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**EL SISTEMA DE APAREAMIENTO POLIGINICO
DEL MURCIELAGO ZAPOTERO
(*Artibeus jamaicensis*) EN YUCATAN**

T E S I S
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Introducción

Structure and social dynamics of harem groups in *Artibeus jamaicensis* (Chiroptera: Phyllostomidae).

Defensive behavior of females by dominant males of *Artibeus jamaicensis* (Chiroptera: Phyllostomidae).

Benefits for males defending harem groups of the Jamaican fruit-eating bat (*Artibeus jamaicensis*).

Discusión

EL SISTEMA DE APAREAMIENTO POLIGÍNICO DEL MURCIÉLAGO ZAPOTERO (*Artibeus jamaicensis*) EN YUCATÁN

RESÚMEN

Los sistemas de apareamiento poligínicos son comunes dentro del grupo de los mamíferos debido principalmente a que durante la lactancia, el macho no participa en el cuidado de las crías e incrementa su adecuación copulando con varias hembras. Los grupos de harén son frecuentes en los murciélagos tropicales que habitan en cuevas. Siendo poliginia por defensa de los recursos cuando los machos defienden el sitio de percha y poliginia por defensa de las hembras cuando los machos defienden el acceso directo a ellas. En este trabajo se describió la estructura y dinámica de los grupos de harén en el murciélago zapotero (*Artibeus jamaicensis*) y las actividades de defensa de los machos que las controlaban. Los grupos de harén variaron de cuatro a 18 hembras por grupo, con uno o dos machos asociados. Los machos adultos en la cueva fueron clasificados como dominantes, siempre presentes en el harén con despliegues de actividad de defensa; secundarios, presentes en los grupos de harén de más de 14 hembras (grupos grandes) pero sin despliegues de actividad de defensa; y satélites machos adultos nunca asociados a los grupos de harén pero que realizaron frecuentes visitas a los sitios de percha de los grupos de harén. Las hembras, más que los machos, son muy móviles entre los distintos sitios de percha. No obstante, los grupos conservaron > 75% de los miembros descritos desde el primer registro. Los machos asociados a los grupos de harén permanecieron siempre en el sitio donde fueron identificados inicialmente. Los movimientos entre los grupos fueron 72% menos frecuentes durante la época de apareamiento que durante la época de no-apareamiento. Se documentaron tres tipos de respuestas (ignorancia, acercamiento y agonística) de los machos dominantes cuando algún murciélago (hembra, juvenil o satélite) llegaba a menos de 10 cm del sitio de percha. Los individuos más agredidos por los dominantes fueron los satélites y los más ignorados fueron las hembras. Durante la época reproductiva las interacciones agonísticas entre machos aumentaron 20% con respecto a las observadas durante la época no reproductiva, aún cuando las visitas fueron más escasas. Se encontró que los grupos grandes (> 14 hembras) presentaron una menor frecuencia de visitas (aprox. 25%) realizadas por satélites que los grupos de menor tamaño.

La tercera parte del trabajo consistió en tres experimentos de remoción de individuos con la finalidad de poner a prueba tres hipótesis sobre las ventajas de asociación cooperativa para los machos presentes en los grupos de harén (dominantes y secundarios). La hipótesis del primer experimento fue que los machos secundarios estaban dentro de los grandes grupos de harén para ocupar el lugar del macho dominante cuando éste estuviera vacante, en tanto que los satélites ocuparían los lugares de los machos dominantes en los grupos pequeños puesto que en éstos no hay secundarios. La manipulación consistió en la remoción de los machos dominantes de grupos grandes (n=4) y pequeños (n=8) por espacio de tres días. Los machos secundarios ocuparon el

puesto vacante 90% del tiempo observado, mientras que los satélites fueron solamente de un 60%. En el segundo experimento, se postuló que la presencia del macho secundario disminuye la frecuencia de visitas realizadas por los machos satélites. Se removieron los machos secundarios de los grupos grandes por tres días y se contabilizó la frecuencia de visitas de los satélites a éstos mismos grupos. Las visitas que realizaron los satélites a los grupos grandes se incrementaron 45% durante la ausencia de los machos secundarios comparadas con las visitas observadas con la presencia de los machos secundarios. De igual forma se observó un incremento de 35% de las actividades de defensa desplegadas por el macho dominante contra los satélites durante la ausencia de los secundarios con respecto a las actividades observadas con la presencia de los machos secundarios. En el tercer experimento, se puso a prueba la hipótesis de que el número de hembras en los grupos determina la presencia de un macho asociado. Al reducir los grupos grandes (> 14 hembras) al número modal de los grupos pequeños (promedio 12 hembras por grupo), se observó que los machos secundarios disminuyeron en un 40% su tiempo de permanencia dentro de los grupos. No se observó un incremento en las actividades de defensa desplegadas por los machos dominantes contra los satélites ni contra los secundarios durante la remoción de las hembras.

Se encontró que la composición de los grupos de harén está dada por las hembras que perchan en grupos discretos dentro de las cavidades de disolución, promoviendo que un macho las acapare y despliegue actividades de defensa que restringen la entrada de otros machos a los sitios de percha. Claramente el número de hembras determina el número de machos que pueden establecerse con el grupo. Comprobé que existen posibles ventajas de asociación cooperativa entre los machos de los grandes grupos, ya que mostraron cambios en su conducta al faltar el otro macho asociado.

ABSTRACT

Polygyny is considered the typical mating system in mammals. Males never raise the broods and copulate with several females to increase their reproductive success. Lactation is an exclusive activity for females and they raise their cubs by alone. Harem groups are a common social structure in the bats of the tropical areas, where several authors reported resource defense polygyny when bats defended the roosting sites and female defense polygyny when some male allowed the access to females to other males. Dynamics and social structure of the harem groups the Jamaican fruit-eating bats (*Artibeus jamaicensis*), and the strategy of the male to defend females was described. Groups contained between four to 18 females with one or two associated males. Dominant males were defined when some adult male defended females (present in all the harem groups); secondary males were registered in the largest groups (> 14 females) but never defended females, and satellite males never associated to some harem group and performed visits or frequent intrusions to the harem groups. Females performed frequent movements between the different roosting sites, but males showed more stability in their sites. By two years, the 75% of the members of the harem groups belonged to their original roosting site. Female movements were less frequent during the breeding season (< 72%) compared with the non-breeding season. When some bat arrived to the roosting site (female, juvenile or adult male), I documented the reactions of the dominant male to this arrival. I proposed three different reactions: ignorance (when the dominant male never moved from its site), approach (when dominant approach to the visitor but without agonistic activities) and agonistic (when dominant approach to the visitor with agonistic activities). Satellite males received the majority of the agonistic reactions, followed by juveniles and females. Those activities showed a 20% of increment during the breeding season compared with the non-breeding season. Large groups (> 14 females) received 25% less visits performed by satellites than small groups (< 14 females).

The third part of the thesis was projected to answer several questions related with the mating system and the association of the bat in the roosting sites. I considered than secondary males are present in the harem groups because they have a chance to substitute the dominant males in a long-term period. Besides satellite males are going to occupy the empty places in the small groups, where secondary male status is not present. Dominant males of large groups (n=4) and small groups (n=8) were removed. Secondary males occupied the empty place in the large groups and satellite in the small groups. During three days secondary males spent in the groups the 80% of his time, compared with the 60% of the satellites in the small groups. I considered than secondary males inhibited the frequency of visits performed by satellites to the large groups. In the second experiment, I removed secondary males of the four large groups and compared the frequency of visits performed by satellites during two times (with and without secondary males). Visits performed by satellites showed an increment of 45% during the absence of the secondary males (compared with its presence). Besides, I observed an increment (35%) in the number of

agonistic responses performed by dominants toward satellites in the same observational periods. On the third experiment, I reduced the number of females from > 14 individuals to less than 14. I considered that the number of females in the groups allowed the permanence of secondary males in the large groups. These males belonged with the groups 40% less time than when the number of females raised more than 14. I not registered and increment in the number of agonistic responses from the dominant toward secondary males in this removal time.

Females in the caves of Yucatan promote the formation of harem groups in the solution cavities. These females are the basis of the harem groups and probably males sited around this social structure. One dominant males monopolizes the harem groups and performed defense activities toward its potential competitors. Secondary males are tolerated in the large groups, probably because both males have advantages of this association. The habitual behavior of the males changes when the other resident male is removed.

INTRODUCCIÓN

Tradicionalmente los sistemas de apareamiento han sido definidos con base en la asociación de los individuos para obtener pareja y para cuidar a las crías (Emlen y Oring, 1977). Entre los parámetros que se utilizan en la clasificación de sistemas de apareamiento destacan el número de parejas que un individuo acopia en la temporada reproductiva y la forma en que se adquieren o compiten por esas parejas. Aunque recientemente se han incorporado nuevos parámetros que consideran la variación que existe entre individuos en la forma y manera del cuidado parental, el tiempo de duración con la pareja, el número de parejas en una época reproductiva, la forma de cortejo, la coerción y la competencia por la pareja, los recursos defendidos y el tiempo que dura la elección de la pareja, así como las relaciones de parentesco (Reynolds, 1996).

La mayoría de los mamíferos presenta un sistema de apareamiento poligínico, en el cual un macho copula con dos o más hembras durante una temporada reproductiva dada (Eisenberg, 1981; Clutton-Brock, 1989; Davies, 1991). En los mamíferos, las hembras alimentan a las crías a través de la lactación, por lo que la participación de los machos en la crianza está restringida a las actividades de protección de las crías. Por esta restricción, los machos ganan más adecuación copulando con varias hembras durante una misma época reproductiva que contribuyendo con una sola pareja en la crianza y defensa (Ostfeld, 1987). Lo anterior determina que los machos, para aumentar su paternidad de crías y así su adecuación, destinen la mayoría de su gasto energético en la obtención de las hembras y en impedir el acceso a otros machos, que constituyen posibles competidores (Emlen y Oring, 1977; Morrison y Morrison, 1981; Kunz et al., 1998). Diversos trabajos muestran que los machos que invierten gran cantidad de energía en la obtención y cuidado de la pareja obtienen una mayor certeza de la paternidad de las crías (Emlen, 1995). Un harén está constituido por un grupo estable de hembras y al menos un macho que excluye activamente a otros machos. Se considera que casi todos los harenes son agrupaciones verdaderas porque la permanencia de los individuos es estable, en muchos casos los miembros pueden estar emparentados y quizás reconocerse a través de un código olfativo y visual (Morrison y Handley, 1991). La estabilidad del grupo podría establecer patrones de dispersión y de filopatría

basados en relaciones de parentesco entre los miembros del grupo (Greenwood, 1980). En un ambiente poliginico los harenes son monopolizados por uno o unos pocos machos, los que pueden ser considerados miembros del grupo social. Algunos grupos de harén presentan una composición definida durante determinadas épocas del año (e.g., grupos de harén de leones marinos en época reproductiva (*Mirounga angustirostris*); Eisenberg, 1981); o bien de forma permanente (e.g. grupos de harén del murciélago de lanza (*Phyllostomus hastatus*); McCracken y Bradbury, 1977). El sistema de apareamiento varía dependiendo de la disponibilidad de los recursos o bien de las actividades de los individuos que lleven a un máximo a su adecuación. Por ejemplo, el recurso zona de playa en los leones marinos determina a cantidad de hembras que se pueden monopolizar en determinada zona, y un incremento en la zona de playa trae como consecuencia una mayor monopolización de hembras.

Desde el punto de vista de las hembras de mamíferos, esperaríamos que su función dentro del grupo fuera la de alimentar a las crías para lograr su sobrevivencia (Eisenberg, 1981; Ostfeld, 1987). Ya que en los mamíferos los machos no participan directamente en las actividades de crianza, esperaríamos que su función fuera él de controlar el acceso a las hembras a posibles competidores para aumentar su adecuación (Eisenberg, 1981). Existen diversas estrategias reproductivas de los machos que permiten establecer el control de las hembras como son los enfrentamientos directos con los rivales (e.g. peleas entre machos de *Kobus vardonii*; Balmford et al., 1992), continuas inspecciones a los grupos de harén (e.g. vuelos cortos alrededor de los grupos por machos de *Carollia perspicillata*; Williams, 1986), defensa de los sitios de percha o área de forrajeo (e.g. defensa de huecos de árboles por *Artibeus jamaicensis*; Morrison, 1981), cooperación entre varios machos (e.g. defensa de grupos por varios machos de *Panthera leo*; Packer y Pusey, 1982). La descripción de la forma en como el macho controla a los grupos, permite establecer su estrategia reproductiva; por lo cual se esperaría que entre más efectiva sea la actividad de control más posibilidades tiene el macho de tener el control de acceso a las hembras y potencialmente la paternidad de las crías. Por el otro lado, los individuos excluidos de las hembras reproductivas, o satélites, tendrán que buscar estrategias alternativas para estar junto a las hembras y obtener cópulas, como pueden ser coaliciones entre ellos para desplazar al

macho dominante, intromisiones continuas a los grupos, robo de cópulas, o permanecer como individuo subordinado, etc. (Axelrod y Hamilton, 1981; Ligon, 1991; Wilkinson, 1987).

La presencia de éstos machos secundarios se ha reportado en repetidas ocasiones para diversos grupos de mamíferos como son leones (Grinnell et al., 1995), mangostas (Clutton-Brock et al., 1998); o murciélagos (Kunz et al., 1998). Existen diversas explicaciones que sugieren ventajas de la asociación como son las de carácter genético en el altruismo entre machos emparentados (Grinnell et al., 1995); o bien la cooperación para la obtención de un mayor número de parejas per capita entre machos no emparentados (McDonald y Potts, 1994). Las ventajas de la asociación para el macho dominante son inmediatas y éstas pueden ser tener acceso a copular con un mayor número de hembras, una reducción del gasto energético en la defensa del grupo u la obtención de la paternidad de una mayor cantidad de crías. Mientras que para el macho secundario las ventajas inmediatas pueden ser un mayor número de hembras, permanecer en un sitio con mejores recursos; o bien a largo plazo como la obtención del lugar del macho dominante cuando éste falte (McDonald y Potts, 1994). Se ha sugerido que la presencia de un segundo macho en un grupo se puede explicar porque trae más beneficios que desventajas al macho dominante que lo está tolerando en el grupo.

El murciélago zapotero (*Artibeus jamaicensis*) es una especie que muestra variantes en el sistema de apareamiento poliginico dependiendo del ambiente de percha en donde se encuentre. Dentro de los troncos huecos y follaje se ha determinado que éste murciélago presenta un sistema de poliginia por defensa de los recursos (Kunz et al., 1983). En este sistema algunos individuos (< 10 individuos por sitio de percha; un macho y cuatro o cinco hembras) se agrupan en un sitio (Morrison, 1979; Kunz y McCracken, 1995). En las cuevas se ha postulado que el murciélago zapotero presenta un sistema de apareamiento del tipo poliginia por defensa de las hembras debido a que no existen diferencias microclimáticas y fisiográficas significativas entre las cavidades de disolución ocupadas y desocupadas por los murciélagos (Kunz et al., 1983). La especie presenta un patrón reproductivo del tipo poliéstrico bimodal con dos picos de nacimientos correlacionados con la producción de frutos de los que se alimenta (Heithaus et al., 1975). Las

hembras son receptivas después del postparto, registrándose la cópula entre el segundo y vigésimo quinto día después del nacimiento de las crías (Keast y Handley, 1991).

En Yucatán, *Artibeus jamaicensis* percha en una gran cantidad de sitios como son cuevas, troncos de los árboles y follaje. Se le encuentra formando grandes colonias dentro de las cuevas (> 200 individuos) en forma agregada, presenta un sistema reproductivo poliginico del tipo harén, un patrón reproductivo restringido a una época del año y se ha reportado la presencia de más de un macho en los grupos de harén (Arita y Vargas, 1995). Sin embargo, no se tiene información sobre la estructura y dinámica de los grupos, las estrategias reproductivas de sus miembros y la variabilidad de las mismas en los diferentes grupos de harén. De igual forma la presencia de dos machos en los grupos de harén permite poner a prueba hipótesis sobre porque la asistencia de ambos en un mismo grupo.

