

Instituto de Ecología, Universidad Nacional Autónoma de México

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

Jorge Ortega & Héctor T. Arita

Ortega, J. & Arita, H. T. 2000: Defence of females by dominant males of *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Ethology* **106**, 395–407.

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.

Corresponding author: Jorge Ortega, Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70 275, 04510, México, Distrito Federal, México. E-mail: jortega@miranda.ecologia.unam.mx

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 post-partum 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

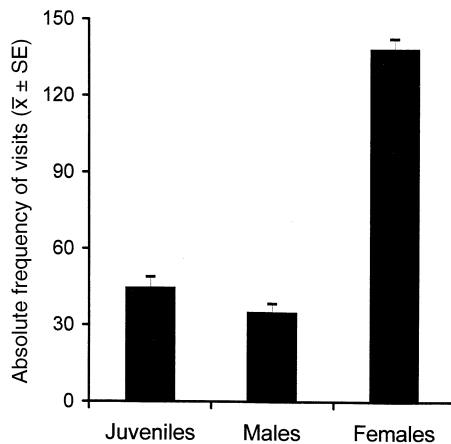


Fig. 1: Absolute frequencies of visits analysed by sex and age of the visitors during the entire study. Females made more visits to the harem groups than juveniles and males. Values shown are $\bar{x} \pm \text{SE}$

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

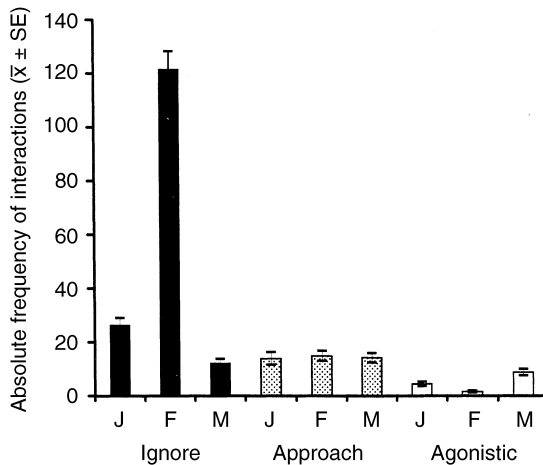


Fig. 2: Absolute frequencies of responses by dominant males. Adult females (F) were ignored more often and assaulted less often than adult males (M), with responses to juveniles (J) being intermediate. The frequency of the approach response was similar for females, males and juveniles. Values shown are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

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

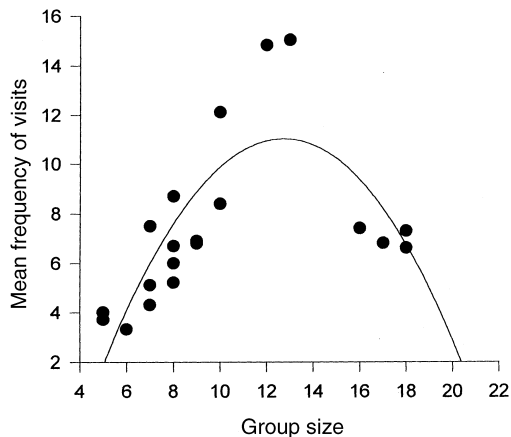


Fig. 3: Mean frequencies of visits by adult males to harem groups of different sizes (quadratic model: $y = -5.60 + 4.3080x - 0.17x^2$, $r^2 = 0.628$, $p < 0.05$). Medium-sized harem groups were more frequently visited than small or large harem groups

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).

Acknowledgements

We are grateful to H. Drummond, L. Eguiarte, and J. L. Osorno for their comments to the text. J. Brockmann, T. H. Fleming, C. Iudica and one anonymous reviewer made useful suggestions and comments on the manuscript. The study was supported by a grant from the Dirección General de Asuntos del Personal Académico (DGAPA, project number IN 208495) of the Universidad Nacional Autónoma de México (UNAM). JO received financial support from the Consejo Nacional de Ciencia y Tecnología (CONACyT 93710). Field assistance was provided by R. Avila, R. Cerritos, F. Colchero, J. J. Flores, G. Guerrero, X. López, M. Santos, G. Steers, G. Súzan, G. Tellez, E. Tobón, and H. Zarza.

