Tent, Tent who made the Tent: An analysis of observations on tent making by *Artibeus watsoni* (Phyllostomidae) in Costa Rica

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498 project
Introduction

The choice of a roost is a very important factor for bats because they are highly susceptible to environmental conditions and predation when in their daily torpor. The proposed primitive condition for bat roosts is in caves (Kunz, 1982). From this primitive location bats diversified and began using tree hollows and external roosts. External roosting has the advantage of being closer to food sources and is not a limiting factor because the number of available leaves or trees is high. External roosting suffers, however, from a poor microclimate and a higher chance of predation. The shift to tent making was probably in response to these disadvantages (Timm & Clauson, 1990).

Bats modify leaves by chewing at the veins branching out from the midrib so that the leaf collapses along the weakened line but does not fall off. The hollow formed by the alteration is then used as a roost by the bat(s). The tent provides a suitable microclimate which resists temperature, humidity and light changes more effectively than an external roost and also provides protection from predators (Timm & Clauson, 1990). The roosts are also superior sites for newborn bats. These nonvolant juveniles need a safe roost for protection from predators when they are left alone during parental foraging and they require an appropriate microclimate as they cannot thermoregulate very well.

The first suggestion that bats were altering leaves to make roosts came from Thomas Barbour in 1932 when he observed a *Uroderma bilobatum* roosting in a curiously shaped leaf he called a tent. Since that time, 14 Phyllostomidae, 1 Vespertilionidae and 2 Pteropodidae have been observed roosting in altered leaves (Kunz et. al., 1993) and upwards of 40 papers (pers. obs.) have been published on bats roosting in tents. Despite the attention given to this curious roosting behaviour, no one has ever witnessed a bat altering a leaf and there are still doubts whether they actually do so (Eisentraut, 1975). It is the purpose of this paper to
demonstrate that bats are indeed responsible for making these tents and it is, in fact single male bats who do so, by referring to observations collected on *Artibeus watsoni* (Phyllostomidae) over a one month period at Cano Palma reserve in Costa Rica.

**Materials and Methods**

**Study site**

The research was conducted at the Cano Palma biological station in Guanacaste province, Costa Rica from December 15, 1992 to January 7, 1993. The station is located approximately 10 km north of Tortuguero village. The area is classified as Tropical Wet Forest life zone (Holdridge, 1967) and consists largely of primary swamp forest. The most common plant in the study site was *Manicaria saccifera* and this was the plant that the *Artibeus watsoni* was making into tents.

**Site preparation**

The area was surveyed over a three day period in order to determine the location of all bat tents. 75 tents were found and numbered with a small piece of flagging tape concealed at the base of the stem. A map of the study site is shown in Appendix A. Once the tents were marked, we proceeded to capture the bats occupying tents using a hand net. The bats were marked with ball and chain necklaces that had a colour coded band on them for individual identification. The area was then surveyed on a daily basis to determine where bats were roosting.

A secondary site was also prepared 300 m to the north of the site shown in Appendix A. The purpose of the secondary site was to establish suitable conditions for observing a bat(s) in the act of constructing a tent. To accomplish this goal, all of the tents were removed from a 1 hectare area plot and this area was surveyed every other day to check for tents under construction. When these tents
were found, they were observed at night using a night vision scope to see how many bats were making the tent and how the construction was undertaken.

Collateral data

In addition to the direct observations of tent construction, further data was collected to corroborate the identity of the tent constructors. A series of measurements from the primary study site was taken on each tent that reflected the tent's overall architecture (Appendix B). Distance measurements were taken with a tape measure and angles with a protractor. A set of discrete tent architecture data was also collected by observation. In addition to these measures, data was collected on which tent a bat would fly to upon release or being disturbed for purposes of determining which bats inhabited which tents.

Analysis of collateral data

Principle component analysis and a minimum spanning tree were calculated for the continuous tent architecture data while Jaccards and Simple-Matching coefficients were calculated for the discrete. Computer programs were from the Numerical Taxonomy System of Multivariate Statistical Programs (Rising, 1991). The data was clustered using the unweighted pair group on arithmetic means from the average taxonomic distance, Pearson's correlation and Manhattan distance matrixes computed by the program. The minimum spanning tree was calculated using average taxonomic distance and superimposed onto the two dimensional principal component diagram of the first two factors. The PCA was performed on the character correlation matrix.