En este trabajo se describe la estructura y dinámica social de los grupos de harén de *Artibeus jamaicensis*, así como las estrategias reproductivas de los murciélagos de un mismo grupos de harén y la variabilidad entre los diferentes grupos. El trabajo se dividió en dos capítulos descriptivos y uno experimental. En el primer capítulo se describe la estructura y dinámica social dentro de los grupos de harén. Al registrar la fidelidad de las hembras marcadas al sitio en donde regularmente se les encontraba (sitio de percha), se logró identificar a los miembros permanentes del grupo y a los miembros ocasionales de los mismos. La dinámica social del grupo fue definida como los movimientos de entradas y salidas diarios que realizaron las hembras del grupo al sitio de percha. Los datos fueron divididos en etapas reproductivas y no reproductivas para comparar la actividad que realizaron los animales entre estos periodos. Además, se determinó la residencia de los machos en los grupos de harén al establecer su tiempo de permanencia en el mismo y se describieron sus características físicas y condición reproductiva para caracterizarlos. Por último, también se contabilizaron sus movimientos diarios para completar la descripción de dinámica social del grupo.

En el capítulo dos se describe la actividad de los machos dominantes en los grupos de harén. Se determinó la forma en que los machos controlaron el acceso a las hembras y las variantes en su defensa. Se establecieron las diferentes respuestas que presentaron los

machos dominantes al momento de que otro murciélago entraba a la cavidad de disolución y ésta se correlacionó con la identidad del recién llegado (miembro del grupo o no; macho, hembra o juvenil). Los datos se dividieron en épocas reproductivas y no reproductivas para evaluar si la cantidad de actividades de defensa desplegadas se encontraba asociada al periodo receptivo de las hembras después del parto. Se analizó la frecuencia de respuestas presentadas por los diferentes machos dominantes para establecer si el número de hembras afectaba la cantidad de respuestas del macho dominante. Este capítulo permitió establecer el papel del macho dominante dentro de los grupos así como las actividades que éste realiza para asegurar el acceso exclusivo de las hembras.

En el tercer capítulo se analizaron los posibles beneficios de la asociación de los machos presentes en los grupos de harén. Para ello se probaron diferentes hipótesis con base en los resultados encontrados en los dos capítulos anteriores: *Experimento 1.-* Sobre la hipótesis de que el macho secundario sustituiría al dominante al momento de remover a éste, se predijo que los machos secundarios ocuparían el lugar vacante debido a que son miembros permanentes de los grupos de harén. Se observó la presencia de dos machos (dominante y secundario) en los grupos grandes de > 14 hembras por grupo. Los primeros no mostraron actividades conductuales de defensa mientras que los segundos sí las presentaron principalmente dirigidas contra los machos no asociados a ningún harén y que visitaban el sitio de percha (satélite; capítulo dos). Al ocupar esta nueva función dentro de los grupos de harén, los machos secundarios desplegarán actividades conductuales similares a las que se reportaron para los machos dominantes (capítulo 2). En este primer experimento se planteó que el beneficio para el macho secundario es a largo plazo, donde obtiene el puesto del macho dominante una vez que este falte en el grupo.

Experimento 2.- Se postuló la hipótesis de que la presencia del macho secundario en los grupos grandes inhibía las visitas de los machos satélites. Se predijo que con la remoción del macho secundario se incrementarán las visitas realizadas por los satélites a los grupos grandes. Como consecuencia directa del incremento en el número de visitas, se predijo que el macho dominante desplegaría una mayor cantidad de actividades conductuales contra los satélites. En los resultados del primer capítulo se observó que los machos satélites intentaron penetrar a los

sitios de percha (visitas) donde están agrupadas las hembras mediante intromisiones a la cavidad de disolución. Los resultados descriptivos del capítulo dos mostraron que las visitas de otros machos a los grupos grandes (> 14 hembras) fueron menos frecuentes que las visitas observadas a los otros grupos (< 14 hembras). En este experimento se planteó un beneficio directo a corto plazo para el dominante, en donde la presencia del macho secundario contribuye a disminuir la visita de los machos satélites y posiblemente represente un menor gasto energético en la defensa de las hembras para el dominante.

Experimento 3.- Se planteó la hipótesis de que reduciendo el número de hembras en los grupos se reduciría el número de machos. Durante la fase descriptiva de éste trabajo que únicamente los grupos de más de 14 hembras presentaban dos machos asociados a ellos, Se predijo que la reducción en el número de hembras de los grupos de grandes hasta < de 14 hembras por grupo (igualando a los grupos medianos) traerá como consecuencia que los machos secundarios abandonarán el sitio de percha. En éste tercer experimento se consideró que grupos con más de 14 hembras favorecían la asociación entre dos machos debido a que posiblemente es un número muy alto de hembras para ser cuidado por un solo individuo, así como la reducción en el mismo traería como consecuencia la disolución de ésta asociación. Con los tres experimentos se intentaron probar los beneficios más evidentes de la presencia de dos machos en un mismo harén, esta asociación produce beneficios para ambos machos cuando el número de hembras por defender y copular es grande.

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Structure and social dynamics of
harem groups in *Artibeus jamaicensis*
(Chiroptera: Phyllostomidae)

STRUCTURE AND SOCIAL DYNAMICS OF HAREM GROUPS IN *ARTIBEUS JAMAICENSIS* (CHIROPTERA: PHYLLOSTOMIDAE)

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The Jamaican fruit-eating bat (*Artibeus jamaicensis*) is one of the most common Neotropical chiropterans, but comparatively little is known about structure and dynamics of its social groups. In two caves of the Yucatán Peninsula, Mexico, we found Jamaican fruit-eating bats forming harem groups, consisting of 4–18 females and 1–2 males, inside solution cavities that develop on the ceiling of caves. Other individuals roosted solitary in the same caves, but outside solution cavities. We identified three types of males: dominants (one in each harem group), subordinates (present only in the largest harems), and satellites (not associated with a harem). Dominants were larger and heavier than males of the other two categories. During the 2-year study, harem groups always roosted in the same cavity and presented a high degree of stability, with few changes in composition. Satellite males and solitary females, in contrast, shifted roosting sites frequently and never formed cohesive groups. Adult females performed more movements from and to harem groups than males, and those movements were less frequent during the breeding season. Harems of the Jamaican fruit-eating bat presented subordinate males in large groups and differ from those of other phyllostomids in the lower degree of cohesiveness shown by females.

Key words: *Artibeus jamaicensis*, bats, behavior, caves, harems, Mexico, social organization

The Jamaican fruit-eating bat (*Artibeus jamaicensis*) is one of the most widely distributed and locally abundant phyllostomids in the Neotropics (Arita, 1993b; Gardner et al., 1991; Timm et al., 1989). It lives in a wide range of habitats, such as tropical rain, dry, and cloud forests, savannas, brushland, and agricultural land (Fenton et al., 1992; Handley, 1976; Heithaus et al., 1975; Morrison, 1979; Orozco-Segovia and Vázquez-Yanes, 1982). This species uses a wide variety of roosting sites, including caves, hollow trees, foliage, undersides of large leaves, and abandoned buildings (Foster and Timm, 1976; Goodwin, 1934; Hatt, 1938; Kunz and McCracken, 1995; Kunz et al., 1983, 1994; Morrison and Handley, 1991; Tuttle, 1976b). Jamaican fruit-eating bats are mostly frugivorous, and their reproductive cycle is linked closely to the

phenology of fruit-producing trees (Eisenberg, 1989; Heithaus et al., 1975; Novick, 1960; Wilson, 1973, 1979; Wilson et al., 1991).

Comparatively little is known about social organization of *A. jamaicensis*. In Puerto Rico, Jamaican fruit-eating bats form harems inside solution cavities that develop on the ceiling of limestone caves (Kunz et al., 1983). Harems form compact and stable groups including 2–14 adult females and a single adult male. Apart from harems, solitary individuals form loose bachelor clusters on walls and ceiling of caves, without any apparent social link. A similar structure exists in caves of Yucatán, Mexico (Arita, 1996; Arita and Vargas, 1995).

Bats are among the few vertebrates that can use caves as permanent refuges (Kunz, 1982). Caves provide protection against

predators and adverse weather conditions, thereby producing adequate roosting sites for more than one-half of the species of bats of a given area (Arita, 1993a; Culver, 1986; Dalquest and Walton, 1970). Studies have shown that resting is the main activity of roosting bats (Burnett and August, 1981; Kunz, 1982; Winchell and Kunz, 1996), while the remaining time is spent in making recognition flights (Bradbury and Emmons, 1974), grooming activities (Bradbury and Vehrencamp, 1976; Wilkinson, 1986), sharing food with conspecifics (McCracken and Gustin, 1991; Wilkinson, 1984), copulating (McCracken and Bradbury, 1981), and commuting between roosting places (Burnett and August, 1981).

The environmental constancy and predictability of cave roosts promotes development of social groups of bats with a high degree of stability in terms of membership. This stability, in turn, allows for development of complex social interactions among individual bats because interactions are stronger in groups with higher degree of stability and with a certain degree of familiarity among members (Wilkinson, 1987). Our objective was to describe social structure of harems of the Jamaican fruit-eating bat in caves of Yucatán. We systematically evaluated dynamics of such groups and identified roles played by different members of groups.

MATERIALS AND METHODS

The state of Yucatán is located in the northwestern part of the Yucatán Peninsula, where the karstic terrain favors development of numerous caves that are used as roosting sites by ≥ 17 species of bats (Arita, 1996; Arita and Vargas, 1995). Because the Peninsula is flat and environmental conditions vary little from place to place, caves in Yucatán can provide true replicates in comparative studies. The Jamaican fruit-eating bat is one of the most abundant and the second most widespread cave bat in Yucatán (Arita, 1996). It occurs in different types of aggregations from small groups of <12 individuals to large colonies of >500 bats (Arita and Vargas, 1995).

Our study was conducted from January 1996 to February 1998 in the Akil (20°14'N, 89°22'W) and Murciélagos (20°09'N, 89°13'W) caves, near Tekax, southeastern Yucatán, Mexico. Both caves are located in the low-elevation mountain range called Sierrita de Ticul at 90 m above mean sea level. The original vegetation of the zone, tropical deciduous forest (Rzedowski, 1978), has been replaced in most parts by cropland (Arita and Vargas, 1995). These two caves were selected from 35 caves with known populations of bats (Arita, 1996) because of the continuous presence of sizable populations of Jamaican fruit-eating bats.

Both caves were multi-chambered and harbored populations of other species of bats besides Jamaican fruit-eating bats, including *Peropteryx macrotis*, *Mormoops megalophylla*, *Pteronotus davyi*, *P. parnellii*, *Glossophaga soricina*, *Carollia perspicillata*, *Mimon bennettii*, *Desmodus rotundus*, and *Natalus stramineus* (Arita and Vargas, 1995). In both caves, groups of Jamaican fruit-eating bats were located in chambers close (<100 m) to the entrance, where *A. jamaicensis* was the most abundant species. Although individuals of other species frequented areas occupied by Jamaican fruit-eating bats and used those sites as flyways, they never formed permanent roosting groups there. Those chambers were sufficiently far from cave entrances to present almost constant temperature (27.4°C) and relative humidity (>90%) year around.

The chamber in Murciélagos Cave was at the end of a 80 m long tunnel. Dimensions of the chamber were 20 by 30 m, with an average height of 5 m. In Akil Cave, Jamaican fruit-eating bats roosted in a 10 by 10 m chamber with an average height of 2.5 m that was connected to an external rock shelter. In both caves, the ceiling was punctuated by several solution cavities, some of which were occupied by groups of *A. jamaicensis*. Other individuals roosted alone or formed small loose groups that disintegrated at the slightest perturbation.

Individuals of groups roosting inside solution cavities were captured using a bucket trap (Kunz et al., 1983; McCracken and Bradbury, 1981) 0.5 m wide and 0.7 m deep. We routinely captured >95% of individuals of a given group with that trap. Bats roosting solitarily on the walls and ceiling were captured from their roost site using a hand-held net or, after being disturbed, by catching them in mist nets (Kunz et al.,

1996). With those bats, our capture rate was lower, but we were able to catch >75% of the individuals that roosted alone. Bats were marked on the forearm with colored plastic rings (Avinet, Inc., Dryden, NY; XB size/4.0 mm diameter) for visual identification. We used a color code that allowed us to identify individuals and determine their original location in the cave (if they were solitary or belonged to a given group). After being marked, all individuals were released at the site of capture. We observed no apparent detrimental effects of bands on bats, and our subsequent rate of recapture showed that marks did not affect the long-term performance or survival of bats.

We considered all individuals with completely ossified epiphyses as adults, and those with cartilaginous joints as juveniles. We corroborated that categorization by measuring body mass, using a spring scale with a precision of 0.1 g, and length of forearm, using a mechanical caliper with a precision of 0.1 mm. Adults always were heavier and had longer forearms than juveniles. Reproductive condition was recorded for males as having abdominal or scrotal testes and for females as pregnant, lactating, or without reproductive signs. The breeding season of colonies was defined as extending from March to August when >80% of adult females were lactating. From September to February, most adult females showed no sign of reproductive activity.

Size of populations of Jamaican fruit-eating bats in both caves was estimated visually (Thomas and LaVal, 1988) and from our capture and marking procedure. We used binoculars, headlamps, and a chronometer to observe and time behavior of bats as described below. White-light was diffused and never aimed directly at bats.

We focused our observations on groups roosting inside solution cavities because they showed greater stability and less sensitivity to disturbance. Each group was monitored once a month during the 2-year study. Observational sessions were 0700–0900, 1000–1200, and 1300–1500 h, for a total of 6 h/group each month. Size of groups could be determined by direct count of bats, while composition was determined by identifying individuals by their marks. Bats were classified as permanent members of a group if they stayed inside the solution cavity for ≥ 3 –6 h of observation. Otherwise, they were considered transients.

Stability and dynamics of groups were ana-

lyzed by documenting permanence, movements, and reproductive activity of individuals. Turn-over of individuals within groups was measured to estimate fidelity of members to their original group. We documented if new members came from other groups or from the pool of individuals roosting on walls and ceiling of the caves. We also recorded the new roosting site of individuals abandoning a group. We also documented cases in which a member changed its membership from permanent to transient within a given group. Number of newborns produced was documented by direct observation. Juveniles were captured, marked, sexed, and eventually monitored to determine their position after they abandoned the group.

We monitored activity of males within and around groups in solution cavities. Marks allowed us to identify individuals, and we could establish hierarchies among males by the proportion of time spent inside cavities or within a radius of 15 cm from the edge. Every month of the study, position and status of individuals were determined to estimate stability of hierarchies among males.

We observed activity of bats inside solution cavities. Activities were classified in two general categories: resting behavior when the bats appeared to be sleeping and active behavior, including self grooming, agonistic interactions, alert activities, and individual movements. Movements included visits of individuals to groups in solution cavities and departure of bats belonging to those groups. During each daily observation period, we measured time spent by individuals in each activity. On a given day, observations were focused on activity of members of a particular group.

A visit was defined as the arrival to a group by an individual from another roosting site, with a residence time of <20 min. In all cases, we were able to determine if the visitor came from another group or from the pool of solitary bats roosting on the walls and ceiling. A departure occurred when an individual abandoned its roosting site for <20 min. We noted the sex of visiting and departing bats and evaluated the relationships of males and females with the reproductive activity of females.

