

## **Subordinate Males in Harem Groups of Jamaican Fruit-Eating Bats (*Artibeus jamaicensis*): Satellites or Sneaks?**

Jorge Ortega & Héctor T. Arita

*Instituto de Ecología, Universidad Nacional Autónoma de México, Mexico*

### **Abstract**

In the caves of Yucatan, Mexico, the Jamaican fruit-eating bat, *Artibeus jamaicensis*, forms harems consisting of four to 18 females and a dominant male that defends the group against foreign males. Large groups (> 14 females) contain an additional subordinate male. In theory, subordinate males can associate with harem groups either as satellites, if they provide at least some benefits to the dominant male, or as sneaks, if they only impose costs on the dominant male. We assessed the costs and benefits of subordinate males in three removal experiments. In the first experiment, when a dominant male was removed from its group, its role was occupied by the subordinate male (in large groups) or by a foreign male (in small groups). Former subordinate males took less time to gain control of the harems and stayed longer with the groups than foreign males. In the second experiment, when a subordinate male was removed, the rate of visitation by foreign males and the number of agonistic displays by the dominant male both increased. In the third experiment, when the number of females in large groups was reduced, subordinate males spent less time with their groups and the rate of visitation by foreign males increased. However, the frequency of agonistic displays by dominant males towards subordinate males did not change. Dominant males invest large amounts of energy in defending the harems, but obtain direct and immediate benefits from the presence of subordinate males in the form of access to a larger number of females, and suffer no obvious costs. Subordinate males apparently invest little energy in defending the harems, obtain no obvious immediate benefit, but gain long-term benefits by having priority access to vacant positions left by dominant males. Subordinate males in harem groups of the Jamaican fruit-eating bat can be considered satellites because their presence brings immediate benefits to the dominant males.

Corresponding author: Héctor T. Arita, Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510, México, Distrito Federal, Mexico. E-mail: arita@miranda.ecologia.unam.mx

### Introduction

Most mammals are polygynous (Greenwood 1980; Clutton-Brock 1989; Davies and Houston 1991). Because of pregnancy and lactation, the bulk of the cost of rearing and feeding the young is on females; so, in general, mammalian males are not 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; Ostfeld 1987). Although exceptions exist (Jennions and MacDonald 1994), males of most mammalian species maximize their fitness by fathering several young with many females, rather than investing time and energy in the rearing of a few young (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 aggregate 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 Boeuf 1974; some bats, *Saccopteryx bilineata*, *Peropteryx kappleri* – Bradbury and Vehrencamp 1977; Voigt et al. 2001; antelopes, *Kobus vardonii*, *Damaliscus lunatus* – Balmford et al. 1992).

In some systems, one or more males may gain access to another male's territory or group of defended females. Sometimes the intruders invade the territory of a dominant male or secure access to its resources by sneaking, and thus impose costs on the dominant male without producing any benefit (Davies and Houston 1984). In other cases, the dominant male tolerates the presence of other males within its territory or close to its defended resources because the subordinate males bring benefits that compensate for their costs. In these cases, subordinates are called 'satellites' to distinguish them from 'sneakers' (Davies and Houston 1984).

In a few cases, groups of females are defended not by a single male, but by a coalition of two or more males that, through co-operation, can control a resource that would otherwise be inaccessible (Connor et al. 1992; Grinnell et al. 1995; Clutton-Brock et al. 1998). Prides of female lions (*P. leo*), for example, are controlled by coalitions of two to six males that associate to defend females against intrusions by foreign males (Bygott et al. 1979; Packer and Pusey 1982; Grinnell et al. 1995). In coalitions of lions, one of the males is dominant and obtains a larger number of copulations than the subordinates. However, it is still advantageous for subordinate males to participate in the coalition because they obtain direct and immediate benefits (some copulations and a share of the paternity of young) that they could not obtain as solitary males (Grinnell et al. 1995).

Co-operative behaviour between males to obtain reproductive benefits can arise even when females do not form permanent groups. Coalitions of

bottle-nosed dolphins (*Tursiops* sp.), for example, sequester receptive females by herding them with co-operative actions, which additionally allow males to control and defend the groups of females from intruders (Connor et al. 1992; Smolker and Pepper 1999). In this species, higher-level alliances have been reported in which members of two or more coalitions co-operate to gain access to a large number of females. Apparently, all participants in coalitions of bottle-nosed dolphins copulate with the sequestered females (Connor et al. 1992), thus gaining direct and immediate benefits from the alliance.

