Leaf selection on *Manicaria saccifera* (Palmae) by the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in Costa Rica

Bruce O'Toole

890531010

The first bat to alter leaves for a diurnal roost was discovered by Barbour (1932) in Panama. The bat, *Uroderma bilobatum*, was found in a palm leaf which it had altered by cutting the leaves. In the same year Chapman (1932) discovered *Artibeus watsoni* roosting in altered leaves and introduced the term tents for these roosts. Subsequently, seventeen different species of bats world wide have been found roosting in tents. Fourteen species of neotropical and three species of paleotropical bats have been found in over 60 different plants (Kunz et al, in press). The neotropical species *Artibeus watsoni* has been found roosting in twenty species of plants: nine from the family Palmae, four in the family Cylanthaceae, one species in the family Musaceae, four species in the family Helicioniaceae, and one species in each of the families Marataceae and Araceae.

Although there are many reports of bats using tents there are few accounts on the choice of leaves that the bats alter. One study on *Artibeus watsoni* roost site selection (Choe and Timm, 1985) concluded that leaves of *Anthurium ravenii* were selected based on their size and location on the plant. The use of specific leaves as diurnal roosts in this study suggests that bats choose leaves based on certain characteristics.The leaf choice by bats can be summarized into two questions:(1) Are the bats choosing characteristics of the particular leaf? or (2) Are the bats choosing the position of the leaf on the plant?

Methods

The study was conducted at the Cano Palma Biological station in the Guanacaste province of Costa Rica (10 30'N, 83 45'W) from December 15 1992 to January 7 1993. Cano Palma is a Canadian research station approximately a 10 minute boat ride north of Tortuguero.

The 30 hectare station was systematically searched for *Artibeus watsoni* tents. The tents were marked and mapped, the majority of altered leaves were from the palm species *Manicaria saccifera*. Each altered leaf was scored on 12 measured characters (Figure 1). The length of the leaf along the midrib (MR and ML) was measured from the attachment of the leaf on the stem to the end of the midrib. The length of the basal and side sections (BL, BR, SL, SR) were measured from corner to corner, not the curved length. The length of the front part of the leaf (FL and FR) was measured from the tip of the leaf to the midrib. The angle measured (AN) was that between the two basal sides at the point of attachment to the stem. The height (HT) was taken from the point of leaf attachment at the stem to the ground or water below. The direction of the leaf (DIR) was the compass direction that the leaf's midrib pointed towards. The age of the leaf (AGE) was determined by numbering the leaves based on their relative position on the plant. New leaves of *Manicaria saccifera* grow on the inner portion of the plant, therefore older leaves (higher numbers) were on the peripheral area of the plant while younger leaves (lower numbers) were on the inner part of the plant. The midrib length, basal length, side length and front length were measured for both the left and right side of the leaf in all cases. This was due to the leaves not being perfectly symmetrical. These eight measurements were done in centimeters as was the height. The angle and direction were both measured in degrees while age had no units since it was a relative measurement.

The leaves scored on these 12 measurements were from three distinct groups; altered leaves, a random set of unaltered leaves, and a random set of unaltered leaves on the same plant as altered leaves. All leaves were from the juvenile stage of the plant, the adult plant has separated leaves which were never found altered.

The data was analyzed using SAS computer programs. The means and basic statistics were calculated for each group (Table 1) based on each measurement. Then each group was tested against the other two to determine if the differences in their means was statistically significant, a one-way analysis of variance was used to determine differences (Table 2). The final test of the data was a discriminant functions analysis of the *a priori* determined groups to determine if the groups were significantly different in multivariate space.

Results

The results of the ANOVA (Table 2) show that the random leaves (Group 0) are significantly different from the altered leaves (Group 2) in all but 4 measurements, which are basal length of the right side of the plant, angle, direction and age of the leaf. The other 8 measures are significant ($P< 0.05$) and in each case the altered leaves have greater means than the random population of unaltered leaves. The ANOVA of the altered leaves versus the unaltered leaves on the same plant as a tent (Group 1) has somewhat different results. Only six of the 12 measurements are significant in this analysis. The side and front lengths, both left and right, are significant, the height of the leaf and the age of the leaf are also significant. The final pairwise comparison, the two unaltered groups, had only one significantly different value, basal length of the left side.

The discriminant functions analysis of the entire group was significant, Wilks' Lambda was significant ($P<0.05$). The histogram of the data scored on discriminant functions shows three groups (Figure2). The two unaltered leaf groups were only significantly different for one of the 12 measurements, therefore an analysis was performed comparing only the random unaltered (group 0) and the altered leaves. The discriminant functions analysis of the random leaves versus the altered leaves was also significantly different with the first discriminant function account for 36% of the variance (squared canonical correlation=0.36). The histogram of group 0 versus group 2 by the discriminant function score shows the groups clearly separated (Figure 3). The discriminant functions analysis of the two types of random leaves were not significantly different in multivariate space.