RESULTS

Group structure.—Populations of Jamaican fruit-eating bats in the Akil and Mur-

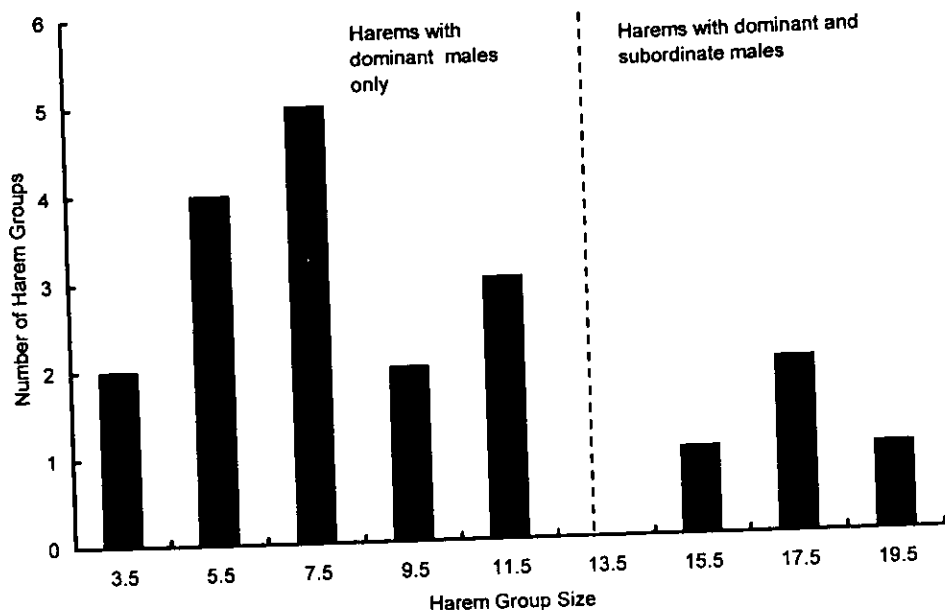


FIG. 1.—Frequency distribution of the number of female Jamaican fruit-eating bats associated with harem groups. Numbers show the 24-month means for 20 harems in two caves of Yucatán, Mexico. Small groups (with ≤ 12 females) included a single dominant male; larger groups (with ≥ 15 females) included one dominant and one subordinate male each.

ciélagos caves were ca. 200 and 250 individuals, respectively. About 75% of those individuals were captured and marked at the beginning of the study. Most marked bats (68%) roosted solitarily or formed loose and unstructured groups on the walls and ceiling of the caves, whereas the remainder (32%) clustered in discrete, stable groups inside solution cavities. Composition of those clusters (several adult females and one or two adult males) was typical of harem groups described for Jamaican fruit-eating bats (Kunz et al., 1983) and other phyllostomids (McCracken and Bradbury, 1981; Wilkinson, 1985; Williams, 1986). Bats that roosted outside harem groups were mostly juveniles (67%) that were observed only in exposed areas of caves, never inside or close to solution cavities as reported for a Puerto Rican cave (Kunz et al., 1983). Some of those bats formed tempo-

rary clusters of individuals of both sexes, but we did not observe groups of bachelor males as described by Kunz et al. (1983).

All harem groups in both caves were sampled to determine their composition. Of the 20 such groups, we captured and marked all individuals in 17 cases, and $>95\%$ of the individuals in the remaining three groups. Akil Cave contained eight groups, but Murciélagos Cave harbored 12. Size of harem was 4–18 females/group (9.7 females ± 0.08 SE, $n = 24$ months $\times 20$ groups; Fig. 1). Sixteen harem groups included <14 females and only one adult male, but the four largest groups (>15 females) contained two adult males. Composition of groups showed little seasonal variation. No significant difference between breeding and non-breeding seasons was found for mean size of group (paired t -test, $t = 0.68$, $d.f. = 19$, $P = 0.5$) or the variance

in number of individuals among groups (Bartlett's test, $F = 2.20$, $d.f. = 19, 19$, $P > 0.05$).

We documented a low, but noticeable, rate of turnover by females within harem groups. During our study, 22 juvenile females and 9 adult females integrated as permanent members in 17 of the existing harem groups. In the same period, 29 adult females (25% of the total) shifted from one harem group to another. With the exception of two females that originally belonged to harem groups that disintegrated, no member of a harem associated with the pool of solitary individuals. We never documented integration of adult males with existing harem groups. Overall, most adult females and all adult males that belonged to a harem group remained in the same group during this study.

Among bats that roosted singly or in loose groups, sex ratio did not differ from unity. With data for both caves pooled, juveniles were represented by 54 males and 60 females (two-tailed binomial test, $P = 0.64$), while adults were represented by 32 males and 34 females ($P = 0.90$). In contrast, permanent members of harem groups showed a highly biased sex ratio (22 males, 101 females, $P < 0.001$).

Harem groups showed a lower degree of sensitivity to disturbance than did loose groups. At the beginning of the daily observation periods, members of harem groups dispersed in response to disturbance by observers. Shortly afterward (<15 min after disturbance), however, groups reintegrated, conserving their original structure and position in the solution cavities. Bats outside harems, in contrast, shifted positions continuously, and composition of loose groups changed accordingly.

Harem groups showed a high degree of stability. During the 2-year study, formation of new harems and disintegration of existing ones were uncommon. We documented only two newly formed harem groups, both in Murciélagos Cave in months 17 (June 1997) and 21 (October 1997) of the study.

Those new groups contained three and four adult females, respectively, and a single adult male in each group. Of the members of the new groups, 78% came from the pool of solitary adult individuals, and only 22% from existing harem groups. One group at Akil Cave disintegrated during month 19 (August 1997) of the study. This was a medium-sized group, containing six females, four of which integrated into another harem group while the remaining two moved to the pool of solitary adults. The dominant male of this group was never seen again in the cave.

A continuous, year-around reproductive pattern has been reported for the Jamaican fruit-eating bat in the Yucatán Peninsula (Jones et al., 1973). In contrast, we observed a distinctive seasonal pattern for females in our two caves, with a in peak parturition between late March and early April. About 75% of all documented births occurred within this period, and newborns remained close to their mothers for 2.5 months. By the end of June, all young-of-the-year had moved out of the harem groups inside solution cavities and associated with the pool of solitary individuals on the walls and ceiling of the caves. Our samples of newborns showed no deviation from a 1:1 sex ratio (two tailed binomial test—Murciélagos Cave, 19 males, 22 females, $P = 0.76$, Akil Cave, 19 males, 19 females, $P = 1.0$).

Hierarchy of adult males.—We classified adult males in three categories according to their permanence and position in harem groups: dominant, subordinate, and satellite males. Dominants (35% of captured males) stayed inside solution cavities or within a radius of 15 cm for an average of ≥ 4 of the 6 daily h of observation. Our sample of dominant males stayed inside or close to their harems 99.4% of the time that they were observed (average for 20 males observed for 6 h every month of the 2-year period). Subordinates (7% of captured males) remained within a radius of 15 cm from solution cavities occupied by harem

groups for 2–4 of the 6 h of observation. Those individuals were considered permanent members of harems because they stayed inside or close to the solution cavities 87.5% of the time that they were observed (average for four males for 6 h for 24 months). Satellites (58% of captured males) were seen inside or close to solution cavities for <2 of the 6 h of observation. They remained close to the harems only 6.8% of the time (average for 30 males for 6 h of observation for 24 months).

One dominant male defended each of the 20 observed groups, and a subordinate male was present in each of the four largest groups. Dominant males spent most of the time outside the cluster of females, patrolling edges of the solution cavities, and rarely ventured >15 cm from the harem group. In contrast, subordinates spent >80% of the time inside the solution cavities, in close contact with females. The brief visits by satellite males occurred with equal frequency on edges (50%) and in the interior of solution cavities (50%).

Adult males varied in size according to their hierarchical status. Both length of forearm and body mass differed among the three categories of males (one-way ANOVA, $F = 8.50$, $d.f. = 2, 51$, $P < 0.005$ for length of forearm, $F = 5.83$, $d.f. = 2, 51$, $P < 0.01$ for body mass, $n = 54$ males in both cases; Fig. 2). Subsequent multiple comparisons showed no difference between dominant and subordinate males (Tukey test, $q = 3.25$ for length of forearm, $q = 0.10$ for body mass, $P > 0.05$ in both cases), or between subordinate and satellite males ($q = 0.27$ for length of forearm, $q = 2.45$ for body mass, $P > 0.05$ in both cases), but they demonstrated that dominant males were larger and heavier than satellite males (Tukey test, $q = 5.72$ for length of forearm, $q = 4.67$ for body mass, $P < 0.05$ in both cases), as reported for groups of Jamaican fruit-eating bats in Puerto Rican caves (Kunz et al., 1983). Among dominant males, larger individuals controlled larger groups of females (correlation analysis be-

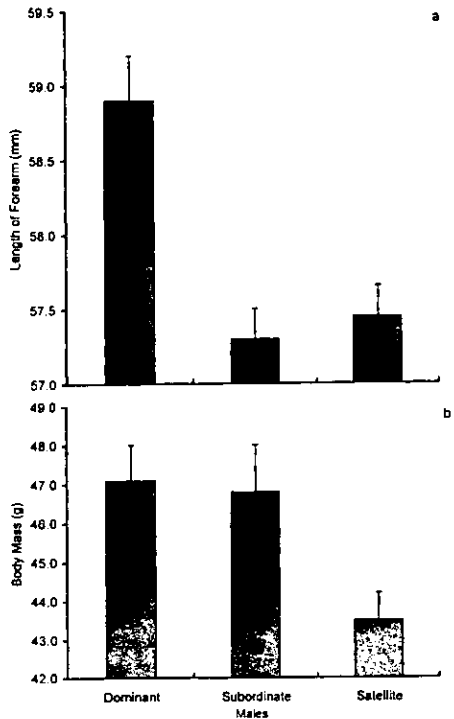


FIG. 2.—Comparison of a) length of forearm and b) body mass among dominant, subordinate, and satellite male Jamaican fruit-eating bats in two caves of Yucatán, Mexico. Dominants consistently had longer forearms and were heavier than individuals of the other two categories.

tween number of females in the group and length of forearm of the male, $r = 0.66$, $n = 20$, $P < 0.001$).

Reproductive condition of males varied according to their hierarchical status. In months prior to the peak of parturition, all dominant and subordinate males had scrotal testes, but only 50% of satellite male showed such condition. During breeding months, dominant males and subordinate males maintained their condition, but percentage of satellite males with scrotal testes increased to 80%.

Hierarchical status of males showed little variation during the 2-year study, with 93%

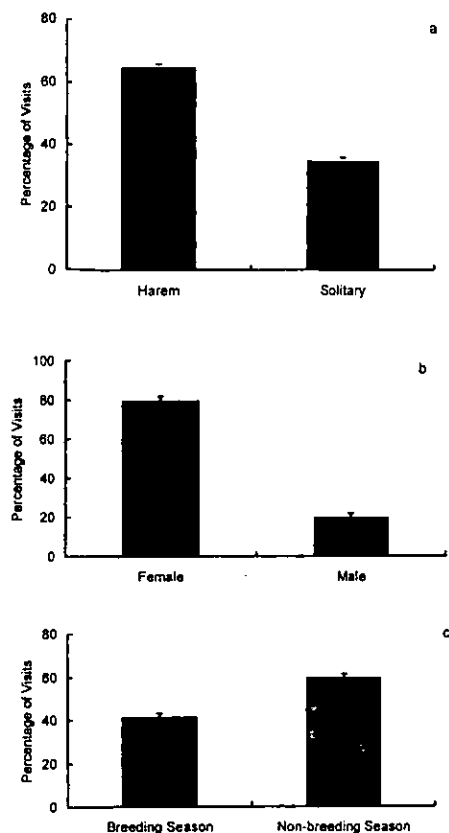


FIG. 3.—Comparison of the number of visits by Jamaican fruit-eating bats to harem groups performed by solitary bats and individuals belonging to a) another harem, b) females and males, and c) during the breeding and non-breeding seasons. Bars represent standard errors.

of adults maintaining their original status. All dominant males conserved their status, with the exception of one individual that disappeared from Akil Cave. Two satellite males became dominant in two newly formed groups, and retained their status at least until the end of the study.

Group dynamics.—Resting accounted for 66% of the time budget of roosting bats. Typical visits to roosts were of short duration, with bats arriving in the proximity of

the solution cavity, climbing with their thumbs and feet into the dome of the cavity, and staying among the harem females for 5–10 min. Visits by members of other harem groups were more frequent than by bats arriving from the pool of solitary individuals (194.65 visits by harem bats \pm 5.23 SE, 105.40 visits by non-harem bats \pm 5.87 SE, $n = 20$ groups, $t = 13.38$, $d.f. = 19$, $P < 0.001$; Fig. 3a). However, the difference was not significant after taking into account the proportion of harem and non-harem individuals in the whole population (pooled data, binomial test comparing the observed proportion of visits by harem-non-harem bats against the proportion in the whole population, 123 versus 66, $P = 0.62$). Visits by females were more frequent than by males (186.7 visits by females \pm 6.09 SE, 46.1 visits by males \pm 3.33 SE, $n = 20$ groups, $t = 16.95$, $d.f. = 19$, $P < 0.001$; Fig. 3b). Visits were more frequent during the non-breeding season than when females were rearing young (110.50 visits during the breeding seasons \pm 5.0 SE, 153.75 visits during the non-breeding seasons \pm 3.11 SE, $n = 20$ groups, $t = 7.26$, $d.f. = 19$, $P < 0.001$; Fig. 3c).

Individuals that temporally departed from harem groups typically moved to the edge of the solution cavity, took flight, and were absent for 15–20 min. Most departures were performed by females (52.05 leaves by females \pm 6.67 SE, 9.80 leaves by males \pm 1.47 SE, $n = 20$ groups, $t = 7.26$, $d.f. = 19$, $P < 0.001$; Fig. 4a). The difference was significant even after taking into account the proportion of females and males in the whole group (pooled data, binomial test comparing the observed proportion of departures by males-females against the proportion of the whole population, 22–101, $P = 0.002$). The frequency of departures varied according to the breeding season (16.45 leaves during the breeding seasons \pm 2.36 SE, 59.20 departures during the non-breeding seasons \pm 6.82 SE, $n = 20$ groups, $t = 8.82$, $d.f. = 19$, $P < 0.001$; Fig. 4b).

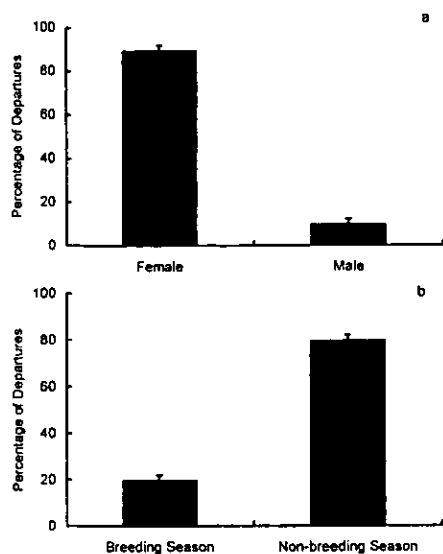


FIG. 4.—Comparison of the number of departures by Jamaican fruit-eating bats from harem groups formed by a) adult male and female bats, and b) during the breeding and non-breeding seasons. Bars represent standard errors.

DISCUSSION

The continuous presence of groups of females inside solution cavities constitutes the basis for social organization of Jamaican fruit-eating bats in the caves of Yucatán. The low variability in size and composition in these groups, contrasting with the instability shown by the diffuse groups of adults and juveniles roosting outside cavities, is evidence of the central role that harem groups play in colonies of *A. jamaicensis*. Similar patterns have been reported for colonies of Jamaican fruit-eating bats roosting in caves (Kunz et al., 1983; Wilkinson, 1987), hollow trees (Morrison, 1979), and tents constructed from leaves (Kunz and McCracken, 1995).

Harems found in caves show more stability than groups roosting in other situations because number of potential roosts for harems in caves is virtually unlimited (Kunz et al., 1983). In our caves, we de-

tected many unoccupied solution cavities, some of which showed evidence of past occupancy—dark spots produced by the excrement of bats. Coinciding with Kunz et al. (1983), we found no noticeable difference between occupied and unoccupied cavities in terms of configuration, position in the cave, or microclimatic conditions. We documented several instances of harem groups moving freely from one solution cavity to another. In other tropical areas, where caves are scarce, availability and permanence of potential roosting sites are lower. For example, in the tropical dry forest of Jalisco, Mexico, hollow trees constitute a highly contested roosting site for groups of Jamaican fruit-eating bats (Morrison, 1980a). Similarly, leaves with adequate position and developmental stage are a limited and ephemeral resource for tent-making bats (Brooke, 1987; Foster and Timm, 1976; Kunz and McCracken, 1995). These unpredictable roosts may not allow development of stable cohesive groups like those found in caves. Migratory bats, such as the lesser long-nosed bat (*Leptonycteris curasoae*), do not form stable groups even when roosting in caves, as they switch roosting places several times each year (Fleming et al., 1998).

