

Synchrony does not explain extrapair paternity rate variation in northern or southern house wrens

Katie LaBarbera,^a Paulo E. Llambías,^b Emily R. A. Cramer,^c Taza D. Schaming,^d and Irby J. Lovette^a

^aFuller Evolutionary Biology Program, Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA, ^bEcología del Comportamiento Animal, Instituto Argentino de Investigaciones de las Zonas Áridas, Centro Científico Tecnológico - Mendoza, Consejo Nacional de Investigaciones Científicas y Técnicas de la Argentina (CCT - Mendoza CONICET), Avenida Ruiz Leal s/n Parque General San Martín, 5500 Mendoza, Argentina, ^cDepartment of Neurobiology and Behavior, Cornell University, Seeley G. Mudd Hall, Ithaca, NY 14853, USA, and ^dDepartment of Natural Resources, Cornell University, Fernow Hall, Ithaca, NY 14853, USA

Rates of extrapair paternity (EPP) vary widely among and within bird species, and 2 hypotheses suggest that this variation is driven by variation in breeding synchrony. These hypotheses make contradictory predictions, and each has some support from field studies, but the general relationship between EPP and synchrony remains unclear. We investigated EPP in relation to population-wide and local breeding synchrony in 2 populations of house wrens (*Troglodytes aedon*)—a migratory northern temperate (New York, USA) and a sedentary southern temperate (Buenos Aires, Argentina) population—that differ in numerous life-history traits. The northern population had significantly higher EPP rates and modestly but significantly higher local breeding synchrony. Population-wide breeding synchrony did not differ between populations. The proportion of extrapair young within a nest was not related to the nest's population-wide or local synchrony index in either population. These results suggest that across divergent life histories in this species, breeding synchrony does not account for within-population variation in EPP. *Key words:* breeding synchrony, extrapair paternity, south temperate ecology, *Troglodytes aedon*. [*Behav Ecol* 21:773–780 (2010)]

In birds, rates of extrapair paternity (EPP)—the siring of offspring by a male other than the social mate of the mother—vary widely both among and within species: socially monogamous birds have population-wide EPP rates ranging from 0% to 55% of offspring (Griffith et al. 2002). This variation is noteworthy because cases of EPP simultaneously influence the fitness of several individuals. Minimally, EPP (or lack thereof) affects the reproductive success of the social male and any cuckolding males. The fitness of the female and her offspring may also be affected via a variety of direct or indirect mechanisms: positive fitness effects include potentially increased quality or genetic heterozygosity of offspring, whereas negative effects could result from punitive reduction in offspring provisioning or nest defense by the cuckolded social male (Masters et al. 2003; Westneat and Stewart 2003; Rubenstein 2007). These and other fitness implications have inspired substantial research on EPP variation, yet many of the determinants of this variation remain uncertain.

Although EPP, like most life-history traits, is probably influenced by a suite of interacting variables, in some situations, it may be possible to disentangle their effects in order to study the relationship between individual variables and EPP rates. A substantial literature addresses how EPP rates may be related to breeding synchrony (the degree of overlap of females' fertile periods in a given population or a subset of a population)

which is a measure of the temporal density of extrapair fertilization opportunities (Birkhead and Biggins 1987; Westneat et al. 1990; Stutchbury and Morton 1995; Weatherhead and Yezerinac 1998). The “simultaneous display” hypothesis suggests that more synchronous populations have higher EPP rates because the temporal clumping of mating opportunities induces males to display more synchronously, facilitating comparison between males and allowing females to more accurately select the best-quality extrapair sires (Stutchbury and Morton 1995; Stutchbury 1998a, 1998b; but see Weatherhead and Yezerinac 1998). The “mate guarding” hypothesis makes the opposite prediction: that more synchronous breeding leads to lower EPP rates because males are constrained in seeking extrapair copulations by the need for mate guarding when their mates are fertile (Birkhead and Biggins 1987; Westneat et al. 1990).

Overall, the empirical evidence for a synchrony–EPP rate relationship is inconclusive and in some cases contradictory. For example, higher synchrony is associated with higher EPP rates in the black-throated blue warbler (*Dendroica caerulescens*; Chuang et al. 1999) and, albeit weakly, in a population of red-winged blackbirds (*Agelaius phoeniceus*; Westneat and Gray 1998). A different population of red-winged blackbirds exhibits a negative synchrony–EPP rate relationship (Westneat and Gray 1998), as do yellow warblers (*Dendroica petechia*; Yezerinac and Weatherhead 1997), common yellowthroats (*Geothlypis trichas*; Thusius et al. 2001), great tits (*Parus major*; Strohbach et al. 1998), and experimentally manipulated populations of house sparrows (*Passer domesticus*; Vaclav and Hoi 2007) and northern house wrens (*Troglodytes aedon*; Johnson et al. 2002). Synchrony and EPP rates are not related in

Address correspondence to K. LaBarbera. E-mail: kl343@cornell.edu.

Received 2 November 2009; revised 17 March 2010; accepted 18 March 2010.

a population of great reed warblers (*Acrocephalus arundinaceus*) (Arlt et al. 2004).

Different relationships between EPP and breeding synchrony may occur because other life-history parameters that influence EPP also vary among species. A recent comparative analysis showed that breeding synchrony and EPP rate are positively correlated across species (Stutchbury and Morton 2008), although the power of such comparative studies is limited in part by the existing sampling bias toward northern temperate species that generally have short, highly synchronous breeding seasons. In contrast, several other reviews have commented on the lack of a consistent interspecific relationship across species between breeding synchrony and EPP rates (Westneat and Sherman 1997; Griffith et al. 2002). Because other factors that covary with breeding synchrony could strongly influence EPP rates (see below), it is useful to study additional species with wide variation in these life-history traits.

