

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 solitarily 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 ($20^{\circ}14'N$, $89^{\circ}22'W$) and Murciélagos ($20^{\circ}09'N$, $89^{\circ}13'W$) 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 ($27.4^{\circ}C$) 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. Turnover 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-

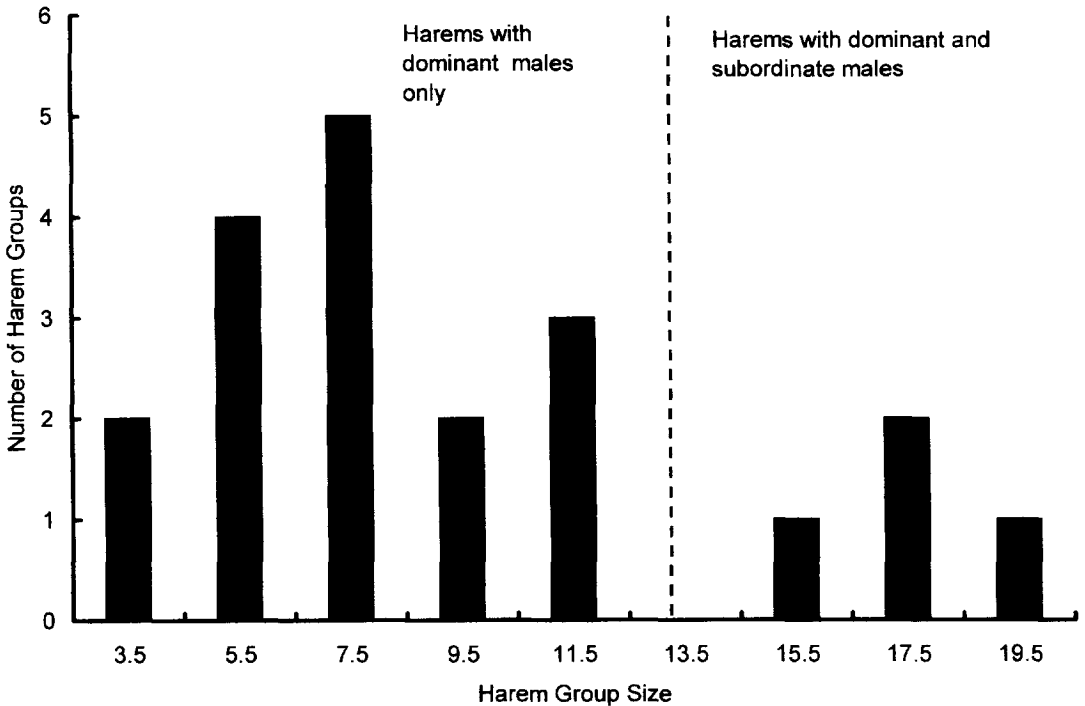


FIG. 1.—Frequency distribution of the number of female Jamaican fruit-eating bats associated with harem groups. Numbers show the 24-month means for 20 harems in two caves of Yucatán, Mexico. Small groups (with ≤ 12 females) included a single dominant male; larger groups (with ≥ 15 females) included one 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 \pm 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, $t = 0.68$, $df. = 19$, $P = 0.5$) 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-

