

**Social Organization in *Artibeus watsoni* (Chiroptera:  
Phyllostomidae) in Costa Rica**

by T. L. Mulcahy  
April 19, 1993  
ZOO498Y

## Introduction

Tent construction in the neotropics is exclusive to members of the Phyllostomidae subfamilies Stenodermatinae and Carollinae (Timm, 1987; Kunz et al. in press). Of the fourteen species of New world tent-roosting bats, *Artibeus watsoni* modifies the greatest number of plant species and has the most diverse tent styles. Thomas' fruit-eating bat (*Artibeus watsoni*) has been observed roosting under the leaves of 20 different broadleaved plant species (Timm, 1987).

*Artibeus watsoni* has been found to roost singly and within groups (Timm & Clauson, 1990). The number of roosting individuals within a tent is likely to be dependent upon the time of year and the reproductive strategy of *A. watsoni* (seasonal polyestry). Similarly, the little permanence of foliage-roosts, compared to caves or tree hollows, is likely to influence the social behaviours of tent-making bats. Although several species have long been known to modify leaves, and roost beneath these structures in clusters, few studies have examined the roosting behaviour or social organization of these species (Lewis, 1992; Brooke, 1987).

This study provides the first description of *Artibeus watsoni* roosting within altered leaves of *Manicaria saccifera* and the first investigation of the social organization of *Artibeus watsoni*.

## Methods

This study was conducted at Cano Palma biological station, 2.4 km NW of Tortuguero, in the Caribbean lowlands of Costa Rica (10°30'N, 83°45'W) between 15 December 1992 and 7 January 1993. Cano Palma lies within the Tropical Wet Forest zone (Holdridge, 1967) and is largely primary forest. One evident feature of

the subcanopy of the forest at Cano Palma is the abundance of dwarf palms, most notably *Manicaria saccifera*.

All Royal palm (*Manicaria saccifera*) leaves that had been altered within a 1.4 km area were mapped and marked with flagging tape near the base of the stalk. The height, size, age, and location of the tents were also noted for other studies on the same population. Throughout the study the area was searched for any new tents constructed since our initial mapping. Each of the tents were inspected daily for roosting *Artibeus watsoni*. Inspections were carried out in the early morning when the bats were the least restless (Lewis, 1992; personal observations). Bats found roosting in tents were captured using a hoop, 1 m in diameter, loosely strung with mist netting. The hoop was fitted with a long handle allowing the net to be quickly raised, entangling the bats as they dropped just prior to flight. Additionally, *Artibeus watsoni* individuals caught in mist nets located in the study area were necklaced.

Sex, weight, forearm length, ear length, and reproductive condition (reproductively active-in estrus or scrotal, or non-breeding) were recorded for each individual caught in the area. When a reproductively active male was captured the length and width of the testes was also recorded. No lactating or pregnant female *A. watsoni* were observed because our study overlapped with the beginning of the first breeding season of the year (Fleming et. al, 1972). Heavy pigmentation of the vulva was used to determine if a female was in estrus (Handley et. al, 1991). All linear measurements were taken to the millimeter and body mass was measured with a Pesola spring scale. We recorded all masses only to the nearest gram, assuming that greater accuracy is unrealistic. Bats were marked by placing a steel ball-chain necklace (no. 3) holding an aluminum band covered in 3-M colour reflective tape on the neck of the bat in individually recognizable patterns. The advantage of necklacing is that it is harmless to bats

as long as they are properly fitted (Handley et. al, 1991). This was ensured by noting necklace circumference (X= 15 balls). A month following the study, further work was done on the same population and only one necklace was found to be irritating the bat.

High diurnal roosts and clustered individuals within a tent made observations difficult. Individual recognition was aided by the use of binoculars (8x30) or by shining a headlamp on the roosting bats. Despite these measures, bats often had to be hand-netted in order to distinguish the banding patterns.

