

Canines as a measuring tool for leaf tent construction in *Dermanura watsoni*

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Many animals are capable of constructing structures to modify the environment for their own benefit. The design of these structures requires animals to perceive dimensions. However, how animals take measurements to achieve the final design of the structures they construct is known for only very few species. In the Neotropics, a few bat species build roosts or leaf tents that serve different purposes. Thomas's fruit-eating bat (*Dermanura watsoni*) constructs tents that have complex designs, when compared to other tent building bats. The bifid tent is a design built by producing a long, J-shaped cut on each side of understory plant leaves. We expect that to accomplish this complex design bats would require precise measurements during tent construction. We measured several bat morphological traits to infer which of them, if any, was used by the bats as a measuring device. *Dermanura watsoni* uses the distance between their lower canines to increase the perpendicular distance of the J-cut to the central vein of the leaf along the J-cut. The bat adds the distance between the canines to each subsequent secondary vein cut. This is the first study to infer which body part *D. watsoni* most likely uses as a measuring tool. Our results provide new insight into the evolution of body parts as measuring devices during tent construction in related and unrelated tent-building bat species.

Key words: tent-making bats, *Dermanura watsoni*, web construction, understory palms

INTRODUCTION

The ability to build structures has evolved independently in different groups of animals (Hansell, 2005). In all cases, animals build structures to modify their environment for their own benefit, and in most cases these structures serve multiple purposes for the builder. For instance, they are often designed to protect animals from predation, parasitism, and harsh environmental conditions (Jeanne, 1975; Skutch, 1976; Hansell, 1993; Nalepa and Bell, 1997; Foelix, 2011). In other cases, they increase capture effectiveness (e.g., spider webs) and reproductive success (e.g., bird and insect nests — Skutch, 1976; Eberhard, 1990a; Perna *et al.*, 2008).

Structures built by animals vary widely in design and materials across different groups, within groups and often even within the same individuals (Jeanne, 1975; Barrantes and Eberhard, 2012). All constructions have dimensions and therefore the builder is expected to have a perception of such dimensions. In other words, an animal constructing a particular structure is expected to be able to conduct some measurements in order to achieve the final design of the structure. However, details of how animals

perform these measurements during construction are known for only some spiders (Vollrath, 1987; Eberhard and Hesselberg, 2012), a few wasp species (West-Eberhard, 1969), and with less detail for a few bird species (Collias and Collias, 1970; Skutch, 1976).

In all known cases, animals use some body parts to measure distances during construction (e.g., retreats and breeding sites). Therefore, considering that construction of different structures is so widespread among animals, it is also expected that using body parts as measuring devices would be equally widespread. We will focus on leaf tents to investigate which body parts bats likely use to perform the measurements during tent construction. Nearly half of all bat species use different plant parts as roosts (Timm, 1987; Rodríguez-Herrera *et al.*, 2007). For many species roosts consist of unmodified leaves or natural tree cavities, but a small number of bat species (i.e., 22 species), most of them Neotropical, modify leaves to construct their roosts or tents (Rodríguez-Herrera *et al.*, 2007). It is as yet unknown if all 22 species construct their own roosts or if some of these species use leaves modified by other bats. Bats construct their roosts by biting or

chewing the leaf veins producing different designs, depending on the plant species on which the tent is constructed (Timm and Mortimer, 1976; Timm, 1984, 1987; Choe and Timm, 1985; Kunz *et al.*, 1994; Choe, 1997; Rodríguez-Herrera *et al.*, 2006, 2007). In the Neotropics, the tent building process has only been directly observed in the Honduran white bat, *Ectophylla alba* (LaVal and Rodríguez-Herrera, 2002; Rodríguez-Herrera *et al.*, 2006, 2011) and field information strongly suggests that Thomas's fruit eating bat, *Dermanura watsoni* also constructs tents (Choe and Timm, 1985; Chaverri and Kunz, 2006). Field observations and experiments conducted to measure the force needed to cut through the secondary veins of some palms used by *Uroderma* indicate that this species is also capable of constructing their own tents (B. Rodríguez-Herrera, unpublished data).