Here, we explore alternative explanations for this inconsistency of support for a breeding synchrony–EPP rate relationship within and between species. Within species, the number of territories which a bird can cross may be limited by territorial defense, making the region in which breeding synchrony affects the EPP opportunities of any given individual smaller than the entire study site (Johnson et al. 2002). Therefore, local breeding synchrony may have an effect on EPP that studies of population-wide breeding synchrony are unable to detect. Between species, numerous other environmental variables may alter the context of breeding synchrony without necessarily driving EPP rate variation themselves. Breeding density may affect breeding synchrony's influence on EPP rates by altering both the proximity of any fertile females (increasing extrapair copulation opportunities) and of neighboring males (reducing extrapair copulation opportunities by stimulating increased mate guarding). The migratory or resident status of a population could affect the direction of any synchrony–EPP rate relationship by altering the relationship between nest synchrony and male quality because early breeding often correlates with high male quality (e.g., Møller 1994; Nyström 1997) and high fledging success in migratory species but not necessarily in resident species (Tieleman et al. 2006). Annual mortality, usually higher in migratory species (Spottiswoode and Møller 2004), may affect the potential for retaliation by a cuckolded male and therefore the cost of EPP for the female (Mauck et al. 1999). Breeding synchrony's effects on EPP rates may hence vary among environmental situations.

The broadly distributed house wren (*T. aedon*) provides an appropriate system in which to explore the effects of variation in life-history traits on the breeding synchrony–EPP rate relationship. In one population each of northern and southern house wrens, we examined whether the context of synchrony affects the relationship between breeding synchrony and EPP rates. If EPP rate variation is driven in part by breeding synchrony unrelated to life-history context, the direction (if not the magnitude) of the synchrony–EPP rate association should be the same for both populations. If variation in context affects the direction of synchrony's effects on EPP rate, then these 2 populations may exhibit dissimilar synchrony–EPP rate associations. Alternatively, failure to find a clear synchrony–EPP rate variation relationship in either population would suggest that these variables are not directly related.

MATERIALS AND METHODS

Study species

The house wren is a small (10–12 g), sexually monomorphic passerine with the broadest latitudinal range of any New World

songbird (Johnson 1998). We studied 2 forms—the northern house wren (*Troglodytes aedon aedon*) and southern house wren (*T. a. bonariensis*)—which are generally considered conspecific (American Ornithologists' Union 1998) but are sometimes classified as separate taxa within a superspecies complex (Brumfield and Capparella 1996).

Throughout most of eastern North America, the northern house wren is migratory, with males generally preceding females to the breeding grounds so that their territories are established by the time females arrive. In most southern temperate regions, southern house wrens reside year-round on their territories (Llambías and Fernández 2009). In our study sites, monogamous northern house wren males have larger territories than southern house wren males (mean \pm standard error: northern, 1766.5 ± 136.1 m²; southern, 753.7 ± 51.3 m²) (Llambías 2009). Males sing to attract females to nest sites within their territories. Both forms nest in either natural cavities or man-made nest-boxes. Nesting in nest-boxes instead of natural cavities increases nest success in both northern and southern house wrens; in northern but not southern house wrens, clutch size also increases in nest-boxes (Purcell et al. 1997; Llambías and Fernández 2009). In nest-boxes, females lay one egg per day for a modal clutch size of 6 in the northern and 5 in the southern house wren (Young 1996; Llambías and Fernández 2009). Females incubate and brood the nestlings, but both parents generally feed the chicks, which fledge 14–19 days after hatching (Johnson et al. 2004). Some northern house wren males attract a second female, whom they typically do not assist with provisioning the nestlings (Johnson et al. 1993). Southern house wren males in our Buenos Aires study population do not advertise for a second mate, and social polygyny is extremely rare (1%; Llambías and Fernández 2009).

EPP has been intensively explored in several populations of the northern house wren, in which late-breeding males experience elevated rates of cuckoldry, and socially polygynous males are more likely to be cuckolded in their secondary nests (Soukup and Thompson 1997; Johnson et al. 2002; Poirier et al. 2004). EPP has not previously been studied in the southern house wren.

Field procedures

We studied 2 populations of house wrens breeding in nest-boxes: northern house wrens in Ithaca (lat 42°31'N, long 76°28'W), NY, USA and southern house wrens in General Lavalle (lat 36°26'S, long 56°25'W), Buenos Aires Province, Argentina.

During April–August 2004 and 2008, we studied northern house wrens on mixed deciduous forest patches at Cornell University Experimental Ponds Units 1 (24.3 ha) and 2 (41.3 ha). These units were treated separately in population-wide breeding synchrony analyses (see below) because they are separated by 3 km. During October–January 2003 and 2004, we studied southern house wrens in a cattle ranch, Los Zorzales. This Argentina study site consisted of 3 forest fragments (total area = 4.1 ha), each separated by about 50 m of pasture.

We checked active nests at least every other day until all nestlings fledged or the nesting attempt failed. We captured breeding adults in mist nets near the nest or with hand nets on the nest, marked each bird with a unique combination of colored leg bands for identification, and collected 50–100 μ l of blood for paternity analysis. We confirmed social parents by repeatedly observing individuals defending nest-boxes and provisioning nestlings. We banded nestlings with US Fish and Wildlife Service metal bands (USA) or numbered bands (Argentina) and obtained blood samples (\sim 50 μ l) at 7–11 days of age. All blood was collected from the brachial wing vein and stored

in lysis buffer (0.1 M Tris [pH 8.0], 0.1 M ethylenediaminetetraacetic acid, 10 mM NaCl, 0.5% sodium dodecyl sulfate; White and Densmore 1992).

