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ORIGINAL ARTICLE

Male condition and group heterogeneity predict extra-group paternity in a Neotropical bat

Danielle M. Adams[1] · Gerald S. Wilkinson[1]

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Abstract

Extra-group paternity, in which offspring are sired by a male outside the breeding group, may alter the distribution of reproductive success in a population, thus affecting the opportunity for sexual selection. Both inter- and intraspecific studies have focused largely on mating systems in which females choose their social mates, and less is known about extra-group paternity in polygynous systems in which social mates are largely dictated by male-male competition. In this study, we examine the frequency and distribution of extra-group paternity in a harem-forming bat, *Phyllostomus hastatus*. We find that despite aggressive harem defense, males are unable to fully monopolize reproduction within their harem and over 70% of harems contain extra-group offspring. Harem males in better body condition suffered less paternity loss, but we found no effect of male age or body size. Even though the age and size of individual females did not predict offspring paternity, we found a significant effect of age heterogeneity within the group. Harems composed of differently aged females were more likely to contain extra-group offspring. Our results not only provide evidence for the role of male defense in preventing extra-group paternity but also suggest that social group composition has consequences for male reproductive success.

Significance statement

In polygynous societies, the ability to monopolize mating is critical to reproductive success. As the group size increases, defense often becomes more difficult, resulting in increased rates of extra-group paternity. We find that among greater spear-nosed bats, extra-group offspring occur in most harems, but the overall rate of extra-group paternity is relatively low despite their large harems (15–30 females). Variation in the rate of extra-group paternity between harems is explained by male body condition (i.e., relative mass) but not harem size. Additionally, the rate of extra-group paternity is not explained entirely by male attributes, as we find that age heterogeneity within the female group is a significant predictor of the extra-group paternity rate. Our results support the hypothesis that not only the physical condition of a male influences his ability to monopolize reproduction but also the group composition influences the female mating behavior.

Keywords Extra-pair paternity · Female-defense polygyny · Chiroptera · *Phyllostomus hastatus* · Sexual selection

Introduction

The social associations of breeding males and females often fail to accurately reflect the genetic mating system of a species due to extra-group paternity, in which offspring are sired by a male outside the social breeding group. Among socially monogamous birds, extra-group paternity, also known as extra-pair paternity, is remarkably common (Griffith et al. 2002). Similarly, extra-group paternity has been documented in several taxa that exhibit a range of social mating systems, including various forms of social polygyny (e.g., birds (Griffith et al. 2002), mammals (Clutton-Brock and Isvaran 2007), fish (Bose et al. 2019), and reptiles (Uller and Olsson 2008)).

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✉ Danielle M. Adams
dadams37@umd.edu

[1] Department of Biology, University of Maryland, College Park, MD 20742, USA

Because such extra-group paternity alters the variance in male reproductive success, it affects the opportunity for sexual selection (Wade and Arnold 1980), and thus can have evolutionary consequences.

Much research has focused on the adaptive value of extra-pair mating from the female perspective (Petrie and Kempenaers 1998; Jennions and Petrie 2000; Griffith et al. 2002), because multiple mating is typically not expected to increase female reproductive success (Trivers 1972). Potential benefits to females include fertility assurance (Hasson and Stone 2009), good genes (Richardson et al. 2005; Brouwer et al. 2010; Reid and Sardell 2012), and compatible genes (Jennions and Petrie 2000; Mays and Hill 2004; Cohas et al. 2007). This emphasis on female choice in the literature is largely driven by a taxonomic bias toward socially monogamous birds, in which female choice has been inferred or demonstrated experimentally (Hasselquist and Sherman 2001; Ferree and Dickinson 2011).

However, some extra-group copulations are not driven by female choice, but rather by opportunistic and coercive males (McKinney et al. 1983; Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005). Socially polygynous species are predicted to exhibit greater variance in male reproductive success, as fewer males have access to reproductive females (Shuster and Wade 2003; Wade and Shuster 2004). As the likelihood of obtaining access to social mates decreases, less competitive males may attempt coercive mating tactics (Parker 1990; Clutton-Brock and Parker 1995). Such tactics may further select for mate defense or guarding by social mates (Harts et al. 2016), but this effect is complicated by several trade-offs faced by both extra- and within-group males (Hasselquist and Bensch 1991; Kokko and Morrell 2005). Mate guarding not only may restrict female opportunities for mate choice but may also benefit females as coercive extra-group copulations are often costly (Leboeuf and Mesnick 1991) and could result in genetically inferior offspring (Townsend et al. 2010). Therefore, the pressures shaping extra-group mating will likely differ among different social mating system types.

Bats are a diverse mammalian order that exhibit the full range of social mating systems, from monogamy to lek polygyny (McCracken and Wilkinson 2000). Both female choice (Bradbury 1977; Voigt et al. 2005; Rossiter et al. 2006; Murray and Fleming 2008) and mate defense (e.g. McCracken and Bradbury 1981; Kunz et al. 1983; Dechmann et al. 2005) have been documented within the order. Extra-group paternity has been investigated in a few socially polygynous species, and estimates vary widely among species (McCracken and Bradbury 1977; Heckel et al. 1999; Storz et al. 2001; Heckel and von Helversen 2003; Ortega et al. 2003; Dechmann et al. 2005). For example, male greater sac-winged bats (*Saccopteryx bilineata*) not only defend small harems but also court females with elaborate, multi-modal displays. The rate of extra-group paternity can exceed 60% in *S. bilineata* harems and is likely due to female choice for high-quality displays and the inability of males to effectively defend their harems (Heckel et al. 1999; Voigt et al. 2005). Female defense plays a more prominent role in the mating system of Jamaican fruit-eating bats (*Artibeus jamaicensis*), in which the rate of extra-group paternity is positively correlated with the harem size. However, the largest harems have reduced rates of extra-group paternity due to the presence of a subordinate male who helps deter intrusions by extra-group males in exchange for reproductive opportunities (Ortega and Arita 2002; Ortega et al. 2008).