Ectophylla alba constructs only a relatively simple tent type (inverted-boat tent) which consists of one long cut on each side of the main vein of *Heliconia* leaves. Thus, the main vein likely serves

as a guide for the bat to cut the secondary veins of *Heliconia* leaves (Rodríguez-Herrera *et al.*, 2006). In contrast, *D. watsoni* constructs their tents with various designs, apparently influenced by the size and shape of the leaf (Kunz *et al.*, 1994). Palms (e.g., Arecaceae: *Asterogyne martiana*) and Panama hat plants (e.g., Cyclanthaceae: *Carludovica palmata*) are two of the plant species most frequently used by *D. watsoni* to construct their tents. On *A. martiana*, *D. watsoni* constructs a bifid tent that consist of two J-shaped cuts along nearly half the length of the central vein, one on each side of the main leaf vein (Fig. 1A). Each J-cut apparently consists of two sections, in the first section the bat chews the secondary veins nearly parallel to the main vein while in the second section the distance from the main vein to the J-cut increases gradually. This type of tent is constructed only on leaves that have bifurcated tips, so that the two cuts make one tip fold over the other as the leaf blade slants downward (Fig. 1B). In contrast to the relatively simple design of the tent constructed by *E. alba*, the cuts produced by

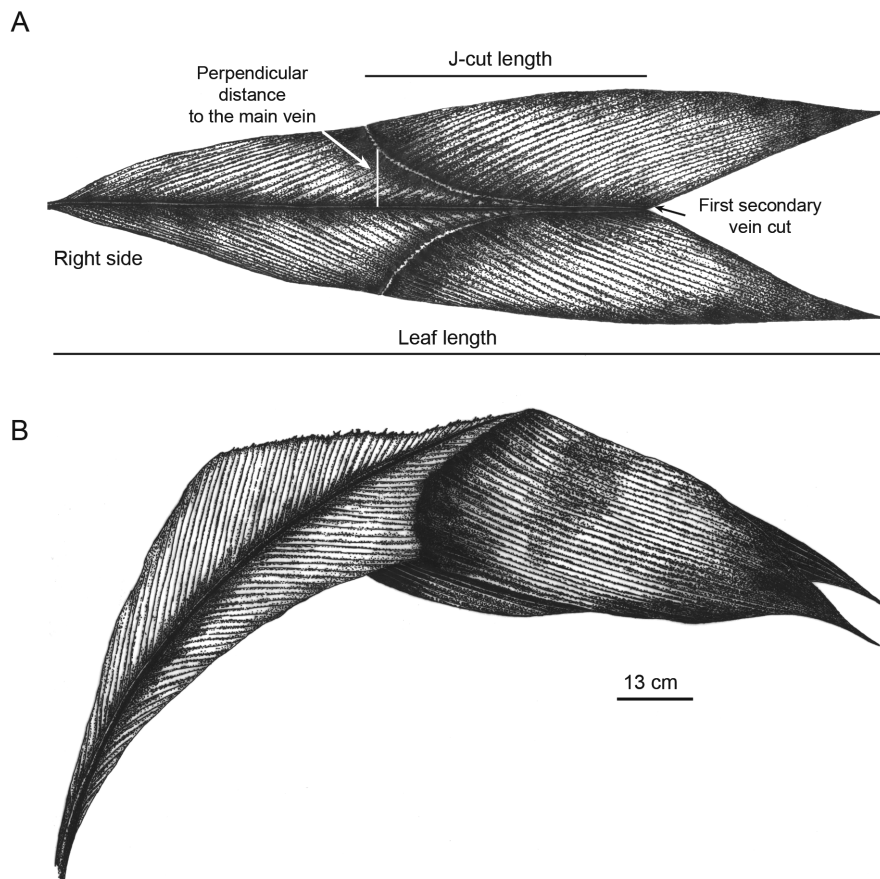


FIG. 1. Leaf tents constructed by *D. watsoni*: A — leaf tent showing the J-cuts and the dimensions measured for the analyses; B — leaf tent in its natural position

D. watsoni on leaves of *A. martiana* deviate away from the main vein from the tip toward the proximal section of the leaf and the cuts on each side of the main vein appear highly symmetrical.