In New York in 2004, we followed 46 nests from first lay date to the onset of incubation (from which data we calculated synchrony measures); for 29 of these nests, we obtained blood for paternity analysis. In 2008, we obtained synchrony information for 70 nests, of which 53 could be analyzed for paternity. In Buenos Aires, we obtained synchrony information for 55 nests (2003) and 53 nests (2004), of which 26 (2003) and 14 (2004) could be analyzed for paternity.

Paternity analysis

Genomic DNA was extracted from whole blood in lysis buffer using Perfect gDNA Blood Mini Kits (Eppendorf, Hamburg, Germany) or Qiagen DNeasy Blood and Tissue Kits (Qiagen, Valencia, CA) according to the manufacturer's instructions. Polymerase chain reaction (PCR) was used to identify alleles at 7 microsatellite loci: TA-A5-2, TA-A5-15, TA-B4-2, TA-C3(B)-2, and TA-C6-7 (Cabe and Marshall 2001); PCA3 (Dawson et al. 2000); and ThPI-14 (Brar et al. 2007). All loci were modified as in Makarewich et al. (2009) with the addition of a 5'-end fluorescent label (FAM, NED, PET, or VIC; Applied Biosystems, Foster City, CA) to the forward primer and the use of a "pigtailed" reverse primer.

The first 4 loci were PCR amplified together in a multiplexed panel, as were PCA3 and TA-C6-7 in a second panel; ThPI-14 was amplified individually. PCRs were carried out in 10 μ l reactions consisting of 20 mM Tris, 50 mM KCl, 3.25 mM MgCl₂, 200 μ M dNTPs, 0.025 U of Jumpstart *Taq* polymerase, and 120 nmol each of the fluorescently labeled forward primer(s) and the corresponding pigtailed reverse primer(s). For TA-A5-15, only 70 nmol each of the forward and reverse primers was used. For PCRs with ThPI-14, the MgCl₂ concentration was reduced to 2.0 mM. We used the following PCR protocol for all loci except ThPI-14: 1 cycle of 94 °C for 3 min; then 35 cycles of 94 °C denaturing for 1 min, 55 °C annealing for 1 min, and 72 °C extension for 1 min; and finally 1 cycle of 72 °C for 45 min. For ThPI-14, the annealing temperature was increased from 55 to 60 °C.

Labeled PCR products were analyzed on a PRISM 3100 Genetic Analyzer (Applied Biosystems), and allele sizes were estimated using a GeneScan-500 LIZ size standard. Alleles were viewed on GeneMapper version 3.7 software (Applied Biosystems). We used Cervus version 3.0.3 (Kalinowski et al. 2007) to determine the exclusion power of our microsatellite loci, to determine whether they were in Hardy-Weinberg equilibrium, and to determine the number of allele mismatches between each chick and its social father. We repeated the PCR amplification and genotyping analysis to confirm all social father

mismatches; we considered only chicks with at least one confirmed mismatch with their social father to be extrapair.

Population-wide breeding synchrony analysis

We calculated population-wide synchrony indices following Kempnaers (1993) to determine the proportion of females in the population that were fertile during each focal female's fertile period. This synchrony index sums all females that were fertile for each day of the focal female's fertile period, then divides this sum by the total possible fertile females (obtained by multiplying the number of total females in the population, minus the focal female, by the number of days that the focal female was fertile). A synchrony index of 0 indicates a completely asynchronous population with no overlap of fertile periods, whereas a synchrony index of 1 indicates a completely synchronous population. We assumed that females became fertile 5 days prior to the laying of the first egg and stayed fertile until they laid the penultimate egg (Yezerinac and Weatherhead 1997; Johnson et al. 2002). All nesting attempts that resulted in at least one egg were included in our calculations, although many of these were depredated or destroyed before blood samples were taken.

In 6 of 116 (5.2%) northern house wren nests and in 14 of 108 (12.9%) southern house wren nests, we estimated some nesting attempt parameters from other data. For instance, when first lay date was not observed, we back-calculated the lay date from the hatch date of the first egg using the mean incubation period in that population. In the few cases where the final clutch size was unknown, we used the mean population clutch size.

Local breeding synchrony analysis

We calculated a local breeding synchrony index that attempts to take into account only those territories near enough to the focal territory to influence the EPP opportunities of its residents, which may be more biologically relevant than the population-wide synchrony index. To determine the "local" region, we used Cervus version 3.0.3 (Kalinowski et al. 2007) to assign parentage to extrapair chicks. We then calculated the distance (both in meters and in number of intervening territories) between the primary nest-box of each extrapair male and that of the male he cuckolded (Table 1 and Figure 1). In this analysis, we used only extrapair sires that could be assigned with 95% confidence.

Because 90% of known extrapair sires were territorial neighbors or only one territory removed from the cuckolded male's nest-box (Figure 1), we defined a radius of 2 territories around each nest-box as the most biologically relevant local region for each resident female. We then calculated local

Table 1
EPP, breeding synchrony, and related measures in northern and southern house wrens

	Northern	N _{Northern}	Southern	N _{Southern}	Statistic	P
Proportion of broods with extrapair young	0.537	82	0.325	40	$\chi^2 = 4.84$	0.028*
Proportion of chicks which were extrapair	0.249	377	0.157	166	$\chi^2 = 5.23$	0.022*
Mean territories crossed to obtain extrapair fertilization \pm SE	0.54 \pm 0.11	48	0.43 \pm 0.25	14	Z = -1.37	0.170
Mean distance (in m) traveled to obtain extrapair fertilization \pm SE	253.5 \pm 31.1	46	80.7 \pm 20.8	14	Z = -3.84	<0.001*
Mean number of local females \pm SE	16.2 \pm 0.49	116	20.1 \pm 0.43	108	Z = 5.81	<0.001*
Mean population-wide synchrony index \pm SE	0.25 \pm 0.01	116	0.23 \pm 0.01	108	Z = -1.10	0.272
Mean local synchrony index \pm SE	0.22 \pm 0.01	116	0.18 \pm 0.01	108	Z = -3.38	<0.001*

P values were calculated using a chi-squared test (statistic: χ^2) or 2-sample Wilcoxon test (statistic: Z); SE, standard error; * marks P values < 0.05.