Therefore the leaves which the bats alter are not a random selection from the population but a specific subset of the available leaves. The selected leaves are longer, MR and ML are larger, wider, and higher. The bats are also selecting specific leaves on a plant. They choose the older leaves on the plant, mean age of 3.46 for altered leaves versus a means age of 3.97 for the unaltered leaves on the same plants.

Discussion

Manicaria saccifera is the dominant palm species at the Cano Palma Biological station, while *Artibeus watsoni* is the most common tent-making species in the area. The only other tent-making bat species found in the area were *Vampressa nymphaea*, *Uroderma bilobatum* and *Artibeus jamacensis*. The other species were found in small numbers and only *V. nymphaea* were found in tents. There are no other known reports of *Artibeus watsoni* constructing tents in this species of palm.

Artibeus watsoni do select particular leaves to alter for their diurnal roosts. They choose both specific leaves and position of leaves on the plant. They prefer larger leaves which are high off the ground. The height they choose is limited by the growth pattern of the plant, once *M. saccifera* matures the leaves are no longer the same as in the younger forms. The leaf separates along the rib forming a typical palm-like leaf, these leaves are less suitable for tent use by the bats and subsequently none of these leaves were found altered. Since they were never found altered, these mature leaves were not considered in the random data set. Therefore *A. watsoni* chooses the high larger juvenile leaves to make their roosts in. The selection of the plant and position of the leaf in the plant are also not randomly chosen by the bats. Only the juvenile plants had altered leaves and the higher older leaves of the plant were selected over the other leaves on the plant. Thus A. watsoni chooses both specific leaves and position of leaves on the plant in constructing tents.

Since bats are making a choice of the leaves they alter into tents then there must be some reason why these particular leaves are chosen. There are several possibilities to explain leaf choice:(1) The bats are phylogenetically constrained, and leaf choice has no real advantage to them. (2) The microhabitat of larger, higher and older leaves is advantageous. (3) The selection of the leaf site conceals or prevents attack by predators. (4) They select leaves which have the easiest access for entry by flight.

The first option seems unlikely since the behavior, tent construction, is fairly wide spread and considered convergent (Kunz et al, in press). There is no reliable phylogenetic analysis of Phyllostominae using species as the operational units. Thus the character, tent-making, could not be optimized onto the cladogram to determine if this is a trait that the ancestor of *A. watsoni* had. If it were determined that tent construction was a plesiomorphic character for *A. watsoni*'s group then there may not be any advantage to the individual bats, it could be a character which has no selective advantage but remains since it is not disadvantageous.

The second explanation, microhabitat, cannot be determined without more research. The microhabitat of altered leaves of different sizes and unaltered leaves could be recorded under various conditions. If it were found that large altered leaves maintained a better microhabitat for the bats then this could explain the leaf choice. This type of study could also be used to determine if the level of illumination was also being selected for, if microhabitat is important then the position of the plant and the amount of sunlight it receives may also be important.

The seasonal difference in climate may also change leaf selection and roosting behavior, more bats may roost together in colder seasons to conserve heat, thus a larger leaf would be needed.

This line of inquiry could explain the choice of leaf but it could not explain the choice of leaf position on the plant. The third option may explain these factors. Since new leaves grow from the middle of the plant they push older leaves out. Therefore the older leaves are further away from other leaves on the plant. This would allow better protection from certain predators. For instance snakes can climb up the plant to attack the bats, if the tent is further away from other stems then an attacking snake would have to climb up the stem of the tent. The bats would be alerted of the predator as soon as it touched the stem. Boinski and Timm (1985) determined that squirrel monkeys (*Saimiri oerstedi*) recognize tents and attack them. The older males are the best hunters of tent roosting bats and attack from above. They locate a tent then jump onto it trapping the bats inside and stunning them when they hit the ground. Therefore it would seem that better concealed tents afford more protection, but at Cano Palma the tents tend to be high and in the open. This may be due to the absence of squirrel monkeys in the area, there are howler monkeys and spider monkeys but no squirrel monkeys were ever seen. These other species of monkeys may also prey upon bats but the level of predation, if it exists, was very low and did not seem to affect the bats. Over 70 tents were checked daily and none of the tents were ever found destroyed by monkeys. Boinski and Timm (1985) also documented predation by double-toothed kites (*Harpagus bidentatus*) on disturbed tent roosting bats. The birds followed the monkeys and attacked any bats that escaped from the monkeys. Monkeys were not disturbing the bats at Cano Palma but many bats were disturbed during the study, none of the bats were seen attacked by double-tooth kites or any other bird.