Our data suggest a system of female-defense polygyny for the Jamaican fruit-eating bat, with males defending groups of females. A system of resource-defense polygyny, with males defending roosting sites as a resource, is highly unlikely in our caves, given availability of an almost unlimited number of unoccupied solution cavities. Development and maintenance of a female-defense system are conditioned to a high degree of association among females belonging to harem groups and to ability of males to defend such groups (Clutton-Brock, 1988; Emlen and Oring, 1977). Structure and dynamics of groups inside solution cavities and behavior of males associated with such groups show that those conditions are met in the social system of the Jamaican fruit-eating bat.

Harem groups in our caves showed a moderate level of cohesiveness. Female spear-nosed bats (*Phyllostomus hastatus*) show a higher degree of fidelity to harem groups, with most members remaining in the same group at roosting and foraging (Boughman, 1997; McCracken and Bradbury, 1981; Wilkinson and Boughman, 1998). In the later species, members of a given group are of the same age and come from the pool of bachelor individuals roosting alone. In contrast, we documented several cases of female Jamaican fruit-eating bats moving from one harem to another, indicating low fidelity to their groups, in a fashion similar to the one documented for Barro Colorado Island in Panama (Morrison and Handley, 1991). Incorporation of new individuals to harem groups from the pool of solitary bats shows that females in a harem are not all of the same age. Similarly, in the two events of formation of new groups, individuals came from different roosting sites, suggesting that members of new groups had no previous social relation among them. Lack of fidelity to harems by females might be caused by a low degree of relatedness among them (Wilkinson, 1987).

We documented a sex ratio not different from 1:1 among newborns and among individuals roosting alone. However, the sex ratio in harem groups was obviously skewed toward females, suggesting that reproductive opportunities for males are unevenly distributed and dependent on ability to control a group of females. We observed satellite males copulating with females not belonging to harems, showing that reproduction is not limited to individuals of harem groups. However, dominant males that defend groups of females might have the advantage of not competing directly for copulations with other males.

Size and structure of harems in our caves were similar to those reported by Kunz et al. (1983). We documented two categories of adult males associated with the largest harem groups similar to the adult and sub-

adult males reported for *P. hastatus* in Trinidad (Kunz et al., 1998). In previous studies of Jamaican fruit-eating bats, a single adult male (which we call dominant) invariably was associated with a group of females (Kunz et al. 1983; Morrison and Handley, 1991). Similarly, in other species of bats, harems always are guarded by a single adult male (*Myotis adversus*—Dwyer, 1970; *P. hastatus*—Kunz et al. 1998; *Pipistrellus nanus*—O'Shea, 1980; *D. rotundus*—Park, 1991; *C. perspicillata*—Porter, 1979; Williams, 1986). In our caves, the largest groups (>14 females) contained an additional adult male that we call a subordinate. Statistically, we found no difference in size between subordinate and dominant males, possibly due to the small sample for the former. However, the fact that dominant males were significantly larger than satellite males suggests a size-biased hierarchy for males in the social system of the Jamaican fruit-eating bat—pattern that has been shown in other species of vertebrates (Archer, 1988).

The hierarchy among males showed little variation during our study. In short-tailed bats (*C. perspicillata*), dominant males stay with groups of females only for a brief period during the breeding season (Fleming, 1988; Williams, 1986). In contrast, dominant spear-nosed bats (*P. hastatus*) retained their positions close to harem groups for ≥ 3 years (McCracken and Bradbury, 1981). We documented only one case of a dominant male disappearing from the population and the formation of two new groups of females, defended by new dominant males. This stability of hierarchies among males shows that Jamaican fruit-eating bats have a social system similar to that of spear-nosed bats.

Dominant and subordinate males showed scrotal testes continuously during our study. Satellite males had abdominal testes most of the time, except when females were lactating. A post-partum estrous had been reported for the Jamaican fruit-eating bats (Fleming, 1971; Fleming et al., 1972; Wilson, 1979; Wilson et al., 1991). This pattern

occurs in Yucatán; the increase in number of satellite males with scrotal testis could be a response to increased availability of reproductive females (Fleming et al., 1972; Wilson et al., 1991). A second response might be an increase in number of agonistic interactions by dominant males during the breeding season to defend groups of receptive females inside solution cavities. By defending harems, dominant males can assure paternity of individuals born to harem females, producing a biased distribution of reproductive success among males, similar to that described for spear-nosed bats (McCracken and Bradbury, 1977) and long-fingered bats (*Miniopterus minor*—McWilliam, 1990).

Jamaican fruit-eating bats spent a high proportion of their time at rest inside the cave, as reported for little brown bats (*Myotis lucifugus*—Burnett and August, 1981) and eastern pipistrelles (*Pipistrellus subflavus*—Winchell and Kunz, 1996). Visits to harem groups by members of another harem were more frequent than visits by solitary individuals. More adult females also visited these groups than did adult males, probably because conflicts for roost position are more pronounced between males (Bradbury and Emmons, 1974; Nelson, 1965) and guarding of harems requires a high investment of energy (Balasingh et al., 1995; Morrison, 1978, 1980b, 1980c; Morrison and Morrison, 1981; Ramírez-Pulido and Armella, 1987).

We observed fewer movements by females during the breeding season. A reduction in capacity of movements by females has been reported for several species during the breeding season (*Artibeus lituratus*, *Corynorhinus townsendii*, *Eptesicus fuscus*, *Lasiurus borealis*—Fenton, 1969; *Myotis lucifugus*—Humphrey, 1975; *Tadarida brasiliensis*—McCracken and Gustin, 1991; *Myotis grisescens*—Tuttle, 1976a), due to the increase in time that females have to invest in feeding and taking care of newborns (Dalquest, 1970; Fenton, 1969). This lowered mobility produces more stability

within groups during the reproductive season. Shortly after the breeding season when young bats learn to fly, we observed an increase in frequency of movements by females.

Our observations provide clues to understanding processes that maintain social structure of Jamaican fruit-eating bats in caves. Several questions, however, remain unanswered. For example, advantages of clustering for females were not clear to us. Patterns of recruitment and formation of new groups did not show any apparent altruistic or cooperative benefit for females. In the same way, possible mutual benefits for the two males that coexisted in larger groups were unclear. Alternative explanations for formation of groups include mutual defense against predators (August, 1979, 1985) and benefits of foraging flocks (Dalquest, 1953; Handley et al., 1991; Heithaus et al., 1975; LaVal, 1970; Wilkinson and Boughman, 1998). An examination of the degree of relatedness among members of groups might provide a better understanding of social organization of the Jamaican fruit-eating bat. It is clear, nonetheless, that structure and dynamics of cave colonies in this species are determined primarily by presence of well-structured, cohesive harem groups.

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Defence of females by dominant
males of *Artibeus jamaicensis*
(Chiroptera: Phyllostomidae)

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Defence of Females by Dominant Males of *Artibeus jamaicensis* (Chiroptera: Phyllostomidae)

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Abstract

Defence of females by dominant males of the Jamaican fruit-eating bat *Artibeus jamaicensis* was observed in two natural colonies over 2 yr. A log-linear model was used to evaluate the frequency distribution of visits to harems by sex, season and agonistic interaction of dominant males. Harem group size varied from four to 18 females, with one adult male in the small and medium-sized groups and two males in the large groups (> 14 females). A highly significant interaction was noted between the age and sex of the visitor and the response of the dominant male. Male visitors were attacked more often than female and juvenile visitors. Aggressive defence increased during the reproductive seasons, with dominant males showing more agonistic responses towards male visitors. An increase in the frequency of visits by male visitors was noted in harem groups that ranged in size from four to 12 females, but the frequency of male visits declined in harem groups that contained more than 14 females.

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Introduction

Polygyny, the monopolization of several females by one male during the breeding season (Emlen & Oring 1977), is the most frequently reported mating system in mammals (Eisenberg 1981). Bats exhibit a variety of social systems, ranging from monogamy in some carnivorous species (Vehrencamp et al. 1977) to polygyny in several species of fruit-eating bats (Bradbury 1977; McCracken & Bradbury 1977; Morrison 1979; Kunz et al. 1983). As in other animal species, polygyny in bats often shows characteristic patterns: a marked sexual dimorphism, with males larger than females; the rearing of young by females; a definite age

structure in social groups, and an operational sex ratio biased towards females (Orians 1969; Alexander 1974; Ralls 1977). These patterns are formed by the mechanisms by which one male is able to gain control over several females and reduce competition with other males (Orians 1969; Bradbury 1977).

The Jamaican fruit-eating bat *Artibeus jamaicensis*, which is considered a polygynous species, is one of the most common bats in the Neotropics, living in a great diversity of habitats (Kunz 1982). In Puerto Rico, compact and stable year-round groups of one male and several females roost inside solution cavities that develop on the ceilings of limestone caves. These cavities are numerous, and the environmental and topographic conditions inside caves are constant, allowing the development and maintenance of a female-defence type of polygynous mating system (Kunz et al. 1983). In other localities, individuals and small harem groups have been found roosting inside hollow trees (Morrison 1978). The availability of tree holes and their defensibility by male fruit-eating bats promotes roost fidelity and the maintenance of harem groups that exhibit high roost fidelity (Morrison 1979). Frequent patrolling movements and short foraging flights are used by males to defend roosting sites (Morrison & Morrison 1981). Ephemeral roosting sites, such as the tents that bats build under the leaves of some tropical plants (Foster & Timm 1976), are used by small harem groups of *A. jamaicensis*, which can be defended only for brief periods of time (Kunz & McCracken 1995).

This paper describes the behaviour of male Jamaican fruit-eating bats (*Artibeus jamaicensis*) while defending harem groups from the intrusions of other males in a female-defence polygynous mating system. The assemblage consisted of groups of *A. jamaicensis* roosting inside solution cavities in limestone caves on the Yucatan peninsula in Mexico (Ortega & Arita 1999). We investigated the defensive behaviour displayed by dominant males towards various visitors (female, male or juvenile) in different seasons (breeding and non-breeding), to determine whether this behaviour is affected by the characteristics of the cave or by the reproductive season of the females.

Methods

Research was conducted for 24 mo, from Jan. 1996 to Feb. 1998, at two caves in Yucatan, Mexico: Akil (20°14' N, 89°22' W) and Murciélagos (20°09' N, 89°13' W). Caves are in the south-eastern Mexican state of Yucatan. Both caves are located 90 m above sea level and are separated by a distance of 30 km. The entire peninsula is a flat limestone block that favours the development of abundant caves. Because of its flatness, the northern part of the peninsula shows very little variation in topography, low habitat heterogeneity, and nearly uniform vegetation cover, consisting of highly disturbed tropical dry forest that has been replaced for the most part by cropland (Arita & Vargas 1995). As a consequence of the low heterogeneity of the peninsula, conditions in the caves are very similar, allowing true replication in comparative studies. The two caves included in this study were selected from a pool of 36 caves in the area with populations of bats (Arita & Vargas 1995).

Caves are the preferred roosting sites for at least half of the bat species reported

for the Yucatan (Arita 1996). The Jamaican fruit-eating bat is the second most common species in the Yucatan caves, and one of the most abundant and widespread bats in the area (Arita & Vargas 1995). In both caves, *A. jamaicensis* formed permanent colonies of approximately 200 individuals situated close to the entrance (< 100 m). The caves showed a marked constancy in ambient temperature ($27.4 \pm 2.34^\circ\text{C}$) and relative humidity (> 90%) throughout the year. The ceilings of both caves included numerous solution cavities. Groups of *A. jamaicensis* choose these cavities as diurnal roosting sites, although several solitary individuals roost alone on exposed sites on the walls and ceilings of the chambers. In both caves, more than 75% of the estimated population of fruit-eating bats were captured and marked. The population at Akil Cave was estimated at 200 individuals, and Murciélagos Cave harboured approximately 250 bats.

Individuals roosting inside solution cavities were captured using a bucket trap (Kunz et al. 1996) 0.5 m wide and 0.7 m deep. Solitary bats were captured with a hand-held net or with mist nets set at strategic places inside the caves. All individuals were marked on the forearm with three coloured, plastic split rings (Avinet Inc., XB size/4.0 mm diameter) for visual identification (Kunz 1996). Animals were released at the exact location of their roosting site after being marked. Subsequent observations showed no detrimental effects of the plastic split rings on bats. Moreover, split rings showed little wear and could be easily read throughout the 24-mo study.

Individuals were considered to be adults when the wing epiphyses were completely ossified, and to be juveniles when the joints were cartilaginous. Standard morphological measurements were taken to corroborate this classification. A spring scale (exact to 0.1 mm) was used for measuring body mass; a mechanical calliper (exact to 0.1 mm) was used for measuring total length and length of the forearm. The position of the testes (abdominal or scrotal) was used to assess the reproductive condition of adult males. Females were classified as pregnant, lactating or without reproductive signs according to external factors, such as the presence of a palpable foetus or swollen nipples with traces of milk (Racey 1988).

Males roosting permanently inside solution caves were considered dominant and were the focus of our observations. Each dominant male was observed once a month during the 2-yr study. Observation sessions started at 07:00 h and finished at 15:00 h, with 1 h of resting between 2 h of continuous watching. Time allocated to the observation of each dominant male was 6 h mo⁻¹. Binoculars, headlamps and a stopwatch were used to observe and to quantify the behaviour of dominant males. To avoid disturbing the natural behaviour of bats, light was diffused and never aimed directly at the groups.

We tallied the number of visits made by identifiable individuals to solution cavities. A visit was defined as a bat arriving at the group from another roosting site, and remaining there for less than 20 min. The forearm bands allowed us to determine the sex and age categories of each visitor. We evaluated the relationship between number of visits made by adult males and harem group size to test whether there was an effect of group size on the visitation rate.

Defensive behaviour performed by dominant males in response to the presence

of a visitor was quantified using a classification of three possible responses. An 'ignore' response was recorded when the dominant male remained motionless when the visitor arrived at the solution cavity. An 'approach' response occurred when the dominant male moved from his patrolling site, at the border of the solution cavity, towards the intruder but displayed no apparent aggressive behaviour. Finally, an 'agonistic' response occurred when the dominant male approached the visiting individual and performed aggressive displays, such as vocalizations, wing flicks, and direct chasing (Williams 1986). In addition, we recorded the number of copulation postures exhibited by dominant males, and this was used to quantify their reproductive activity. A copulation posture occurred when a dominant male approached and mated with a female during an observational period.

We compared the defensive behaviour displayed by dominant males during the breeding and non-breeding seasons. The breeding season extended from Mar. to Aug. More than 80% of the adult females showed signs of reproductive activity during these months. As previously reported for the same species in Panama (Fleming 1971), most female fruit-eating bats carried newborns and exhibited postpartum oestrus during this period. From Sep. to Feb. (non-breeding season), most females showed no apparent reproductive characteristics and were not receptive. Because of the changes in the receptivity of females, we expected differences in the defensive behaviour of dominant males between the breeding and non-breeding seasons, since females are more attractive to non-resident adult males in the breeding season than at other times.

We used a log-linear model (Sokal & Rohlf 1981) to analyse statistically the frequency distribution of visits according to three classification criteria: sex and age of the visitor (juvenile, adult male or adult female); season (breeding or non-breeding), and response of the dominant male (ignore, approach or agonistic behaviour). We tallied each visit documented during the 24-mo study by assigning each observation to one of 18 cells in a three-dimensional table formed by the combinations of three rows (sex and age categories), two columns (season category), and three tiers (types of response). The model was

$$\log \hat{f}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{jk} + \alpha\beta\gamma_{ijk},$$

where \hat{f}_{ijk} represents the expected frequency of visits for the cell corresponding to row i , column j and tier k ; μ is the mean of the log values of the expected frequencies; α , β and γ represent the effects of sex, season and response, and $\alpha\beta$, $\alpha\gamma$, $\beta\gamma$ and $\alpha\beta\gamma$ represent the pairwise and three-way interactions of variables.