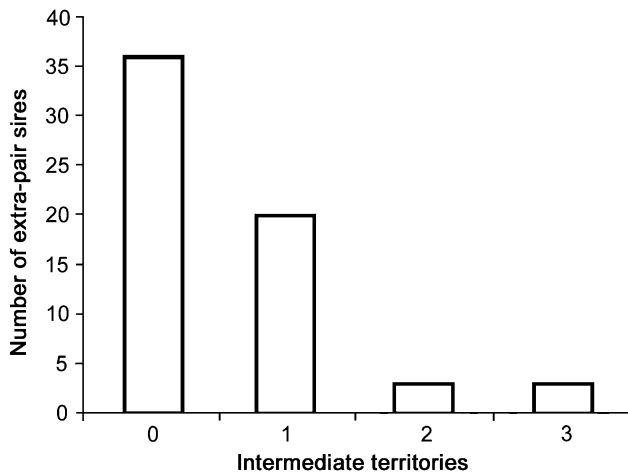


Figure 1

The number of territories between the territory of the extrapair sire and the territory of the cuckolded male. Both northern and southern populations are combined here because they were not significantly different. 90% of extrapair males were no more than one territory from the territory of the male they cuckolded, and no extrapair males were more than 3 territories away. It is unknown whether males or females forayed off their home territory to obtain these extrapair matings.

synchrony indices as above (Kempnaers 1993), except that only females residing in nest-boxes within the local region were included in the calculation. We also used the number of local females per nest as a measure of biologically relevant breeding density as this accounts for limited mobility through neighboring territories by using territories instead of distance as the spatial measure.

Statistical analysis

We compared both population-wide and local synchrony indices between populations using a 2-sample Wilcoxon test. We were not able to formally test for correlation between local and population-wide synchrony measures because the synchrony indices of nesting attempts with overlapping local regions are not independent, and subsampling to perform statistics on independent local regions resulted in inadequate sample size. However, for illustrative purposes, we performed a least squares fit of local synchrony index against population-wide synchrony index, population, and the interaction term of those variables, which is not intended to be interpreted as a statistically robust model. Because we were unable to obtain complete blood samples for many nests for which we had detailed observational data (due to early nest failure, predation, or wary social parents), nests with full genetic paternity data ($n = 122$ nests) were a subset of nests with synchrony indices ($n = 224$ nests).

We used a 2-sample Wilcoxon test to compare distances traveled and territories crossed to obtain extrapair fertilizations between populations and to compare the number of local females per nest between populations. All statistical tests described above were performed in JMP v. 7.0 (1989–2007).

We compared both the overall proportions of extrapair young and the overall proportions of broods containing extrapair young between populations using a chi-squared test.

In R v. 2.9.2 (R Development Core Team 2009), we used generalized linear mixed models fit by the Laplace approximation (the glmer function from the package lme4 [Bates and Maechler 2009]) with a binomial distribution and logit link function to examine how the proportion of extrapair young per brood, weighted by the number of chicks tested

in that brood, varied with fixed effects. We tested all possible combinations of the following fixed effects, with the restriction that only one measure of synchrony (population-wide or local) could be included in any model: population, population-wide nest synchrony index, local nest synchrony index, standardized first egg date (to detect any effect of temporal synchrony context, i.e., early asynchrony vs. late asynchrony), number of local females, and pairwise interactions between these variables. We specified year as a random effect in all models. We evaluated our models using Akaike's information criterion (AIC); the model with the lowest AIC score is the best-supported model (Akaike 1974).

RESULTS

Microsatellite loci

All microsatellite loci were highly variable, with means of 13.1 alleles per locus in northern house wrens and 8.3 alleles per locus in southern house wrens. No locus deviated significantly from Hardy–Weinberg equilibrium in either population.

Nonexclusion probabilities describe the likelihood of failing to exclude a male that is not a chick's true genetic sire as a potential sire, with small nonexclusion probabilities indicating a high power to detect extrapair young. For all loci combined, second parent nonexclusion probabilities for northern house wrens in 2004 and 2008 were 0.0009 and 0.0001, respectively, and for southern house wrens in 2003 and 2004, they were both 0.006.

Extrapair paternity

In New York, 54% of broods (44 of 82) summed over both years contained extrapair young, and 25% of offspring (94 of 377) were extrapair. In Buenos Aires, 33% of broods (13 of 40) summed over both years contained extrapair young, and 16% of offspring (26 of 166) were extrapair (Table 1). Within broods containing at least one extrapair chick, a mean of 46% of young were extrapair in both New York and Buenos Aires. The New York population had significantly higher EPP than the Buenos Aires population in both measures (proportion of broods containing extrapair young: $\chi^2 = 4.835$, degrees of freedom [df] = 1, $P = 0.028$; overall proportion of extrapair young: $\chi^2 = 5.228$, df = 1, $P = 0.022$).

Breeding biology and synchrony

Birds in the New York population traveled farther to obtain extrapair fertilizations than did birds in Buenos Aires (2-sample Wilcoxon test; $Z = -3.84$, $P = 0.0001$) but did not cross significantly more occupied territories in so doing (2-sample Wilcoxon test; $Z = -1.37$, $P = 0.170$; Table 1). The higher density of the Buenos Aires population also caused it to have significantly more local females per nest than the New York population (2-sample Wilcoxon test; $Z = 5.81$, $P < 0.0001$; Table 1).