The greater spear-nosed bat (*Phyllostomus hastatus*) is a large sexually dimorphic bat with female-defense polygyny. Females roost in groups (harems) of 15–20 predominantly unrelated individuals, and each group is defended by a single adult male. Group formation is not initiated or controlled by the harem male, as both natural turnover and experimental removal of males do not disrupt group composition. Instead, groups appear to form for cooperative benefits associated with foraging (McCracken and Bradbury 1981; Wilkinson and Boughman 1998) and pup defense (Bohn et al. 2009). Females leave their natal group after weaning and either join an existing group or roost with other first-year females. Group fidelity is subsequently high, and most females switch groups no more than once as adults, resulting in the average female occupying 1.5 groups over her lifetime (Wilkinson et al. 2016).

Competition to become a harem male is intense, and unsuccessful competitors reside in bachelor groups. On average, harem males are heavier than bachelor males, despite having the same skeletal body size (Adams et al. 2018). Harem males defend their females year-round, and although they aggressively drive away approaching males, they do not appear to restrict or police the movement of females. This affords females the opportunity to visit other males in pursuit of extra-group copulations. On average, a harem male retains tenure for 2 years before being displaced by another male (Wilkinson et al. 2016). Harem status is thought to be a terminal position, as former harem males have never been seen in the colony (McCracken and Bradbury 1981; Wilkinson et al. 2016). How males are displaced and which bachelor males are most likely to acquire harems are still open questions.

Initial estimates indicated extra-group paternity is rare (McCracken and Bradbury 1977; McCracken and Bradbury 1981), suggesting that either extra-group copulations are rare or extra-group copulations rarely result in successful fertilizations. Extra-group copulations may be rare if females do not pursue them or if harem males successfully prevent them. Alternatively, harem males may rely on repeated copulations to outcompete extra-group males via sperm competition (Parker 1990; Birkhead and Møller 1991). In the latter case, we would expect males to have large testes to successfully fertilize the large number of females despite sperm competition (Parker and Ball 2005). However, compared with other species in the same family (Phyllostomidae), male *P. hastatus* have small testes for their body size (Adams et al. 2020), suggesting that sperm competition is not a major selective force. Moreover, male-biased sexual dimorphism in body size and canine length (Adams et al. 2020), along with their aggressive behaviors, are consistent with intense pre-copulatory competition. These traits are likely beneficial for harem acquisition as well as long-term harem defense.

In this study, we consider the potential causes of extra-group paternity from three perspectives. First, we examine the effect of harem male attributes, specifically male age, body size, and body condition, on extra-group paternity. If male defense is important for excluding extra-group males, we expect older, larger, and heavier males to suffer less paternity loss. Because the composition of the female group may influence defensibility or the willingness of individuals to engage in extra-group mating, we investigate the effect of several features of the harem group. Specifically, we consider if the composition of each group with respect to female age, body size, and birth synchrony affects the rate of extra-group paternity. This analysis could reveal if males are more able to control paternity if, for example, females within the group show less reproductive synchrony or are more similar in size or age. Finally, we examine if maternal attributes, such as female age, body size, and relative timing of parturition, predict paternity (within- vs. extra-group) of the offspring. An increase in extra-group paternities among smaller, younger females may, for example, suggest that extra-group copulations are coercive and those females are less able to resist.

Methods

Study population and sample collection

For this study, we observed and sampled *P. hastatus* individuals over a 25-year period (1990–2015; cf. Wilkinson et al. 2016) from three wild, cave-roosting colonies in Trinidad, West Indies: Tamana cave (10.4711° N, 61.1958° W), Caura cave (10.7019° N, 61.3614° W), and Guanapo cave (10.6942° N, 61.2654° W). Tamana cave is the largest and contains approximately 20–30 harem groups, which are unevenly distributed among three connected chambers. Guanapo cave is the smallest but contains the second largest colony with 15–20 harems. Caura cave is intermediate in physical size but houses the smallest colony with only 4 harem groups. In Trinidad, *P. hastatus* exhibit a single breeding season from November to January, with most pups born in April (McCracken and Bradbury 1981; Porter and Wilkinson 2001). Mating has been observed in caves, but it is unknown if any copulations occur outside the cave (McCracken and Bradbury 1981). There is no evidence of induced ovulation, sperm storage, or extended reproductive delay in *P. hastatus* (James 1977), yet parturition is highly synchronized. In Trinidad, the birth peak occurs in April–May and synchrony at the colony level appears to track rainfall from east to west across the island. Within colonies, births are further synchronized within harem groups, such that female group-mates typically give birth within 19 days of each other (Porter and Wilkinson 2001).

Each harem typically occupies a separate solution depression in the cave ceiling (Fig. 1), which allowed us to capture an entire group at once using a bucket trap extended to the cave ceiling on a pole. Immediately after capture, bats were held individually in cloth bags while each bat was processed. Previously banded bats were identified by band number, and unbanded bats were fitted with a numbered metal band (Monel, National Band and Tag, Newport, KY, USA) on their forearm, with males banded on the right wing and females banded on the left. We recorded the mass (Pesola spring scale), forearm length (digital caliper; Chicago Brand, Medford, OR, USA), and degree of tooth wear (using a 5-category scale, cf. McCracken and Bradbury 1981) for each individual. Unless individuals were banded as juveniles, tooth wear is the only way at present to estimate the age of living adult bats (Brunet-Rossinni and Wilkinson 2009). We also collected one or two wing tissue samples from each individual, including pups, using a 3-mm-diameter biopsy punch. Samples were stored in saturated DMSO solution or 95% ethanol and kept at − 4 to − 80 °C. In total, 17 harem groups consisting of 561 individuals were captured in April, shortly after the pups were born. Twelve harems were from Tamana cave (2001 and 2013), three harems from Caura cave (2013), and three harems from Guanapo cave (1995 and 2001).