Here we report the case of a mammalian polygynous system in which females are defended by a dominant male, which in some cases tolerates the presence of a second, subordinate male. In the caves of the Yucatan peninsula of Mexico, Jamaican fruit-eating bats (*Artibeus jamaicensis*) form large colonies of more than 200 individuals. Juveniles, solitary adult males and some adult females roost on the ceiling and walls of the caves, forming loose and unstable groups. Other females roost inside solution cavities that develop on the ceiling of limestone caves, forming cohesive groups (harems) guarded by a dominant male that copulates with them frequently (Ortega and Arita 1999). The size of these groups varies from four to 18 females, with a mean of 10 individuals. Large groups (> 14 females) contain a second adult male, called a subordinate, that does not participate actively in the defence of the harem, but whose presence seemingly reduces the frequency of visits by unfamiliar males, called foreigners, to the solution cavity (Ortega and Arita 2000). Subordinate males roost in close contact with the group of females (Ortega and Arita 1999, 2000). A polygynous mating system is common among tropical bats (Kunz et al. 1983; McCracken and Wilkinson 2000), and the presence of subordinate males has been reported in some species (e.g. *Carollia perspicillata*, Williams 1986; *Desmodus rotundus*, Denault and McFarlane 1995; *Phyllostomus hastatus*, Kunz et al. 1998; *A. jamaicensis*, Ortega and Arita 1999, 2000), but the role of these males has not been clarified.

Here we report the results of a series of experiments designed to define the role of subordinate males of the Jamaican fruit-eating bat by documenting benefits and costs for dominant and subordinate males associated in harem groups. Specifically, we tested three hypotheses. (1) Subordinate males roost with the large groups, even at the cost of delaying their own reproduction, because they expect a future but predictable benefit. (2) The presence of subordinate males inhibits visits by intruders, thereby providing a benefit to dominant males. (3) Groups containing more than 14 females are too large to be defended by a single male.

## Methods

### Study Site

The Yucatan peninsula of eastern Mexico is a limestone shelf projecting northward from Central America and lying between the Gulf of Mexico on the

west and north, and the Caribbean Sea on the east. In the north-western part of the peninsula, corresponding to the Mexican State of Yucatan, the climate is hot (mean annual temperature 25.9°C) and dry (mean annual rainfall 949 mm), with a definite dry season extending from Nov. to May. The original vegetation (tropical dry forest) has been replaced in most parts by agricultural and cattle pastures, leaving only isolated patches of secondary forest. The entire peninsula is composed of porous limestone karst that promotes the development of numerous caves and natural wells.

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

We conducted the study in two caves in the vicinity of Tekax, on the Sierrita de Ticul. Murciélagos cave (20°09'N, 89°13'W) is a hot cavern harbouring nine species of bats (Arita 1996). Fruit-eating bats roost in the second chamber of this cave, closer to the entrance than the other eight chiropteran species (Ortega and Arita 1999). Temperature and humidity in this site are constant (29°C, > 95% relative humidity), with almost no daily or yearly variation. The chamber contains numerous solution cavities, most of them unoccupied, and a few (10) inhabited by harem groups of fruit-eating bats. Akil cave (20°14'N, 89°22'W) is a short cave with a spacious main chamber that contains the solution cavities in which fruit-eating bats roost. This cave is inhabited only by Jamaican fruit-eating bats and sheath-tailed bats (*P. macrotis*).

### General Methods

The study groups have been observed since 1996. Early that year, a high proportion (> 75%) of the females and all males in the harem groups were marked with three coloured plastic bands attached to the forearm of individuals in such a way that a unique colour code was created for each bat (Ortega and Arita 1999, 2000). Experiments, involving the removal of one type of individual (females, dominant males, or subordinate males) from the roosting sites and the observation of the behaviour of the remaining bats, were performed in 1997 and 1998. To remove bats, we used a bucket trap (Kunz et al. 1983) to capture most of the individuals roosting in a solution cavity. Experimental individuals were detained for 3 d following the removals, whereas the others were released immediately in the same cavity where they had been captured. Experimental individuals were maintained in cages (50 × 70 cm) in the laboratory, with 12-h cycles of constant-intensity artificial light provided by a 60-W conventional bulb. Constant high humidity was maintained with an electric humidifier, and bats were fed fruit (banana and papaya) and provided with water ad libitum.

**Experiment 1: Removal of Dominant Males**

One conceivable benefit to subordinate males of associating with large harem groups is the possibility of taking over the role of the dominant male once this bat disappears from the group (Kunz et al. 1998). In small groups, in which there are no subordinate males, the disappearance of dominant males would afford foreign males the possibility to acquire dominance over a harem. To test these possibilities, we performed a series of experiments in which dominant males were temporarily removed from their groups, and the performance of replacement males was evaluated.