The southern house wrens were significantly less synchronous than the northern house wrens in local (2-sample Wilcoxon test; $Z = -3.38$, $P = 0.0007$) but not in population-wide measures (2-sample Wilcoxon test; $Z = -1.10$, $P = 0.272$; Table 1). In a least squares fit, population-wide synchrony index was predictive of local synchrony index in both populations, although the relationship between the 2 measures differed between populations (population-wide synchrony index: t ratio = 18.26, $P < 0.0001$; population: t ratio = -3.57 , $P = 0.0004$; population by population-wide synchrony index interaction: t ratio = -2.08 , $P = 0.039$; but see caution in MATERIALS AND METHODS; Figure 2).

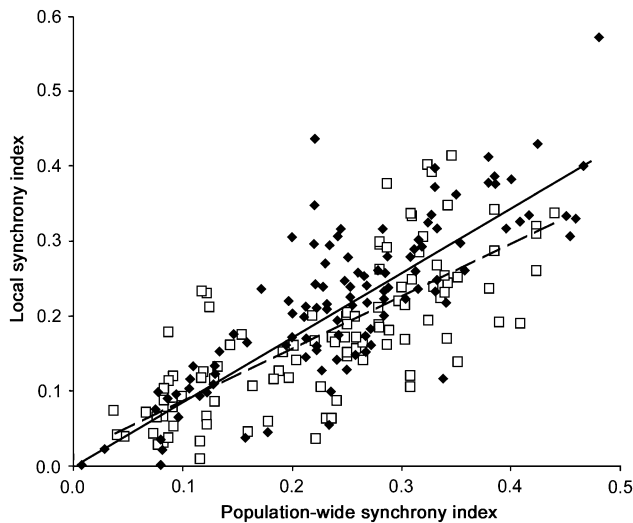


Figure 2
Local and population-wide synchrony in northern and southern house wrens. Northern house wrens are represented by filled diamonds and the solid regression line; southern house wrens are represented by open squares and the dashed regression line. Both synchrony measures showed similar patterns, although their relationship differed between the populations.

Breeding synchrony and EPP rates

Neither the population-wide nor the local synchrony index was related to the proportion of extrapair young in full models, in models with synchrony as the only predictor (population-wide synchrony index: 0.31 ± 1.16 , $z_{117} = 0.27$, $P = 0.79$; local synchrony index: -0.40 ± 1.13 , $z_{117} = -0.35$, $P = 0.72$), or in any other model (Table 2; Figure 3; see MATERIALS AND METHODS for details on the models tested). The best-supported model did not include any measure of synchrony.

In the 2 best-supported models, population, first egg date, and the population by first egg date interaction were significantly related to proportion of extrapair young (best-supported model, with these 3 variables as the only fixed effects: population (Buenos Aires vs. New York): 2.14 ± 0.76 , $z_{117} = 2.82$, $P = 0.005$; first egg date: 0.03 ± 0.02 , $z_{117} = 2.16$, $P = 0.03$; population by first egg date

interaction: -0.04 ± 0.02 , $z_{117} = -2.25$, $P = 0.02$. The second best-supported model included the same significant effects, as well as a nonsignificant term of population breeding synchrony). When first egg date was tested in each population separately, to explore the patterns underlying the significance of the population by first egg date interaction term, it was nonsignificant in New York (-0.004 ± 0.006 , $z_{117} = -0.67$, $P = 0.50$) and significant in Buenos Aires (0.03 ± 0.02 , $z_{117} = 1.97$, $P = 0.05$).

Removing polygynous nests (10 in New York, none in Buenos Aires) from the sample never changed estimates of EPP or local or population-wide synchrony by more than 0.005, and did not change the conclusions of any statistical analyses. The results presented are those with the polygynous nests included.

DISCUSSION

Hemispheric comparisons of breeding synchrony and EPP rates

Southern house wrens had a moderate rate of EPP (33% of broods and 16% extrapair offspring), significantly lower than their northern counterparts (54% of broods and 25% of offspring). Few opportunities exist to compare EPP rates between closely related populations of passerine birds that breed in northern temperate and southern temperate regions, and information on EPP rates of southern temperate species is also generally sparse. Our Argentinean southern house wren population was overall less locally synchronous than the northern house wren population. The lower EPP rate and lower local breeding synchrony in the southern population is consistent with hypotheses of a general association between EPP rate variation and synchrony (Stutchbury and Morton 1995; Stutchbury 1998a, 1998b). However, the differences in synchrony are small (0.23 vs. 0.25; Table 1) and seem unlikely to drive the much larger differences in EPP rates.

Influence of migratory context and other life-history variables

Migration could be one cause of the higher EPP rates in the migratory northern house wrens compared with the resident southern house wrens. Spottiswoode and Møller (2004) suggest that migration might lead to higher EPP rates if 1) the pressure to commence breeding quickly leads to hasty mate choice, such that females become socially mated to males which do not maximize the genetic quality of their offspring, with the females subsequently seeking extrapair copulations with more optimal males; 2) females use arrival time to assess relative male quality, increasing females' potential benefits of EPP by enabling them to better select highest quality extrapair partners; or 3) higher gene flow in migratory populations in house wrens (Arguedas and Parker 2000) leads to higher male genetic variance, increasing the potential benefits to females of EPP. The significant effect of the population by first egg date interaction on EPP in our analysis may be due to migration: the timing of breeding could be determined by different factors in a resident versus a migratory population, and thereby be related differently to EPP rates in the 2 populations.

