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Extra-pair paternity in a population of Chilean Swallows breeding at 54 degrees south

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ABSTRACT. Geographic patterns of variation in life-history traits have puzzled researchers for decades. However, the widely accepted idea that mating systems exhibit a tropical–temperate latitudinal trend, with extra-pair mating systems being the norm among temperate species and genetic monogamy the norm among tropical species, is supported by sparse data, particularly for birds breeding in the tropics and even more so for birds that breed in the southern hemisphere temperate zone. Our objective was to examine the genetic mating system of Chilean Swallows (*Tachycineta meyeni*) breeding at 54°S in Tierra del Fuego, Argentina. From 2006 to 2009, we examined the paternity of young in 52 broods. Contrary to predictions based on their congeners that breed at equivalent latitudes in the northern hemisphere, Chilean Swallows in our study had low rates of extra-pair paternity (EPP), with 13.5% of nests ($N = 52$) having at least one extra-pair young and 6.8% of all nestlings ($N = 161$) fathered by extra-pair males. These rates are also lower than those reported for species of *Tachycineta* swallows that breed at tropical latitudes. We found no support for a tropical–south temperate latitudinal cline in EPP rates. The highly unpredictable weather of the island of Tierra del Fuego might be influencing parental investment at this site; small clutch sizes and low EPP rates are expected if biparental attention is crucial for chick survival and reproductive success for these aerial insectivores. We argue that the sparse sampling of mating systems in birds worldwide may have contributed to a misapprehension of a global pattern. More studies of tropical and south-temperate systems are needed to build on theories based on a wider set of taxa.

RESUMEN. **Paternidad extra-pareja en una población de Golondrina Patagónica a los 54 grados sur**

Los patrones de variación geográficos en rasgos de historias de vida han intrigado a los investigadores por décadas. Sin embargo, la idea ampliamente aceptada que establece que los sistemas de apareamiento presentan una tendencia latitudinal del trópico a las latitudes templadas, con sistemas de apareamiento extra-pareja siendo la norma en las especies templadas, y la monogamia genética la norma entre especies tropicales, se apoya en muy pocos datos; en especial para especies de aves que se reproducen en el trópico, y más aun para aquellas de la zona templada del hemisferio sur. Nuestro objetivo fue estudiar el sistema genético de apareamiento de la golondrina Patagónica *Tachycineta meyeni* a los 54°S en Tierra del Fuego, Argentina. Entre 2006–2009 examinamos la paternidad de los polluelos de 52 nidadas. Contrario a nuestras predicciones basadas en los congéneres que se reproducen en latitudes equivalentes del hemisferio norte, en nuestro estudio las golondrinas Patagónicas tienen tasas muy bajas de paternidad extra-pareja con 13.5% de nidos con por lo menos un polluelo extra-pareja ($N = 52$) y 6.8% de polluelos extra-pareja en la población ($N = 161$). Estas tasas son más bajas que las encontradas en especies de golondrinas *Tachycineta* tropicales. No encontramos apoyo para la existencia de una clina latitudinal de los trópicos al sur templado en tasas de paternidad extra-pareja. El tiempo altamente impredecible de la isla de Tierra del Fuego puede estar influyendo sobre la inversión parental en este sitio: se espera que los tamaños de puesta sean pequeños y las tasas de paternidad extra-pareja bajas si la atención biparental es crucial para la supervivencia de los pichones y el éxito reproductivo de estos insectívoros aéreos. Sostenemos que el escaso muestreo de los sistemas de apareamiento en aves

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a nivel mundial ha contribuido a esta evaluación equivocada del patrón general. Más estudios deberían enfocarse en los sistemas tropicales y del sur templado para reforzar las teorías basadas en un set más amplio de taxones.