The experiments were conducted on 12 harem groups from Mar. to Jun. 1997, that is, during the breeding season (Ortega and Arita 1999). Eight of the groups were small harems (< 14 females) with no subordinate male and four were large harems (> 14 females) with subordinate and dominant males. In the first round of removals, we randomly selected two of the groups. During 3 d, we made observations (described below) on the two groups, followed by the removal of the dominant males. The male from one of the groups was held in the laboratory for 3 d, while the other one, serving as a control, was returned to its original roosting site after 2 h. During the banding procedure in 1996, we had observed that, after disturbance, members of a group took, on average, 2 h to return to their roosting site and resume normal activities. Because our capture method involved the disturbance of the entire group, we retained the control male for 2 h until the rest of the members of the harem had returned to the roosting site.

Groups were observed from 09.00 to 16.00 h for three consecutive days, starting at the moment when the control male was returned to its roosting site. Our pilot observations made in a different cave in 1997 had shown that after the removal of the dominant male, it took, on average, 3.12 d for a different male to acquire complete dominance over the harem, spending at least 80% of its time patrolling the group (SE = 0.44, n = 8 groups). On the morning of the fourth day, the male that had been removed was returned to its roosting site, and observations were continued for three additional days to document activities after the reintroduction of the dominant male. Thus, the observational period consisted of 9 d: three before the removal of the dominant male, three in the absence of the dominant male, and three after its reintroduction. After concluding the observations of the first pair of groups, a second pair was randomly selected and the experimental procedure was repeated. The sequence was iterated until all 12 groups had been manipulated.

Our observations focused on two aspects: the identity of the male that assumed the role of the dominant male and the time it took this male to gain full control of the female group. Focal-animal sampling was used to document the presence or absence of the incoming male as percentages of 1-h observational periods, such that we amassed eight daily periods of observations (from hour 0 to hour 7). A new dominant male was considered to have full control of the group when it stayed at least 80% of 1-h period patrolling the edges of the solution cavity, assuming the normal behaviour of a dominant male. After a male had

attained full control, we measured its persistence as the number of intervals in which it was present, patrolling the harem group. We tested for temporal changes in the attendance by the new dominant male by quantifying its presence in the roosting site in 1-h periods using Cochran's Q-test (Sokal and Rohlf 1981), analysing small (< 14 females) and large groups separately. We also compared the number of visits by foreign males with the harem groups before and during the forced absence of the dominant male.

### **Experiment 2: Removal of Subordinate Males**

A dominant male can be affected by the presence of a subordinate male if the subordinate has the possibility of displacing the dominant male. In contrast, a dominant male can benefit from the presence of a subordinate male if its presence somehow reduces the frequency or success of intrusions by foreign males. Hence, our second experiment was aimed at quantifying changes in the frequency of visits by foreign males to harems from which the subordinate male had been experimentally removed. We also documented changes in the agonistic behaviour of dominant males towards intruders in the absence of subordinate males.

We performed the second experiment 1 mo after the first experiment, simultaneously on the four groups that contained both a dominant and a subordinate male. Observations were made 3 d before the removal of the subordinate males, 3 d in the absence of these bats, and 3 d after the individuals had been returned to their roosting site. We recorded visits by foreign males and agonistic responses by dominant males from 09.00 to 16.00 h every day. An agonistic response consisted of one of the following activities performed by dominant males in response to the presence of a foreign male: wing flicks, short chases, and attempts to bite the visiting male (Ortega and Arita 2000). Aggressive responses by dominant males towards subordinate males were also recorded before and after the removal.

### **Experiment 3: Removal of Females**

If the presence of a subordinate male in the roosting site allows the dominant male to control a larger number of females, and the costs to the dominant male of sharing females are not too high, then it is to the dominant male's advantage to tolerate the presence of the subordinate. If the dominant male somehow lost that benefit, then we would expect that its tolerance towards the subordinate male would decrease. In the third experiment, we experimentally reduced the number of females in the groups with two males to document possible changes in the interactions between dominant and subordinate males.

In the summer of 1998, a year after the previous two experiments, we removed some of the females from the four large groups to reduce the harem size from > 15 (original sizes: 16, 18, 19, 21 females) to 12 individuals, which is the average number of females in the medium groups in our system (Ortega and Arita 2000). Females that had been removed were held in cages for 3 d and then

released back into their roosting sites. During the experiment, we also observed four control groups under natural conditions that contained 11, 11, 12 and 12 females. Control groups were disturbed in the same manner as the experimental groups, but without detaining females. Control groups were used to compare the activity in the groups that were experimentally reduced in size to 12 females with that of groups naturally containing that number of females.