The final explanation, access, could explain the position and height of the altered leaves. The bat must be able to enter and leave the tent unobstructed. By altering higher leaves which are farther out from the plant there are less obstacles. The altered leaves found in the study tended to be in the open, they were along paths and in open areas of the forest, when tents were found in denser areas they were high up and the entrance was clear.

The tent roosting species *Artibeus watsoni* preferentially select larger leaves which are on the periphery of the plant, the older leaves on the plant. These leaves are higher up than the average juvenile leaf, but they are not as high as the mature leaves. The mature leaves are not used by the bats as tents. The selective advantage, if there is one, of choosing these leaves is unknown but most likely a combination of several factors. The leaf must be accessible for easy entrance, it must be large enough to house several bats, it must provide a suitable microhabitat and it must give protection against predators.

References

Barbour, T. 1932.. A peculiar roosting habit of bats. *Quarterly Review of Biology*. 7:307-312.

Boinski, S and Timm, R.M. 1985. Predation by squirrel monkeys and double-toothed kites on tent-making bats. *Journal of Primatology*. 9:121-127.

Chapman, F.M. 1932. A home-making bat. *Natural History*. 32:555-556.

Choe, J.C. and Timm, R.M. 1985. Roosting site selection by *Artibeus watsoni* (Chiroptera:Phyllostomidae) on *Anturium ravenii* (Araceae) in Costa Rica. *Journal of Tropical Ecology*. 1:241-247.

Kunz,T.H., Fujita, M.S., Brooke, A.P. & McCracken,G. 1993. Bats and tents: Convergence in tent architecture and tent-making behavior among neotropical and paleotropical species. in press.

	Group 0 vs Group 1	Group1 vs Group2	Group 0 vs Group2
MR	NS (0.12)	NS (0.06)	S (0.0005)
ML	NS (0.12)	NS (0.41)	S (0.01)
BL	S (0.01)	NS (0.09)	S (0.002)
BR	NS (0.12)	NS (0.66)	NS (0.06)
SL	NS (0.13)	S (0.04)	S (0.0001)
SR	NS (0.23)	S (0.02)	S (0.0004)
FL	NS (0.06)	S (0.005)	S (0.0001)
FR	NS (0.10)	S (0.004)	S (0.001)
AN	NS (0.07)	NS (0.35)	NS (0.31)
HT	NS (0.82)	S (0.01)	S (0.04)
DIR	NS (0.16)	NS (0.13)	NS (0.97)
AGE	NS (0.49)	S (0.04)	NS (0.16)

Table 2: The P-values from the pairwise ANOVAs. The groups and characters are the same used in Table 1. The level of significance was $P<0.05$. NS=not significantly different, S=significantly different.

	Group 0	Group 1	Group 2
ML (cm)	38.4	42.7	48.4
MR (cm)	38.8	43.0	45.5
BL (cm)	51.5	56.2	59.7
BR (cm)	53.6	56.6	57.5
SL (cm)	26.8	30.0	36.6
SR (cm)	27.2	29.8	35.6
FL (cm)	25.7	27.8	32.6
FR (cm)	25.6	27.3	31.8
AN (degrees)	76.8	73.4	75.0
HT (cm)	235.3	239.0	272.9
DIR (degrees)	164.7	194.7	165.5
AGE	3.1	3.0	3.5

Table 1: Means for the three groups based on the 12 measurements. M=midrib length for left and right, B=basal length for left and right, S=side length for left and right, F=front length for left and right, AN=angle at the base of the leaf, HT=height of leaf, DIR=compass direction leaf facing, AGE=the relative age of the leaf. Group 0= random unaltered leaves (N=60), Group 1= random unaltered leaves on the same plant with a tent (N=60), Group 2= altered leaves (N=50).