We used forearm length (FA) to estimate pup age, in days, using the formula (age = 0.77 × FA − 24.605) developed by

Fig. 1 Photograph of several harems in Tamana cave (second chamber). Each harem occupies a discrete solution depression. In this part of the cave, harems are tightly clustered, whereas other areas (not shown) have more space between solution depressions (photo credit: G.S. Wilkinson)

Stern and Kunz (1998), and then determined each pup's likely birth date by counting back from the day they were captured and measured. For each group, we determined the birth peak for a given year as the median birth date. We then calculated the number of days before or after the peak each pup was born. To quantify each group's degree of synchrony, we calculated the mean absolute deviation from the group median.

Body mass is correlated with skeletal body size and also decreases throughout the day, as the time since last feeding increases. To estimate male body condition, we calculated the relative body mass via the residuals from a linear regression of mass on forearm length, time of capture, and their interaction (Online Resource Table S1). We used all measurements of 112 harem males captured between 1990 and 2015 to fit the regression ($N = 168$ captures), and then predicted the mass of the harem males in this study using their forearm length and time of capture. Thirty-three harem males were captured multiple times (mean ± SD 2.70 ± 0.15 captures per male), so we calculated a single average forearm length, as this is not expected to change once males reach adult size. Because repeat capture events were sometimes at different times of day and male mass can fluctuate between days, we used the time of capture and the male's average forearm length to predict the body mass and calculate the residual mass for each independent capture event. To generate a single condition score for each male, the residuals were averaged across all captures within 1 year of the relevant parturition month (e.g., April 2012 to April 2014). We chose to use the average condition because a single measure of mass is influenced by time since feeding and excretion rate. By averaging across this time period, we could identify males that were consistently in high or low condition.

Maternity assignment

Pups are non-volant until 6–7 weeks of age (Stern et al. 1997) and spend much of their time nursing. As a result, we could determine the mother's identity when the pup was still nursing during capture. However, as pups get older, they spend less time nursing and are more likely to separate from their mother during capture. Because they were still non-volant during the capture period, we infer that the mother is a member of the harem group, but we rely on genetic analyses to identify the specific female (see below).

Because the number of pups caught unattached to mothers was relatively high in Tamana cave in 2013, we used mitochondrial haplotypes to reduce the pool of candidate mothers. We extracted DNA from wing punches using a Puregene tissue kit (Qiagen). To identify potential mothers, we amplified a region of the mitochondrial control region via polymerase chain reaction (PCR) using primers P* (Wilkinson et al. 1997) and E (Wilkinson and Chapman 1991). All reactions had a final volume of 25 μL with 1.5 mM $MgCl_2$, 0.2 mM dNTP mix, 1.25 U Taq polymerase (2X Taq Master Mix, Apex Bioresearch), and 0.24 mM of each primer. We used an annealing temperature of 55 °C and the thermal cycling program described by Meyer et al. (2009). PCR products were subsequently purified and sequenced from the P* end on an ABI 3730xl by Eton Bioscience Inc. We screened and aligned sequences using Sequencher v. 5.4 (Gene Codes Corp).

We used eight microsatellite loci for genotyping, of which three were previously used in this species, one was previously developed for *Desmodus rotundus*, and four were newly developed based on 454 junior pyrosequencing data (Online Resource Tables S2, S3). All PCRs were performed using either a fluorescently labeled forward primer or M-13-labeled forward primer with an M-13-labeled fluorophore (Schuelke 2000). All reactions had a total volume of 10 μL with 1.5 mM $MgCl_2$, 0.2 mM dNTP mix, and 1.25 U Taq polymerase (2X Taq Master Mix, Apex Bioresearch). When the forward primer was fluorescently labeled, the final concentration of each primer was 0.5 mM. When using the M-13 method, the forward primer had a final concentration of 0.13 mM while the reverse primer and the M-13-labeled fluorophore each had final concentrations of 0.5 mM. All PCR reactions were run on a touchdown thermal cycling program with the annealing temperature descending from 64 to 50 °C (3 min at 95 °C, (15 cycles: 30 s at 95 °C, 45 s at annealing, 1-min extension at 72 °C), (26 cycles: 30 s at 95 °C, 45 s at 50 °C, 1-min extension at 72 °C), 5-min final extension at 72 °C). The fluorescently labeled PCR products were separated on an ABI 3730xl DNA Analyzer (Applied Biosystems), and we used GeneMapper 4.0 (Applied Biosystems) to size and score alleles. Allele scoring was done blind to familial relationships to minimize potential bias.

Across the eight loci, the mean allelic diversity is 6.13 ± 2.17 alleles (Online Resource Table S3). We used GenAlEx v6.5 (Peakall 2012) to calculate Jost's pairwise D_{est} to evaluate genetic differentiation between the three cave populations (Jost 2008). Because populations show significant genetic structuring ($D_{est} = 0.04$, $p < 0.01$), the subsequent genetic analyses were performed separately for each cave. To estimate allele frequencies and test for deviations from the Hardy-Weinberg equilibrium (HWE), we used only adult genotypes to avoid introducing bias from mother-offspring and half-sibling relatedness. Tests for HWE were performed in GENEPOP for R (Rousset 2008), and the rate of allelic drop-out was estimated with CERVUS 3.0.7 (Marshall et al. 1998; Kalinowski et al. 2007).

