

Male dominance, paternity, and relatedness in the Jamaican fruit-eating bat (*Artibeus jamaicensis*)

JORGE ORTEGA,* JESÚS E. MALDONADO,* GERALD S. WILKINSON,+ HÉCTOR T. ARITA‡ and ROBERT C. FLEISCHER*

*Genetics Program, National Museum of Natural History, Smithsonian Institution, 3001 Connecticut Ave., Washington, DC, 20008, USA; †Department of Biology, University of Maryland, College Park, Maryland, 20742, USA; ‡Instituto de Ecología, UNAM, Circuito Exterior junto a Jardín Botánico, Apdo. Postal 70–275, México, D.F., 04510, México

Abstract

We analysed variation at 14 nuclear microsatellite loci to assess the genetic structure, relatedness, and paternity of polygynous Jamaican fruit-eating bats. A total of 84 adults captured in two caves exhibited little genetic differentiation between caves ($F_{ST} = 0.008$). Average relatedness among adult females in 10 harem groups was very low ($R = 0.014 \pm 0.011$), providing no evidence of harem structure. Dominant and subordinate males shared paternity in large groups, while dominant and satellite males shared paternity in smaller groups. However, our results suggest that male rank influences paternity. Dominant males fathered 69% of 40 offspring, followed by satellite (22%) and subordinate males (9%). Overall adult male bats are not closely related, however, in large harem groups we found that subordinate and dominant males exhibited relatedness values consistent with a father-offspring relationship. Because dominant and subordinate males also sired all the pups in large groups, we propose that their association provides inclusive fitness to them.

Keywords: *Artibeus jamaicensis*, genetic structure, male dominance, microsatellites, paternity, relatedness

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Introduction

The Jamaican fruit-eating bat (*Artibeus jamaicensis*) is considered a polygynous species, ranging from female defense polygyny in caves (Kunz *et al.* 1983; Ortega & Arita 1999) to resource defense polygyny in hollow trees and leaf tents (Morrison 1979; Kunz & McCracken 1995). The species is found in all neotropical habitats, and uses caves, hollow trees, dense foliage, buildings and leaf tents as roost sites (Ortega & Castro-Arellano 2001). In a survey conducted in caves in the State of Yucatan, Mexico harem groups of the Jamaican fruit-eating bat were found to roost exclusively inside solution cavities or small holes in the ceiling formed by percolating water (Ortega & Arita 1999). Groups of females, ranging from four to 14 individuals, usually include one dominant adult male (Ortega & Arita 1999). Larger groups (> 14 females) contain two adult males (dominant and subordinate) that roost in close

contact with the female group (Ortega & Arita 1999). During the day dominant individuals stay inside solution cavities or within a radius of 15 cm, in close contact with their harem (Ortega & Arita 1999). Harem groups show a high degree of stability as indicated by their continuous presence in the caves and their low exchange of members. Bats that roost outside harem groups form diffuse groups that are composed mostly of adult males (satellites), juveniles and a few females. These groups shift positions continuously, and their composition changes according to the season (Ortega & Arita 1999).

Dominant males show a high degree of roost fidelity and display agonistic behaviour against satellite males. Aggressive behaviours are more frequent during the breeding season (April to July), but are never directed toward subordinates, which are tolerated in the harem groups (Ortega & Arita 2000). Satellite males visit larger groups less often than medium-sized groups, suggesting that dominant and subordinate males may cooperate to control access by other males to harem females (Ortega & Arita 2000). Removal experiments revealed mutual benefits

Correspondence: Jorge Ortega. Fax: (202) 673–4648; Tel. (202) 673–4781, E-mail: artibeus2@aol.com.

for dominant and subordinate males. Subordinate males assume the place of removed dominants, and the number of visits by satellite males increases in the absence of subordinate males (Ortega & Arita 2002).