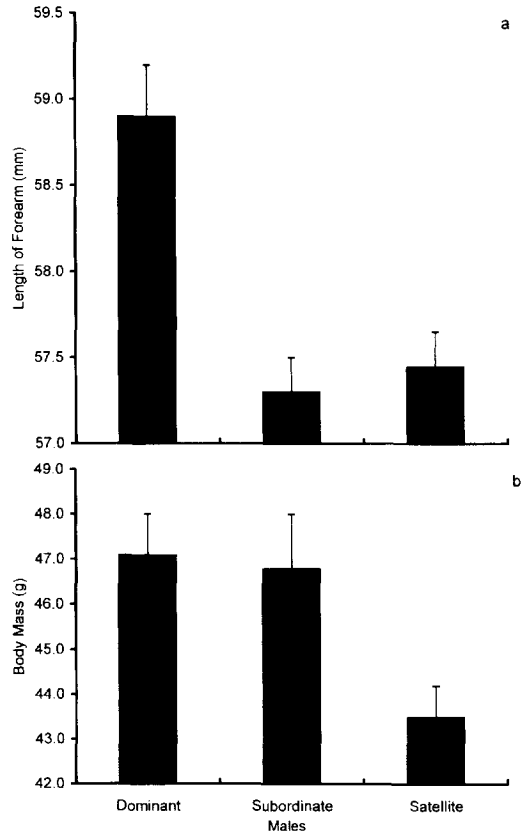


FIG. 2.—Comparison of a) length of forearm and b) body mass among dominant, subordinate, and satellite male Jamaican fruit-eating bats in two caves of Yucatán, Mexico. Dominants consistently had longer forearms and were heavier than individuals of the other two categories.

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 males 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%

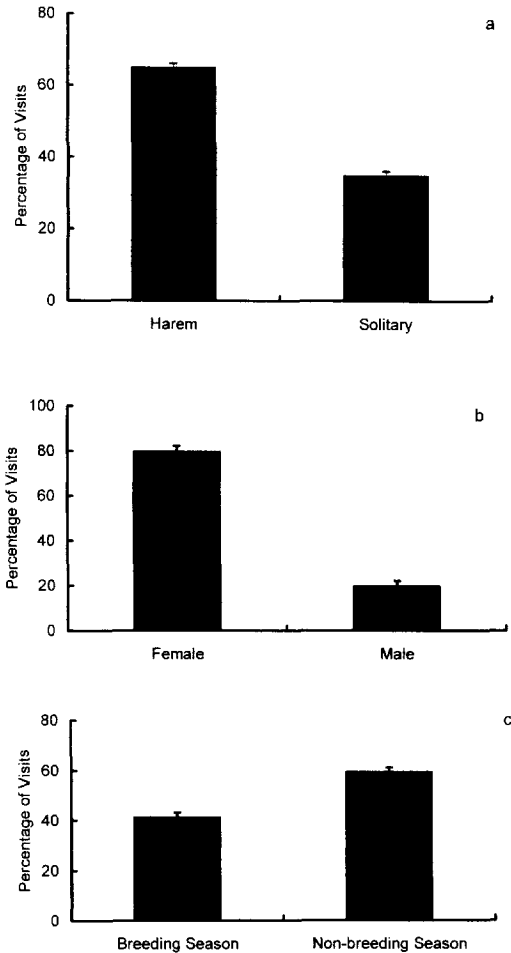


FIG. 3.—Comparison of the number of visits by Jamaican fruit-eating bats to harem groups performed by solitary bats and individuals belonging to a) another harem, b) females and males, and c) during the breeding and non-breeding seasons. Bars represent standard errors.

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).

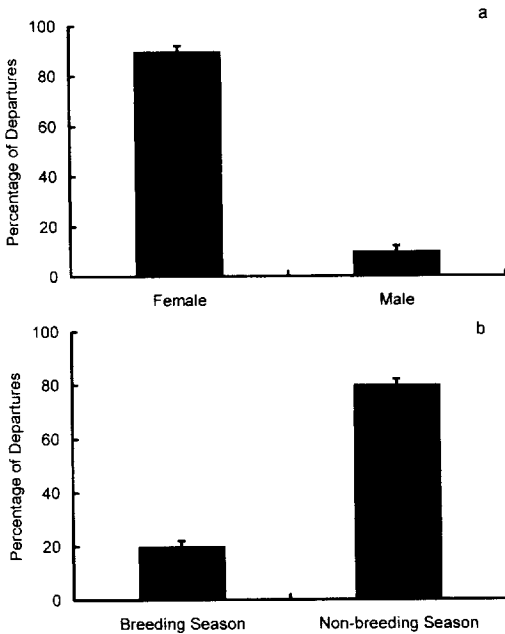


FIG. 4.—Comparison of the number of departures by Jamaican fruit-eating bats from harem groups formed by a) adult male and female bats, and b) during the breeding and non-breeding seasons. Bars represent standard errors.

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 times (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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