For each pup, the initial pool of candidate mothers included all females in the harem group that did not have a known pup. Although we were often able to capture all females present at the harem, it is possible that some members of the group were not present at the time of capture; therefore, we also included females that were present in the harem during the breeding season. This breeding season information was available for seven of the ten groups surveyed in 2013. We narrowed the pool of candidate mothers to only those with the same haplotype as the given pup. If pups had two or more candidate mothers, we used CERVUS to identify the most probable mother at a minimum of 95% confidence. For all parentage analyses, we use a 1% genotyping error rate, which is based on the mean mistyping rate calculated by CERVUS across known mother-pup pairs. Additionally, we required a minimum of four genotyped loci per individual. The mean proportions of loci typed per cave are 0.89 (Tamana), 0.74 (Guanapo), and 0.95 (Caura).

Paternity exclusion

To evaluate paternity, we used the likelihood-based exclusion method described by Lemons et al. (2015). Typically, CERVUS is used to assign parentage to specific individuals; however, with a slight modification, the same computational framework can be used to estimate the likelihood that a pup is not directly related to the focal male. Pups were classified as extra-group offspring if we could exclude the resident harem male with 95% confidence. Because this approach requires the user to estimate the number of candidate males and the proportion of candidate males sampled, we repeated the simulation under a range of parameter estimates to assess the robustness of the results. The number of candidate males was varied from 8 to 32 males, and the proportion of males sampled varied from 0.64 to 0.84. We ran at least ten simulations using different parameter combinations for each cave. The proportion of loci typed and the 1% error rate were the same as those in the maternity assignment analysis. With the exception of two pups, assignments were consistent across parameter variations. The two pups with inconsistent results were classified as extra-group offspring under most parameter estimates, and each mismatched their respective harem males at one locus. As a result, we classified them as extra-group offspring.

Based on the social mating system and previous evidence (McCracken and Bradbury 1977), the harem male is expected to sire most offspring. Therefore, if the resident male could not have fathered most of the offspring within the group, we assumed that he either was a temporary visitor who happened to be there at the time of capture or became the resident male after the end of the mating period. After a preliminary review of extra-group paternity, we found two groups to be outliers with 73% and 100% extra-group paternity, while the other groups ranged from 0 to 54% (mean ± SE 13.4 ± 3.7%). Therefore, we did not consider that male to be the resident harem male in those two groups and they were re-analyzed assuming the harem male was unknown. For these two groups, along with two groups for which the harem male was never captured, we inferred the paternal genotype that could best account for the greatest number of offspring in the group. This method is likely to underestimate the rate of extra-group paternity, as we are more likely to infer a heterozygous genotype when the group of pups has more than 2 alleles at a given locus. When a group contained three or more extra-group pups, regardless of whether the harem male was known, we used a similar approach to infer the minimum number of extra-group sires necessary to account for all extra-group pups in a harem.

Relatedness among candidate males can limit the ability to accurately exclude or assign paternity to potential sires. To determine if the candidate males in our samples were related, we used the R package *related* (Pew et al. 2014) to measure average relatedness among males within Tamana and Caura caves, the two colonies for which we sampled multiple males from the same year. Among the 20 males (2 harem and 18 bachelor) sampled in Caura, the mean pairwise relatedness (*Wang's estimator*) among all males was 0.003 (CI − 0.05, 0.05). Among the ten harem males sampled in Tamana, the mean pairwise relatedness was − 0.02 (CI − 0.09, 0.06). Because we did not detect any significant relatedness among candidate sires, we did not account for relatedness among males in subsequent analyses.

Because we captured multiple harems from Tamana in 2013, we could then ask if other harem males are potential sires of the extra-group offspring. To address this question, we used the same exclusion methods as above, but the set of candidate sires included all harem males sampled from Tamana in 2013.

Paternity exclusion provides a minimum estimate of the rate of extra-group paternity. It is possible, however, that there are additional extra-group offspring for which we do not have the power to exclude the harem male. To estimate an upper bound on extra-group paternity, we also used CERVUS to assign paternity in the groups for which the harem male was known ($N = 13$ groups). All adult males from the relevant cave and year were included as potential candidates, and we evaluate assignments using 85% and 95% confidence thresholds. Additional parameter details are available in the Online Resource.

Statistical analyses

Using generalized linear models (GLM), we evaluated the effect of harem male attributes on the rate of extra-group paternity (number of extra-group offspring/total number of offspring). The independent variables include male tooth wear, forearm length, body condition, number of adult females in the group (group size), and all first-order interactions. Continuous predictors were centered and scaled prior to analysis, and because the response is the proportion of extra-group paternity per group, we fit the model with a binomial error distribution and a logit link function and weighted it by the total number of pups in the group. All possible models were ranked via the corrected Akaike's information criterion

(AICc), and models within two AICc of the top model (ΔAICc < 2) were averaged (Barton 2017). We report full averages, such that coefficients are averaged across all models, not just the subset in which the variable appears.

We fit a second set of GLMs to evaluate the effect of female group attributes. By fitting these models separately from the models of harem male attributes, we can include data for the four harems for which we do not have a known harem male. Predictor variables included mean forearm length and mean tooth wear as proxies for the average age and size of females within the group, because females' size and experience may influence their ability to resist coercion and exercise a mating preference. We also included standard deviations of tooth wear and forearm length to evaluate the degree to which variation within the female group affects mating decisions. Finally, we included birth synchrony (mean absolute deviation from group median) as a predictor to evaluate if female synchrony affects the ability of males to defend and monopolize mating within the group.