In this study we use genetic variation assessed by microsatellite genotyping to examine the genetic structure, relatedness and paternity in Jamaican fruit-eating bats. Kinship is an important factor that can influence the evolution of sociality. High stability in harem groups of *A. jamaicensis* can lead to high levels of relatedness between females if dispersal is uncommon and we expect to find greater than random levels of relatedness among females. However, previous studies have shown that relatedness in social groups can also be low as a consequence of immigration between colonies, small litter size, elevated infant mortality, and short harem tenure of males (Wilkinson 1987). In addition, considering the high degree of roost fidelity and active defense exhibited by dominant males, we hypothesize that dominant males should control paternity. We studied fitness relevance of the different adult males in the harem. In some cases monopolization of paternity by the dominant males is incomplete due to alternative strategies performed by satellite males to gain copulations. These alternative strategies include coalitions, forced copulations, or sperm competition (Clutton-Brock *et al.* 1989). Therefore the permanent presence of subordinate males in the larger groups in conjunction with reduced aggression between dominant and subordinate males, raises the possibility that these males might be related. Subordinate males may not obtain an immediate reward if the dominant male fathers all of the young. The objectives of this study are (i) to compare genetic variability of bats from two geographically distant caves and to assess group structure between them; (ii) to ascertain the degree of relatedness between members of different harem groups using a maximum likelihood approach; and (iii) to assign paternities and determine how dominance influences reproductive competition among adult males.

Methods

Population sampling and genotyping

We sampled all adults and offspring of 12 groups in two caves in the Yucatan peninsula during the breeding season of 1999. The Akil (20°14' N, 89°22' W) and Murciélagos (20°09' N, 89°13' W) caves are located 11 km apart in the Sierra de Ticul, a low-elevation mountain range 90 m above mean sea level (Ortega & Arita 1999). Ten harem groups roosting inside solution cavities were captured using a bucket trap (Kunz *et al.* 1983). Two diffuse groups composed of bats that roosted solitarily or that formed loose groups, were captured from their roost sites using a hand-held net in both caves. Adult bats were identified

using the colour code of the plastic rings placed on their forearms during the previous year (Ortega & Arita 1999). Offspring were recognized by the presence of cartilaginous joints on the epiphyses (Kunz *et al.* 1996). A small piece of wing membrane (5 mm²) was excised from each individual with biopsy punches and stored in 95% ethanol solution.

Total genomic DNA was extracted from wing membrane punches using the DNeasy® tissue kit (QIAGEN®, Valencia, Ca, USA). Fourteen dinucleotide microsatellite loci were screened: AjB464, AjA123, AjA40, AjA47, AjA151, AjA74, AjA185, AjA180, AjA2, AjA84, AjA80, AjA199, AjA107, AjA110 (Ortega *et al.* 2002). We used an annealing temperature of 56 °C for all microsatellites except for AjA123, AjA185, and AjA199 for which an annealing temperature of 60 °C was used. Each locus was amplified using polymerase chain reactions (PCR) in a total volume of 25 µL including: 50–100 ng of DNA, 0.1 U of AmpliTaq® DNA polymerase (Applied Biosystems, Hayward, Ca, USA), 10 µM of both primers, 25 mM of MgCl₂, 10× PCR Buffer II (Applied Biosystems, Hayward, Ca, USA), and 2 mM of FdUTPs (R110; Applied Biosystems, Hayward, Ca, USA), 5 M Betaine (Sigma, St. Louis, Mo, USA) and 10 µg/µL bovine serum albumin (BSA). Alleles were separated on a 5% polyacrylamide gel using an ABI 377 automated sequencer and analysed with GENOTYPER Version 2.1 software (Applied Biosystems, Hayward, Ca, USA).

Statistical analysis

Genetic differentiation between caves and harem groups was examined using a hierarchical analysis of molecular variance (AMOVA; Excoffier *et al.* 1992). *F*-statistics and pairwise *F*_{ST} values were calculated from a distance matrix among genotypes, and significance levels predicted by permutating genotypes between caves using ARLEQUIN 2.0 (Schneider *et al.* 2000). Genetic structure of harem groups within caves was calculated using only adult individuals; bats in a harem group were classified as permanent members if they stayed inside the solution cavity for 3–6 h during one day. Each group was monitored at least twice a month during the 2-year study (Ortega & Arita 1999). Standard errors were calculated by jackknifing across loci.

To evaluate the reproductive success of males we measured paternity of pups born in each harem group. Father-offspring dyads were examined using the likelihood approach implemented in the program CERVUS 1.0 (Marshall *et al.* 1998). This program computes a log-likelihood ratio of the probabilities of parentage for each pair of candidate parents. A total of 10 000 simulations were conducted to assess the significance of the difference between the most likely father and the next most likely father (Δ score). Distributions were used to allocate 80% and 95% confidence levels; when paternity is assigned, the father-offspring relationships can be described as 80% confident (relaxed

paternity) or 95% confident (strict paternity; Marshall *et al.* 1998). All sampled males (dominant, subordinate and satellite) were tested as potential fathers. The total number of significant father-offspring relationships thus provided an estimate of each male's reproductive success during one breeding season.