A stepwise procedure was used to determine the log-linear model that had the best fit to our data on the frequency distribution of visits. Starting with the complete model, including all possible interactions, we subtracted sequentially the effect of the interactions between pairs of classification criteria until we found the model that best fitted the data by yielding a likelihood ratio chi-square value corresponding to a $p > 0.05$, but containing the lowest number of terms (Sokal & Rohlf 1981). Taking advantage of the additive property of log-linear models, we were able to test the significance of the effect of individual terms of the model by comparing the

likelihood ratio chi-square values of the equation with and without that particular term.

Results

The majority of marked bats (68%) roosted on the walls and ceilings of the caves, forming loose groups of mixed sexes with variable proportions of juveniles and adults. These bats were considered to be solitary individuals that did not form structured harem groups. The remaining 32% of individuals clustered in structured harem groups that roosted inside solution cavities throughout the year. Because of their composition (several females and one or two males), we considered the groups inside solution cavities to be harems: groups of females associated with one male (Ortega & Arita 1999). We were able to capture and mark more than 95% of all individuals that roosted in these harem groups.

Akil Cave contained eight harem groups, and Murciélagos Cave harboured 12 harem groups. Harem size varied from four to 18 females per group ($\bar{x} \pm \text{SE} = 9.72 \pm 0.08$ females, $n = 24 \text{ mo} \times 20$ groups). The four largest groups, containing more than 14 females, had two adult males. The secondary male was located at the bottom of the solution cavities and did not display any defensive behaviour (Ortega & Arita 1999). Smaller groups ranged from six to 13 females and contained a single adult male.

We observed visits by juveniles, adult males and adult females (Fig. 1). Visitors typically arrived at the edge of the solution cavity, subsequently climbing with their thumbs and feet into the bottom of the cavity, and staying inside for 5–10 min per visit ($\bar{x} \pm \text{SE} = 6.23 \pm 3.45$ min for the 20 groups). The bats did not engage in boxing matches, but they did perform wing flicks, engage in short chases, and attempt to bite the visiting males. The intensity of agonistic responses was not

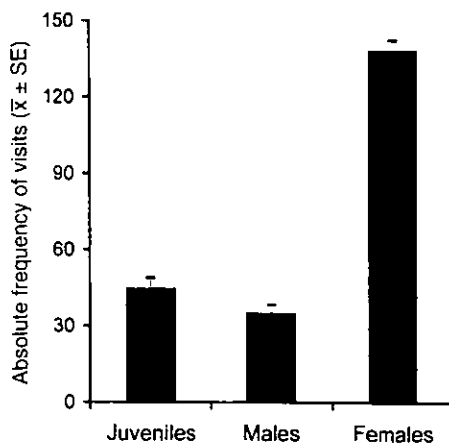


Fig. 1. Absolute frequencies of visits analysed by sex and age of the visitors during the entire study. Females made more visits to the harem groups than juveniles and males. Values shown are $\bar{x} \pm \text{SE}$.

measured, but chases and attempts to bite were not documented in all cases and seemed to constitute the most aggressive responses. Agonistic responses were short, lasting for less than 1 min ($\bar{x} \pm SE = 0.35 \pm 0.29$ min, $n = 12$ groups), with very little year-round variation.

The log-linear model suggested that there was a highly significant interaction between sex and age of visitor and the response of the dominant males (Table 1). The majority (88.3%; $n = 2316$ observed visits) of visits by females were ignored by dominant males, and in most other cases (10.7%) the male approached the visiting female but performed no aggressive display (Fig. 2). Only in 1.03% of the cases did the male display agonistic behaviour towards a visiting female. In contrast, the majority of visits by adult males ($n = 840$ observed visits) elicited

Table 1: The fit of the log-linear model $\log \hat{f}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{jk} + \beta\gamma_{ijk}$ to our data on the frequency of visits classified in terms of age/sex of visitor (α), season (β), and response by the dominant male (γ). The hierarchical analysis showed significant effects of the three pairwise interactions

	Likelihood ratio χ^2	d.f.	Probability
Actual data versus model	5.81	4	0.213
Sex by season	6.42	2	< 0.05
Sex by response	1129.07	4	< 0.0
Season by response	137.29	2	< 0.0

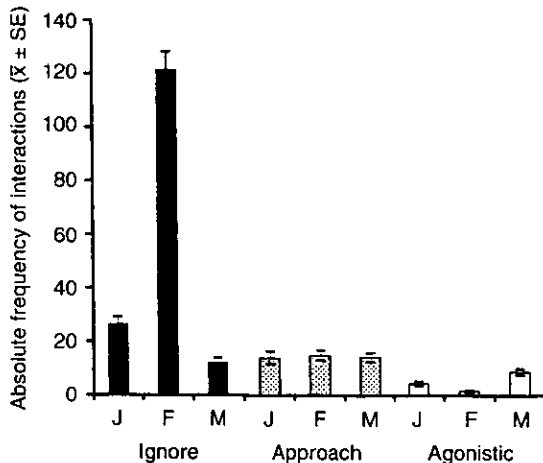


Fig. 2: Absolute frequencies of responses by dominant males. Adult females (F) were ignored more often and assaulted less often than adult males (M), with responses to juveniles (J) being intermediate. The frequency of the approach response was similar for females, males and juveniles. Values shown are $\bar{x} \pm SE$

approaches or aggressive responses by dominant males. Only in 34.9% of cases did the dominant male ignore the visiting male; in 40.4% of cases the dominant males approached the visiting bat, and in 24.7% of cases they displayed aggressive behaviour towards the visitor. A typical aggressive response to a visit by a visiting adult male consisted of a sequence of short and rapid vocalizations, wing flicks, and direct aggression such as chasing or attempts to bite the opponent (Williams 1986). In response to visits by juveniles, dominant males approached the intruder or attacked in 40.8% of cases, ignoring the visit in 59.2% of cases ($n = 1069$ observed visits).

A significant interaction between season (reproductive and non-reproductive) and response by dominant males was demonstrated by the log-linear model. During the non-breeding season only 3.79% ($n = 2649$ observed visits) of all visits elicited an aggressive response by the dominant male, whereas 9.23% ($n = 1576$ observed visits) of such visits were responded to by dominant males with an agonistic display when most adult females were reproductively receptive. In contrast, in the non-breeding season, 82.6% of all visits triggered no response by the dominant male, while this percentage during the breeding season was 65.5%.

The number of visits made by adult males varied according to the number of females belonging to the focal harem group (quadratic model, $y = -5.60 + 4.31x - 0.17x^2$, $r^2 = 0.63$, $n = 20$, $p < 0.05$; Fig. 3). Groups that ranged from four to 10 females received fewer visits than the other groups ($\bar{x} \pm SE = 15.68 \pm 0.48$, $n = 12$ groups). Groups with 10–13 females received most visits ($\bar{x} \pm SE = 23.75 \pm 0.66$, $n = 4$ groups), while the largest groups (> 14 females) received comparatively few visits ($\bar{x} \pm SE = 17.45 \pm 0.77$, $n = 4$ groups).

Aggressive responses were seen in all 20 dominant males included in the study. There was a positive correlation between the number of agonistic responses by a

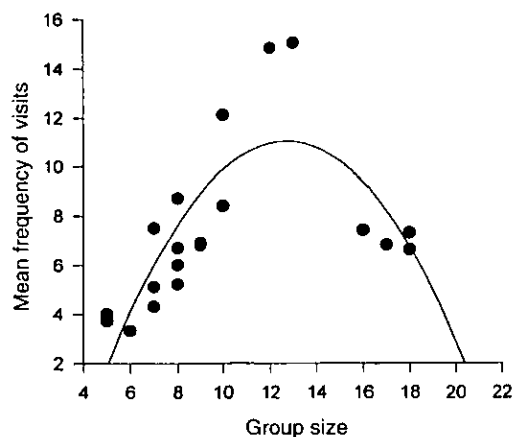


Fig. 3: Mean frequencies of visits by adult males to harem groups of different sizes (quadratic model: $y = -5.60 + 4.3080x - 0.17x^2$, $r^2 = 0.628$, $p < 0.05$). Medium-sized harem groups were more frequently visited than small or large harem groups

given male and the number of births recorded for its group (Pearson's correlation coefficient: $r = 0.74$, $n = 20$, $p < 0.001$). The percentage of dominant males that were observed copulating in a given month was correlated with the number of births documented in the corresponding group ($r = 0.86$, $n = 24$ mo, $p < 0.001$).

Discussion

Dominant males actively defended females. The stereotyped agonistic display performed by dominant males was similar to that described for male short-tailed bats (*Carollia perspicillata*; Porter 1978) and greater spear-nosed bats (*Phyllostomus hastatus*; McCracken & Bradbury 1981). Before attacking a visiting male, short-tailed bats typically produce aggressive vocalizations, display wing flicks, and adopt a 'boxing position' accompanied by swipes with the forearms and closed wings (Porter 1978). In contrast, male spear-nosed bats normally attack an intruder without a previous display (McCracken & Bradbury 1981).

Dominant males largely ignored visits by adult females. Interactions between males and females belonging to the same group have been reported as infrequent, under natural conditions, for short-tailed bats (Williams 1986) and greater spear-nosed bats (McCracken & Bradbury 1981). In both species, dominant males do not try to prevent females from temporarily moving from one group to another. Moreover, male short-tailed bats normally do not show distinct reactions to attempts by visitor females to move into the roosting sites occupied by the male's group (Williams 1986). In captivity, male short-tailed bats actively recruit females into their territories (Porter 1979). In our study, 88.3% of visits by females were completely ignored, 10.7% elicited an approach by the dominant males, and only 1% ended with an aggressive display by dominant males.

Only 34.9% of visits by males were ignored. In 40.4% of cases, the dominant male approached and inspected the visitor, and 24.7% of visits triggered aggressive responses. Clearly, our results are consistent with those reported in field studies for other polygynous bat species, where males show a high degree of roost fidelity and perform agonistic behaviour aimed at visiting males, which constitute potential competitors for females (e.g. *Myotis adversus*, Dwyer 1970; *Saccopteryx bilineata*, *S. leptura*, and *Balantiopteryx plicata*, Bradbury & Emmons 1974; Bradbury & Vehrencamp 1977; *C. perspicillata*, Porter 1978; Williams 1986; *Pipistrellus nanus*, O'Shea 1980; *Desmodus rotundus*, Park 1991).

Dominant males displayed aggressive behaviour more frequently during the breeding season. A similar pattern has been documented for other bat species (Wilkinson 1987). Male short-tailed bats display more agonistic activities during the two birth peaks (which coincide with a post-partum oestrus condition in females) than during the non-breeding season. Similarly, male spear-nosed bats vigorously defend their groups of females during the breeding season. In both cases, however, genetic paternity analysis has shown that the defence behaviour of males is not totally effective, as about 15% of young born to harem females have genotypes that are incompatible with that of the putative father (McCracken & Bradbury 1977; Porter & McCracken 1983).

Observations under natural conditions of colonies of common vampire bats (*Desmodus rotundus*) have shown that high-ranking males achieve a higher rate of copulation than satellite males (Wilkinson 1985). In our system, male Jamaican fruit-eating bats increase their aggressiveness during the breeding season, even though the absolute number of visits to harem groups decreases during the breeding season (Ortega & Arita 1999). In harem groups defended by a single male, control over access to females is possible. However, in larger groups containing several females and two males (a dominant and a subordinate), some sharing of mates is possible, although we did not observe this. Genetic paternity analysis would be necessary to document the effectiveness of the behavioural defence by dominant males, as well as to evaluate the genetic contribution of subordinate males.

The frequency of visits varied according to the size of harem groups. Because of their high concentration of receptive females, we expected to document more visits to the largest groups, especially by males from outside the groups. However, we observed a different pattern in which medium-sized groups (10–13 females) received the most visits, while small (four to 10 females) and large groups (more than 14 females) received visits with approximately the same frequency. The low visitation rate by foreign males to small groups can be explained by the low concentration of females in these harems. The case of the largest harems is more complex. In these groups, in addition to the guarding male that is present in harems of all sizes (the 'dominant male', Ortega & Arita 1999), an additional male (the 'secondary male', Ortega & Arita 1999) roosts in close contact with females. In most polygynous bat species, a single adult male guards the groups of females (McCracken & Bradbury 1981; Williams 1986). The only exceptions are Jamaican fruit-eating bats (Ortega & Arita 1999) and greater spear-nosed bats (Kunz et al. 1998). In the case of the greater spear-nosed bat, membership of a harem group allows a subordinate male to become familiar with the females and subsequently assume the dominant position (Kunz et al. 1998). The fact that in our study the largest groups, which include two adult males, were visited relatively infrequently suggests a possible role of subordinate males in controlling the access of visitors to harem females. Coalitions or cooperative relationships between two or more males are widespread in some mammal groups, such as primates and carnivores (Bygott et al. 1979; Caro & Collins 1987; Noe & Sluiter 1990; Bulger 1993; Herrera & Macdonald 1993; Waser et al. 1994), but are unreported for bats. A more detailed examination of the potential advantages that dominant and subordinate males gain by maintaining large groups of females might show this kind of relationship for Jamaican fruit-eating bats.

The groups of females inside solution cavities formed the typical harem arrangement reported for Jamaican fruit-eating bats at other roosting sites. Similar groups have been described for *A. jamaicensis* in caves (Kunz 1982; Kunz et al. 1983), hollow trees (Morrison 1979), and so-called 'tents', which are roosts built by some species of bats by cutting parts of the leaves of certain tropical plants (Kunz et al. 1994; Kunz & McCracken 1995; Storz et al. 2000a). These harem groups showed very little variation in their composition through time and can be considered as the basis for the social structure of fruit-eating bats in our caves

(Ortega & Arita 1999). The cohesiveness of harems contrasted with the instability of the loose groups formed by juveniles and other solitary bats roosting outside solution cavities (Ortega & Arita 1999). These individuals never formed long-term groups, and showed very little fidelity to their roosting sites, moving frequently from one place to another inside the cave (Ortega & Arita 1999).

Our caves harboured eight (Akil Cave) and 12 (Murciélagos Cave) harems, with group size varying from four to 18 adult females. The number and size of harem groups in fruit-eating bats are determined by the type of roosting site (Morrison & Handley 1991). Ephemeral sites, such as foliage or tents built by bats, provide secure space only for single groups consisting of a single male and two or three adult females (Morrison 1979; Kunz & McCracken 1995). Tree hollows and some small caves can also accommodate only one harem group, but these groups can include up to 14 adult females (Morrison 1979; Arita & Vargas 1995). Large limestone caves provide numerous permanent and predictable roosting sites for several groups of varying size (Kunz et al. 1983).

Adult males showed high roost fidelity, spending most of the daytime inside or around their roosting site (Ortega & Arita 1999). In several bat species, dominant males spend more time within their groups than do females or juveniles (Porter 1979; Morrison & Morrison 1981; Williams 1986; Morrison & Handley 1991; Balasingh et al. 1995; Kunz et al. 1998). Dominant males need to stay close to their roosting sites for longer periods because they have to guard the harems from potential competitors. Being free from that limitation, females of different bat species with polygynous mating systems temporarily change their roosting position several times a day and, in some cases, abandon their groups permanently (e.g. the white lined bat *Saccopteryx bilineata*, Bradbury & Emmons 1974; the short-tailed fruit bat *Carollia perspicillata*, Fleming 1988; the pallid bat *Antrozous pallidus*, Lewis 1996; the fishing bat *Noctilio leporinus*, Brooke 1997; the short-nosed fruit bat *Cynopterus sphinx*, Storz et al. 2000a). In the Jamaican fruit-eating bats in our caves, females showed more mobility than dominant males, making the majority of the visits to other solution cavities, and in some cases making permanent moves from one group to another (Ortega & Arita 1999).