Results

The results from the direct observation proved to be somewhat disappointing. When the tents in the secondary study area were disturbed, the
resident bats simply left the area. It was not until the fourth week of the study that evidence was found of a tent under construction. This tent was observed with a night vision scope from 6:00pm until 8:00pm when a bat showed arrived and landed under the leaf. Because the leaf had already started to bend down it was not possible to determine what the bat was doing beneath the tent. Observations on the following day revealed that more side veins had been cut on the leaf and the fresh cuts were stained purple. Only one bat was observed in the area that evening and its sex was not determined.

The PCA results were also inconclusive. The first three eigenvalues only represent 49.64% of the information, and even when the analysis was done to 13 eigenvalues, the results were still ambiguous. The map of factor 1 vs factor 2 is shown in Appendix C. The eigenvalues produced by the analysis are also indicated in this appendix. Because the eigenvalues for the first two factors were so low, only 37.83% of trace together, the minimum spanning tree was taken as indicative of the relationship presented by the PCA. The minimum spanning tree is shown in Appendix C2, its matrix correlation is 0.45082.

The Jaccards and Simple-Matching results are shown in Appendix D. It can be seen from this phenogram, both gave the same topology so only one was shown in the appendix, that there is evidence for distinct clusters supported by the discrete tent architecture data. The correlation for the phenogram is 0.7193.

The last set of data to consider is which tents have been occupied by bats. The following table summarizes the results based on which tents a group of bats occupied:
In the above table B on Al is the identity (necklace code) of the male bat that was tracked and/or found in the tents 19, 24 and 28. B and W is the identity of the male in the social group but there were also up to three females with him (the number of females varied). W on Y is the male id and he also was found with three females. And the two ? cases represent individual unmarked bats that were disturbed before being caught and then followed to another tent.

Discussion

The assumption taken at the onset of this project was bats are responsible for making their own tents. The goal of the project was to go out in to the field and observe this construction directly to determine how many bats were involved in construction and what sex the bats were. Unfortunately, results only started to come in on January 6, the second last day of the study. An auxiliary project had already been started to account for this lack of results and that then will be the focus of this discussion. The backup project, carried out in the primary study site, was based on the observation that spatial clusters of tents shared unique architectural styles. From this observation, it was hypothesized that a single bat, or small group of bats, was responsible for construction of each of these clusters and there where elements in the architecture that could help identify which bat was responsible for construction. In other words, if tents that were inhabited by a bat
or social group of bats also show up as a distinct cluster based on tent architecture data then this would indicate that the bat or group of bats was responsible for the construction of these tents. To test this hypothesis two assumptions had to be made; one, that bats were responsible for making the tents and two, that specific bats used specific tents to the exclusion of other bats. The discussion will first deal with the justification for these assumptions.

Bats do make tents

The justification for this assumption comes largely from observations made in the last two days on a tent found under construction in the secondary study site. A single bat was observed flying into a partially completed tent during the night and purple stains on the areas of the leaf that had been cut that night were found the next morning. This observation suggests that the bat seen under the leaf was responsible for the work done on the tent over the night and the purple stain was due to the consumption of wild grapes before construction started. This same staining was observed on one of the researcher's gloves when she removed a bat from a mist net after it had been feeding on these same grapes, albeit the stain on the glove was due to feces and not saliva.

Another piece of evidence gathered by observation is the contrast in architecture between leaves modified by insects and those modified by bats. Insects have been cited in the past as being responsible for altering the leaves in which bats are found roosting (Eisentraut, 1975). Appendix E shows reproductions of leaves cut by a) insects, in this case leaf cutter ants, and b) *Artibeus watsoni*. It can be seen that the insect cuts are not in a straight line nor are they confine primarily to the branching veins of the leaf but rather involve removing large segments of the leaf tissue in between veins. The bat cuts, on the other hand, are centered primarily on the veins themselves and there is no tissue
removal but only some cutting of tissue by the lateral border of the leaf. Furthermore, the cut is in a distinct J shaped pattern not seen in the insect cut leaf.