At the individual level, we examined the effect of maternal attributes on the likelihood of producing an extra-group offspring using a generalized linear mixed model (GLMM) with a binomial error distribution, a logit link function, and harem identity included as a random effect. Again, we include maternal forearm length and tooth wear as proxies for body size and age. In addition to absolute age, we also included female age relative to the group, which we calculated as the difference between the mother's tooth wear and the group median. We also tested for the effect of birth synchrony relative to the group using the absolute difference between the pup's estimated birth date and the harem's median birth date (measured in days). As before, AICc scores were used to rank and select models for averaging. All statistical analyses were performed in R version 3.5.1 (R Core Team 2018).

Results

Maternity assignment

Across all caves and years, 179 of the 223 pups were assigned a mother prior to paternity analyses (Online Resource Table S4). Maternity assignment was made either by co-capture of a nursing pup and lactating female or by mitochondrial sequencing followed by genotypic confirmation. Of the 223 pups, 143 were nursing from an adult female at the time of capture. This rate of co-capture varied between caves. In Caura, Guanapo, and Tamana (2001 only), all pups were nursing at the time of capture, with the exception of one pup in Guanapo and three in Tamana. Using microsatellite genotypes, we were able to assign maternity to one pup at 95% confidence. Of the co-captures, we were unable to obtain sufficient genotypes for five mothers (two were never sampled and three were genotyped at fewer than four loci) and an additional five showed genotypic inconsistencies that could not be explained by allelic dropout. Allonursing is not known in this species, but pups can grab onto another female during the disruption of capture. For subsequent paternity analyses, these pups were treated as though the mother was unassigned.

Due to the high number of pups with ambiguous maternity in Tamana cave in 2013 (76 of 122 pups were not attached to a female when captured), we used mtDNA haplotypes to identify candidate mothers prior to using microsatellite genotypes to assign maternity. A portion of the mtDNA control region was sequenced for 82 pups and 127 adult females captured in Tamana cave in 2013. A total of 31 variable sites were identified in the 325-bp alignment, producing 27 unique haplotypes. On average, each harem group contained 9.44 ± 0.60 (mean ± SE) haplotypes. Within a harem, each detected haplotype was shared by 1.47 ± 0.08 adult females (Online Resource Fig. S1). Sixteen behaviorally determined mother-pup pairs had matching haplotypes, supporting our expectation that females captured with a nursing pup were indeed mother-pup pairs. For pups captured unattached to a female, the number of candidate mothers within the harem ranged from zero to five females (1.76 ± 0.15 females/pups) based on haplotype data. After defining the pool of candidate mothers based on haplotypes, 45 pups were assigned to females based on microsatellite genotypes and 31 pups could not be assigned to any females with at least 95% confidence, presumably because their mother evaded capture.

Paternity exclusion

The power to exclude males as sires is influenced by whether the mother was known and varies among caves due to allelic diversity and variation in the proportion of loci typed. As a result, the combined probabilities of non-exclusion, as calculated by CERVUS, for the 192 pups with a known mother are 1.8% (Tamana), 1.9% (Guanapo), and 3.5% (Caura); for the 31 pups with an unknown mother, the non-exclusion probabilities rise to 11.5% (Tamana) and 12.3% (Guanapo) and 16.5% (Caura).

Among the 223 genotyped pups, we identified 29 pups (13.0%) for which the harem male could be excluded as the sire. Of the 17 groups examined, 12 (70.6%) had at least one extra-group offspring, with an average of 1.70 ± 0.41 extra-group pups per group. The three harems with the greatest number of extra-group offspring (3–5 offspring) had at least two different extra-group sires. No extra-group offspring were detected in Caura (Table 1). Within Tamana, the average per-harem rate of extra-group paternity varied among the three chambers (4.1–27.9%), but not significantly ($F_{2,7} = 2.34$, $p = 0.17$).

Among the ten harems (122 pups) sampled in Tamana in 2013, we detected 19 extra-group offspring. When all harem males from that cave and year are included as potential candidate sires, all males were excluded at 95% confidence for 14

Table 1 Distribution of extra-group paternity among three colonies of greater spear-nosed bats (*Phyllostomus hastatus*) in Trinidad, West Indies

	Tamana	Guanapo	Caura
N groups	11	3	3
N pups	137	51	35
Total extra-group offspring	22	7	0
Overall extra-group paternity rate	16.1%	13.7%	0.0%
Range of extra-group paternity rates per group	0.0–53.8%	5.8–26.3%	0.0%
Mean extra-group paternity rate per group	16.5%	13.0%	0.0%

of the 19 extra-group pups. The remaining five had at least one harem male from a different group that could not be excluded as the potential sire. Therefore, most of the extra-group offspring were sired by males that were not included in our analyses; these could be bachelor males or harem males from the 10–15 unsampled harems.

The 13 groups with a known harem male contained 163 offspring. Through paternity exclusion, we identified 22 extra-group offspring, leaving 141 as presumed within-group offspring. Of those 141 offspring, 71 could be assigned to the resident harem male with at least 95% confidence. Thus, if we were to assume all unassigned pups were extra-group offspring, the overall rate of extra-group paternity could be as high as 56.4%. However, given that these unassigned pups have genotypes consistent with being the offspring of the harem male, it seems more likely that we do not have sufficient power to assign them with 95% confidence. By relaxing the confidence threshold to 85%, 110 pups can be assigned to the harem male, which reduces the estimated upper limit of extra-group paternity to 32.5% (Online Resource Table S4).

Predictors of extra-group paternity

When evaluating the effect of male morphology on the rate of extra-group paternity, three models were within two AICc of the top model. Male condition was the most important variable, appearing in all four models, while forearm length and tooth wear each appeared in a subset of the models (Table 2). After model averaging, male condition was the only predictor with a coefficient different from zero, such that males with greater body condition experience lower rates of cuckoldry (Fig. 2; Table 3).