Key words: Hirundinidae, latitudinal variation, life-history traits, mating system, *Tachycineta meyeni*

In the three decades since DNA-based molecular techniques for assessing parentage were first applied to birds (Burke and Bruford 1987), we have learned that the earlier assumption that 90% of avian taxa are genetically monogamous (Lack 1968) greatly underestimated the prevalence of extra-pair mating. Variation in local ecology likely affects the reproductive tactics and mating decisions of birds exposed to different ecological conditions (Griffith et al. 2002, Wilson 2009) and, therefore, such variation likely influences the genetic mating systems and levels of extra-pair paternity (EPP) of different populations and species. Although we know that the genetic mating systems of populations of the same or closely related bird species may vary (e.g., Moore et al. 1999, LaBarbera et al. 2010, 2012), studies designed to compare this variation among different geographic areas remain scarce. Nonetheless, an emerging paradigm is that tropical species generally have lower rates of EPP than species at higher latitudes (Stutchbury and Morton 2001, 2008, Macedo et al. 2008). Low levels of EPP in the tropics have been related to decreased breeding synchrony and density, slow pair formation by non-migrants, and high adult survival (reviewed in Macedo et al. 2008), all of which co-vary with latitude.

Studies of variation in the mating systems of north-temperate and tropical species have been important for developing hypotheses regarding the possible causes of geographic variation in extra-pair mating (e.g., Stutchbury and Morton 1995). However, there is still relatively little empirical evidence showing that tropical birds are, in fact, different from temperate ones (Macedo et al. 2008), and we should expect lower rates of EPP for tropical species of birds than for temperate species (Stutchbury and Morton 2001). North-temperate birds might behave differently than south-temperate ones, and tropical birds might be more similar to north- or south-temperate species than expected. The point is that we do not know; avian mating systems have been studied extensively, but sample sizes in some regions remain small (Macedo et al. 2008). At present, our knowledge of EPP rates of tropical birds stems from studies of less than 0.1% of the total number of species breeding at those latitudes (passerines and non-passerines, 12 species cited in Macedo et al. 2008, 10 species cited in Stutchbury and Morton 2008, plus six more species have been studied since these reviews were published: Cramer et al. 2011, Maurer et al. 2011, Douglas et al. 2012, Eikenaar et al. 2013, Tarwater et al. 2013, Woolaver et al. 2013). Although these investigators have generally focused on the contrast between tropical and north-temperate species, few have addressed patterns in southern temperate breeding birds.

Why might patterns of extra-pair mating be different in the southern temperate zone than in the northern temperate zone? Differences in climate-related variables between the north and south might modify predictions about geographic variation in mating systems of birds breeding at the same latitude, but in different hemispheres. In particular, continentality (i.e., the proportion of land surface area to ocean surface area) can affect breeding synchrony, migration behavior, and adult survival, variables that can shape mating decisions of birds living in the northern and southern hemispheres. Continentality can have an effect on mean summer and winter temperatures because the caloric capacity of water is greater than that of land. Because water acts as a temperature attenuator, winters tend to be colder and summers hotter in the northern hemisphere than the southern hemisphere (see Rivas-Martínez and Rivas-Sáenz 1996–2015, for detailed world maps depicting differences in continentality) and, in addition, there is greater thermal amplitude and more rapid seasonal change north of the equator (Linacre and Geerts 1997, Gates et al. 1999).

Environmental temperatures, in turn, can have an impact on the length of the breeding season, influencing breeding synchrony, which can indirectly affect EPP rates because females will be better able to compare the quality of displaying males when breeding synchronously, and can base their later mating decisions on this early assessment of quality (Stutchbury 1998). In addition, the harsher climates experienced by birds in the northern hemisphere can differentially affect migratory behavior and adult survival compared to birds that breed at similar latitudes in the south, which can also influence extra-pair mating tactics. For example, if migration selects for early arrival of birds in good condition, high-quality individuals will occupy the best nest sites (Kokko 1999), potentially affecting the pairing dynamics of a population and leading to a latitudinal pattern of variation in EPP (Spottiswoode and Møller 2004). In addition, males usually arrive first in breeding areas (protandry), and this may result in intense sperm competition between males attempting to gain access to the few females arriving early in the breeding season (Kokko et al. 2006) as well as female-driven choice of extra-pair partners by later-arriving females (Spottiswoode and Møller 2004). Migratory birds may be forced to quickly find a mate to start breeding soon after settling in breeding areas, potentially leading to inaccurate assessments of mate quality and, as a result, high rates of EPP (Spottiswoode and Møller 2004). Harsher winter climates and migration can also affect the prospects of survival of adult birds, potentially affecting extra-pair mating decisions; tolerance of extra-pair mating is expected to increase with a decrease in adult survival rates because of the increased chance of not breeding if they desert their social partner due to uncertainty of paternity (Mauck et al. 1999, Wink and Dyrcz 1999). For these reasons, testing hypotheses concerning variation in mating systems in south-temperate as well as north-temperate birds is essential for a better understanding of the variables that affect mating decisions.