The relatedness coefficient (R) between individuals at these 14 loci was inferred using the program RELATEDNESS 5.0. Standard errors were calculated using the jackknife procedure (Queller & Goodnight 1989). For this analysis caves were treated as two separate demes. Consequently relative genotype frequencies for each individual were calculated differently for each cave. We divided samples by sex (male, female) and age (adult, juvenile), and assessed relatedness between individuals in order to evaluate if these categories have an influence on them (Queller & Goodnight 1989; Blouin *et al.* 1996).

We tested whether harem group offspring were half or full siblings using a likelihood approach in the program KINSHIP 1.2 (Goodnight & Queller 1999). Hypotheses about particular pedigree relationships were tested assuming Mendelian gene transmission (Van de Casteele *et al.* 2001). For offspring that were born in the same harem group to different mothers, we tested the hypothesis that alleles were identical by descent (IBD) as a consequence of pups being sired by the same father ($R_p = 0.5, R_m = 0; \beta = 0.2677$). For this comparison, the null hypothesis was that alleles were not IBD because pups were not sired by the same father ($R_p = 0, R_m = 0$). Direct maternal descent ($R_p = 0, R_m = 1.0; \beta = 0.2519$) relationships were evaluated by comparing shared alleles between all mother-offspring dyads in all 10 groups. Adult male relationships were examined using three different hypotheses: father-offspring ($R_p = 1.0, R_m = 0; \beta = 0.4942$), full siblings ($R_p = 0.5, R_m = 0.5; \beta = 0.3783$), and half siblings ($R_p = 0.5, R_m = 0; \beta = 0.2274$), and the null hypothesis for each relationship was $R_p = 0, R_m = 0$. Hypotheses were accepted or rejected on the basis of the log-likelihood ratio between the two hypotheses (primary/null). A high value of the ratio favours the primary hypothesis and a low value rejects it in favour of the null hypo-

thesis (Goodnight & Queller 1999). A simulation based on 10 000 random pair samplings was used to confirm the pedigree relationships specified by the primary and null hypotheses. These data were used to accept or reject the null hypotheses with 95% confidence.

Results

Population variation

Bats were associated in distinct assemblages inside caves. A total of 34 adult males, 50 adult females, and 40 pups were captured. Harem groups ranged from three to 16 females/group (7.4 females \pm 0.6 SE). Eight harem groups included < 14 females and only one adult male, but the two largest groups (> 14 females) contained two adult males. Harem groups roosted inside solution cavities and formed a well-defined cluster. The two diffuse groups included individuals of both sexes (15 males/2 females in Murciélagos Cave, and 7 males/2 females in Akil Cave) and no offspring. Diffuse groups were found only in exposed areas of caves, where they formed a temporary cluster but never a structured harem group.

There was no significant genetic subdivision detected between groups within caves or between caves (Table 1). When caves were considered as independent groups, the overall F_{ST} value was 0.008, which was not significantly different from zero ($P > 0.05$). AMOVA indicates that 94.4% of the variation in allele frequencies is due variation among individuals within caves while only 5.6% of this variation is partitioned between caves (Table 1).

Paternity

Paternity assignment results showed that sampled males sired 32 of 40 pups, and unsampled males sired eight pups. Using the 95% confidence limits for paternity, we found that 22 pups (69%) were sired by dominant males, three pups (9%) were sired by subordinate males, and seven pups (22%) were sired by satellite males. Satellite and

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among caves	1	8.012	0.018 Va	0.31
Among populations within caves	13	76.99	0.018 Vb	0.31
Among individuals within populations	70	434.4	0.296 Vc	94.39
Within individuals	84	471.5	5.613 Vd	4.99
Total	167	990.9	5.946	

Table 1 Hierarchical analysis of molecular variance (AMOVA) within and among 12 harem groups of *Artibeus jamaicensis* from two caves in Yucatan, Mexico. Variance components (Va, Vb, Vc, and Vd) as well as the percentage of variation were calculated from a distance matrix among genotypes