## Results

Over the 1.4 km study area, 75 tents were identified, many of which were never found to be inhabited over the study period. Only a fraction of the altered leaves were occupied by bats on any given day (approx. 1-2 %). When bats were disturbed from a roost they would attempt to return to the same tent or fly to another in the vicinity. On one occasion when a tent was disturbed the bat inhabiting it flew to a nearby palm frond and roosted externally. No *Artibeus watsoni* was found within the same tent on two consecutive days yet individuals were usually found roosting beneath a series of tents scattered within a restricted area of the forest. One group of *A. watsoni* was observed roosting within 8 different tents over the course of the study (sometimes after being disturbed from other tents). Bats were absent from the study area on seven separate days, five of which were the last days of the study. This indicates that the low roost fidelity that we observed may better reflect disturbance caused by our censusing.

During the 21 day study, 29 adult *Artibeus watsoni* were necklaced, 20 of which were captured in diurnal roosts. Of the total number of bats necklaced, 17 were males and 12 were females. The sex ratio of *Artibeus watsoni* found roosting was 2:1, with females being more common. Bats were found to roost singly or in

groups of up to four individuals. On nine occasions a bat was found roosting singly (of which 6 were captured and found to be adult males). Adult males roosting singly that were caught were not reproductively active, with the exception of one male. Five tents were each occupied by two individuals: a male and female in one tent; a male with an unidentified individual in another; and in three cases both sexes were unknown. Two groups were captured that exhibited a harem-like social organization consisting of a single adult male with two or three females. One group was observed on five different days, during which the number and attendance of females varied. On three occasions the male (B-W) was found roosting with three females. On the other two occasions he was found with two females. Females found in the company of a male were never observed roosting with another male over the course of the study.

Our observations, of the morphological characteristics of bachelor and harem males, indicate that there is no significant difference in size between males roosting singly and those roosting with females. Similarly, we did not observe any marked sexual dimorphism in *Artibeus watsoni* (insufficient data to statistically analyze).

It has previously been suggested that some members of the Phyllostomatidae family, in addition to constructing diurnal tents, modify leaves close to foraging areas where they return over the course of an evening to feed on the fruit acquired at nearby trees (Morrison, 1980). We observed an individual *A. watsoni* one evening feeding on piper within a tent that had never been occupied during the day over the course of our study. The quantity of guano observed beneath this foraging roost compared to that at a diurnal roost suggests that foraging roosts, in addition to providing concealment while feeding, ensure that metabolic wastes will not aid predators in detecting conspicuous diurnal roosts containing bats.

## Discussion

Our observations reveal a harem mating system in *A. watsoni*, similar to that described in Brooke's 1987 study (in which she wrongly identified *A. watsoni* as *Vampyressa nymphaea*) and those found in other bat species (McCracken & Bradbury, 1981; Lewis, 1992).

Bat tents themselves limit group size, in turn possibly affecting the social organization of *Artibeus watsoni*. Palm fronds may be unable to support large numbers of roosting *A. watsoni* or they may not afford enough protection to efficiently conceal many individuals.

The evolution of a harem social organization in *Artibeus watsoni* may be explained by one of two systems in which males control females. Female defense polygyny would occur if clustering into groups is beneficial to females, facilitating subsequent monopolization by males. Resource defense polygyny would occur if either food sources or diurnal roosts were essential to females and could be economically defended by males (Emlen & Oring, 1977). While there is not yet a definitive answer to the mechanism involved in the evolution of a harem mating system in *Artibeus watsoni* there is sufficient data to seriously question some hypotheses and to identify areas that warrant further study.

Support for female defense polygyny would require evidence of stable female groups guarded by single male regardless of the groups movement to different roosts or areas (Kunz et. al., 1983). The benefits of female clustering need not be related to reproduction. One explanation for female group roosting when alternative roosts are available is social thermoregulation (Lewis, 1992). Similarly, cooperative predator defense or cooperative rearing of young among females within a cluster may explain female grouping independent of male defense. For unrelated females of *Phyllostomas hastatus* grouping could also be the result of a reciprocal system based on cooperative foraging and defense of foraging sites,

as described by McCracken & Bradbury (1981).

In female defense polygynous species competition for female groups is intense. High sexual dimorphism, elaborate display behaviours, and intense intrasexual selection, are common among these species (Emlen & Oring, 1977).