One final piece of evidence that suggests bats are responsible for altering the leaf is the pattern of puncture marks seen on the leaf itself. The bat cuts by hanging beneath the leaf and making puncture marks with its canines along the side veins. With veins close to the lateral edge of the leaf the biting is concentrated enough to cut through the tissue while closer to the midrib biting only serves to weaken the vein. Measurements taken of the width of these puncture marks range from 4.5–4.7 mm. The canine width of *Artibeus watsoni* was measured at 4.55 mm. The similarity of these two measures indicates that the bats were responsible for constructing the tents.

Clusters used to the exclusion of others

Table 1 shows which tents were used by bats during the study period. Other bats were observed in tents but it was not known what tent they flew to after being disturbed so these cases were not useful for a consideration of clustering. It should be noted that no different bats (i.e., bats outside of the immediate social group) were ever found in a tent that was previously occupied by another group. The cases in table 1 show instances where bats were disturbed or caught and then tracked to another tent. For example, 4 *Artibeus watsoni* were found in tent 65 and caught with a hand net. Upon release, 2 flew to 64, one flew to 66 and one to 68. A few days later the same 4 were found in 71 and when released flew to 72 and 73. They were also caught in tent 69. From this information it is inferred that this social group owns these tents because they were never found outside of this cluster and no other bat was found within the cluster.

Another piece of evidence that demonstrates the exclusive use of a cluster by a social group is the refusal of tired bats to roost in another bat's tent. Bats that are exhausted after handling will roost in a bat bag or on a branch or even hanging
on to a hand, but they will not roost in a tent that is not their own. Presumably they can recognize tents by structure or smell.

One final piece of evidence that lends support to the exclusive use of a group of tents by bats is the clustering of each social group's tents (see outlined tents in Appendix A). A clustering analysis was performed using the DISTRIBUTS program from the ZOO 323 computer program (ZOO 323, 1991) based on the distribution of the tents. The transects were calculated by dividing the study site map into 1 cm by 1 cm squares which represent 8 m by 8 m transects on the actual study site. Cluster analysis was only performed in the on a 2.5 hectare section of the study area as this was the only plot deemed to have a uniform distribution of the plant species, Manicaria saccifera, that Artibeus watsoni was using for tents. The DISTRIBUTS analysis gives a mean=0.2451 and a variance=0.4202 which indicates a clumped distribution. In this case the meaning of clumped distribution is the probability of finding an individual in one location increases if there are other individuals around. This sort of distribution indicates small social groups with large spaces in between. This finding adds further to the conclusion that bats are using their own clump of tents to the exclusion of others.

Recognizing a bat from its tent architecture

With the justification for the assumptions presented, it remains to be seen if the tents used by bats will also cluster together based on tent architecture. Examination of the continuous data on the minimum spanning tree reveals that the conclusions from this source are ambiguous. Consider first the tents used by B on A1. The minimum spanning tree shows tents 19 and 24 to be closely related (1 step away) but neither tent is close to 28 (6 steps away). B and W data is also ambiguous. The tree shows tents 64, 68, 65 to be closest neighbors. These three are then 2 steps away from 72. 66, 69 and 73 are also clumped together but are
about 6 steps away from the first three trees. And finally, tent 71 is found by itself 5 steps from any other tree of these group. The next set of trees comes from W on Y. The two trees in this instance, 3 and 4 are found 12 steps away on the tree and apparently have no relationship at all. The last two set of tents come from single observances of unmarked bats. In this case, tents 6 and 9 are very close (2 steps) as are tents 30a and 39 (3 steps). The results from the minimum spanning tree are somewhat ambiguous. The tree tends to show these clusters grouping close together but not with enough certainty to draw any conclusions. It is most likely due to the poor representation of the actual architecture by the limited measurements taken that the results are so ambiguous.