A pair of groups (one control, one experimental) was observed simultaneously for seven consecutive hours during 3 d before the experimental manipulation. We recorded the number of visits performed by foreign males and counted the number of 1-h intervals in which dominant and subordinate males were present with the harem groups, using the focal-animal sampling method. After performing the experimental manipulation, the same observations were made for three additional days.

Additionally, we recorded the frequency of agonistic acts directed towards subordinate males by dominant males before and after the removal of the females. After the experiment, all females were returned back to their original roosting site and monitored to verify their reintegration into the groups.

## Results

### Experiment 1: Removal of Dominant Males

In each of the 12 experimental groups, a new individual occupied the site of the dominant male that had been removed. In the four large groups, in which a subordinate male was present before the experiment, that individual took over the site of the dominant male and remained there until the end of the experiment. In the eight groups that originally included a single male, a foreign male occupied the vacant site. In five of these groups the first foreign male to arrive remained with the harem until the end of the experiment, while in three groups a different foreign male displaced the first one. The new dominant males took up the same positions as the original dominant males, on the edge of solution cavities, but did not direct any agonistic acts towards intruders. During substitutions, all females remained within their harem groups.

Subordinate males responded more quickly to the removal of dominant males than did foreign males. In the four large groups, subordinate males moved to the position left by the missing dominant male within 2 h of the removal ( $\bar{x} \pm \text{SE} = 1.5 \pm 0.28$  h,  $n = 4$  groups), whereas foreign males took up to 5 h to replace a dominant male in the small groups ( $\bar{x} \pm \text{SE} = 4.09 \pm 0.36$  h after removal,  $n = 8$  groups; Mann–Whitney U-test,  $U = 43$ ,  $p < 0.01$ ).

On day 1 after the removal, former subordinate males spent more time defending their harems ( $\bar{x} \pm \text{SE} = 4.16 \pm 0.35$  h,  $n = 4$  groups) than former foreign males ( $\bar{x} \pm \text{SE} = 1.00 \pm 0.23$  h,  $n = 8$  groups; two-tailed paired-sample t-test,  $t = 4.00$ ,  $df = 3$ ,  $p < 0.05$ ). Afterwards, former foreign males spent increasingly more time with the groups as the experiment progressed, while the time spent by former subordinate males remained constant (Fig. 1). The presence

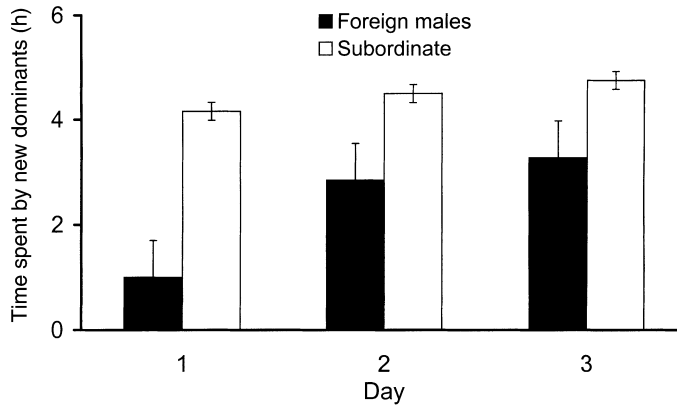


Fig. 1: Mean ( $\pm$ SE) time (in hours) spent by replacement males guarding harems during the 3-d removal of 12 dominant males from harems. Subordinate males replaced dominant males in the four largest groups ( $> 14$  females), while foreign males did so in the remaining eight groups ( $< 14$  females)

of former foreign males within the groups was less predictable than that of former subordinate males. For foreign bats, Cochran's test showed significant differences in the presence of the male when comparing 1-h intervals within groups ( $Q = 6.5$ ,  $df = 2$ ,  $p < 0.05$ ). For former subordinate males, in contrast, no such difference could be detected ( $Q = 2.0$ ,  $df = 2$ ,  $p > 0.05$ ).

The number of visits by foreign males to the groups during the 3-d period before the removal ( $\bar{x} \pm SE = 17.5 \pm 1.75$  visits,  $n = 12$  groups) was not different from the number observed during the absence of the dominant male ( $\bar{x} \pm SE = 21.0 \pm 1.68$  visits,  $n = 12$  groups; Wilcoxon paired test,  $T = 10$ ,  $p > 0.05$ ).