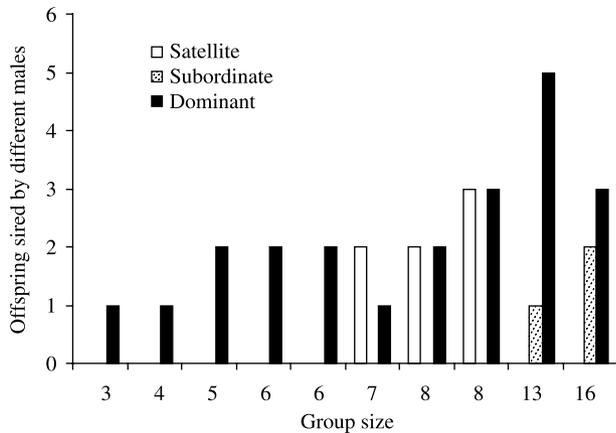


Fig. 1 Distribution of offspring sired by satellite, subordinate and dominant males in three categories of harems ranging from small (3–6), medium (7–8) and large (13–16) group sizes.

subordinate males only sired offspring in groups larger than six individuals (Fig. 1). In almost all cases the most likely father was not disqualified at any loci, but the next most likely father was disqualified by at least one locus. Assignment results were greater than those predicted by the 10 000 simulations. At the 95% confidence level the expected paternity assignments were 32% vs. the 87% observed, demonstrating that proper fathers were included in our sampling. Pups born in harem groups with fewer than six females were sired by dominant males in all cases where the father was known (1.6 offspring \pm 0.4 SE per male, $n = 8$ out of 11). However, these groups also contained three offspring that could not be assigned to any adult male sampled. In groups that ranged from seven to 13 females, five pups (42%) were sired by dominant (1.6 offspring \pm 0.3 SE per male), and seven pups (58%) by satellite males (2.3 offspring \pm 0.3 SE per male) (Fig. 1). There was no significant difference between the frequency of pups sired by dominant and satellite males (Wilcoxon paired test, $Z = 1.41$, $P > 0.05$). In the same groups, five offspring were not sired by any of the sampled males. In groups with more than 14 females, paternity was shared by dominant and subordinate males. All pups captured in these groups could be assigned to either the dominant or subordinate male.

Relatedness

Relatedness was not significantly different from zero between adult individuals and between offspring that inhabit both caves. Considering each group as an independent unit, average relatedness among offspring from the 10 harem groups was $R = -0.003$ [± 0.006 , 95% confidence interval (CI) 0.011 to -0.017], as expected if they were sired by different parents. In both adult sexes,

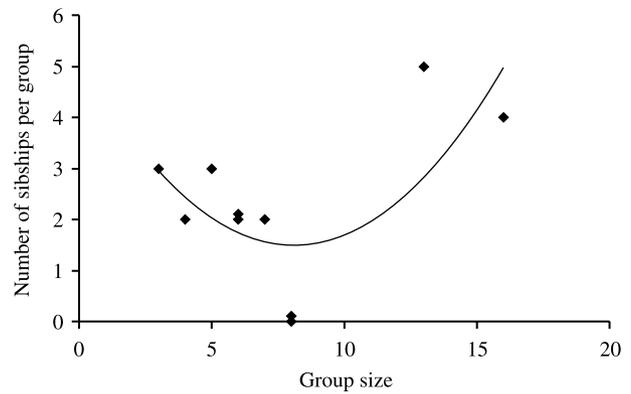


Fig. 2 Distribution of the absolute values of sibships by the dominant males calculated from different sized harem groups (Quadratic model: $y = 7.9 - 3.11x + 0.90x^2$, $r^2 = 0.57$, $P = 0.05$). Harem groups that ranged between six and 13 females showed the lowest values compared with the rest of the groups.

relatedness estimates were also not significantly different from zero. The majority of adult male dyads were unrelated; the average R -value was 0.006 (± 0.007 , 95% CI 0.023 to -0.009). Relatedness among dominant male dyads that defended harem groups was also not significantly different from zero (0.002 ± 0.008 , 95% CI 0.034 to -0.017). Similar results were found between satellite male dyads (0.003 ± 0.004 , 95% CI 0.015 to -0.012). Within the 10 harem groups the degree of relatedness between adult females ranged from unrelated (expected value: $R = 0.0$) to second order relative ($R \leq 0.25$). Average relatedness among adult females within harem groups was 0.014 (± 0.011 , 95% CI 0.040 to -0.010), which did not differ from zero indicating that the majority of the females within harems were not related.