Here we addressed the following questions regarding the expected measurements bats should make to achieve the final design of a bifid tent. First, which part of its body do bats likely use to measure the distance from the main vein, or between successive bites along the J-cuts? Since the first bites of the J-cut are close to the main vein and the distance from the main vein increases gradually along the J-cut, we expect the bat to use a part of its head as a measuring device. Second, does the perpendicular distance from the main vein to the J-cut increase constantly along the main vein? We expect that the increment in the perpendicular distance from the main vein to each point where the bat bites the leaf along the J-cut to be the same as the length of the bat's measuring device. Third, are the cuts on each side of the main vein symmetric? Strict symmetry between both J-cuts in a leaf is possible only if the perpendicular distance measured at any point of the main vein is the same on both sides of the leaf. We also consider in our analyses possible deviations from a strict symmetric design that still yield a functional bifid tent.

MATERIALS AND METHODS

Tent Measurements

We collected 18 leaves of *Asterogyne martiana* (Arecaceae) modified as bifid tents by *D. watsoni* at Tirimbina Biological Research station (10°26'N, 83°59'W; 150 m elevation), and at El Roble (10°26'N, 84°05'W; 110 m elevation), Sarapiquí, Heredia province, Costa Rica, in mature and old growth lowland rainforest. *A. martiana* is the plant most frequently used by *D. watsoni* to construct the bifid tents in the region (Rodríguez-Herrera *et al.*, 2007). We focus on bifid tents because this type of tent offers the opportunity to evaluate the symmetry between the J-cuts that the bat made on each side of the main vein and allows us to investigate which body traits the bats might use to measure where to bite the secondary veins to produce the J-cuts.

In each tent we measured total leaf length, length of the J-cut at each side of the main vein, and the perpendicular distance from the main vein to the point where bats bit each of the secondary veins (hereafter: distance to bitten point) (Fig. 1A). Occasionally a few secondary veins were not bitten by the bats and they were not included in the analyses. To determine whether J-cuts were strictly symmetric in each tent or if they had some deviation from strict symmetry, we defined two variables: count of the veins (1 to x) bitten by the bat along the J-cut, and the perpendicular distances from the main vein to the bites (D_1 to D_x). We numbered the secondary veins from 1 to x , 1 being the first secondary vein bitten of a J-cut at the tip of the leaf, where x corresponds to the last secondary vein bitten by

the bat at the opposite extreme of the J-cut. We measured the perpendicular distance at each bitten point (D_1 to D_x) rather than at fixed intervals along the main vein, because bats specifically bite the secondary veins during the construction of their tents and veins seldom have the same distance between them.

Bat Morphological Traits

We measured the rostrum and head width (at their widest section), head length (from the most distal parts of the back and front of the skull) and distance between upper canine teeth and between lower canine teeth as indicated in Fig. 2 from 24