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

### Experiment 2: Removal of Subordinate Males

The number of visits by foreign males differed among the three observational periods (before the removal, in the absence of the subordinate male, and after the return of the subordinate male; Friedman's test,  $\chi^2 = 6.0$ ,  $df = 2$ ,  $p < 0.05$ ). In the 3-d period before the removal of subordinate males, the number of visits by foreign males was similar to the normal rate reported by Ortega and Arita (2000;  $\bar{x} \pm SE = 5.75 \pm 0.32$  visits/day,  $n = 4$  groups). When subordinate males were removed, the number of visits increased progressively, reaching its peak on the third day ( $\bar{x} \pm SE = 14.83 \pm 1.50$ ; Fig. 2). After subordinate males were



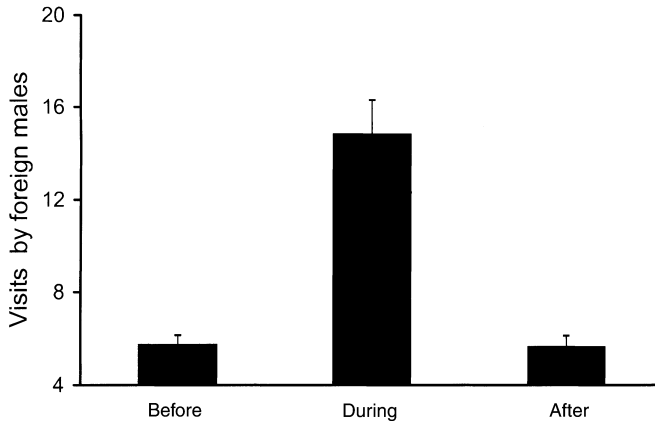


Fig. 2: Visits by foreign males to the four large groups containing dominant and subordinate males. Bars show the mean + SE of visits before subordinate males were removed, during the removal, and after subordinate males were returned

released, the rate of visitation by foreign males returned to its normal level ( $\bar{x} \pm SE = 5.67 \pm 1.61$  visits).

The number of agonistic displays performed by dominant males differed among the three observational periods (Friedman's test,  $\chi^2 = 6.0$ ,  $df = 2$ ,  $p < 0.05$ ). In the 3-d period before the removal of subordinate males, dominant males performed an average of 16.0 aggressive actions/day (SE = 1.06,  $n = 4$  groups), while in the absence of subordinate males, the average number of aggressive acts was  $28.7 \pm 0.94$ . After the release of subordinate males, the number of aggressive acts returned to its normal level ( $\bar{x} \pm SE = 18.5 \pm 0.78$ ).

In the four experimental groups, subordinate males returned to their original positions 2 h after being released back to their roosts. The number of agonistic displays directed at subordinate males by dominant males did not change with the experimental manipulations (before the experiment:  $\bar{x} \pm SE = 4.25 \pm 0.47$  displays/day; after the experiment:  $4.0 \pm 1.08$ ;  $n = 4$ , Wilcoxon paired test,  $T = 10$ ,  $p > 0.05$ ).

### Experiment 3: Removal of Females

Subordinate males spent a lower percentage of the time with the harems after the experimental reduction in the number of females (before the removal:  $\bar{x} \pm SE = 88.0 \pm 4.04\%$ ; after the removal:  $52.25 \pm 3.88\%$ ; two-tailed t-test,  $t = 4.89$ ,  $df = 3$ ,  $p < 0.01$ ). The percentage of time spent by dominant males did not change with the removal of females (before the removal:  $\bar{x} \pm SE = 98.0 \pm 1.22\%$ ; after the removal:  $96.25 \pm 1.75\%$ ; two-tailed paired-sample t-test,  $t = 2.28$ ,  $p < 0.05$ ).

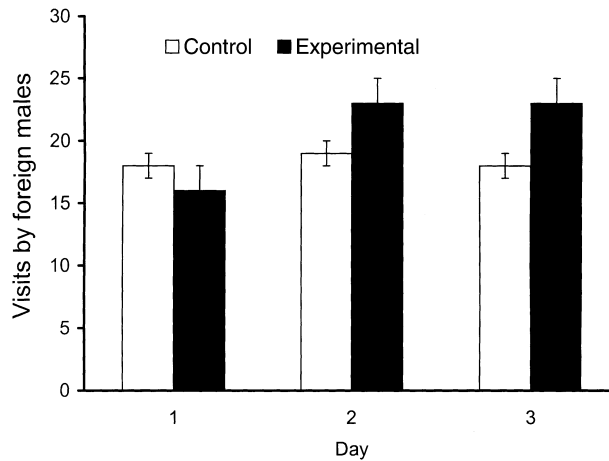


Fig. 3: Visits by foreign males after the experimental removal of some females from four harem groups (to < 12 females per group). Four additional groups served as controls. Mean number of visits ( $\pm$  SE) is shown for three consecutive days after the removal