We identified paternal half-siblings as pups within a harem that were assigned to the same father at the 95% confidence level. A total of eight paternal half-sibships were identified on the basis of paternal allele sharing. Every sibship contained at least two pups and reached a maximum of five pups per harem. Sibships accounted for 71% of the total offspring in the cohort; the rest were not sired by a sampled male or had unique paternal alleles and were not included in the sibships. The number of sibships varied according to the number of females in the harem group (quadratic model, $y = 7.9 - 3.11x + 0.90x^2$, $r^2 = 0.57$, $P = 0.05$; Fig. 2). Groups with less than six females comprised two or three pups per sibship. A group with seven females contained a sibship of two pups, whereas two groups with eight females included one pup sired by a sampled male and one or two pups sired by an unsampled male. Groups with more than 14 females contained sibships that ranged between four or five pups per sibship.

All harem groups contained at least one mother-offspring relationship, ranging from one to five (2.5 female-offspring ± 1.2 SE). Two thirds (67%) of all adult females in the caves

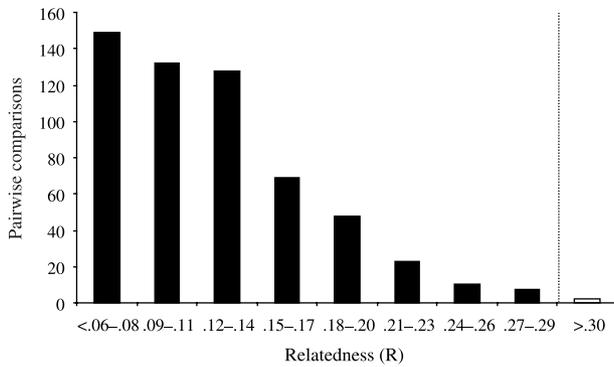


Fig. 3 Distribution of all pairwise comparisons of relatedness values (R) calculated at the father-son level ($R_p = 1.0$, $R_m = 0$; $\beta = 0.4942$). Subordinate and dominant relationships at the 95% CI are greater than 0.3 and are marked in the right column.

roosted with their pups in the harem groups. Mother-offspring dyads were not found in the diffuse groups. Two pups that did not share alleles with any of the potential mothers were excluded from the analysis. Also, harem groups contained one or two adult females without pups, and none of the sampled offspring were indicated by genetic data to be their progeny. When these females were examined ($n = 38$), two thirds of them displayed no signs of lactation.

Overall, adult males were unrelated. Our kinship analysis did not detect any adult male dyads which were related as full siblings. Among satellite males, 89% of dyads were unrelated, but 11% of them were assigned to the half-sibling relationship. No relatedness at any level was found between dominant males from groups with any other adult male in the caves. However, a unique significant result between adult males was found between dominant and subordinate males in the large harem groups. Using the 95% confidence level as the minimum criterion for father-offspring assignment, the most likely fathers of the two subordinate males were, in both cases, the dominant males from the same harem group (Fig. 3).

Discussion

Comparisons between colonies and harem groups

Bats in the two different caves cannot be characterized as distinct subpopulations. Our data showed a low F_{ST} value reflecting no local genetic differentiation. The estimated daily flying route for *Artibeus jamaicensis* is approximately 0.6 km in productive habitats and 8 km in poor habitats (Morrison 1978). The original tropical deciduous forest vegetation of the area around the study site has been replaced in most parts by cropland, producing a highly disturbed habitat with low fruit availability. The geo-

graphical proximity (c. 11 km) may result in high levels of gene flow that prevent genetic differentiation between our study caves. Bat species range from extremely strong usually sex-limited colony fidelity (Rossiter *et al.* 2000; Castella *et al.* 2001; Storz *et al.* 2001a; Kerth *et al.* 2002), to a null exchange of individuals between colonies (Burland *et al.* 1999). Our behavioural observations over a period of 30 months showed a low, but continuous rate of turnover by females in the harem groups (c. 25% females per year). It also showed that formation and disintegration of harem groups was infrequent (Ortega & Arita 1999). Some marked individuals (18%) disappeared and were never seen again in the caves. Although the presence of immigrants was documented, intercave dispersal was not observed (Ortega & Arita 1999). Thus, immigrants must originate from other caves in the area.