Additionally, extrapair mating behavior may have a higher cost for resident southern house wrens than for migratory populations because southern house wren females can remain paired with the same male for several years. If cuckolded males penalize their unfaithful females, for example, by reducing parental care of the young, then for female southern house wrens these long-term costs might not outweigh any benefits of EPP (Mauck et al. 1999).

Table 2
Selected generalized linear mixed models of EPP rate

Fixed effects in model	AIC	ΔAIC
1 Pop. , laydate , pop. × laydate	260.8	0.0
2 Pop. , laydate , pop. × laydate , pop. SI	261.1	0.3
3 Pop.	261.6	1.0
4 Pop. SI	264.0	3.2
5 Local SI	264.0	3.2
6 Pop. , local SI, females, laydate, pop. × local SI, pop. × females, pop. × laydate , local SI × females, local SI × laydate, females × laydate	266.9	6.1
7 Pop., pop. SI, females, laydate, pop. × pop. SI, pop. × females, pop. × laydate , pop. SI × females, pop. SI × laydate, females × laydate	270.5	9.7

1–3 had the 3 lowest AIC scores of all models; 4–5 tested one synchrony measure alone; 6–7 are full models. Fixed effects significant at the $\alpha = 0.05$ level are in bold. Pop., population; pop. SI, population-wide synchrony index; local SI, local synchrony index; lay date, first egg date; females, number of local females.

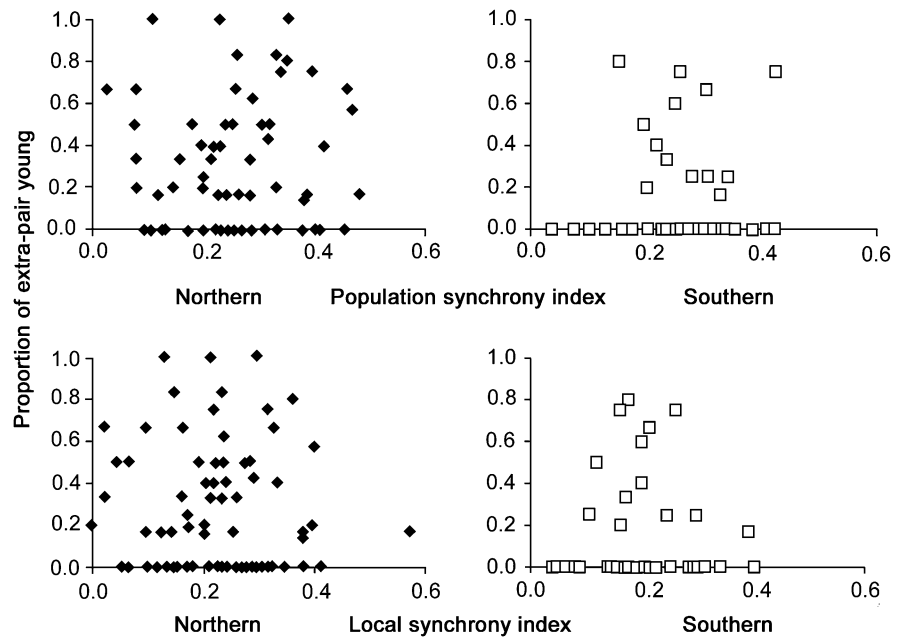


Figure 3
Population-wide and local synchrony indices and proportions of extra-pair young within nests in northern and southern house wrens. EPP was not significantly related to either synchrony index

Breeding density differed significantly between the northern and southern populations, and may affect interpopulation differences in EPP. Higher densities might increase extrapair copulation opportunities but could also stimulate increased mate guarding (Thusius et al. 2001). However, our sample size is too small to test the effects of density or other life-history factors on EPP rates at the interpopulation level. Within populations, local breeding density was not significantly related to variation in EPP rates in either population.

Local versus population-wide measures of breeding synchrony

Although population-wide synchrony and local synchrony followed similar patterns in this study, the significant interpopulation difference in local synchrony was not present in population-wide synchrony. We suggest that researchers in general should be wary of using synchrony measures that are not scaled according to the mobility of their study organism because a simple population-wide synchrony index may not be biologically relevant, and using an incorrect measure could mask an effect of synchrony, especially in populations with high spatial heterogeneity in the timing of females' fertile periods.

Moreover, the apparent relationship between population-wide and local synchrony indices in this study may not generalize to other systems because the association between local and population-wide synchrony indices may depend on the size of local regions relative to the whole study area and on the habitat uniformity across the study area. That is, local and population-wide synchrony indices will be essentially the same for highly mobile organisms or for organisms in patchy habitat, where most individuals in the population are also in the biologically relevant local area. For less mobile animals living in large contiguous populations, population-wide and local synchrony indices may be less similar. That the relationship between local and population-wide synchrony indices differed between the northern and southern populations in this study exemplifies that relationship's potential sensitivity to environmental factors.

Intrapopulation patterns in breeding synchrony and EPP rates

We found no evidence that within-population variation in EPP rates was related to either measure of nest synchrony in either

the northern or the southern house wren, despite substantial variation in these variables. The possibility that the sample size in the Buenos Aires population was insufficient to detect a synchrony–EPP rate relationship in that population cannot be ruled out. Nevertheless, the lack of a strong intrapopulation relationship between EPP and synchrony in house wrens is consistent with some studies of other northern temperate species (Chuang et al. 1999; Johnson et al. 2002; Arlt et al. 2004; Vaclav and Hoi 2007) and suggests that southern temperate species likewise have EPP rate variation which cannot be explained by breeding synchrony variation alone.

What does drive variation in EPP rates?