Under normal conditions, large groups containing > 14 females and two males receive significantly fewer visits by foreign males than medium-sized (12 females) groups (Ortega and Arita 2000). In the 3-d period before the experimental reduction in the number of females, the four experimental groups received the normal number of visits documented in a previous study (Ortega and Arita 2000; 11.21 visits/day  $\pm$  2.24,  $n = 4$ ). After the removal of some of the females, visits by foreign males increased progressively, and on the second day after the removal of females the frequency of visits was comparable with the average of visits to the control medium-sized groups (Fig. 3). In fact, our data suggest that during the 3 d in which the number of females was abnormally low, the experimental groups received a similar number of visits as did the non-experimental medium-sized groups. A Mann–Whitney U-test failed to demonstrate a significant difference between experimental and control groups (experimental:  $\bar{x} \pm \text{SE} = 20.67$  visits/day  $\pm$  4.04; non-experimental:  $18.33 \pm 2.4$ ; Mann–Whitney U-test,  $U = 9$ ,  $p > 0.05$ ) but the result has to be viewed with caution, because the number of available large groups (four) constitutes a very small sample size.

Our data suggest that the average number of aggressive displays by dominant males against subordinate males before the removal ( $\bar{x} \pm \text{SE} = 5.75 \pm 1.09$  aggressions/day,  $n = 4$ ) did not differ after the reduction in the number of females ( $4.75 \pm 0.94$ ; Wilcoxon's paired test,  $T = 6$ ,  $p > 0.05$ ). We never observed agonistic displays by subordinate males against dominant males, either before or during the experiment. Eighty per cent of females that were returned to their roosts were reintegrated quickly into their harems, while the rest shifted their roosting site for some days, eventually returning to their original groups.

### **Discussion**

The effects of removals can be summarized as follows: (1) In the absence of dominant males, subordinate males occupied the vacant places faster than did foreign males, (2) In the same experiments, subordinate males showed more fidelity to their groups than did foreign males, (3) In the absence of subordinate males, the frequency of visits by foreign males to large harems increased, (4) When the number of females was experimentally reduced the rate of visits by foreign males increased, (5) The reduction in the number of females apparently had no effect on the number of agonistic interactions between dominant and subordinate males, (6) All removed bats reintegrated quickly into their original groups and recovered their original status when released back to their roosts.

#### **Costs and Benefits to Dominant Males**

Dominant males obtain direct and immediate benefits, in the form of access to reproductive females, by defending harems. A potential cost is the expenditure of energy in repelling intrusions by foreign males. The presence of a subordinate male in the largest groups deters foreign males from attempting to take over the harems. This effect probably also reduces the behavioural energetic cost that dominant males incur in defending the groups of females.

Dominant males of several bat species invest high levels of time and energy in patrolling their harems, because they are constantly alert to movements by foreign individuals, and need to display expensive agonistic responses towards intruders (Morrison 1978; Morrison and Morrison 1981; Williams 1986; Kunz et al. 1998). We did not measure directly the energy spent by dominant males to defend their groups, but our data suggest that the presence of subordinate males reduces the cost of defending harems by lowering the rate of visits by male intruders and by reducing the number of agonistic responses performed by dominant males.

Furthermore, our data suggest that the presence of a subordinate male allows dominant males to defend larger groups than those held by a single male. The results of our second experiment show that the presence of a subordinate male reduces the number of visits by foreign males, presumably reducing the energetic cost to dominant males of controlling the harems. Thus, by tolerating the presence of a subordinate male, dominant males in large groups gain access to a higher number of females, thereby increasing their potential fitness.

#### **Costs and Benefits to Subordinate Males**

In harems of the Jamaican fruit-eating bat, subordinate males do not perform any obvious defensive behaviours, so there is no apparent energetic cost of belonging to a group. However, because subordinate males are fully adult

individuals (Ortega and Arita 1999), staying with a harem dominated by another male might constitute a cost in the form of delayed reproduction.

Subordinate males obtain no obvious immediate benefit from belonging to large groups. To be profitable for subordinate males, the association with a dominant male has to offer long-term benefits to offset the costs. In most cases of male coalitions, dominant males share reproduction with subordinate males to induce them to remain with the group (Emlen and Oring 1995; Grinnell et al. 1995). Apparently this is not the case with Jamaican fruit-eating bats, because no copulation by a subordinate male has been observed in over 20.00 h of observations (Ortega and Arita 1999, 2000). However, only a direct measure of reproductive output of both dominant and subordinate males, through paternity tests (Hughes 1998), can confirm or reject our field observations.

Our data suggest that subordinate males may obtain a long-term benefit by having priority access to the position of the dominant male once this bat disappears from the roost. A similar situation has been documented for spear-nosed bats (*P. hastatus*, Kunz et al. 1998) and for coalitions of male manakins (*Chiroxiphia linearis*), in which subordinate males perform costly displays to attract females, playing a satellite role but obtaining no immediate reward because the dominant male fathers practically all the young (McDonald and Potts 1994). However, subordinate manakin males obtain a long-term benefit from the association because they readily take the place of the dominant males when these individuals disappear. If subordinate males are related to dominant males, then an additional benefit to subordinate males could take the form of an increase in inclusive fitness through a higher reproductive output for the dominant male (Emlen and Oring 1997; Mesterton-Gibbons and Dugatkin 1992).