Paternity assignments

Our data demonstrated an unequal distribution of reproduction between adult males, where the dominant males obtained higher reproductive skew. Several genetic analyses have shown that paternity is biased in polygynous mating systems. In harem groups of *Phyllostomus hastatus*, about 85% of young have loci that are compatible with the dominant male (McCracken & Bradbury 1977; 1981). In *Cynopterus sphinx*, 64% of pups were sired by territory-holding males in two different breeding seasons (Storz *et al.* 2001b). Territorial males of *Saccopteryx bilineata* showed a higher reproductive success compared with the peripheral males, but those were not excluded from reproduction (Heckel & von Helversen 2002). The estimated paternity for dominant males of *A. jamaicensis* ranged from 33 to 83%. Overall, most adult males belonging to a harem remained as dominants in the same group at least for two reproductive seasons (Ortega & Arita 1999). Dominant males were responsible for almost all fertilizations in large harem groups, and because they maintain their dominant status from one season to the next, we concluded that they have the highest lifetime reproductive success among all adult males. Some satellite males succeeded in siring a few offspring during one reproductive season, but 30% of them disappeared from the caves and were substituted by new satellite males during the next reproductive season (Ortega & Arita 1999). Subordinate males sired some pups in large groups and they remained there for at least two reproductive periods. One consequence of this shared paternity is increased inclusive fitness for both. Studies have demonstrated that dominant males share reproduction with subordinate males in order to induce them to remain with the group, bringing mutual benefits for both partners (Emlen 1997).

In this study we have established the genetic relationship between dominant and subordinate males and shown

that these pairs of males were able to monopolize females in their groups. Dominant males in groups containing from seven to 13 females sired less offspring than might be expected from group size. These groups showed high extra group paternity, with many pups being sired by satellite males. Circumstances such as time constraints of mate guarding, energy invested in mate defence, or the absence of another associated male can promote extra-pair paternity in harem groups (Ligon 1991). Observational studies established that these groups received the most visits by satellite males (Ortega & Arita 2000). Dominant males from groups containing less than seven females sired offspring in the same proportion as dominant males from groups containing more than 13 females. Both kinds of groups received visits at the same frequency (Ortega & Arita 2000). Low visitation rates by foreign males to small size groups can be explained by the low concentration of females in these harems. As a result of this pattern, dominant males in these groups sired almost all of the offspring. In groups with more than 13 females, low visitation rates can be explained by the presence of the subordinate male (Ortega & Arita 2002).

Relatedness analysis

Members of the different harem groups showed a low degree of relatedness. Thus affiliations based on kinship cannot be used to explain female group stability in this species. The environmental predictability of cave roosts may encourage cooperative activities for individuals that coexist in the same population (Wilkinson 1987). Cooperative activities described for bats include foraging flocks (Wilkinson & Boughman 1998), defence against predators (August 1985), communal nursing (McCracken 1984; Wilkinson 1992), social grooming (Wilkinson 1986), providing a warm environment (Roverud & Chappell 1991; Lewis 1996), sharing food with conspecifics (Wilkinson 1984), and exchanging information (Wilkinson 1992). Nevertheless, only a few of these cooperative activities have been shown to be correlated with relatedness (Wilkinson 1985; Kerth *et al.* 2000; Burland *et al.* 2001). Some cooperative activities have been described in *A. jamaicensis*. Distress calls used as defence against predators were recorded from different members of the same colony, but the degree of relatedness between individuals is unknown (August 1985). Our data demonstrate that the relationship between dominant and subordinate males in the larger harem groups produces mutual benefits. Dominants perform most of the costly defensive responses, but the presence of subordinate males is correlated with a lower rate of intrusions by foreign males (Ortega & Arita 2000). The absence of subordinate males increases the rate of visits by extraneous males and the number of agonistic responses performed by dominant males (Ortega & Arita 2002). In removal experiments,

subordinate males obtain access to vacant positions of dominants, when dominant males disappear (Ortega & Arita 2002). Our relatedness estimates support a genetic relationship among dominant and subordinate males. We found that both pairs were most consistent with a parent-offspring relationship. Because dominant and subordinate males monopolize larger groups of females, cooperative activities can be based on kinship ties with positive results for both males (Emlen & Oring 1977; Emlen 1997). We conclude, that our paternity analysis demonstrates that dominant males sired most of the offspring in harem groups. Inclusive fitness is high for dominant males that monopolize large harem groups and receive the help of related subordinate males.

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Jorge Ortega is a Smithsonian postdoctoral Fellow at the Genetics program, headed by Dr. Robert Fleischer. Jorge Ortega is interested in behavioural and genetic studies, addressing questions in how relatedness and kinships affects social structure and mating systems in vertebrates. Jesus Maldonado's primary interests are the evolutionary genetics and conservation biology of mammals. Jerry Wilkinson conducts research on the evolution of social behavior and the outcome of evolution and how behavior may affect genetic population structure. Hector T. Arita is the director of the Instituto de Ecología, UNAM, working on the macroecology and biogeography of New World bats.