When examining harem attributes, the top model set (ΔAICc < 2) contained two models (Table 4). Among these models, the standard deviation of female tooth wear and birth synchrony were the most important predictors, but tooth wear variation was the only predictor with a non-zero coefficient in the averaged model (Table 5). When considering male and female attributes simultaneously, male condition is the only significant predictor of the extra-group paternity rate. Variation in female tooth wear is no longer significant, but this difference is likely due to the reduced sample size (*N* = 13; Online Resource Tables S5, S6).

Modeling paternity at the level of the individual female produced six models with ΔAICc < 2, of which, the null model had the lowest AICc (Table 6). Measures of female tooth wear and forearm length, both absolute and relative to group medians, do not predict offspring paternity and neither does timing of parturition relative to the group. Morphologically, mothers of within-group pups are not different from mothers of extra-group pups with regard to forearm length ($t_{25.8} = 0.42$, $p = 0.68$) and tooth wear ($t_{23.5} = 1.31$, $p = 0.20$).

Discussion

We examined the occurrence of extra-group paternity in three wild colonies of greater spear-nosed bats, *Phyllostomus hastatus*. This species' social mating system is one of strong female-defense polygyny, but genetically, we find that males are often unable to defend female groups completely. Across all groups, at least 13% of the offspring are sired by a male other than the resident harem male, although the rate of extra-group paternity varies between caves and among harems. We did not detect any extra-group offspring within one colony, while the others averaged 15.6% extra-group paternity. Most harems had at least one extra-group offspring, with the average harem having approximately two extra-group offspring. Variation in the rate of extra-group paternity within a harem is inversely related to the body

Table 2 Generalized linear models predicting the effect of male attributes and group size on the proportion of extra-group offspring present in the harems of *Phyllostomus hastatus* (*N* = 13). Presented are the models with ΔAICc < 4; however, only models with ΔAICc < 2 (italicized) contribute to the averaged model. *C* body condition, *T* tooth wear, *F* forearm length, *G* group size

Model	df	logLik	AICc	Delta	Weight
C	*2*	*− 21.46*	*48.11*	*0*	*0.32*
C + F	*3*	*− 19.97*	*48.61*	*0.50*	*0.25*
C + T	*3*	*− 20.50*	*49.66*	*1.55*	*0.15*
C + F + T	*4*	*− 18.51*	*50.02*	*1.91*	*0.12*
C ∗ F	4	− 19.12	51.24	3.12	0.07
C + G	3	− 21.44	51.54	3.43	0.06
C ∗ F + T	5	− 16.64	51.85	3.73	0.05

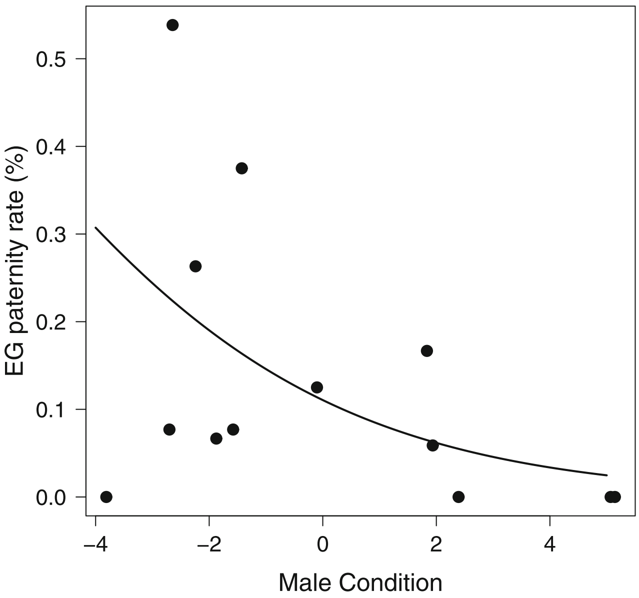

Fig. 2 The rate of extra-group paternity detected within a harem as a function of harem male body condition. Each point represents a single harem, and the line represents the extra-group paternity rate predicted by the average model, while holding the other terms at zero (i.e., the mean after centering the data)

Table 4 Generalized linear models predicting the effect of group attributes on the proportion of extra-group offspring present in the harems of *Phyllostomus hastatus* ($N = 17$). Presented are the models with ΔAICc < 4; however, only models with ΔAICc < 2 (italicized) contribute to the averaged model. *B* birth synchrony, *T* average female tooth wear, *F* average female forearm length, *sT* standard deviation of tooth wear, *sF* standard deviation of forearm length, *G* group size

Model	df	logLik	AICc	Delta	Weight
sT + B + G	*4*	*− 27.69*	*66.71*	*0.00*	*0.25*
sT + B + T	*4*	*− 27.76*	*66.85*	*0.14*	*0.24*
sT + B + T ∗ F	6	− 24.24	68.87	2.17	0.09
sT + G + sF	4	− 29.08	69.49	2.78	0.06
sT + T + sF	4	− 29.31	69.95	3.24	0.05
sT + B + T + F	5	− 27.36	70.18	3.47	0.04
B + G	3	− 31.22	70.28	3.58	0.04
B + T	3	− 31.39	70.63	3.92	0.04
sT + B + G + F	5	− 27.63	70.71	4.00	0.03

condition of the harem male and positively correlated with variation in female age (as measured by tooth wear) within the harem. We found no effect of male age or group size. Additionally, female age, body size, and birth synchrony did not predict the paternity of individual pups.