That within-population variation in EPP is not related to synchrony suggests that EPP in these wrens is not primarily constrained by the availability of fertile females. Extrapair copulations may not be driven simply by opportunistic males (as in the mate-guarding hypothesis); instead, individual variation in attributes such as male or female quality, age, genetic makeup, territory quality, or personality (van Oers et al. 2008) could influence extrapair behavior or affect the success of extrapair fertilization attempts, complicating patterns of EPP. The significant positive association between first egg date and EPP in our analysis may indicate an effect of male and/or territory quality, if, for instance, better territories support earlier breeding. It is unlikely that this association is due to the positive association of male arrival time on the breeding grounds with male quality often seen in migratory populations because we found no significant association between first egg date and EPP when we analyzed our migratory population alone.

Alternatively, fertile female presence may contribute to variation in EPP, but the synchrony index may not measure fertile female presence in a way that is relevant to the behaviors that influence EPP rates. Either males (e.g., via mate guarding) or females (e.g., via rejecting some extrapair copulation attempts) could alter the effective availability of fertile females in a way that is not directly related to the simple number of fertile females, and therefore would not be reflected in the synchrony index. In golden whistlers (*Pachycephala pectoralis*), for example, increased male mate-guarding effort when synchrony is low may render the synchrony index an inaccurate measure of fertile female availability (van Dongen 2008).

In contrast to our results, several studies of other avian taxa have found a significant intrapopulation relationship between EPP rates and breeding synchrony (Strohbach et al. 1998; Westneat and Gray 1998; Thusius et al. 2001). It may be that breeding synchrony is an important factor under circumstances that were not present in our study populations. Alternatively, variables that do drive EPP rate variation may covary with synchrony in some populations, leading to the semblance of a causal synchrony–EPP rate relationship. Our results, however, add to the growing evidence that across divergent life histories, EPP rates are often not driven by breeding synchrony (Westneat and Sherman 1997; Griffith et al. 2002; Arlt et al. 2004).

FUNDING

Fuller Evolutionary Biology Program support to K.L., a Howard Hughes Summer Scholarship to K.L.; Mario Einaudi Center for International Studies International Research Travel Grant to P.E.L.; Organization of American States Graduate Fellowship to P.E.L.; The Scientific Research Society to P.E.L.; American Ornithological Union Research Award to P.E.L.; Andrew W. Mellon Student Research Grant to P.E.L.; Cornell Chapter of Sigma Xi Grant to E.R.A.C.; Cornell University College of Agriculture and Life Sciences Science Fellowship to T.D.S.; National Sigma Xi Grant-In-Aid-of-Research (G200803150162 to T.D.S.).

We thank Laura Stenzler, Amanda Talaba, Douglas Morin, Chris Makarewicz, Andrea Townsend, and Benjamin Winger for their laboratory assistance and advice. We thank Gustavo Fernández, Myriam Mermoz, and Pablo Rodríguez for help in the field; the Whisky-Michelli family for allowing us to work on their ranches; and Mario Beade for logistical support. We thank Bob Johnson, Janis Dickinson, Andre Dhondt, Caren Cooper, and Margaret Voss for logistical support at Cornell Experimental Ponds.

REFERENCES

Akaike H. 1974. A new look at the statistical model identification. *IEEE Trans Automat Contr*. AC19:716–723.

American Ornithologists' Union. 1998. Checklist of North American birds. 7th ed. Washington (DC): American Ornithologists' Union. p. 480–481.

Arguedas N, Parker PG. 2000. Seasonal migration and genetic population structure in house wrens. *Condor*. 102:517–528.

Arlt D, Hansson B, Bensch S, von Schantz T, Hasselquist D. 2004. Breeding synchrony does not affect extra-pair paternity in great reed warblers. *Behaviour*. 141:863–880.

Bates D, Maechler M. 2009. lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999375-31 [Internet]. Available from: <http://lme4.r-forge.r-project.org/>.

Birkhead TR, Biggins JD. 1987. Reproductive synchrony and extra-pair copulation in birds. *Ethology*. 74:320–334.

Brar RK, Schoenle LA, Stenzler LM, Halls ML, Vehrencamp SL, Lovette IJ. 2007. Eleven microsatellite loci isolated from the banded wren (*Thryothorus pleurostictus*). *Mol Ecol Notes*. 7:69–71.

Brumfield RT, Capparella AP. 1996. Genetic differentiation and taxonomy in the House Wren species group. *Condor*. 98:547–556.

Cabe PR, Marshall KE. 2001. Microsatellite loci from the house wren (*Troglodytes aedon*). *Mol Ecol Notes*. 1:155–156.

Chuang HC, Webster MS, Holmes RT. 1999. Extra-pair paternity and local synchrony in the black-throated blue warbler. *Auk*. 116:726–736.

Dawson DA, Hanotte O, Greig C, Stewart IRK, Burke T. 2000. Polymorphic microsatellites in the blue tit *Parus caeruleus* and their cross-species utility in 20 songbird families. *Mol Ecol*. 9:1941–1944.

van Dongen WFD. 2008. Mate guarding and territorial aggression vary with breeding synchrony in golden whistlers (*Pachycephala pectoralis*). *Naturwissenschaften*. 95:537–545.

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol Ecol*. 11:2195–2212.

JMP. 1989–2007. Version 7. Cary (NC): SAS Institute Inc.

Johnson LS. 1998. House Wren (*Troglodytes aedon*). In: Poole A, editor. The birds of North America Online [Internet]. Ithaca (NY): Cornell Lab of Ornithology; [cited 2009 October 24]. Available from: <http://bna.birds.cornell.edu/bna/species/380>.

Johnson LS, Hicks BG, Masters BS. 2002. Increased cuckoldry as a cost of breeding late for male house wrens (*Troglodytes aedon*). *Behav Ecol*. 13:670–675.

