG. 3. Mate-following behavior ($\bar{x} \pm SE$) by male (solid bars) and female (open bars) Mangrove Swallows during the prefertile ($n = 8$ pairs) and fertile periods ($n = 6$).

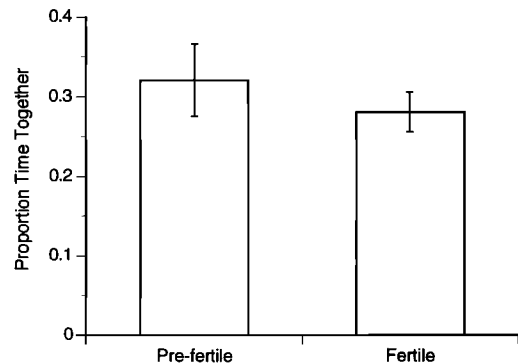


FIG. 4. Proportion of time ($\bar{x} \pm SE$) Mangrove Swallow pairs spent together during the prefertile ($n = 8$ pairs) and fertile periods ($n = 6$).

TABLE 3. Comparison of Mangrove Swallows (this study) and Tree Swallows for extrapair paternity (Liffield et al. 1993, Dunn et al. 1994a), breeding synchrony and testis mass (Stutchbury and Morton 1995), nearest-neighbor distance (Dunn et al. 1994b), and copulation rate (Beasley 1996). Values are $\bar{x} \pm SE$, with n in parentheses. Asterisks denote statistical significance between species for Fisher exact test (extrapair paternity) or t -tests (all other variables).

Variable	Mangrove Swallow	Tree Swallow
Extrapair paternity		
% of broods***	26	72
% of nestlings***	15	47
Breeding-synchrony index (%)***	7.7 \pm 0.5 (48)	47 \pm 3.2 (57)
Testis mass/body mass***	0.002 \pm 0 (3)	0.035 \pm 0.001 (21)
Nearest-neighbor distance (m)	313 \pm 51.8 (33)	26 to 152 ^a
Copulation rate (no. per h)		
Prefertile period	0 \pm 0 (8)	3.8 \pm 1.48 (14)
Fertile period**	0.33 \pm 0.12 (6)	5.4 \pm 1.28 (14)

** , $P < 0.01$; *** , $P < 0.001$.

^a NND = 26 m for nests in grids, 152 m for solitary nests.

creased density does not necessarily result in more EPFs within species (Tarof et al. 1998). This population of Mangrove Swallows did have a lower breeding density than many populations of Tree Swallows (Table 3). Tree Swallows breeding at low density (nearest-neighbor distances of 100 to 643 m), comparable to that of Mangrove Swallows, nevertheless had a high frequency of EPFs (75% of broods; Dunn et al. 1994b). Therefore, low breeding density cannot explain the low EPF frequency in Mangrove Swallows. For Mangrove Swallows, we were able to exclude most neighbors as extrapair fathers, suggesting that extrapair matings occur far from the nest site. Similarly, in Tree Swallows extrapair fathers seldom are immediate neighbors (Dunn et al. 1994a).

Paternity-assurance behaviors.—One paternity-assurance behavior, within-pair copulation frequency, was significantly lower in Mangrove Swallows than in Tree Swallows (Table 3). Furthermore, Mangrove Swallows had a relative testis mass less than one-tenth that of Tree Swallows (Table 3), reflecting the low copulation frequency and the likely low level of sperm competition (Møller and Briskie 1995). We did not observe extrapair copulations in Mangrove Swallows, which are frequent and conspicuous in Tree Swallows (Venier et al. 1993). Neither species exhibits close mate guarding during the fertile period (Leffelaar and Robertson 1984), although mate guarding has evolved in a close relative, the Violet-green Swallow (*Tachycineta thalassina*; Beasley 1996). Paternity guards, like the frequent copulation seen in Tree Swallows, likely evolve in response to a

high frequency of EPF behavior. In a similar comparison of temperate-zone congeners that differ in breeding synchrony, Morton et al. (1998) found that the frequency of EPF in the synchronously breeding Red-eyed Vireo (*Vireo olivaceus*) was significantly higher than in the less-synchronous Blue-headed Vireo (*Vireo solitarius*). Red-eyed Vireos exhibit close mate guarding and conspicuous EPC attempts, whereas Blue-headed Vireos do not.

Although studies comparing two closely related species cannot be generalized to broad correlations (or causations), they nevertheless allow one to test *a priori* predictions about the presence of extrapair behavior. Comparisons of temperate-zone and tropical congeners, like our comparison of Mangrove Swallows and Tree Swallows, are powerful tools for understanding what ecological and social conditions lead to the evolution of EPF behavior. Many life-history traits besides breeding synchrony differ between the temperate zone and the tropics, most notably clutch size, adult longevity, and nest predation (Skutch 1985, Martin 1996). It is not known whether these other life-history traits affect the evolution of EPF behavior. We urge more study of tropical species, and of latitudinal differences in EPF frequency within species, to further test the breeding-synchrony hypothesis for the evolution of extrapair behavior in birds.

ACKNOWLEDGMENTS

We thank the Smithsonian Tropical Research Institute for logistic support, INRENARE for permis-

sion to conduct research at the Barro Colorado Island Biological Reserve, A. J. Jeffreys for minisatellite probes, and P. Boag for microsatellite primers for swallows. P. Dunn, S. A. Gill, E. Morton, T. Pitcher, and R. Wagner commented on the manuscript. This research was supported by a grant from the Purple Martin Conservation Association and grants to BJMS and JSQ from the Natural Sciences and Engineering Research Council of Canada.

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Associate Editor: J. Ekman