Literature Cited

- Alexander, R. D. 1974: The evolution of social behavior. *Ann. Rev. Ecol. Syst.* **5**, 325—383.
- Arita, H. T. 1996: The conservation of cave roosting bats in Yucatan. *Mexico Biol. Conserv.* **76**, 177—185.
- Arita, H. T. & Vargas, J. A. 1995: Natural history, interspecific associations, and incidence of the cave bats of Yucatan. *Mexico Southwest. Naturalist* **40**, 29—37.
- Balasingh, J., Koilraj, J. & Kunz, T. H. 1995: Tent construction by the short-nosed fruit bat *Cynopterus sphinx* (Chiroptera: Pteropodidae) in southern India. *Ethology* **100**, 210—229.
- Bradbury, J. W. 1977: Social organization and communication. In: *Biology of Bats*, Vol. III (Wimsatt, W. A., ed.). Academic Press, New York, pp. 1—72.
- Bradbury, J. W. & Emmons, L. 1974: Social organization of some Trinidad bats. I. Emballonuridae. *Z. Tierpsychologie* **36**, 137—183.
- Bradbury, J. W. & Vehrencamp, S. L. 1977: Social organization and foraging in emballonurid bats. III. Mating systems. *Behav. Ecol. Sociobiol.* **1**, 1—17.
- Brooke, A. P. 1987: Tent selection, roosting ecology and social organization of the tent-making bat, *Ectophylla alba* in Costa Rica. *J. Zool. (London)* **221**, 11—19.
- Brooke, A. P. 1997: Social organization and foraging behaviour of the fishing bat, *Noctilio leporinus* (Chiroptera: Noctilionidae). *Ethology* **103**, 421—436.
- Bulger, J. B. 1993: Dominance rank and access to estrous females in male savanna baboons. *Behaviour* **127**, 67—103.
- Bygott, J. D., Bertram, B. C. R. & Hanby, J. P. 1979: Male lions in large coalitions gain reproductive advantages. *Nature* **282**, 839—841.
- Caro, T. M. & Collins, D. A. 1987: Male cheetah social organization and territoriality. *Ethology* **74**, 52—64.
- Dwyer, P. D. 1970: Social organization of the bat *Myotis adversus*. *Science* **168**, 1006—1008.
- Eisenberg, J. F. 1981: *The Mammalian Radiations, an Analysis of Trends in Evolution. Adaptations and Behavior.* The Univ. of Chicago Press, Chicago.
- Emlen, S. T. & Oring, L. W. 1977: Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215—223.
- Fleming, T. H. 1971: *Artibeus jamaicensis*: delayed embryonic development in a Neotropical bat. *Science* **171**, 402—404.
- Fleming, T. H. 1988: *The Short-Tailed Fruit Bat.* Univ. of Chicago Press, Chicago.
- Foster, M. S. & Timm, R. M. 1976: Tent-making by *Artibeus jamaicensis* (Chiroptera: Phyllostomidae) with comments on plants used by bats for tents. *Biotropica* **8**, 265—269.
- Herrera, E. A. & Macdonald, D. W. 1993: Aggression, dominance, and mating success among capybara males (*Hydrochoerus hydrochaeris*). *Behav. Ecol.* **4**, 114—119.
- Kunz, T. H. 1982: Roosting ecology of bats. In: *Ecology of Bats* (Kunz, T. H., ed.). Plenum Publ. Corp., New York, pp. 1—56.
- Kunz, T. H. 1996: Methods for marking bats. In: *Measuring and Monitoring Biological Diversity. Standard Methods for Mammals* (Wilson, D. E., Cole, F. R., Nichols, J. D., Rudran, R. & Foster, M. S., eds). Smithsonian Institution Press, Washington, pp. 304—310.
- Kunz, T. H. & McCracken, G. F. 1995: Tents and harems: apparent defense of foliage roost by tent-making bats. *J. Trop. Ecol.* **11**, 1—17.