Johnson LS, Kermott LH, Lein MR. 1993. The cost of polygyny in the house wren *Troglodytes aedon*. *J Anim Ecol*. 62:669–682.

Johnson LS, Rauch RL, Dellone SN. 2004. The process and causes of fledging in a cavity-nesting passerine bird, the house wren (*Troglodytes aedon*). *Ethology*. 110:693–705.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol*. 16:1099–11006.

Kempnaers B. 1993. The use of a breeding synchrony index. *Ornis Scand*. 24:84.

Llambías PE. 2009. Why monogamy? Comparing House Wren social mating systems in two hemispheres [PhD dissertation]. New York: Cornell University.

Llambías PE, Fernández GJ. 2009. Effects of nestboxes on the breeding biology of Southern House Wrens *Troglodytes aedon bonariensis* in the southern temperate zone. *Ibis*. 151:113–121.

Makarewicz CA, Stenzler LM, Ferretti V, Winkler DW, Lovette IJ. 2009. Isolation and characterization of microsatellite markers from three species of swallows in the genus *Tachycineta*: *T. albilinea*, *T. bicolor* and *T. leucorhoa*. *Mol Ecol Resour*. 9:631–635.

Masters BS, Hicks BG, Johnson LS, Erb LA. 2003. Genotype and extra-pair paternity in the house wren: a rare-male effect? *Proc R Soc B Biol Sci*. 270:1393–1397.

Mauck RA, Marschall EA, Parker PG. 1999. Adult survival and imperfect assessment of parentage: effects on male parenting decisions. *Am Nat*. 154:99–109.

Møller AP. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav Ecol Sociobiol*. 35:115–122.

Nyström KGK. 1997. Food density, song rate, and body condition in territory-establishing willow warblers (*Phylloscopus trochilus*). *Can J Zool*. 75:47–58.

van Oers K, Drent PJ, Dingemanse NJ, Kempenaers B. 2008. Personality is associated with extra-pair paternity in great tits, *Parus major*. *Anim Behav*. 76:555–563.

Poirier NE, Whittingham LA, Dunn PO. 2004. Males achieve greater reproductive success through multiple broods than through extra-pair mating in house wrens. *Anim Behav*. 67:1109–1116.

Purcell KL, Verner J, Oring LW. 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. *Auk*. 114:646–656.

R Development Core Team. 2009. R: a language and environment for statistical computing [Internet]. Vienna (Austria): R Foundation for Statistical Computing; [cited 2009 December 30]. Available from: <http://www.R-project.org>.

Rubenstein DR. 2007. Female extra-pair mate choice in a cooperative breeder: trading sex for help and increasing offspring heterozygosity. *Proc R Soc B Biol Sci*. 274:1895–1903.

Soukup SS, Thompson CF. 1997. Social mating system affects the frequency of extra-pair paternity in house wrens. *Anim Behav*. 54:1089–1105.

Spottiswoode C, Møller AP. 2004. Extra-pair paternity, migration, and breeding synchrony in birds. *Behav Ecol*. 15:41–57.

Strohbach S, Curio E, Bathen A, Epplen JT, Lubjuhn T. 1998. Extra-pair paternity in the great tit (*Parus major*): a test of the “good genes” hypothesis. *Behav Ecol*. 9:388–396.

Stutchbury BJ, Morton ES. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour*. 132:675–690.

Stutchbury BJM. 1998a. Breeding synchrony best explains variation in extra-pair mating system among avian species. *Behav Ecol Sociobiol*. 43:221–222.

Stutchbury BJM. 1998b. Female mate choice of extra-pair males: breeding synchrony is important. *Behav Ecol Sociobiol*. 43:213–215.

- Stutchbury BJM, Morton ES. 2008. Recent advances in the behavioral ecology of tropical birds: the 2005 Margaret Morse Nice lecture. *Wilson J Ornithol.* 120:26–37.
- Thusius KJ, Dunn PO, Peterson KA, Whittingham LA. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. *Behav Ecol.* 12:633–639.
- Tieleman BI, Dijkstra TH, Lasky JR, Mauck RA, Visser GH, Williams JB. 2006. Physiological and behavioural correlates of life-history variation: a comparison between tropical and temperate House Wrens. *Funct Ecol.* 20:491–499.
- Vaclav R, Hoi H. 2007. Experimental manipulation of timing of breeding suggests laying order instead of breeding synchrony affects extra-pair paternity in house sparrows. *J Ornithol.* 148:395–400.
- Weatherhead PJ, Yezerinac SM. 1998. Breeding synchrony and extra-pair mating in birds. *Behav Ecol Sociobiol.* 43:217–219.
- Westneat DF, Gray EM. 1998. Breeding synchrony and extrapair fertilizations in two populations of red-winged blackbirds. *Behav Ecol.* 9:456–464.
- Westneat DF, Sherman PW. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. *Behav Ecol Sociobiol.* 41: 205–215.
- Westneat DF, Sherman PW, Morton ML. 1990. The ecology and evolution of extra-pair copulations in birds. *Curr Ornithol.* 7: 331–369.
- Westneat DF, Stewart IRK. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Ann Rev Ecol Evol Syst.* 34:365–396.
- White PS, Densmore LD. 1992. Mitochondrial DNA isolation. In: Hoelzel AR, editor. *Molecular genetic analysis of populations: a practical approach.* Oxford: IRL Press at Oxford University Press. p. 50–51.
- Yezerinac SM, Weatherhead PJ. 1997. Reproductive synchrony and extra-pair mating strategy in a socially monogamous bird, *Dendroica petechia*. *Anim Behav.* 54:1393–1403.
- Young BE. 1996. An experimental analysis of small clutch size in tropical House Wrens. *Ecology.* 77:472–488.