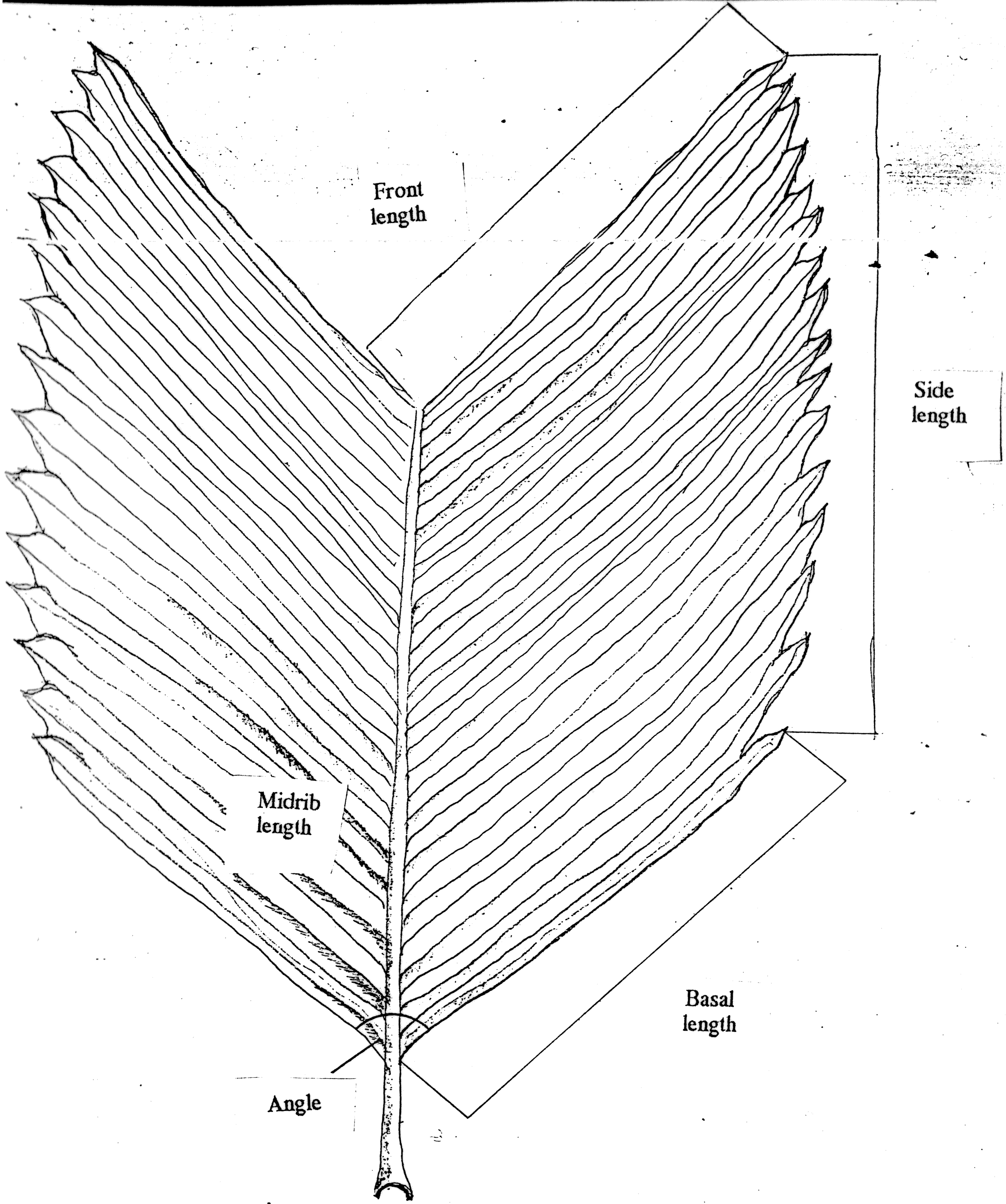

Figure 1: Drawing of *Manicaria sacciferawith* measured section indicated.

FREQUENCY OF CAN1

```
CAN1                                                   CUM              CUM
MIDPOINT                                         FREQ  FREQ  PERCENT  PERCENT
      |
-4.2  |0                                            1     1     0.59     0.59
-3.0  |                                             0     1     0.00     0.59
-1.8  |000001112                                   18    19    10.59    11.18
-0.6  |0000000000000000011111111111111111112222    80    99    47.06    58.24
 0.6  |00000001111111222222222                     45   144    26.47    84.71
 1.8  |01122222222                                 21   165    12.35    97.06
 3.0  |22                                           3   168     1.76    98.82
 4.2  |2                                            1   169     0.59    99.41
 5.4  |2                                            1   170     0.59   100.00
      -----+----+----+----+----+----+----+----+
          10   20   30   40   50   60   70   80

              FREQUENCY
```

Figure 2:Histogram from dfa analysis of all three groups together.
Group 0=random unaltered leaves, Group 1=unaltered leaves on the same plant as tents, Group 2=altered leaves.

```
                              FREQUENCY OF CAN1

 CAN1                                                        CUM                CUM
MIDPOINT                                               FREQ. FREQ   PERCENT   PERCENT
         |
 -3.5    |0                                              1      1      0.91      0.91
 -2.5    |0                                              1      2      0.91      1.82
 -1.5    |000000000000000002                            18     20     16.36     18.18
 -0.5    |0000000000000000000000000000002222222222      40     60     36.36     54.55
  0.5    |0000000002222222222222222                     25     85     22.73     77.27
  1.5    |000222222222222222                            18    103     16.36     93.64
  2.5    |222222                                         6    109      5.45     99.09
  3.5    |                                               0    109      0.00     99.09
  4.5    |2                                              1    110      0.91    100.00
         -----+----+----+----+----+----+----+----+
              5   10   15   20   25   30   35   40

                        FREQUENCY
```

Figure 3: Hisrogram from the discriminant functions analysis of altered versus random unaltered leaves (Group 2 vs Group 0)