Our observations suggest that female *Artibeus watsoni* groups are not stable. Throughout our study females were found consistently with the same male but the size and make-up of female groups with a given male changed daily. If the harem organization of *A. watsoni* was female defense-based we would expect female groups to be roosting at diurnal tents in the absence of a male. On no occasion was a female or group of females not attended by a single male. Additionally, a female defense system does not account for two occasions when a male was found roosting with a single female. Our observations that there was no difference in body size between males roosting alone or with females suggests that successful harem acquisition is not dependent on the size of the male. Although no aggressive behaviours were observed during our study it is likely that intraspecific interactions do occur in *Artibeus watsoni* as they have been observed in other members of the Phyllostomatidae family (Fenton & Kunz, 1977). However, this aggression may be more a result of limited food resources and roost sites than of competition for females.

Segregation of harem roost sites could be the result of harem males defending a large area that includes foraging sites as well as diurnal roosts. Harem males would allow only those females they roost with to forage within their territory. This system would require individual recognition of those females that a male roosts with. Bradbury & Vehrencamp (1977) proposed a resource defense polygynous system in emballonurids, with males defending foraging grounds. When foraging, *Artibeus watsoni* do not feed on a fruit at the tree but carry the fruit to a nearby roosting tent (personal observation). This feeding behaviour is similar to that of other neotropical frugivores (Morrison, 1980) where many bats converge on the

same tree and feeding individuals change fruiting trees several times a night.

Although it is not fully known where most mating in *A. watsoni* occurs it seems likely that a substantial portion would occur in diurnal roosts, as suggested in emballonurids (Bradbury & Vehrencamp, 1977). If this is the case then the defense of foraging grounds is not energetically feasible if males can only benefit from this defense at the diurnal roost. Additionally, the small size of the harem organization in *A. watsoni* would not make defense of a fruiting tree cost-effective.

If *Artibeus watsoni* males were defending a fruiting tree (or a portion of) we would expect the males to depart the diurnal roost before and return after the females. Evidence of males always at a fruiting source where females are present would also aid in identifying the social structure as resource-based (food).

Resource defense polygyny in *A. watsoni* would be explained if males alone constructed tents and females preferentially selected roosts. The selection of a tent by females may be dependent on a number of factors; proximity to prime food resources, ability to provide concealment from predators, and protection from rain, wind, and sun. If the latter was the case we would expect females to select such features of the tent as; size, height above ground, and age of the leaf. Although a female may select a tent for reasons independent of the male that constructed it, a male that can construct and defend a tent having these qualities may be more aggressive, attractive, or possess other traits that would increase his fitness (Morrison, 1979). Female clustering would only be a result of limited acceptable roosting sites if resource defense polygyny was the explanation for a harem social organization. So that the chance of obtaining more mates would increase as the critical resource (tents) became more unevenly distributed (Emlen & Oring, 1977). Morrison (1979) suggested that resource defense polygyny was not feasible in *Artibeus jamaicensis* when roosting in foliage because leaves available for tents were not in limited supply. However, although the abundance of plants available for diurnal roosts is



substantial, the tents within which females may roost are likely to be limited in number. Within the study site 75 *Manicaria saccifera* fronds were modified into tents however, these tents represent only a small portion of the total leaves available. Additionally, if female bats within a population are sexually receptive in unison, monopolization by males becomes increasingly more difficult. Throughout our study both females in estrus and non-reproductive females were observed. The length of time over which female receptivity lasts is unknown.

Considering the short duration of the present study, it is difficult to draw any substantial conclusions as to the mechanism underlying the evolution of a harem mating system in *A. watsoni*.