Our objective was to characterize the genetic mating system of Chilean Swallows (*Tachycineta meyeni*) at a site in Tierra del Fuego at 54°S latitude. The mating systems of other swallows in the genus *Tachycineta* have been the focus of extensive past research, particularly, but not exclusively, northern temperate breeding species (e.g., Moore et al. 1999, Jones 2003, Ferretti and Winkler 2009, Ferretti et al. 2011). All species in the genus *Tachycineta* are socially monogamous (Turner and Rose 1989, Turner 2004), but rates of EPP vary. In the northernmost study conducted to date, O'Brien and Dawson (2007) reported that 85% of nests had at least one extra-pair young (EPY) in a population of Tree Swallows (*T. bicolor*) breeding at 53°N. In contrast, Moore et al. (1999) found at least one EPY in 26% of nests of Mangrove Swallows (*T. albilinea*) breeding in the tropics at 9°N, and Ferretti et al. (2011) reported that 78% of nests had EPY in a population of White-rumped Swallows (*T. leucorrhoa*) breeding at 35°S. In addition, Moore et al. (1999) compared their results to those for Tree Swallows and concluded that differences in EPP rates between these species were likely due to latitudinal differences in breeding synchrony. Given this variation among latitudes and different species of swallows and the apparent positive correlation between EPP rates and latitude, we expected that Chilean Swallows would exhibit high rates of EPP, similar to those reported for Tree Swallows at high northern latitudes by O'Brien and Dawson (2007).

METHODS

Chilean Swallows are found in open and semi-open grasslands and wetlands, usually near water, and are secondary cavity nesters that readily nest in nest boxes. The species breeds from Tierra del Fuego (Argentina and Chile) in the south to central Chile and southwest Argentina further north. During the southern winter, these birds migrate north to northern Argentina, southeast Brazil, and Paraguay (Turner 2004).

Field protocol. We studied Chilean Swallows breeding in nest boxes at a site located at 54°44′S 68°12′W, 15 km from the city of Ushuaia (Tierra del Fuego, Argentina), from 2006 to 2009. We set up 118 nest boxes in 2006 before the breeding season started and added 100 additional nest boxes in 2007. The percent occupancy of these boxes varied from 19% to 28% during our study (i.e., nests with at least one egg) (Liljesthröm 2011). We checked nest contents every other day for the duration of the breeding season (late October through January).

For every nesting attempt, we captured both adults attending nests using box traps (see http://golondrinas.cornell.edu for details on boxes and traps). We banded adults with individually numbered aluminum bands, and banded nestlings when they were 7- to 9-d-old. We also collected 20–70 µl of blood from adults and nestlings using heparinized capillary tubes and brachial venipuncture, and stored the blood in Queen's lysis buffer (Seutin et al. 1991). When nestlings were found dead in the nest before they were banded and bled, we dissected them and collected a sample of pectoral muscle and stored it in 96% ethanol. If eggs failed to hatch, but showed some embryonic development, we dissected the egg and collected tissue from the embryo that was stored in 96% ethanol.