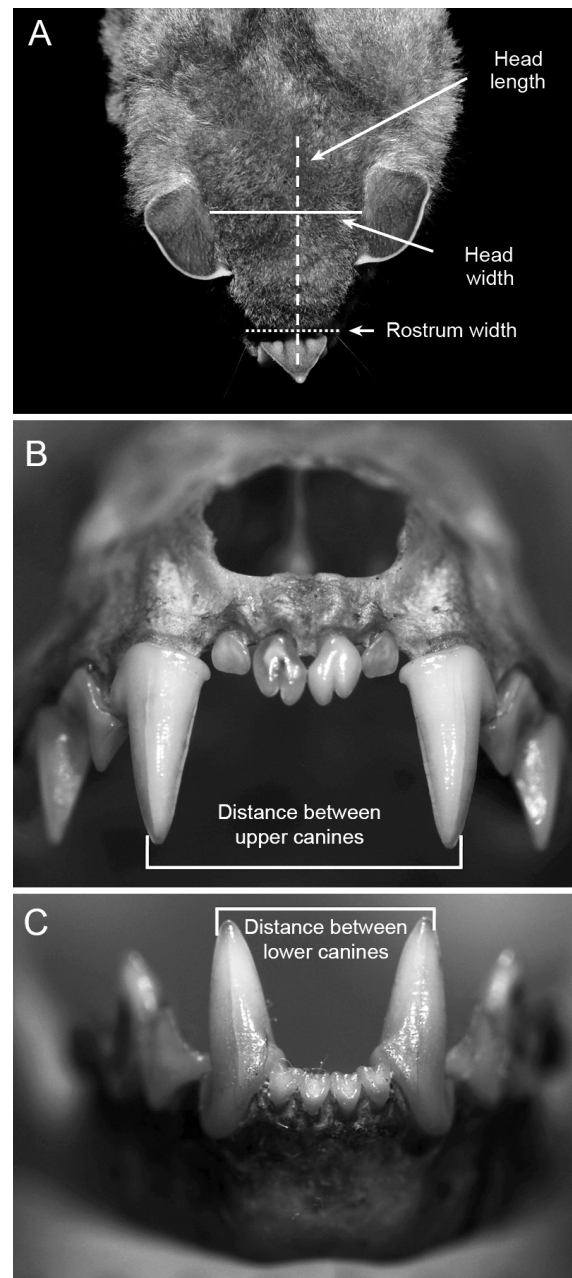


FIG. 2. Morphological features measured in *D. watsoni*. Dimensions of these features were used to infer which feature was used as a measuring devise during tent construction

specimens (8 ♀♀, 16 ♂♂) of *D. watsoni* preserved in alcohol in the Mammalogy Collection of the Museo de Zoología, Universidad de Costa Rica (catalog serial no: MZUCR1779–1783, 896–899, 901–906, 3550–3554, 2164–2166), using a digital caliper (Mitutoyo CD-8°C; ± 0.01). Only five specimens were collected in the region where the study was conducted which may introduce some additional variation in the analyses. We thought that one or some of these body parts might be used to measure distances during tent construction (Rodríguez-Herrera *et al.*, 2006), and included both males and females because it is unknown which sex builds the tents. The information available indicates that bats use their teeth to chew sections of the leaves to construct their tents (Choe and Timm, 1985; Chaverri and Kunz, 2006; Rodríguez-Herrera *et al.*, 2006, 2011). Additionally, the characteristics of the J-cut, first bites close to the main vein and the distance from the main vein increasing gradually along the J-cut, suggest that the distance between canine teeth or other dimensions of the head could be used by *D. watsoni* as a measuring device.

Statistical Analyses

To examine the increase in the perpendicular distance from the J-cut to the main vein from the tip to the basal section of the leaf (Fig. 1A), we regressed the position of the secondary vein (position 1 corresponded to secondary vein closest to the tip of the leaf), against the perpendicular distance of the corresponding secondary vein (dependent variable — Fig. 1A) for each side of each tent. The slope of this regression represents the increase in the perpendicular distance between the main vein and the J-cut performed by the bat. This increase should correspond to a bat's body part. In all cases we compared the fit between a simple linear regressions and segmented regressions via Akaike Information Criterion (AIC). Segmented regression allows us to test whether there is a constant increase of the perpendicular distances along the entire J-cut or if the increase changes significantly along different sections of the J-cut. The point where a significant change in the increase (slope) occurs is defined as a breaking point in the slope.

In *D. watsoni* it is unknown if males, females or both construct the tent. Therefore, before testing which morphological trait is more likely to be used by *D. watsoni* as a measuring device, we compared these traits between sexes using a multivariate analysis of variance. We then used a one-way ANOVA to compare the mean size of all morphological traits and the mean of the slopes of the regression described in the preceding paragraph. A mean of the slopes (right and left) was calculated for each section (prior to and after the breaking point) estimated by the segmented regression for each leaf. Including the slopes in the ANOVA allows us to compare whether the increase in the perpendicular distance along the J-cuts (from 1 to x) was statistically similar to the dimension of one or more of the morphological traits included. If the mean of the slopes does not differ from the mean of one (or more) morphological trait, it indicates that the J-cut increases by that dimension suggesting that this trait is likely to be used by the bat as a measuring device.