In polygynous mating systems in which the limiting resource is a territory (e.g. tree holes or leaf tents built by the bats), male bats normally move frequently around the roosting place to prevent invasions by other males, and perform short foraging flights (Morrison 1978, 1980; Morrison & Morrison 1981; Brooke 1987; McWilliam 1990; Morrison & Handley 1991; Kunz & McCracken 1995; Kunz et al. 1998; Storz et al. 2000b). In our system, roosting sites (solution cavities on the ceiling of the caves) are not a limited resource (Ortega & Arita 1999) and males do not perform patrolling activities around the holes. Furthermore, agonistic displays by dominant males are directed in most cases at other males, with few displays directed at juveniles, and very few aimed at females. These observations support the hypothesis that the mating system of Jamaican fruit-eating bats in the Yucatan caves is a case of female-defence polygyny (Ortega & Arita 1999), but male activities are probably related to dispersion of resources and females. These factors could be studied with the help of removal experiments to assess the relative importance of each (Ostfeld 1987).

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**Benefits of males defending harem
groups of the Jamaican fruit-eating
bat (*Artibeus jamaicensis*)**

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8 Benefits for males defending harem groups of the Jamaican fruit-eating bat

9 (Artibeus jamaicensis)

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24 ABSTRACT

25 In the caves of Yucatan, Mexico, the Jamaican fruit-eating bat, Artibeus
26 jamaicensis, forms harems of 4 to 18 females controlled by dominant males that
27 defend groups from foreign, satellite males. Large groups (>14 females) contain
28 an additional, secondary male. In theory, an association between dominant and
29 secondary males can evolve only if both participants obtain benefits from the
30 relationship. With three removal experiments, we tested for such benefits. In the
31 first experiment, when a dominant male was removed from its group, its role was
32 occupied by the associated secondary male (in large groups) or by a satellite male
33 (in small groups). Former secondary males took less time to gain control of the
34 harems and stayed more time with the groups than former satellites. In the second
35 experiment, when a secondary male was removed, the rate of visitation by foreign
36 males and the number of agonistic displays by the dominant both increased. In the
37 third experiment, when the number of females in large groups was reduced,
38 secondary males spent less time with their groups and the rate of visitation by
39 foreign males increased. However, the frequency of agonistic displays by
40 dominant males toward secondary males did not change. Dominant males invest
41 large amounts of energy in defending the harems, but obtain direct and immediate
42 benefits from the presence of secondary males in the form of access to a larger
43 number of females. Secondary males apparently invest little energy in defending
44 the harems, obtain no obvious immediate benefit, but gain long-term benefits by
45 having priority access to vacant positions left by dominants.

INTRODUCTION

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Most mammals are polygynous (Greenwood 1980; Clutton-Brock 1989; Davies 1991). Because of the phenomena of pregnancy and lactation, the bulk of the cost of rearing and feeding the young is on females, so in general mammalian males do not get deeply involved in caring for the young. Under these circumstances, it is more advantageous for males to attempt to mate with as many females as possible, rather than to form monogamous pairs (Emlen and Oring 1977; Osfeld 1987). Thus, although exceptions do exist (Jennions and MacDonald 1994), males of most mammalian species maximise their fitness by fathering several young with many females, rather than investing time and energy in the rearing of a few young (Brown 1987; Ligon 1991; Dugatkin 1997, 1998).

In several mammalian species (e.g. howler monkeys, Alouatta seniculus; lions, Panthera leo; suricates, Suricata suricatta), males compete to gain dominance over rich territories where females concentrate to feed or to seek refuge from predators (Rood 1989; Pope 1990; Clutton-Brock et al. 1998; Doolan and MacDonald 1999). These cases of resource-defence polygyny contrast with those in which females form cohesive groups that, from a male's perspective, constitute a resource that can be defended against other males, giving rise to a system of female-defence polygyny (e.g. elephant seals, Mirounga angustirostris Le Beouf 1974; some bats, Saccopteryx bilineata, Peropteryx kappleri Bradbury and Vehrencamp 1977; antelopes, Kobus vardonii, Damaliscus lunatus Balmford et al. 1992).

68 In a few cases, groups of females are defended not by a single male, but by
69 a coalition of two or more males that, through co-operation, can control a resource
70 that would be inaccessible otherwise (Connor et al. 1992; Grinnell et al. 1995;
71 Clutton-Brock et al. 1998). Prides of female lions (Panthera leo), for example, are
72 controlled by coalitions of two to six males that co-operate in defending the groups
73 against intrusions from foreign males (Bygott et al. 1979; Packer and Pusey 1982;
74 Grinnell et al. 1995). In coalitions of lions, one of the males is dominant and
75 obtains a larger number of copulations with the females than the other, secondary
76 males. However, for secondary males it is still advantageous to participate in the
77 coalition because they obtain direct and immediate benefits (some copulations
78 and fatherhood of some young) to which they would not have access by
79 themselves (Grinnell et al. 1995).

80 Co-operative behaviour between males to obtain reproductive benefits can
81 arise even when females do not form permanent groups. Coalitions of bottle-
82 nosed dolphins (Tursiops sp.), for example, sequester receptive females by
83 herding them with co-operative actions, which additionally allow males to control
84 and defend the groups of females from intruders (Connor et al. 1992; Smolker and
85 Pepper 1999). In this species, higher-level alliances have been reported in which
86 members of two or more coalitions co-operate to gain access to a large number of
87 females. Apparently, all participants in coalitions of bottle-nosed dolphins copulate
88 with the sequestered females (Connor et al. 1992), therefore gaining direct and
89 immediate benefits from the alliance.

90 Here we report the case of a mammalian polygynous system in which two
91 males contribute to the defence of a group of females, but apparently only one of
92 them obtains direct and immediate benefits. In the caves of the Yucatan peninsula
93 of Mexico, Jamaican fruit-eating bats (Artibeus jamaicensis) form large colonies of
94 more than 200 individuals. Juveniles, solitary adult males and some adult females
95 roost on the ceiling and walls of the caves, forming loose and unstable groups.
96 Other females roost inside solution cavities that develop on the ceiling of
97 limestone caves, forming cohesive groups (harems) guarded by a single, dominant
98 male that copulates frequently with them (Ortega and Arita 1999). Size of these
99 groups varies from four to 18 females, with a mean of 10 individuals. Large groups
100 (> 14 females) contain a second adult male, called secondary, which does not
101 participate actively in the defence of the harem, but whose presence seemingly
102 reduces the frequency of visits by extraneous males, called satellites, to the
103 solution cavity (Ortega and Arita 2000). Secondary males roost in close contact
104 with the group of females, but no instance of copulation by these males has been
105 documented in more than 2,000 hours of observations in four harem groups
106 (Ortega and Arita 1999; 2000). The polygynous mating system is frequent among
107 tropical bats (Kunz et al. 1983; McCracken and Wilkinson in press). The presence
108 of secondary males has been reported in some species (e.g. Carollia
109 perspicillata—Williams 1986; Desmodus rotundus—DeNault and McFarlane 1995;
110 Phyllostomus hastatus—Kunz et al. 1998; Artibeus jamaicensis—Ortega and Arita
111 1999; 2000), but the role of these males has not been clarified.

133 peninsula is composed of porous limestone that promotes the development of
134 numerous caves and natural wells.

135 The northern part of the peninsula lacks high mountain ranges. The only
136 significant range, the Sierrita de Ticul, is a 100-km chain of low (<200 m) hills
137 punctuated with numerous caves that harbour large populations of bats (Arita
138 1996). On the ceiling of some of these caves, percolating water forms solution
139 cavities, small (<1 m in diameter) holes that constitute ideal roosting sites for
140 several species of bats (Arita 1996). In particular, harem groups of the Jamaican
141 fruit-eating bat in Yucatan roost exclusively inside these solution cavities.

142 We conducted the study in two caves in the vicinity of Tekax, on the Sierrita
143 de Ticul. Bat cave (20° 09' N, 89° 13' W) is a hot cavern harbouring nine species
144 of bats (Arita 1996). Fruit-eating bats roost in the second chamber of this cave,
145 closer to the entrance than the other eight chiropteran species (Ortega and Arita
146 1999). Temperature and humidity in this site are almost constant (29° C, >95%
147 relative humidity), with almost not daily or yearly variation. The chamber contains
148 numerous solution cavities, most of them unoccupied, and a few (10) inhabited by
149 harem groups of fruit-eating bats. Akil cave (20° 14' N, 89° 22' W) is a short cave
150 with a spacious main chamber that contains the solution cavities in which fruit-
151 eating bats roost. This cave is inhabited only by Jamaican fruit-eating bat and
152 sheath-tailed bats (Peropteryx macrotis).

153 General methods

154 The study groups have been observed since 1996. Early that year, a high
155 proportion (> 75%) of the females and all males in the harem groups were marked
156 with three coloured plastic bands attached to the forearm of individuals in such a
157 way that a unique colour code was created for each bat (Ortega and Arita 1999;
158 2000). Experiments, consisting in the removal of one type of individuals (females,
159 dominant males, or secondary males) from the roosting sites and the observation
160 of the behaviour of the remaining bats, were performed in 1997 and 1998. To
161 remove bats, we used a bucket trap (Kunz et al. 1983) to capture most of the
162 individuals roosting in a solution cavity. Experimental individuals were retained by
163 three days during the removals, whereas the rest were released immediately in the
164 same cavity where they had been captured. Experimental individuals were kept in
165 cages (50 cm x 70 cm) in the laboratory, with 12-hour cycles of constant-intensity
166 artificial light provided by a 60-watt conventional bulb. A constantly high humidity
167 was maintained with an electric humidifier, and bats were fed fruit (banana and
168 papaya) and were provided water ad libitum.

169 Experiment 1: Removal of dominant males

170 One conceivable long-term benefit for secondary males of being associated
171 with large harem groups is the possibility of taking over the role of the dominant
172 once this bat disappears from the group. In small groups, in which there are no
173 secondary males, the disappearance of dominant males would open the possibility
174 for satellite males to acquire dominance over a harem. To test these possibilities,

175 we performed a series of experiments in which dominant males were temporarily
176 removed from their groups, and the performance of substituting males was
177 evaluated.

178 The experiments were conducted on 12 harem groups from March to June
179 1997, that is, during the breeding season (Ortega and Arita 1999). Eight of the
180 groups were small harems (<14 females) with no secondary male and four were
181 large harems (>14 females) with secondary and dominant males. In the first round
182 of removals, we randomly selected two of the groups. During three days, we made
183 observations (described below) on the two groups, and then the dominant males
184 were removed. The male from one of the groups was retained in the laboratory for
185 three days, while the other one, serving as a control, was returned to its roosting
186 site after two hours. During the banding procedure in 1996 we had observed that,
187 after disturbance, members of a group took an average of two hours to return to
188 their roosting site and reassume normal activities. Because our capturing method
189 involved the disturbance of the whole group, we retained the control male for two
190 hours until the rest of the members of the harem had returned to the roosting site.

191 Groups were observed from 0900 to 1600 hours for three consecutive days,
192 starting at the moment when the control male was returned to its roosting site. Our
193 pilot observations made in a different cave in 1997 had shown that, after the
194 removal of the dominant male, it took an average of 3.12 days for a different male
195 to acquire full dominance over the harem, staying at least 80% of the time
196 patrolling the group ($SE=0.44$, $n=8$ groups). On the morning of the fourth day, the

197 removed male was returned to its roosting site, and observations were continued
198 for three additional days to document the activity after the reinstatement of the
199 dominant male. Thus, the observational period consisted of nine days: three
200 before the removal of the dominant male, three in the absence of the dominant,
201 and three after its reinstatement. After concluding the observations of the first pair
202 of groups, a second pair was randomly selected and the experimental procedure
203 was repeated. The sequence was iterated until all 12 groups were manipulated.

204 Observations were focused on two aspects: the identity of the male taking
205 over the role of dominant male and the time it took this male to gain full control of
206 the group of females. Focal-animal sampling was used to document the presence
207 or absence of the incoming male as percentages of one—hour observational
208 periods, so we had eight daily periods of observations (from hour 0 to hour 7). A
209 new dominant male was considered to have full control of the group when it stayed
210 at least 80% of one-hour period patrolling the edges of the solution cavity,
211 assuming the normal attitude of a dominant male. After a male had attained full
212 control, we measured its persistence as the number of intervals in which it was
213 present, patrolling the harem group. We tested for temporal changes in the
214 attendance by the new dominant by quantifying its presence in the roosting site in
215 days periods using Cochran's Q -test (Sokal and Rohlf 1981), analysing small (<14
216 females) and large groups separately. We also compared the number of visits
217 performed by satellite males to the harem groups before and during the removal.
218 Experiment 2: Removal of secondary males

219 A dominant male can obtain a benefit from the presence of a secondary
220 male if such presence somehow reduces the frequency or success of intrusions by
221 foreign males. Our second experiment was aimed at quantifying changes in the
222 frequency of visits by foreign males to harems from which the secondary male had
223 been experimentally removed. We also documented changes in the agonistic
224 behaviour of dominants toward intruders in the absence of secondary males.

225 We performed the second experiment one month after the first experiment,
226 simultaneously on the four groups that contained both a dominant and a
227 secondary male. Observations were made three days before the removal of the
228 secondary males, three days in the absence of these bats, and three days after
229 the individuals had been returned to their roosting site. We tallied visits by foreign
230 males and agonistic responses by dominants from 0900 to 1600 every day. An
231 agonistic response consisted in one of the following activities performed by
232 dominant males in response to the presence of a foreign male: wing flicks, short
233 chases, and attempts to bite the visiting male (Ortega and Arita 2000). Aggressive
234 responses by dominant males toward secondary males were also recorded before
235 and after the removal.

236 Experiment 3: Removal of females

237 If the presence of a secondary male in the roosting site allows the dominant
238 to control a larger number of females, and the costs for the dominant are not too
239 high, then it is to the dominant's advantage to tolerate the presence of the
240 subordinate. If the dominant somehow loses that advantage, then it would be

241 predictable that its tolerance toward the secondary male would decrease. In the
242 third experiment, we experimentally reduced the number of females in the groups
243 with two males to document possible changes in the interactions between
244 dominants and secondary males.

245 In the summer of 1998, a year after the previous two experiments, we
246 removed some of the females from the four large groups to reduce the harem size
247 from >15 (original sizes:16, 18, 19, 21 females) to 12 individuals, which is the
248 average number of females in the medium groups in our system (Ortega and Arita
249 2000). Removed females were retained in cages for three days and then released
250 back into their roosting sites. During the experiment, we also observed four control
251 groups containing, under natural conditions, 11, 11, 12, and 12 females. Control
252 groups were disturbed in the same manner as the experimental groups, but
253 without retaining females. Control groups were used to compare the activity in the
254 groups that were experimentally reduced in size to 12 females with that of groups
255 naturally containing that number of females.

256 A pair of groups (one control, one experimental) was observed
257 simultaneously for seven consecutive hours during three days before the
258 experimental manipulation. We tallied the number of visits performed by satellite
259 males and counted the number of one-hour intervals in which dominant and
260 secondary males were present with the harem groups, using the focal--animal
261 sampling method. After performing the experimental manipulation, the same
262 observations were made for three additional days.

284 groups). The difference is statistically significant (Mann-Whitney U -test, $U=43$,
285 $P<0.01$).

286 On day 1 after the removal, former secondary males spent more time
287 defending their harems ($\bar{x} \pm \text{SE} = 4.16 \pm 0.35$ hours, $n=4$ groups) than former
288 satellites ($\bar{x} \pm \text{SE} = 1.00 \pm 0.23$ hours, $n=8$ groups; prueba de t con dos muestras,
289 $t=4.00$, $df=3$, $P<0.05$). Afterwards, former satellites spent increasingly more time
290 with the groups as the experiment progressed, while the time spent by former
291 secondary males remained constant (Fig. 1). The presence of former satellite
292 males within the group was less predictable, as shown by significant differences in
293 one-hour intervals (Cochran's $Q=6.5$, $df=2$, $P<0.05$) than that of former secondary
294 males (Cochran's $Q=2.0$, $df=2$, $P>0.05$).

295 The number of visits by satellite males to the groups during the three-day
296 period before the removal ($\bar{x} \pm \text{SE} = 17.5 \pm 1.75$ visits, $n=12$ groups) was not
297 different from the figure observed during the absence of the dominant male ($\bar{x} \pm \text{SE}$
298 $= 21.0 \pm 1.68$ visits, $n=12$ groups; Wilcoxon paired test, $T=10$, $P>0.05$).