Genetic analyses. We extracted DNA from blood and muscle samples using DNA purification kits (Qiagen, Valencia, CA). Extracted DNA was diluted 1:10 in ultrapurified H_2O and then amplified at a panel of 10–11 highly polymorphic microsatellite loci (Makarewich et al. 2009). Samples from 2006 to 2008 were genotyped at 10 loci; samples from 2009 were genotyped at the same 10 loci plus an additional locus (Table 1). The combined exclusion probability for all loci was >0.9999 for both runs using 10 and 11 loci. We used the program Cervus v.3.0 (Marshall et al. 1998, Kalinowski et al. 2007, 2010) for the calculation of population genetic and parentage analyses. For likelihood calculations in Cervus, we used the following simulation parameters for 2006–2008 and 2009: proportion of fathers sampled in the population for both time periods was 90% (this proportion was taken directly from our field observations of active nests in the area, and the males captured at these nests), 10,000 offspring, 80% relaxed and 95% strict confidence levels, 100% and 97% of loci typed for each time period sampled, respectively, and 1% of loci mistyped, as calculated by the program from our data. With these parameters, we obtained a 99% and 95% assignment rate for each time period under the strict confidence level, respectively. Details on the PCR (Polymerase Chain Reaction) cycling profiles, additional paternity assessment methods, and software used are provided in Ferretti et al. (2011).

We only analyzed nests where we collected tissue samples (blood, pectoral muscle, or embryo) from all eggs/nestlings in the brood and both social parents. We first compared the nestlings' genotypes with the genotype of the adult female attending their nest (i.e., the putative mother). As expected, most nestlings shared at least one allele at each of the amplified loci with their putative mother. Eight nestlings mismatched the genotype of the mother at one locus; we regard these nestlings as offspring of their putative mothers, and assume this single-locus allele difference to be a result of rare mutations or genotyping errors (Fernando et al. 2001). We found no cases of mismatches between offspring and their putative mothers at two or more loci. Genotypes of nestlings were then compared to those of their putative father, and we considered nestlings to be EPY if they mismatched the social father's genotype at two or more loci. Fourteen nestlings mismatched their social father's genotype at only one locus.

Lastly, we compared EPP rates (measured as the proportion of nests with at least one extra-pair offspring, and the proportion of extra-pair offspring in the population) for each year of our study with Fisher's exact test using the web tool provided by http://in-silico.net/tools. We tested the null hypothesis that these proportions did not differ across the years of our study.

RESULTS

Mean clutch size in our population was 3.8 ± 0.05 eggs ($N = 157$), and mean brood size at hatching was 3.2 ± 0.08 nestlings ($N = 134$). During our study, we captured and banded 73 adult females and 60 adult males, and analyzed 52 broods with complete information (male and female and nestlings or eggs). We extracted DNA from 24 nestlings found dead in nests and eight eggs that did not hatch, which were part of these broods. Seven of the 52 broods (13.5%) had at least one extra-pair nestling. Of 161 nestlings in these broods, 11 were EPY (6.8%). Five of the seven broods with EPY had only one extra-pair nestling, one brood had two, and one brood had four. Of the 161 nestlings, we were able to assign paternity-status, given a known mother, for 154 under the strict confidence level (61 for 2006–2008, and 93 for 2009).

In 2006 and 2007, we found no extra-pair offspring ($N = 6$ nests and 17 nestlings for both years combined). In 2008 ($N = 19$ nests and 55 nestlings), 15.8% of nests had at least one EPY and 7.3% of all nestlings were EPY. In 2009 ($N = 27$ nests and 89 nestlings), 14.8% of nests had at least one EPY and 7.9% of all nestlings were EPY. These differences among years were not significant (Fisher's exact two-tailed test, $P = 0.84$ for percentage of EPY and $P > 0.99$ for percentage of nests with EPY).

DISCUSSION

Breeding populations of swallows in the genus *Tachycineta* are distributed throughout the Americas, ranging from Alaska to Tierra del

Table 1. Microsatellite primers used for genotyping Chilean Swallows (from Makarewich et al. 2009).