To measure the symmetry between the perpendicular distances on both J-cuts of each leaf we tested the following four scenarios. First, the perpendicular distances from the J-cut to the central vein could be the same on both sides of the leaf, at each measuring point. This will yield a strong correlation between perpendicular distances on both sides of the main vein. A regression of perpendicular distances from the right side against

the perpendicular distances of the left side will have a slope $b = 1$, an intercept $a = 0$, and a coefficient of determination $r^2 = 1$ producing a strictly symmetric design (S1). In a second scenario (S2) all perpendicular distances of one J-cut are larger by a constant dimension than the distances of the opposite J-cut (e.g., all perpendicular distances of the left J-cut are 3 mm longer than those of the right J-cut). In such a case we would have: $b = 1$, $a \neq 0$, $r^2 = 1$. In a third scenario (S3) the differences between opposite perpendicular distances vary randomly (random distribution of residuals along the fitted line) along J-cuts; under this scenario $b = 1$, $a = 0$, $r^2 < 1$. Finally, in the fourth scenario (S4) the perpendicular distances may all be larger on one side along a given section of the leaf, but with the opposite pattern for another section of the leaf, producing a curvilinear, non-random distribution of residuals along the adjusted line, resulting in $b \neq 1$ and $a \neq 0$, $r^2 < 1$. If the distribution of residuals is not random along the adjusted line, it may also have the following parameters: $b = 1$, $a = 0$, $r^2 < 1$; so that S3 and S4 may yield the same results. Hence, to have another statistical criterion we conducted runs tests to examine the distribution of residuals along the adjusted line of each leaf tent. For this test we considered a run as a series of either consecutive negative (i.e., residuals below the adjusted line) or positive residuals (i.e., residuals above the adjusted line) (Zar, 1984). With this additional criterion if we have a leaf tent whose regression yielded $b = 1$, $a = 0$, and $r^2 < 1$, with non-randomly distributed residuals along the adjusted line, we assign this leaf tent as S4. For the purpose of these analyses we considered values of $r^2 \geq 0.99$ as 1, since such a small deviation could be caused by measurement imprecisions. We used the R statistical Language, version 2.15.3 (R Development Core Team, 2013) for all statistical analyses.

RESULTS

Tent Morphology

Leaf tents had a total mean length of 122.9 ± 20.5 cm (range: 93.4–160.1 cm, $n = 18$), whereas the left and right J-cuts made by the bats on the leaves measured 39.7 ± 8.1 cm and 39.0 ± 7.5 cm, respectively. The length of J-cuts on each side of the leaf differed from 0.3 cm to 5.5 cm ($2.4 \text{ cm} \pm 1.9 \text{ cm}$) between sides and the longer cut was not always on the same side. Of the 18 tents, 11 had a difference of one cm or more between lengths of the J-cuts.

Based on information obtained from an independent study, we know that *D. watsoni* often constructed tents during a single night (B. Rodríguez-Herrera, unpublished data). However, occasionally the bat fails to finish the tent during one night. In these unfinished tents bats produced one J-cut and the leaf blade on the opposite side of the main vein is intact or nearly so. This information indicates that at least some bats produce one J-cut on the leaf blade first, and then the other on the opposite side of the main vein.

Morphological Variables of *D. watsoni*

There was a significant correlation between rostrum width and distance between lower canine teeth ($r = 0.49$, $P = 0.015$), rostrum width and head length ($r = 0.64$, $P < 0.001$), distance between lower canine teeth and head length ($r = 0.47$, $P = 0.022$) and a marginal correlation with distance between lower and distance between upper canine teeth ($r = 0.39$, $P = 0.06$; in all cases $n = 24$). Morphological variables did not differ between sexes (MANOVA Pillai test = 0.44, $d.f. = 1, 22$, $P = 0.15$).

Segmented Slope

Segmented regression analyses yielded two slopes, rather than one (based on Akaike information criterion) for each side of all 18 tents (Fig. 3). For a more general approach, we ran the same analysis for the values of the left sides of all 18 tents and then for values of all 18 right sides (Fig. 4). For this analysis, the first slope that corresponded to the

section of the tent within the first 11.83 cm (± 2.33 cm) from the initial construction point was $b = 0.78$ (CI 95%: 0.37–1.08) for the left side and $b = 0.62$ (0.30–0.97) for the right side. The second slope that corresponded to the rest of the leaf tent was $b = 2.85$ (2.69–3.02) for the left side and 3.03 (2.90–3.16) for the right side. Slope values did not differ significantly between the right and left sides of the first section of the J-cut (Tukey HSD test, $P = 0.996$, $n = 18$), nor did they differ between both sides of the second section of the J-cut (Tukey HSD test, $P = 0.916$, $n = 18$).