#### **Satellites or Sneaks?**

Dominant males obtain benefits by tolerating the presence of subordinate males and apparently incur little or no cost in doing so. Thus, the relationship between dominant and subordinate Jamaican fruit-eating bats can be described as a dominant/satellite association that functions to retain a large number of females in the harem. The association can be considered a long-term relationship, because pairs of dominant/subordinate individuals have been observed roosting together for at least two continuous years (Ortega and Arita 1999, 2000). However, the conditions and mechanisms under which subordinate males are incorporated into the harem groups remain unclear.

Dominant males perform all the costly defensive behaviours and apparently obtain most or all the copulations with females. The presence of subordinate males is correlated with a higher number of females in the harem and reduces the rate of intrusions by foreign males, thereby lowering energy expenditures for dominant males. Subordinate males invest little energy in defending the harem but obtain no obvious reproductive benefit. In addition, subordinate males obtain a

long-term benefit in the form of priority access to vacant positions of dominance and, probably, in the form of an increased inclusive fitness. Clearly, subordinate males are not sneaks, because dominant males derive obvious benefits from their presence.

A stable dominant/satellite association, such as the one observed in our system, can evolve only if (1) both males obtain some kind of benefit; (2) for dominant males, the cost of tolerating the presence of subordinate males (which constitute potential competitors) is offset by the benefits gained because of the help provided by subordinate males in defending a larger group of females and (3) the cost of being a subordinate male (and obtaining few or no copulations) is offset by present or future benefits (Alexander 1974; Axelrod and Hamilton 1981; Emlen and Oring 1982; Davies and Houston 1984). Our data suggest that all of these conditions are met in the polygynous system of the Jamaican fruit-eating bat in the caves of Yucatán.

### Acknowledgements

We are indebted to H. Drummond for advice and comments on the design of this project. We also thank J. L. Osorno for statistical assistance and suggestions on experimental design. C. Macías and L. Eguiarte provided helpful comments on the manuscript. Funding was provided by DGAPA-UNAM (IN-208495), CONACyT (25685-N) and CONABIO (H-180). CONACyT supported the first author through scholarship 93710. R. Avila, R. Cerritos, F. Colchero, J. J. Flores, X. López, M. Santos, G. Steers, G. Suzán, G. Téllez, E. Tobón and H. Zarza provided field assistance. Fieldwork was made possible under a permit from the Mexican Ministry of the Environment granted to H. T. Arita. Experiments were performed in accordance with current Mexican law.

### 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.
- Axelrod, R. & Hamilton, W. D. 1981: The evolution of cooperation. *Science* **211**, 1390—1396.
- Balmford, A., Rosser, A. M. & Albon, S. D. 1992: Correlates of female choice in resource-defending antelope. *Behav. Ecol. Sociobiol.* **31**, 107—114.
- Bradbury, J. W. & Vehrencamp, S. L. 1977: Social organization and foraging in Emballonurid bats. III Mating systems. *Behav. Ecol. Sociobiol.* **2**, 1—17.
- Bygott, J. D., Bertram, B. C. R. & Hanby, J. P. 1979: Male lions in a large coalitions gain reproductive advantage. *Nature* **282**, 839—841.
- Clutton-Brock, T. H. 1989: Mammalian mating systems. *Proc. Royal Soc. London B* **236**, 339—372.
- Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A. D. C., McIlrath, G., Chadwick, P., Brotherthorn, P. N. M., O'Riain, J. M., Manser, M. & Skinner, J. D. 1998: Cost of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. Royal Soc. London B* **265**, 185—190.
- Connor, R. C., Smolker, R. A. & Richards, A. F. 1992: Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc. Nat. Acad. Sci. USA* **89**, 987—990.
- Davies, N. B. & Houston, A. I. 1984: Territory economics. In: *Behavioural Ecology: An Evolutionary Approach* (Krebs, J. R. & Davies, N. B., eds). Sinauer Associates, Sunderland, Massachusetts, pp. 148—169.
- Davies, N. B. & Houston, A. I. 1991: Mating systems. In: *Behavioral Ecology: An Evolutionary Approach* (Krebs, J. R. & Davies N. B., eds). Blackwell Scientific Publications, Oxford, pp. 263—294.