Compared with other mammals, the observed rate of extra-group paternity in *P. hastatus* is relatively low. Across the 26 species reviewed by Isvaran and Clutton-Brock (2007), the mean extra-group paternity rate is 18%; however, that mean rises to 29% when considering only those species that have at least some extra-group paternity. Species with larger female breeding groups tend to have higher rates of extra-group paternity. Many of the species included in recent interspecific analyses have small harems of 4–5 females (Isvaran and Clutton-Brock 2007; Lukas and Clutton-Brock 2014; Isvaran and Sankaran 2017) with one notable exception, the Southern elephant seal (*Mirounga leonina*). With harems often exceeding 40 individuals, extra-group paternity rates range from 25 to 40% among seal populations (Hoelzel et al. 1999; Fabiani et al. 2004). Blue monkeys (*Cercopithecus mitis*) also defend large harems (5–25 females), and approximately 40% of offspring in single-male groups are sired by an extra-group male (Roberts et al. 2014). Given the large harems of *P. hastatus*, averaging 19 females per harem, one might have predicted a greater rate of extra-group paternity than we observed. The high mobility of the harem males combined with the tight clustering of females within the roost improves defensibility, likely limiting opportunities for extra-group copulations. One caveat is that extra-group paternity based on exclusions is minimum estimate. Paternity assignment estimates indicate that we cannot rule out the possibility of some additional extra-group paternity.

Among harems, the rate of extra-group paternity is influenced by harem male body condition, but not skeletal body size. Harem males that are heavier for their size have lower rates of extra-group paternity within their harem. This finding is consistent with the expectation that stronger, more

Table 3 Model-averaged coefficients ± SE for models predicting the effect of male attributes and group size on the proportion of extra-group offspring present in the harems of *Phyllostomus hastatus*. Coefficient estimates are full averages calculated over the set of models with ΔAICc < 2, as detailed in Table 2

Variable	Estimate ± SE	95% CI	Importance
Intercept	− 2.16 ± 0.32	(− 2.86, − 1.46)	
Male condition	− 0.32 ± 0.12	(− 0.59, − 0.06)	1.00
Male forearm	− 0.13 ± 0.18	(− 0.49, 0.24)	0.44
Male tooth wear	− 0.24 ± 0.45	(− 1.18, 0.70)	0.32

Table 5 Model-averaged coefficients ± SE for models predicting the effect of group attributes on the proportion of extra-group offspring present in the harems of *Phyllostomus hastatus*. Coefficient estimates are full averages calculated over the set of models with ΔAICc < 2, as detailed in Table 4

Variable	Estimate ± SE	95% CI	Importance
Intercept	−2.13 ± 0.24	(− 2.64, −1.61)	
Tooth wear SD	2.68 ± 1.05	(0.39, 4.93)	1.00
Birth sync	0.39 ± 0.21	(− 0.07, 0.86)	1.00
Group size	0.02 ± 0.04	(− 0.06, 0.11)	0.52
Mean tooth wear	− 0.21 ± 0.42	(− 1.10, 0.68)	0.48

Table 6 Generalized linear mixed-models predicting paternity (extra-group or within-group) of *Phyllostomus hastatus* pups in response to maternal attributes and birth timing ($N = 175$). Presented are the top-ranked models (ΔAICc < 2). *TD* difference between maternal tooth wear and group median, *T* maternal tooth wear, *BD* difference between birth date and group median birth date, *F* maternal forearm

Model	df	logLik	AICc	Delta	Weight
Null	2	− 59.49	123.04	0	0.25
TD	3	− 58.64	123.42	0.37	0.21
T	3	− 58.71	123.56	0.51	0.19
T ∗ F	5	− 56.86	124.08	1.03	0.15
BD	3	− 59.22	124.58	1.54	0.11
F	3	− 59.43	125.01	1.96	0.09

competitive males will be heavier and better at defending females (Andersson 1994). In *P. hastatus*, harem males are in better condition than bachelor males (Adams et al. 2018). Although correlational, this evidence suggests that good condition is necessary for harem acquisition. Given the energetic demands of defense (Kunz et al. 1998), it seems less likely that condition increases as a result of harem acquisition. The effect of variation in condition that we find in this study indicates that condition is important for the continued defense of the harem.

From behavioral observations, we know that the resident male will approach and repel males that attempt to enter his harem site (McCracken and Bradbury 1981). Extra-group mating has not been directly observed in this species, but it seems unlikely that extra-group mating would successfully occur while the harem male is present, regardless of his condition. These interactions, however, may allow males to communicate their strength and the risk of retaliation to opportunistic extra-group males.

At night, females typically forage in one or two long bouts, but harem males forage in short bouts, making frequent trips back to the roost. This strategy is energetically costly but allows males to maintain vigilance at the roost site (Kunz et al. 1998). Furthermore, we have observed males temporarily occupying an empty harem site that is not their own at night, perhaps waiting for unattended females to return. Daytime interactions between males may communicate the harem male's strength and dissuade extra-group males from seeking copulations with unattended females. Greater body condition may also allow males to reduce foraging trips and allocate more time to vigilance. A more careful examination of which locations are visited by extra-group males at night, as well as when and where extra-group copulations occur, will allow us to better understand how males in good condition maintain better control over within-group paternity. While male-male competition and female defense are clearly important in this mating system, we also cannot exclude the possibility that heavier males are more attractive to females, and thus, females are less likely to seek extra-group copulations when the harem male is in good condition.

We found no effect of male age on the rate of extra-group paternity in his harem. The harem males included in our study, however, have limited variation in tooth wear (2–3.5 on a 5-point scale). Our extensive mark-recapture records (see Wilkinson et al. 2016) show that the average male's harem tenure is 2 years and their lifespan is short compared with that of females. In that dataset, we have 464 males for which we have minimum age estimates and less than 2% of males reach 5 years of age and only a single male reached 9 years of age. By contrast, the females in this study show much greater variation in tooth wear (1–5) and the mark-recapture records indicate that females live considerably longer than males. Of the 1835 females for which we have minimum age estimates, 18% lived at least 5 years and 5% lived at least 10 years. These differences in longevity and reproductive life histories are consistent with intense male-male competition (Promislow 1992; Clutton-Brock and Isvaran 2007; Lukas and Clutton-Brock 2014), and given the limited time during which males retain harem status, a lack of an age effect is perhaps unsurprising. How age influences a male's ability to gain extra-group fertilizations is not yet known, as we could not unambiguously identify extra-group sires. In other species, older males are more successful at securing extra-group paternities, particularly when older males are better at competing for the resources necessary to attract females (Ward et al. 2014; Michálková et al. 2019).