When we compared the slopes with the morphological traits, the distance between lower canines did not differ significantly from the mean of slopes corresponding to the second section of the J-cut (Tukey HSD test, $P = 0.09$), indicating a possible use of the distance between these canines as a measuring tool during tent construction. The distance between lower canines was also the closest morphological distance to the slopes of the first section of the J-cut

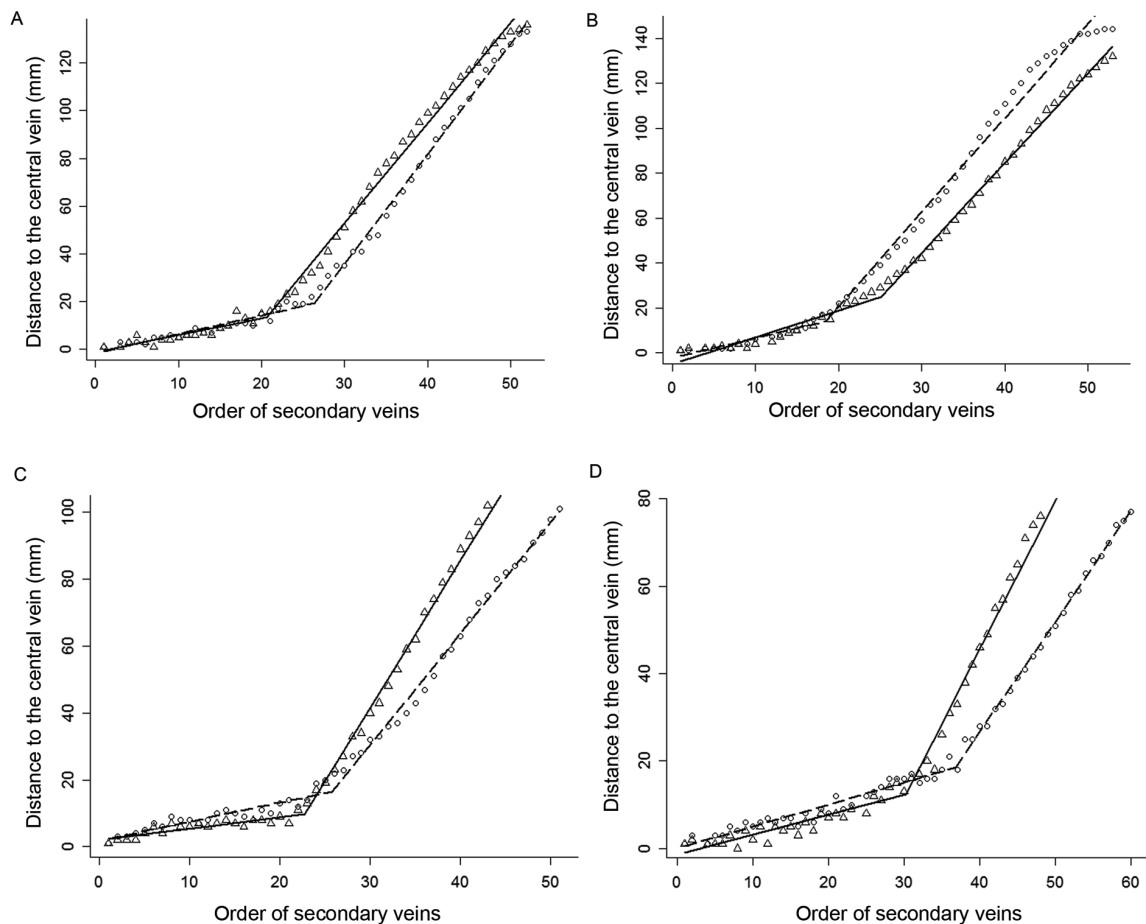


FIG. 3. Slopes for segmented regression of four of the 18 leaf tents. For each tent, the slopes of the right (dashed line) and left (continuous line) sides are presented. Other tents had similar pattern