Locus	*N*[a]	Na[b]	Ho[c]	He[d]	Ann Temp[e]	Primer concentration (pM)
Tabi1	53	8	0.849	0.786	56	1.2
Tabi4	53	7	0.755	0.724	56	4.8
Tal6	53	4	0.245	0.238	58	1.6
Tal8	53	34	1.000	0.965	58	3.6
Tal7	53	24	0.774	0.930	56	1.2
Tle17	53	6	0.509	0.512	56	2.4
Tle19	53	4	0.472	0.429	56	1.0
Tle21	53	4	0.245	0.225	58	1.2
Tle4	53	25	0.943	0.948	56	2.4
Tle8	53	8	0.698	0.692	56	1.2
Tle11	60	19	0.883	0.854	58	1.2

[a] *N*, number of unrelated individuals genotyped.
[b] Na, number of alleles.
[c] Ho, observed heterozygosity.
[d] He, expected heterozygosity.
[e] Ann Temp, annealing temperature.

Fuego, and studies to date suggest a tropical–temperate pattern of variation in rates of EPP. Temperate Tree and White-rumped swallows have high rates of EPP (e.g., Dunn and Robertson 1993, Lifjeld et al. 1993, Ferretti et al. 2011), and tropical Mangrove Swallows have lower rates of EPP (Moore et al. 1999). We found that Chilean Swallows in a population breeding at 54°S in Tierra del Fuego, Argentina, had relatively low rates of EPP, and rates lower than that of their tropical congener, the Mangrove Swallow.

Our results did not support our initial prediction that Chilean Swallows would have EPP rates similar to those reported for the northernmost breeding populations of Tree Swallows (O'Brien and Dawson 2007), that is, we found no support for a tropical–temperate latitudinal gradient in EPP. This could be because our prediction was based on the results of studies of relatively few tropical species. Alternatively, our population of Chilean Swallows in Tierra del Fuego may be an outlier in an otherwise strong tropical–temperate latitudinal cline because Tierra del Fuego is an island at the tip of South America with an oceanic (Rivas-Martínez and Rivas-Sáenz 1996–2015) and somewhat unpredictable climate (Tuhkanen 1992), that is, dramatic changes in temperature and precipitation throughout the day can be frequent, snowfall can be expected in the summer months, and wind is a constant stress factor that could subject the population to location-specific ecological dynamics. For example, bad weather conditions can affect food supply and foraging success of aerial insectivores such as these *Tachycineta* swallows, directly affecting their nesting success, as reported for Tree Swallows (McCarty and Winkler 1993, 1999). With unpredictable weather conditions, the degree of parental care received by each nestling might be crucial for survival, so smaller clutch sizes and increased male and female attention to the nest should be favored, limiting the opportunities for seeking extra-pair copulations. In fact, Liljesthröm et al. (2012) found that clutch sizes in this population of swallows were smaller than those of their tropical congeners, *T. albilinea*. Moreover, Chilean Swallows in Tierra del Fuego have one of the smallest clutch sizes in the genus *Tachycineta* (only tropical *T. stolzmanni* and *T. cyaneoviridis* have smaller clutches) and, in addition, do not follow the general trend for species in this genus for larger clutches at higher latitudes (Winkler et al. 2014). This supports our hypothesis that the population we studied is an outlier, likely due to the unpredictable environmental idiosyncrasies of the study site.

In contrast to our study site, birds breeding at high latitudes in continental North America or Patagonia may not experience such dramatic and rapid changes in weather. If so, clutch sizes would be expected to be larger because food availability would likely not exhibit as much variation as in Tierra del Fuego, and the longer periods of daylight at higher latitudes might mean more food can be delivered to nestlings. This additional time would likely also provide adults with more opportunities to engage in extra-pair matings. Testing this hypothesis will require data from continental populations of Chilean Swallows breeding at different latitudes.

In summary, we found that Chilean Swallows in Tierra del Fuego have lower EPP rates than expected based on the predicted latitudinal cline in this parameter. This may be because there is no such cline or because the particular environmental and ecological conditions at our study site have favored low rates of EPP. Further study is needed to determine which of these two alternatives best explains our results and, more generally, to better understand the possible effect of latitude on variation in rates of EPP.

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