If extra-group matings are coerced, we expect that larger or older females would be better able to resist coercive males, and thus be less likely to have extra-group offspring. Alternatively, we might expect the reverse pattern if a female's ability to express choice for extra-group sires is restricted by a physically controlling social mate. Among our study population, we found no relationship between maternal age or size and the paternity of her offspring. Thus, if extra-group copulations are coerced, larger females do not have any resistance advantage. However, males are larger than females and possess larger canine teeth (Adams et al. 2020), so it is also possible that females, regardless of size or age, do not attempt to resist due to the risk of injury (Smuts and Smuts 1993; Wong and Candolin 2005). Harem male *P. hastatus* do not restrict female movement (McCracken and Bradbury 1981), and thus, females do not need to be larger or older to overcome or escape their social mate.

Although we found no effect of the average age and size of females within a harem, the variation in female age within the group influences the rate of extra-group paternity. Harems with a heterogeneous age structure have higher rates of extra-group paternity than more uniformly aged groups. However, neither the oldest nor youngest members of the harem are more likely to produce extra-group offspring. The overall effect of age heterogeneity suggests extra-group paternity rate is a "meta-trait" of the group, driven by the social dynamics within the harem, rather than individual mating strategies (Maldonado-Chaparro et al. 2018). Group heterogeneity likely reflects its history. When females disperse from their natal group, they may form new groups with members of the same cohort, or join existing groups (McCracken and Bradbury 1981). As a result, new harems will have less age variation than existing harems with recent additions. Additionally, adult females occasionally switch groups (Wilkinson et al. 2016), and if this movement increases age heterogeneity and females mate prior to moving, then we could see the observed association between age heterogeneity and extra-group paternity. Further examination of the ecological and social factors that influence harem formation and stability may explain the observed relationship between age heterogeneity and paternity.

As mentioned previously, interspecific (Isvaran and Clutton-Brock 2007) and intraspecific (Ortega and Arita 2002) patterns reveal that monopolizing paternity is more difficult when harems are large. However, we did not find an effect of group size; large harems were no more susceptible to cuckoldry than small harems. Among blue monkeys, the number of females simultaneously in estrus affected the siring success of the resident male (Roberts et al. 2014); therefore, female synchrony may be the more important measure. We found no significant effect of birth synchrony, but this may not be a reliable proxy of estrus synchrony, as bats are often able to manipulate the timing of fertilization and gestation (Racey and Entwistle 2000). Additionally, increasing the number of females in the group may not actually increase defense requirements because they are spatially discrete and females roost in tightly packed groups.

The spatial distribution of breeding pairs has been proposed to explain variation in extra-pair paternity among birds (Birkhead 1978); however, support has been mixed (Westneat and Sherman 1997; Westneat and Mays 2005; Schlicht et al. 2015). Qualitatively, the difference in extra-group paternity rates between the caves suggests that the density and spatial distribution of harems within a colony may influence defensibility. The colony in Caura cave, in which we detected no extra-group paternity, is the smallest of the colonies with only 3–5 harems present each year we visited. The solution depressions in which they roost are in close proximity to one another but are very deep. In contrast, Guanapo cave is smaller but houses a much larger colony. Many of the roost sites are in very close proximity, and the depressions are relatively shallow, making it easier to move between sites. Tamana cave is much larger and also contains a large colony with the harems distributed among three connected chambers. Although the extra-group paternity rate did not differ significantly between chambers, the variation qualitatively reflects the spatial distribution of the harems. The chamber with the fewest harems and most space between harems had the lowest rate of extra-group paternity (4.2%), while the chamber with the most tightly packed groups had the highest rate of extra-group paternity (27.8%).

Furthermore, different roost sites may vary in quality. When social mate pairing is based on resource defense, location within the colony may reflect male quality. For example, male great cormorants (*Phalacrocorax carbo sinensis*) that nest at the periphery of the colony are of inferior quality and also suffer greater rates of extra-pair paternity, regardless of the overall nesting density (Minias et al. 2016). Within the caves used by *P. hastatus*, different roost sites may be more favorable than others due to risk of predation by snakes, which we have observed crawling along the cave ceiling. However, in this female-defense system, males are not defending roost sites to attract females. Instead, the females occupy the roost and are subsequently defended by the male (McCracken and Bradbury 1981). The location and quality of the roost site may influence recruitment and stability of the female group. The potential effect of spatial distribution may be worthy of further study, especially if additional colonies of varying density and distribution can be located.

In summary, we found that despite their large size and highly mobile females, *P. hastatus* harems contain few extra-group offspring. Variation between harems suggests that prevention of extra-group paternity is driven by a male's ability to defend his harem, as males in better body condition suffer fewer paternity losses. This finding is also consistent with a female preference for high-condition males, and teasing apart these effects will require further investigation. Furthermore, the effect of female age heterogeneity on the rate of extra-group paternity raises several interesting questions about how within-group dynamics affect the genetic mating system.

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Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All procedures performed in studies involving animals were in accordance with the ethical standards set forth by the American Society of Mammalogists (Sikes 2016) and were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol # R-11-21). Permission to work with wild populations was granted by the Forestry Division of Trinidad and Tobago.

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