299 In all cases, after being released back, the original dominant males
300 reclaimed their physical position and status in the harem groups. Displaced
301 secondary males returned to their original site in the roost, while displaced
302 satellites reintegrated to the loose groups of bats roosting on the ceiling and walls
303 of the cave. All females remained with their respective harems.

304 Experiment 2: Removal of secondary males

305 The number of visits by foreign males differed among the three
306 observational periods (before the removal, in the absence of the secondary male,
307 and after the return of the secondary male; Friedman's test, $\chi^2=6.0$, $df=2$,
308 $P<0.05$). In the three-day period before the removal of secondary males, the
309 number of visits by foreign males was similar to the normal rate reported by
310 Ortega and Arita (2000; $\bar{x} \pm \text{SE} = 5.75 \pm 0.32$ visits/day, $n=4$ groups). When
311 secondary males were removed, the number of visits increased progressively,
312 reaching its peak on the third day; ($\bar{x} \pm \text{SE} = 14.83 \pm 1.50$; Fig. 2). After secondary
313 males were released back, the rate of visitation by foreign males returned to its
314 normal level ($\bar{x} \pm \text{SE} = 5.67 \pm 1.61$ visits).

315 The number of agonistic displays performed by dominants differed among
316 the three observational periods (Friedman's test, $\chi^2=6.0$, $df=2$, $P<0.05$). In the
317 three-day period before the removal of secondary males, dominant males
318 performed an average of 16.0 aggressive actions/day ($\text{SE}=1.06$, $n=4$ groups),
319 while in the absence of secondary males the average number of aggressions was
320 28.7 ± 0.94 aggressions. After the release of secondary males, the number of
321 aggressions returned to its normal levels ($\bar{x} \pm \text{SE} = 18.5 \pm 0.78$).

322 In the four experimental groups secondary males returned to their original
323 positions two hours after being released back in their roosts. The number of
324 agonistic displays by dominants aimed at secondary males did not change with the
325 experimental manipulations (before the experiment: $\bar{x} \pm \text{SE} = 4.25 \pm 0.47$

326 displays/day; after the experiment: 4.0 ± 1.08 ; $n=4$, Cambiar por t pareada
327 Wilcoxon paired test, $T=10$, $P>0.05$).

328 Experiment 3: Removal of females

329 Secondary males spent a lower percentage of the time with the harems
330 after the experimental reduction in the number of females (before the removal:
331 $\bar{x} \pm SE=88.0\% \pm 4.04$; after the removal: $52.25\% \pm 3.88$; two-tailed paired-sample t
332 test, $t=4.89$, $df=3$, $P<0.02$). The percentage of time spent by dominant males did
333 not change with the removal of females (before the removal: $\bar{x} \pm SE=98.0\% \pm 1.22$;
334 after the removal: $96.25\% \pm 1.75$; two-tailed paired-sample t test, $t=2.78$, $P>0.05$).

335 Under normal conditions, large groups containing >15 females and two
336 males receive significantly fewer visits by foreign males than medium-sized (12
337 females) groups (Ortega & Arita 2000). In the three-day period before the
338 experimental reduction in the number of females, the four experimental groups
339 received the normal number of visits documented in a previous article (Ortega &
340 Arita 2000; 11.21 visits/day ± 2.24 , $n=4$). After the removal of some of the females,
341 visits by foreign males increased progressively, and on the second day after the
342 removal of females the frequency of visits was comparable to the average of visits
343 to the control medium-sized groups (Fig. 3). In fact, our data suggest that during
344 the three days in which the number of females was abnormally low, the
345 experimental groups received a similar number of visits as did the non-
346 experimental medium-sized groups. A Mann-Whitney U-test failed to demonstrate
347 a difference between the experimental and the control groups

348 (experimental: $\bar{x} \pm \text{SE} = 20.67 \text{ visits/day} \pm 4.04$; non-experimental: 18.33 ± 2.4 ;
349 Mann-Whitney U-test, $U=9$, $P>0.05$) but the result has to be taken with reserve,
350 because the number of available large groups (four) constitutes a very small
351 sample size.

352 Our data suggest that the average number of aggressive displays by
353 dominant males against secondary males before the removal ($\bar{x} \pm \text{SE} = 5.75 \pm 1.09$
354 aggressions/day, $n=4$) did not differ after the reduction in the number of females
355 (4.75 ± 0.94 ; Prueba de t pareada Wilcoxon's paired test, $I=6$, $P>0.05$). We never
356 observed agonistic displays by secondary males against dominant males, either
357 before or during the experiment. Eighty percent of females that were returned back
358 to their roosts reincorporated quickly to their harems, while the rest shifted their
359 roosting site for some days, eventually returning to their original groups.

360 DISCUSSION

361 The effects of removals can be summarised as follows. (1) In the absence
362 of dominant males, secondary males occupied the vacant places faster than
363 satellite males. (2) In the same experiments, secondary males showed more
364 fidelity to their groups than satellite males. (3) In the absence of secondary males,
365 the frequency of visits by foreign males to large harems increased. (4) When the
366 number of females was experimentally reduced the rate of visits by foreign males
367 increased. (5) The reduction in the number of females apparently had no effect on
368 the number of agonistic interactions between dominant and secondary males. (6)

369 All removed bats reintegrated quickly to their original groups and recovered their
370 original status when released back to their roosts.

371 An association between a dominant and a secondary male to defend a
372 group of females can evolve only if (1) both males obtain some kind of benefit; (2)
373 for dominant males, the cost of tolerating the presence of secondary males (which
374 constitute potential competitors) is overcome by the benefits gained due to the
375 help provided by secondary males in defending the group of females; and (3) the
376 cost of being a secondary male (and obtaining fewer or no copulation) is
377 overcome by present or future benefits (Alexander 1974; Axelrod and Hamilton
378 1981; Emlen 1982). Our results suggest that both dominant and secondary males
379 associated in harems of the Jamaican fruit-eating bat obtain benefits from the
380 relationship.

381 Costs and benefits for dominant males

382 Dominant males obtain direct and immediate benefits, in the form of access
383 to reproductive females, by defending harems. A potential cost is the expenditure
384 of energy in repelling intrusions by foreign males. The presence of a secondary
385 male in the largest groups deters foreign males from attempting to take over the
386 harems. This effect probably also reduces the behavioural energetic cost in which
387 dominants incur to defend the groups of females.

388 Dominant males of several bat species invest high levels of time and energy
389 in patrolling their harems, because they are constantly alert to movements by
390 foreign individuals, and need to display expensive agonistic responses toward

391 intruders (Morrison 1978; Morrison and Morrison 1981; Williams 1986; Kunz et al.
392 1998). We did not measure directly the energy spent by dominants to defend their
393 groups, but our data suggest that the presence of secondary males reduces the
394 cost of defending harems by lowering the rate of visits by extraneous males and
395 by reducing the number of agonistic responses performed by dominants.

396 Furthermore, our data suggest that the presence of a secondary male
397 allows dominants to defend larger groups than those held by a single male. The
398 results of our second experiment show that the presence of a secondary male
399 reduces the number of visits by satellite males, presumably reducing the energetic
400 cost for dominants to control the harems. Thus, by tolerating the presence of a
401 secondary male, dominants in large groups gain access to a higher number of
402 females, thereby increasing their potential fitness.

403 Costs and benefits for secondary males

404 In harems of the Jamaican fruit-eating bat, secondary males do not perform
405 evident defence activities, so there is no apparent energetic cost of belonging to
406 the groups. However, because secondary males are fully adult individuals (Ortega
407 and Arita 1999), staying with a harem dominated by another male without
408 obtaining copulations might constitute a cost in the form of a delayed reproduction.
409 To be profitable for a secondary male, the association with a dominant has to offer
410 long-term benefits to overcome the costs.

411 Secondary males obtain no obvious immediate benefit from belonging to
412 large groups. The fact that no copulation by a secondary male has been observed

413 in 2000 hours of observations indicates that there is no direct reproductive benefit
414 for these individuals. In most cases of male coalitions, dominants share
415 reproduction with secondary males in order to induce the subordinates to remain
416 with the group (Emlen 1995, Grinnell et al. 1995). Apparently this is not the case
417 with Jamaican fruit-eating bats, as suggested by our observations (Ortega & Arita
418 1999, 2000). However, only a direct measure of reproductive output of both
419 dominant and secondary males, through paternity tests (Hughes 1998) can
420 confirm or reject our field observations.

421 Our data suggest that secondary males may obtain a long-term benefit by
422 having priority access to the position of the dominant once this bat disappears
423 from the roost. A similar situation has been documented for coalitions of male
424 manakins (Chiroxiphia linearis), in which secondary males perform costly displays
425 to attract females, but obtain no immediate reward because the dominant male
426 fathers practically all the young (McDonald and Potts 1994). However, a
427 secondary male obtains a long-term benefit from the association because it readily
428 takes the place of the dominant when this individual disappears. If secondary
429 males are related to dominants, then an additional benefit for secondary males
430 could take the form of an increase in inclusive fitness through a higher
431 reproductive output for the dominant (Emlen 1997; Mesterton-Gibbons and
432 Dugatkin 1999).

433 The relationship between dominant and secondary Jamaican fruit-eating
434 bats can be described as a case of co-operation to retain a large number of

435 females in the harem (Wilkinson 1987). Dominants perform all of the costly
436 defensive responses but apparently obtains most or all of the copulations with the
437 females. The presence of secondary males is correlated with a higher number of
438 females in the harem and reduces the rate of intrusions by foreign males, thereby
439 lowering the energy expenditure by dominants. Secondary males invest little
440 energy in defending the harem but obtain none immediate reproductive benefit.
441 However, they obtain a long-term benefit in the form of priority access to vacant
442 positions of dominance and, probably, in the form of an increased inclusive
443 fitness.

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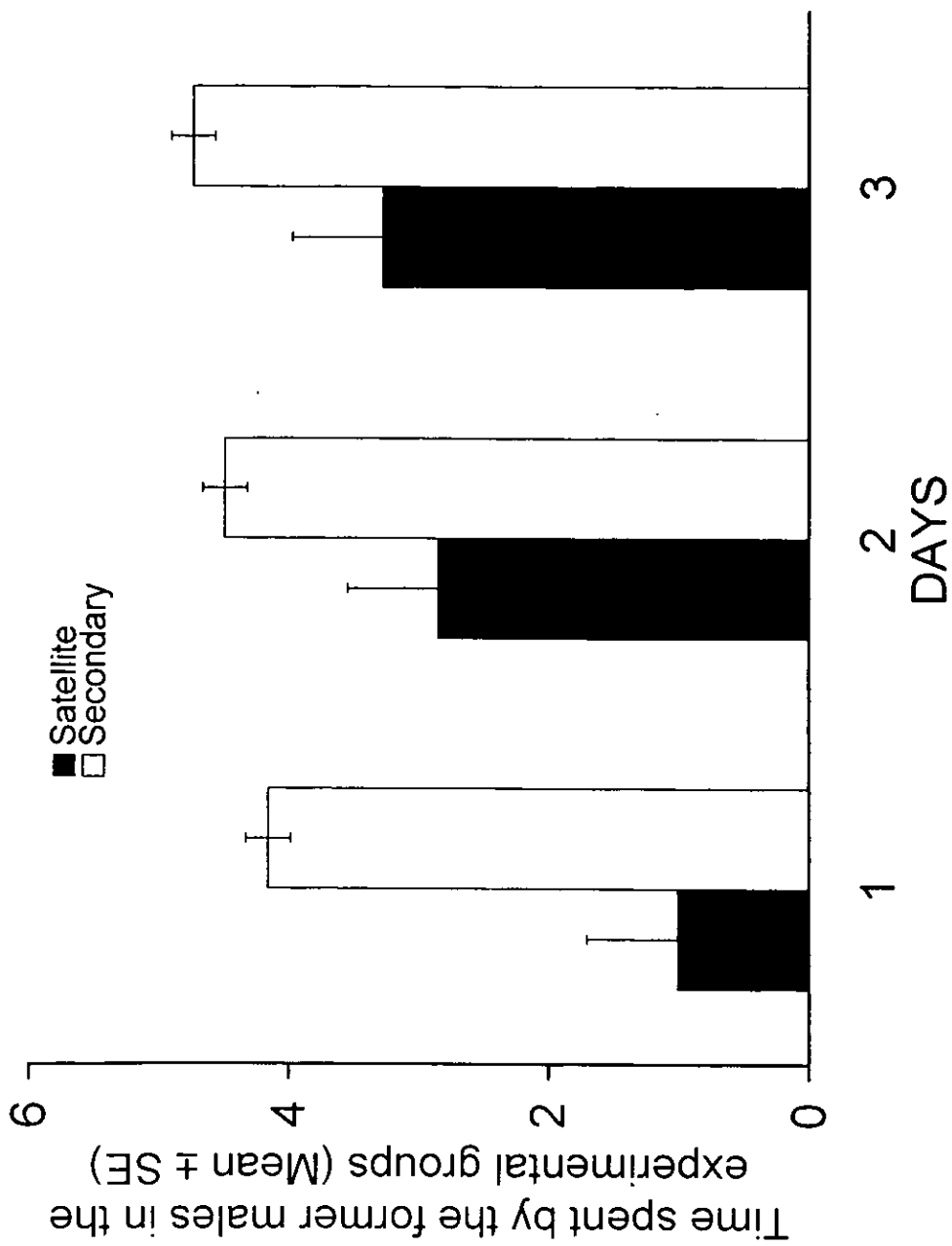
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FIGURE LEGENDS

Figure 1.- Mean (\pm SE) of time spent for substitute males during the removal of 12 resident males. During three days secondary males substituted resident males in the four large groups (> 14 females), fitted there with a great constancy. Satellite males substituted resident males on the 12 medium groups (< 14 females) and spent less time in their new roosting site.

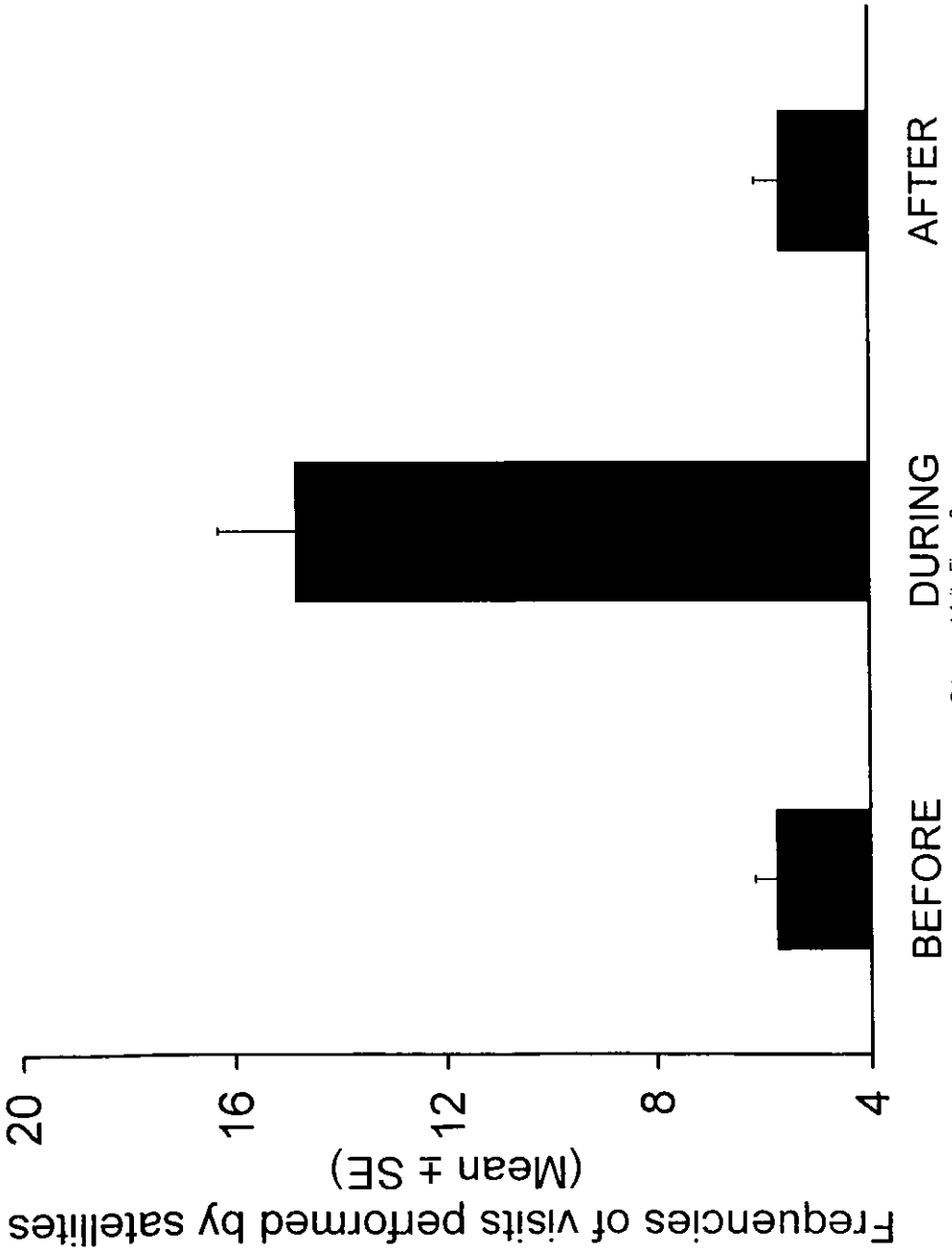
Figure 2.- Frequencies of visits performed by satellite males to the four large groups that contains two associated males (dominant and secondary males). Mean \pm SE is shown in bars for before, during and after the removal of secondary males. Visits were high frequent during the absence of the secondary males than with their presence in the groups.