The next line of evidence to consider is the discrete analysis of the tent architecture. Here, discrete aspects of the cut itself (number of ribs, was midrib cut, J shaped cut or other...) were analyzed using Jaccards and Simple-Matching coefficients. Again the results of this analysis are somewhat ambiguous. While the cluster inhabited by B and W comes out in a very tight cluster, none of the other tents are found with others from their group (24 is found with 28 but 19 is not near any of them). This leaves two possible conclusions to be drawn; the hypothesis that individual bats are responsible for a specific cluster is wrong or the measurements used were ineffective at capturing the tent architecture. Based on an additional set of observations, I will conclude the later.

Further observations

The conclusion that it is the measurements to blame for the ambiguous results stems from three observations. 1) I could tell what cluster of tents I was in by looking at the architecture. For example, an additional set of tents was discovered a few days after four bats were found in tent 65. The new cluster of three tents looked identical in construction to the 64,65,66,68 cluster found earlier. A few days later the four bats from 65 were found in this new cluster (71,72,73).
2) the B and W cluster of tents was remarkable in having a distortion in the J cuts on both sides. While normal J cuts resembled the capitalized letter to a great extent, the B and W cluster had a distinct jag in the J half way up. 3) The measurement were taken in an attempt to recreate the tent architecture as a paper model. Recreation as such a model reveals just how much information is lost. See cut out labelled Appendix F.

Conclusions from tent architecture data

It is to be concluded then, based more on observations taken than the analysis of the data, that the tents occupied by a bat group also cluster together based on architecture. This conclusion leads directly into the next, if a group of tents can be distinguished by peculiarities in its construction (ie jagged J cut) then one individual must be responsible for all of the tents in a cluster. It is tempting to say that the same group of individuals is responsible for the construction of the tent cluster but this is clearly not the case. In each of the tents from the B and W cluster both of the J cuts have the same jag in the same location, half way up the J. One alternative answer is the behaviour is a learned one and this social group all learned to make a jagged J, but then individuals born of the group would also have learned how to make a jagged J and when they went off to start their own group they too would use a jagged J. This is clearly not the case as only one group of bats, or one individual (B and W), uses this type of cut. Therefore, it is concluded that one individual in the group is responsible for the construction of all of the tents.

Determining the sex

This last section of the discussion is not based directly on the findings of this report but relies heavily on the data collected for another report from this study. Mulcahy (1993), concludes in her report that the social structure observed in the tent roosting *Artibeus watsoni* is that of resource defense polygyny. In this
social structure males have a harem and attract females by controlling a limited resource, in this case tents. This finding agrees with the conclusion that a single individual is responsible for the construction of all of the tents in a cluster. If tents are the limiting factor in the scenario then a male that builds a number of tents will attract females to him. The tents would be constructed alone and in a tight cluster for ease of defense, the tents would also be expected to be isolated from other clusters, an observation that is also found (see clusters in appendix A). It can then be speculated that it is a single male who is responsible for constructing the tents in a cluster.

Conclusion

This study concludes that a single individual is responsible for constructing the tents in a given cluster and goes on to speculate that this individual is a male. The deduction that the individual is a male is based largely on conclusion drawn by Mulcahy (1993) that the social structure observed in the Aribesus watsoni on the study site is resource defense polygyny with the tents being the resource defended. While data was collected on tent architecture in order to demonstrate that there was a correlation between tents inhabited and tents constructed, the conclusions drawn from this data were ambiguous. This was due to the nature of the measurements taken. Further research in this area should concentrate more on finding appropriate measurements to establish this correlation and establish an experimental design to observe the act of tent construction directly. While the removal experiment did encourage bats to construct new tents in the study area, the time available and the equipment on hand were not suitable to make appropriate observations. To get a clear view of what goes on during the tent-making process, it is probably necessary to use a film camera with a night scope. The bats would also have to be marked in a clearer manner, the colour coded
necklaces were rarely visible, one suggestion is the use of surgical dye to draw numbers on the head of the bats. If the dye was florescent, it would then be possible to identify the bat without disturbing it. It is only by direct observation that the number of bats responsible for construction and the sex of the bats involved will be known for certain.

References
Holdridge, L.R. 1967. Life zone ecology. Tropical Science Center, San Jose.