- DeNault, L. K. & McFarlane, D. A. 1995: Reciprocal altruism between male vampire bats, *Desmodus rotundus*. *Anim. Behav.* **49**, 855–856.
- Doolan, S. P. & MacDonald, D. W. 1999: Co-operative rearing by Slender-tailed Meerkats (*Suricata suricatta*) in the southern Kalahari. *Ethology* **105**, 851–866.
- Dugatkin, L. A. 1997: The evolution of cooperation. *Bioscience* **47**, 355–362.
- Dugatkin, L. A. 1998: *Cooperation Among Animals. An Evolutionary Perspective*. Oxford Univ. Press, New York.
- Emlen, S. T. & Oring, L. W. 1977: Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.
- Emlen, S. T. & Oring, L. W. 1982: The evolution of helping. II. The role of behavioral conflict. *Am. Nat.* **119**, 40–53.
- Emlen, S. T. & Oring, L. W. 1995: An evolutionary theory of the family. *Proc. Nat. Acad. Sci. USA* **92**, 8092–8099.
- Emlen, S. T. & Oring, L. W. 1997: Predicting family dynamics in social vertebrates. In: *Behavioural Ecology: An Evolutionary Approach* (Krebs, J. R. & Davies, N. B., eds). Blackwell, New York, pp. 228–253.
- Greenwood, P. J. 1980: Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162.
- Grinnell, J., Packer, C. & Pusey, A. E. 1995: Cooperation in male lions: kinship, reciprocity or mutualism? *Anim. Behav.* **49**, 95–105.
- Hughes, C. 1998: Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology* **79**, 381–399.
- Jennions, M. D. & MacDonald, D. W. 1994: Cooperative breeding in mammals. *Trends Ecol. Evol.* **9**, 89–93.
- 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., August, P. V., Burnett, C. D., Robson, S. K. & Nagy, K. A. 1998: Economics of harem maintenance in the greater spear-nosed bat, *Phyllostomus hastatus*. *J. Mamm.* **79**, 631–642.
- Le Boeuf, B. J. 1974: Male–male competition and reproductive success in elephant seal. *Am. Zool.* **14**, 163–176.
- Ligon, J. D. 1991: Co-operation and reciprocity in birds and mammals. In: *Kin Recognition* (Hepper, P. G., ed.). Cambridge Univ. Press, Cambridge, pp. 30–59.
- McCracken, G. F. & Wilkinson, G. S. 2000: Bat mating systems. In: *Reproductive Biology of Bats* (Crichton, E. G. & Krutzsch, P. H., eds). Academic Press, New York, pp. 321–362.
- MacDonald, D. B. & Potts, W. K. 1994: Cooperative display and relatedness among males in a lek-mating bird. *Science* **266**, 1030–1032.
- Mesterton-Gibbons, M. & Dugatkin, L. A. 1992: Cooperation among unrelated individuals: evolutionary factors. *Quat. Rev. Biol.* **67**, 267–281.
- Morrison, D. W. 1978: Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* **59**, 716–723.
- Morrison, D. W. & Morrison, S. H. 1981: Economics of harem maintenance by a neotropical bat. *Ecology* **62**, 864–866.
- Ortega, J. & Arita, H. T. 1999: Structure and social dynamics of harem groups in *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *J. Mamm.* **80**, 1173–1185.
- Ortega, J. & Arita, H. T. 2000: The behavioral defense of resident males of the Jamaican fruit-eating bats (*Artibeus jamaicensis*). *Ethology* **106**, 395–407.
- Ostfeld, R. S. 1987: On the distinction between defense and resource polygyny. *Oikos* **48**, 238–240.
- Packer, C. & Pusey, A. E. 1982: Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* **296**, 740–742.
- Pope, T. R. 1990: The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behav. Ecol. Sociobiol.* **27**, 439–446.
- Rood, J. P. 1989: Male associations in a solitary mongoose. *Anim. Behav.* **38**, 725–728.
- Smolker, R. & Pepper J. W. 1999: Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). *Ethology* **105**, 851–866.

- Sokal, R. R. & Rohlf, F. J. 1981: *Biometry: The Principles and Practice of Statistics in Biological Research*. W. H. Freeman Press, San Francisco.
- Voigt, C. C., von Helversen, O., Michener, R. & Kunz T. H. 2001: The economics of harem maintenance in the sac-winged bat, *Saccopteryx bilineata* (Emballonuridae). *Behav. Ecol. Sociobiol* **50**, 31—36.
- Williams, C. F. 1986: Social organization of the bat *Carollia perspicillata* (Chiroptera: Phyllostomidae). *Ethology* **71**, 265—282.

*Received: January 23, 2002*

*Initial acceptance: March 20, 2002*

*Final acceptance: August 2, 2002 (S. Sakaluk)*