Figure 3.- Visits by satellite males increased progressively after removal of some females in the experimental groups. Mean \pm SE is shown for three consecutive days after female's removal. Both kinds of groups have similar number of visits at the end of the experiment.

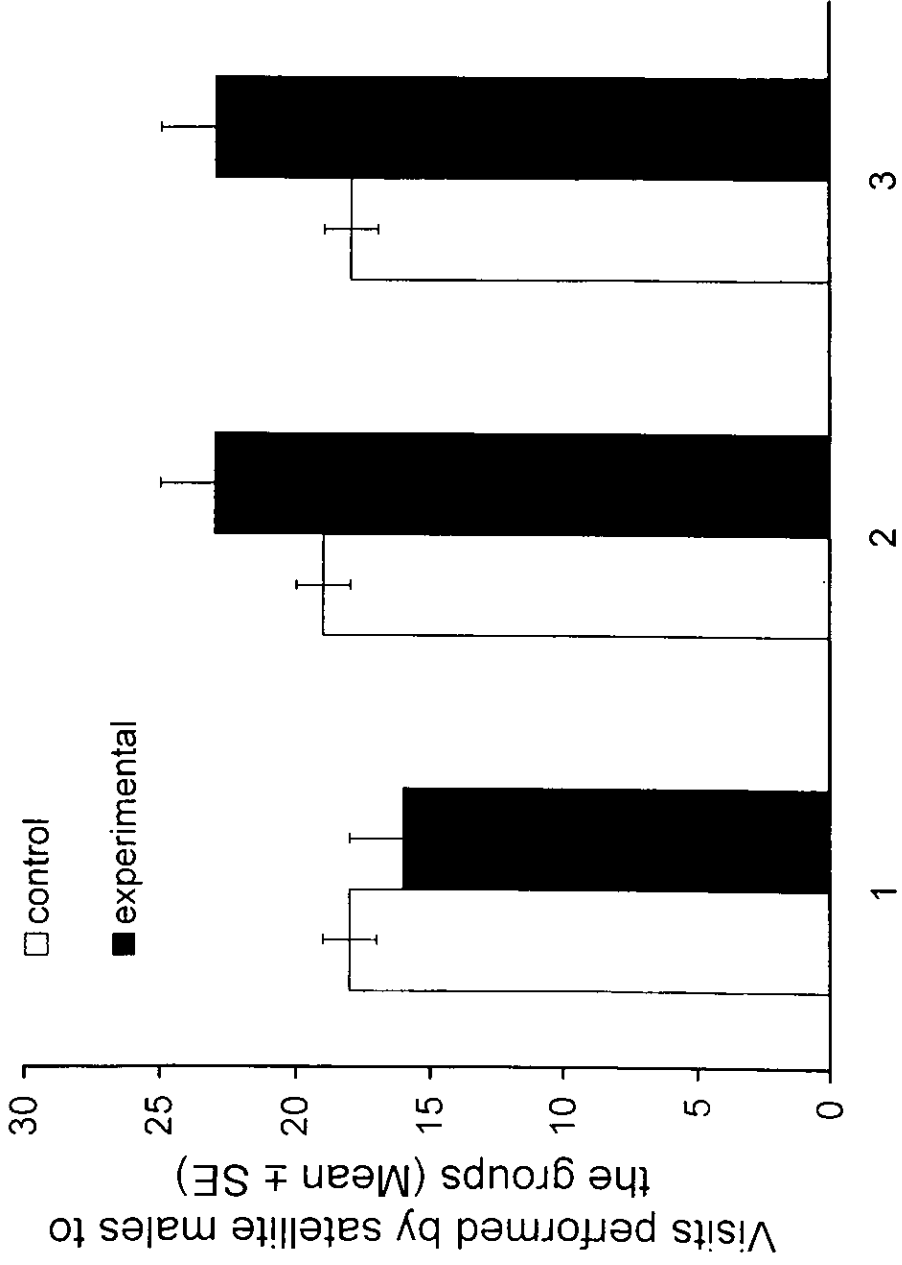


Ortega and Arta Figure 1

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SALIR DE LA BIBLIOTECA



Ortega and Antia Figure 2



DAYS

Ortega and Arifa Figure 3

DISCUSIÓN GENERAL

El presente trabajo aporta información sobre la estructura y dinámica de los grupos de harén, el sistema de defensa que los machos adultos realizan para proteger a las hembras y sobre los beneficios que obtienen los machos adultos en una posible asociación para defender a las hembras de otros machos. El capítulo uno muestra que los grupos están compuestos básicamente por hembras que perchan dentro de las cavidades de disolución, por lo que su forma de agregación facilita que los machos tengan o controlen el acceso directo a ellas, dando como resultado un sistema de apareamiento poligínico. Con base a trabajos anteriores en donde se describe el sistema de apareamiento de *Artibeus jamaicensis* en distintos sitios de percha (Kunz et al., 1983; Momison, 1979), se podría considerar que la especie depende de las características del ambiente físico para presentar un sistema de apareamiento determinado y donde es posible predecir que sistema presentará bajo determinadas circunstancias ambientales, es decir la agrupación de las hembras puede depender de la disponibilidad del sitio de percha, de la variabilidad de las condiciones ambientales que limiten cierto recurso, etc. (Clutton-Brock, 1989). Aunque se tendrían que realizar estudios y experimentos adicionales para examinar el microclima, fisiografía de los sitios de percha, preferencias de las cavidades con respecto al goteo, etc.

La estabilidad de los grupos depende de las tasas de emigración e inmigración de las hembras entre los grupos; situación que rara vez se presenta entre los machos asociados, ya que éstos permanecen por más de dos años en el mismo harén. Se observó que los movimientos de las hembras disminuían durante las épocas reproductivas y aumentaba durante las no reproductivas. Una posible hipótesis del porqué este cambio en los movimientos podría ser que las hembras están restringidas durante la crianza, primero quince días en que las crías no vuelan, pudiéndose presentar actividades de colaboración entre ellas como son: cooperación en la alimentación,

termorregulación de las crías, entre otros. Análisis de paternidad mostrarían si existe entre las hembras relaciones de parentesco, es decir que un vínculo de familiaridad una a las hembras y mantengan la cohesión del grupo. De igual forma se podría especular sobre las hembras que cambian de grupos tienen lazos familiares menos cercanos que con las hembras que forman el núcleo del harén.

Dentro de los grupos pequeños y medianos (entre 5 y 14 hembras) solamente se registró un macho asociado a cada grupo, pero los cuatro grupos grandes (> 14 hembras) incluían dos machos. La presencia de un segundo macho asociado a los grupos grandes de harén es reportada por primera vez para *Artibeus jamaicensis*. La continua permanencia de los machos dominantes en los sitios de percha puede ser explicada por las frecuentes visitas que realizan los machos satélites a los grupos, lo cual requiere de una gran inversión de tiempo y energía por parte de los machos dominantes para evitar éstas intromisiones.

Mis observaciones mostraron que los machos adultos de mayor tamaño y peso son los que se asocian a los grupos de harén, mientras que los de menor tamaño y peso fueron considerados como satélites. Los sitios de percha ocupados y desocupados parecen no tener diferencias significativas en condiciones microclimáticas o fisiográficas, por lo que al parecer el recurso sitio de percha no es relevante para la defensa de los machos. Es posible que la habilidad de controlar el acceso a los grupos de hembras este relacionado con la edad de los machos como ocurre con otros vertebrados (Clutton-Brock, 1988). Es posible que la forma en que opera el sistema dentro de las cuevas consista en que los machos de mayor tamaño tienen acceso directo a las hembras, mientras que los de menor tamaño tengan que recurrir a estrategias alternativas como cópulas forzadas en los sitios de forrajeo, intromisiones furtivas a los grupos de harén, cópulas con las hembras de los grupos difusos. Todas estas suposiciones están supeditadas a observaciones posteriores que complementen las estrategias reproductivas de los

restantes miembros de la colonia. Existe la posibilidad de que exista selección sexual en los grupos, en donde las hembras estén agrupándose alrededor de un macho con mejores características físicas; siendo los machos que no cumplen éstos requisitos, los que no están asociados a los grupos de hembras.

Las actividades conductuales de los machos dominantes fueron similares entre ellos con un patrón definido. Las agresiones consistieron en aleteos, vocalizaciones y mordidas, las cuales ya habían sido reportadas para otras especies de murciélagos (Morrison y Handley, 1991). Los machos satélites fueron los que tuvieron el mayor número de agresiones por parte de los dominantes. Individuos que posiblemente no son considerados como rivales en la obtención de las cópulas de las hembras mostraron una baja tasa de agresiones (e.g. hembras y juveniles). Por otro lado, los machos secundarios de los grupos grandes nunca desplegaron actividades conductuales de defensa, además de que fueron poco agredidos por los machos dominantes. Es posible que los machos secundarios no reciban agresiones dentro de los grupos debido a que su presencia represente una ventaja para el macho dominante o bien que sean los secundarios los que obtienen la mayor cantidad de cópulas con la y que el denominado dominante sea en realidad el subalterno en el sistema. Un análisis de paternidad podría dilucidar cual es el verdadero macho dominante en el sistema y que tipo de recompensa en éxito reproductivo están obteniendo ambos machos dentro de los grupos de harén.

Los machos dominantes fueron extremadamente activos en la defensa durante la época reproductiva, siendo más tolerantes a la intromisión de los satélites durante la época no reproductiva. En el sistema estudiado, es posible que el aumento de interacciones esté relacionado con la protección del recurso hembras receptivas obstruyendo de ésta manera a los competidores potenciales y obteniendo con ello un éxito reproductivo mayor que el de los machos que no acaparan hembras (Emlen y Oring, 1977). Esta última hipótesis necesita ser probada mediante análisis de ADN realizados a

las crías de un mismo harén, para con ello dilucidar si la defensa activa del macho dominante esta dando como resultado la obtención de la paternidad de las crías (Emlen, 1995). De igual forma se podría analizar si la paternidad es compartida entre los dos machos asociados a los grandes grupos, es decir posiblemente exista un costo genético que tenga que compartir el macho dominante con el macho secundario para mantenerlo en el sitio y que sirva en la defensa de las hembras. Finalmente existe la posibilidad de que los machos asociados tengan una relación de parentesco por lo que el compartir la paternidad de las crías tendría beneficios genéticos para ambos.

Dentro del primer experimento del tercer capítulo (remoción de los machos dominantes), se esperaba que su sitio fuera ocupado rápidamente por otro macho adulto debido a que las agrupaciones de tipo harén se presta a ser fácilmente monopolizado. En los grupos grandes se esperaba que los machos secundarios ocuparan el lugar vacante debido a que son miembros habituales del sitio de percha, en cambio se esperaba que en los grupos medianos fueran los satélites los que ocuparan el lugar porque no había ningún otro macho asociado al sitio. Existe la posibilidad de que debido a que los machos secundarios son más pesados que los machos satélites, éstos nunca intentaron desplazar a los secundarios. De esta forma se podría plantear la posibilidad de que por el tamaño los satélites estén en desventaja de ocupar los grupos grandes y de allí que no se observó este tipo de sustitución. De igual forma, se podría considerar que los machos secundarios al ser individuos aceptados dentro del grupo estén habituados al sitio de percha, esta es una ventaja que les permite ocupar el lugar vacante en forma inmediata (Emlen, 1982). Un posible experimento podría ser la remoción de los individuos secundarios recién integrados a los grupos grandes y comparar su fidelidad con satélites en un experimento similar.

El número de visitas realizadas por los satélites a los grupos varió de acuerdo con el tamaño de los mismos. Se esperaba que en donde existiera una mayor cantidad de

hembras receptivas se observaría la mayor cantidad de visitas. Sin embargo, los datos descriptivos mostraron que en los grupos donde se presentó un segundo macho asociado este hecho no ocurre. Con base en ésta predicción de que los grupos grandes reciben menos visitas debido a la presencia del segundo macho, en el segundo experimento se removió a los machos secundarios y se observó que los satélites incrementaban su número de visitas a los grupos aumentando con ello las respuestas agonísticas de los dominantes hacia los intrusos. La posible implicación pudiera ser que la presencia de los machos secundarios disminuya la tasa de visita de los intrusos y resultara en un ahorro en el gasto energético en la defensa de las hembras para los machos dominantes (Kunz et al., 1998). De igual forma se podría suponer que ambos machos están emparentados y que consiguen ventajas familiares al momento de asociarse y defender grupos de hembras grandes. Aunque en esta trabajo no se determinó el mecanismo que influye en la permanencia de los dos machos asociados (altruismo, cooperación, coalición, etc.), si se probó que la ausencia de cualquiera de los machos asociados afecta la actividad de la macho que permanecía en el grupo.

Durante el tercer experimento se encontró que al remover a las hembras hasta reducir los grupos a un tamaño similar a los de tamaño mediano, los secundarios abandonaron el sitio por espacios de tiempo más largos. En este caso se esperaba que el considerable número de hembras en los grandes grupos determinara la presencia de los machos asociados. Es posible que al aumentar el número de hembras en los grupos de harén (> 20 hembras que fue el máximo observado), se incrementara el número de machos asociados. La hipótesis de porqué el macho secundario abandona el sitio de percha puede estar ligada al hecho de que al reducir el número de hembras se reduzcan algunas de las ventajas para ambos machos (e.g. éxito reproductivo), por lo que el secundario abandona el sitio y busca una estrategia reproductiva alterna a la que tenían en el grupo grande. Este postulado no fue probado, pero se podría estudiar en

experimentos similares a largo plazo, además de considerar la paternidad de las crías del secundario cuando cambia su estrategia reproductiva.

Las observaciones descriptivas del sistema muestran que los individuos tenían por lo menos dos años de tener el mismo estatus, el cual conservaron al momento de reintegrarlos al grupo. El factor tiempo de permanencia en un sitio (familiaridad con el lugar) es importante en la conservación del estatus, por lo que considero que el tiempo de remoción de los individuos provoca cambios temporales en la jerarquía de los machos, pero esta se restituye al reintegrarlos a los tres días.

Considero que es necesario estudiar los procesos evolutivos que están influyendo en el sistema de apareamiento del murciélago zapotero en Yucatán. Es factible que los procesos de selección familiar estén influyendo en la estructura de los grupos, así como en la aceptación de un segundo macho en los grandes grupos. Es imprescindible incluir herramientas genéticas que permitan comprender el éxito reproductivo de ambos machos en los grupos grandes, así como las relaciones de parentesco entre los diversos miembros de un harén. De igual forma entender que mecanismos conllevan a que los murciélagos presenten diferentes estrategias reproductivas dentro del sistema y como les reditúan en cuestión de éxito reproductivo a cada uno de ellos.

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