The reproductive pattern of *Artibeus watsoni* needs to be confirmed by long-term studies. If *A. watsoni* are in fact seasonally polyestrous then a year-long study emphasizing the spring and summer months (when births would occur) would be required. A year-long study would elucidate whether males will often only defend the females or resources during the breeding season, or will do so throughout the year. Future research may also emphasize whether the social behaviour changes in different habitats (with more or less food sources), species densities, and under different sex ratios. All of these could be accomplished by comparing different sites. It remains to be determined whether individual bats or several members of a roosting group construct the tents. Evidence of this kind will go far in determining whether the mating system of *A. watsoni* is female or resource defense based. However, detailed knowledge on the social system of *Artibeus watsoni* will be difficult, or impossible, to obtain through observation alone. Confidence about whether members of a roosting group are genetically related will give insight into the genetic and evolutionary mechanisms underlying this harem social system. This is best accomplished by genetic studies using enzyme polymorphisms or DNA fingerprinting (McCracken & Bradbury, 1981). If females within a tent are closely related a female defense mating system would seem

more plausible since nepotism would influence the stability of female groups. Radio-telemetry would be useful coupled with observational data collection to identify the ranges and possibly territories of individual *A. watsoni*. Additionally, although necklacing ensures little disruption to the bats and individual patterns are recognizable when bats are alone, it is not as efficient when bats are clustered in close proximity beneath a diurnal roost. Other methods of individual field identification need to be investigated.

## References

- Boinski, S., R.M. Timm. 1985. Predation by Squirrel Monkeys and Double-toothed Kites on Tent-making Bats. Am. J. Primat., 9: 121-127.
- Bradbury, J.W., S.L. Vehrencamp. 1977. Social Organization and Foraging in Emballonurid Bats. Behav. Ecol. Sociobiol., 2: 1-17.
- Brooke, A.P. 1987. Tent construction and social organization in *Vampyressa nymphaea* (Chiroptera: Phyllostomidae) in Costa Rica. J. Tropical Ecology, 3: 171-175.
- Clutton-Brock, T.H. 1989. Mammalian mating systems. Proc. R. Soc. Lond., 236: 339-372.
- Emlen, S.T., L.W. Oring. 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. Science, 197: 215-222.
- Fenton, M.B., T.H. Kunz. 1977. Movements and Behavior Pp 351-364, in *Biology of bats of the New World family Phyllostomatidae, Part II* (R.J. Baker, J.K. Jones, Jr., and D.C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 13: 1-364.
- Foster, M.S., R.M. Timm. 1976. Tent-Making by *Artibeus jamaicensis* (Chiroptera: Phyllostomatidae) with Comments on Plants Used by Bats for Tents. Biotropica, 8(4): 265-269.
- Handley, C.O., Jr., D.E. Wilson, A.L. Gardner. 1991. Chapter 12: Appendix, in *Demography and Natural History of the Common Fruit Bat, Artibeus jamaicensis, on Barro Colorado Island, Panama* (Handley, C.O., Jr., D.E. Wilson, A.L. Gardner, eds.). 511: 1-173.
- Holdridge, L.R. 1967. Life zone ecology. Tropical Sci. Center, San Jose, Costa Rica, 206 pp.
- Kunz, T.H., P.V. August, and C.D. Burnett. 1983. Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Biotropica, 15(2): 133-138.
- Kunz, T.H., M.S. Fujita, A.P. Brooke, and G.F. McCracken. Bats and tents: convergence in tent architecture and tent-making behavior among neotropical and paleotropical species. *in press*.
- Lewis, S.E. 1992. Behavior of Peter's Tent-making Bat, *Uroderma Bilobatum*, at Maternity Roosts in Costa Rica. J. Mammal., 73(3): 541-546.

McCracken, G.F., J.W. Bradbury. 1981. Social Organization and Kinship in the Polygynous Bat *Phyllostomus hastatus*. Behav. Ecol. Sociobiol., 8: 11-34.

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(1): 20-29.

Timm, R.M. 1987. Tent construction by bats of the genera *Artibeus* and *Uroderma*, in *Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz* (B.D. Patterson & R.M. Timm, eds.). Fieldiana: Zoology (new series), 39: 187-212.

Timm, R.M., B.L. Clauson. 1990. A Roof over their Feet. Nat. Hist., 3:55-58.

Wilson, D.E. 1979. Reproductive Patterns Pp 317-378, in *Biology of bats of the New World family Phyllostomatidae, Part III* (R.J. Baker, J.K. Jones, Jr., and D.C. Carter, eds.). *Special Publications, The Museum, Texas Tech University*, 16: 1-441.