- Kunz, T. H., August, P. V. & Burnett, C. D. 1983: Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica* **15**, 133—138.
- Kunz, T. H., Fujita, M. S., Brooke, A. P. & McCracken, G. F. 1994: Convergence in tent architecture and tent-making behavior among Neotropical and Paleotropical bats. *J. Mammal. Evol.* **2**, 57—78.
- Kunz, T. H., Thomas, D. W., Richards, G. C., Tidemann, C. R., Pierson, E. D. & Racey, P. A. 1996: Observational techniques for bats. In: *Measuring and Monitoring Biological Diversity* (Wilson, D. E., Cole, F. R., Nichols, J. D., Rudran, R. & Foster, M. S., eds). Smithsonian Institution Press, Washington, pp. 105—114.
- Kunz, T. H., Robson, S. K. & Nagy, K. A. 1998: Economics of harem maintenance in the greater spear-nosed bat, *Phyllostomus hastatus*. *J. Mammal.* **79**, 631—642.
- Lewis, S. E. 1996: Low roost-site fidelity in pallid bats: associated factors and effect on group stability. *Behav. Ecol. Sociobiol.* **39**, 335—344.
- McCracken, G. F. & Bradbury, J. W. 1977: Paternity and genetic heterogeneity in the polygynous bat, *Phyllostomus hastatus*. *Science* **198**, 303—306.
- McCracken, G. F. & Bradbury, J. W. 1981: Social organization and kinship in the polygynous bat, *Phyllostomus hastatus*. *Behav. Ecol. Sociobiol.* **8**, 11—34.
- McWilliam, A. N. 1990: Mating system of the bat *Miniopterus minor* (Chiroptera: Vespertilionidae) in Kenya, East Africa: a Lek? *Ethology* **85**, 302—312.
- Morrison, D. W. 1978: Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* **59**, 716—723.
- Morrison, D. W. 1979: Apparent male defense of tree hollows in the fruit bat, *Artibeus jamaicensis*. *J. Mammal.* **60**, 11—15.
- Morrison, D. W. 1980: Foraging and day-roosting dynamics of canopy fruit bats in Panama. *J. Mammal.* **61**, 20—29.
- Morrison, D. W. & Handley, C. O. Jr 1991: Roosting behavior. In: *Demography and Natural History of the Common Fruit Bat, Artibeus jamaicensis*, on Barro Colorado Island, Panama (Handley, C. O. Jr, Wilson, D. E. & Gardner, A. L., eds). Smithsonian Contrib. Zool., Washington, pp. 131—163.
- Morrison, D. W. & Morrison, S. H. 1981: Economics of harem maintenance by a Neotropical bat. *Ecology* **62**, 864—866.
- Noë, R. & Sluijter, A. A. 1990: Reproductive tactics of male savanna baboons. *Behaviour* **113**, 117—169.
- Orians, G. H. 1969: On the evolution of mating systems in birds and mammals. *Am. Nat.* **103**, 589—603.
- Ortega, J. & Arita, H. T. 1999: Structure and social dynamics of harem groups in *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *J. Mammal.* **80**, 1173—1185.
- O'Shea, T. J. 1980: Roosting social organization and the annual cycle of a Kenya population of the bat *Pipistrellus nanus*. *Z. Tierpsychologie* **53**, 171—195.
- Ostfeld, R. S. 1987: On the distinction between female defense and resource defense polygyny. *Oikos* **48**, 238—240.
- Park, S. R. 1991: Development of social structure in a captive colony of the common vampire, *Desmodus rotundus*. *Ethology* **89**, 335—341.
- Porter, F. L. 1978: Roosting patterns and social behavior in captive *Carollia perspicillata*. *J. Mammal.* **59**, 627—630.
- Porter, F. L. 1979: Social behavior in the leaf-nosed bat, *Carollia perspicillata*. I. Social Organization. *Z. Tierpsychologie* **49**, 406—417.
- Porter, F. L. & McCracken, G. F. 1983: Social behavior and allozyme variation in a captive colony of *Carollia perspicillata*. *J. Mammal.* **64**, 295—298.
- Racey, P. A. 1988: Reproductive assessment in bats. In: *Ecological and Behavioral Methods for the Study of Bats* (Kunz, T. H., ed.). Smithsonian Institution Press, Washington, pp. 31—46.
- Ralls, K. 1977: Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* **111**, 917—938.
- Sokal, R. R. & Rohlf, F. J. 1981: *Biometry: the Principles and Practice of Statistics in Biological Research*. W. H. Freeman Press, San Francisco.
- Storz, J. F., Balashing, J., Thiruchenthil, N. P., Emmanuel, K. & Kunz, T. H. 2000a: Dispersion and

- site fidelity in a tent-roosting population of the short-nosed fruit bat (*Cynopterus sphinx*) in southern India. *J. Trop. Ecol.* **16**, 1—15.
- Storz, J. F., Bhat, H. R. & Kunz, T. H. 2000b: Social structure of a polygynous tent-making bat, *Cynopterus sphinx* (Megachiroptera). *J. Zool. (London)*, in press.
- Vehrencamp, S. L., Stiles, F. G. & Bradbury, J. W. 1977: Observations on the foraging behavior and avian prey of the Neotropical carnivorous bat *Vampyrum spectrum*. *J. Mammal.* **58**, 469—478.
- Waser, P. M., Keane, B., Creel, S. R., Elliot, L. F. & Minchella, D. J. 1994: Possible male coalition in a solitary mongoose. *Anim. Behav.* **47**, 289—294.
- Wilkinson, G. S. 1985: The social organization of the common vampire bat. II. Mating system, genetics, structure and relatedness. *Behav. Ecol. Sociobiol.* **17**, 123—134.
- Wilkinson, G. S. 1987: Altruism and co-operation in bats. In: *Recent Advances in the Study of Bats* (Fenton, M. B., Racey, P. A. & Rayner, J. M. V., eds). Cambridge Univ. Press, Cambridge, pp. 299—323.
- Williams, C. F. 1986: Social organization of the bat *Carollia perspicillata* (Chiroptera: Phyllostomidae). *Ethology* **71**, 265—282.

Received: June 7, 1999

Initial acceptance: September 15, 1999

Final acceptance: November 15, 1999 (J. Brockmann)