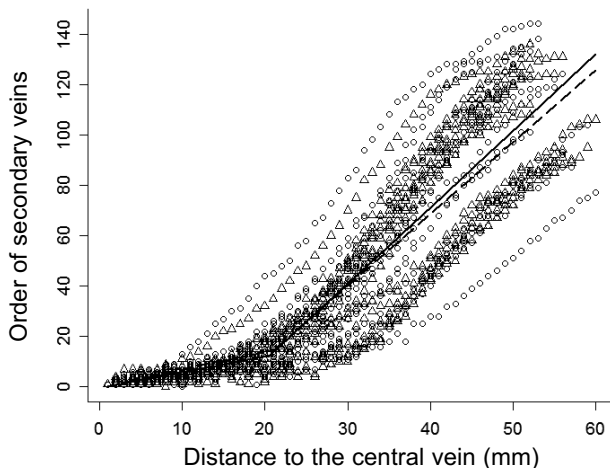


FIG. 4. Slopes of segmented regression for the 18 leaf tents. These include the slopes of the right (dashed line) and left (continuous line) sides. Triangles correspond to the right side of the tents and circles to the left side

(Fig. 5). The distance between lower canines differed significantly from the mean slopes corresponding to the first section of the J-cut ($P < 0.001$).

Tent Symmetry

Nearly all tents had the same, asymmetrical, pattern. Only one tent had strict symmetry (S1). The rest of the tents fitted the S4 scenario (using both statistical criteria). For all tents that fit the scenario S4 the residuals were not randomly distributed along the adjusted line. Similar results were obtained with paired t -tests; in only two out of the 18 tents the opposite perpendicular distances were similar on both sides of the leaf tent (paired t -test, $P > 0.05$).

DISCUSSION

Animals are expected to use body parts to measure dimensions of the structures they build. However, for only a few species is known which body parts are used as measuring devices for building their retreats, nests or snares. In ancient cultures, humans used body parts as measurement tools to record distances and design constructions (O'Brien and Christiansen, 1986; Garegae, 2005; Michailidou, 2010; Olman, 2012). Notably the 'foot' is still a widely used unit of length in the U.S.A. Other animals also use body parts as measuring tools during construction of different structures. For instance, birds used their chest and abdomen as rudimentary tools to build the cavities of their nests (Skutch, 1976; Collias and Collias, 1984). Precise measurements

using body parts are known for even fewer species. For instance, during nest construction *Polistes* wasps measure precisely the dimensions of the reproductive cells using their antennae (West-Eberhard, 1969). Orb-web spiders are also capable of precise measurements during web construction. During the construction of the sticky spiral (the sticky section of the web), these spiders use primarily the front legs to touch other threads previously attached and then decide where to attach the next segment of the sticky spiral thread (Eberhard, 1982; Eberhard and Hesselberg, 2012).

The bifid tents constructed by *D. watsoni* consist of two sections. In the first section that corresponds to the distal section of the leaf, J-cuts are nearly parallel to the main vein. The second section of the bifid tent begins with a drastic change in the slope, which is statistically identified by the breaking point between the two slopes. The slope of the second section of the bifid tent is larger than the slope corresponding to the first section and correlates with the distance between lower canine teeth. The increase in the slope of the second section of the tent produces the J-cuts that makes the leaf blade slant downward, forming an spacious roof where bats hang (position near to the breaking point of the tents). Our results strongly suggest that *D. watsoni* uses the distance between its lower canines to measure where to cut the secondary veins between successive bites along the second section of the J-cuts. With the teeth as a measuring device, bats can increase the perpendicular distance of the J-cut to the central vein of the leaf along the second section of the J-cut by adding the distance between the canines to each subsequent secondary vein cut. The first section of the J-cut is very close, and nearly parallel to the main vein, similar to the cut produced by *E. alba* during its tent construction. *Ectophylla alba* also builds its tent by producing two long cuts parallel to the central vein of *Heliconia* leaves, likely using the central vein as a guide to chew the secondary veins (Rodríguez-Herrera *et al.*, 2006). Thus, it is possible that *D. watsoni* also uses the main vein of the leaf as a guide during the first section of the J-cut, or another morphological feature not considered in this study (e.g., length of vibrissae). Unfortunately, there are no direct observations of how *D. watsoni* build the tents.

The design of the bifid tents constructed by *D. watsoni* deviated from a strict symmetry ($b = 1$, $a = 0$). These deviations may occur if different individuals with different lower-canine distances are involved in the construction of the same tent, by imprecision caused by movement of other individuals

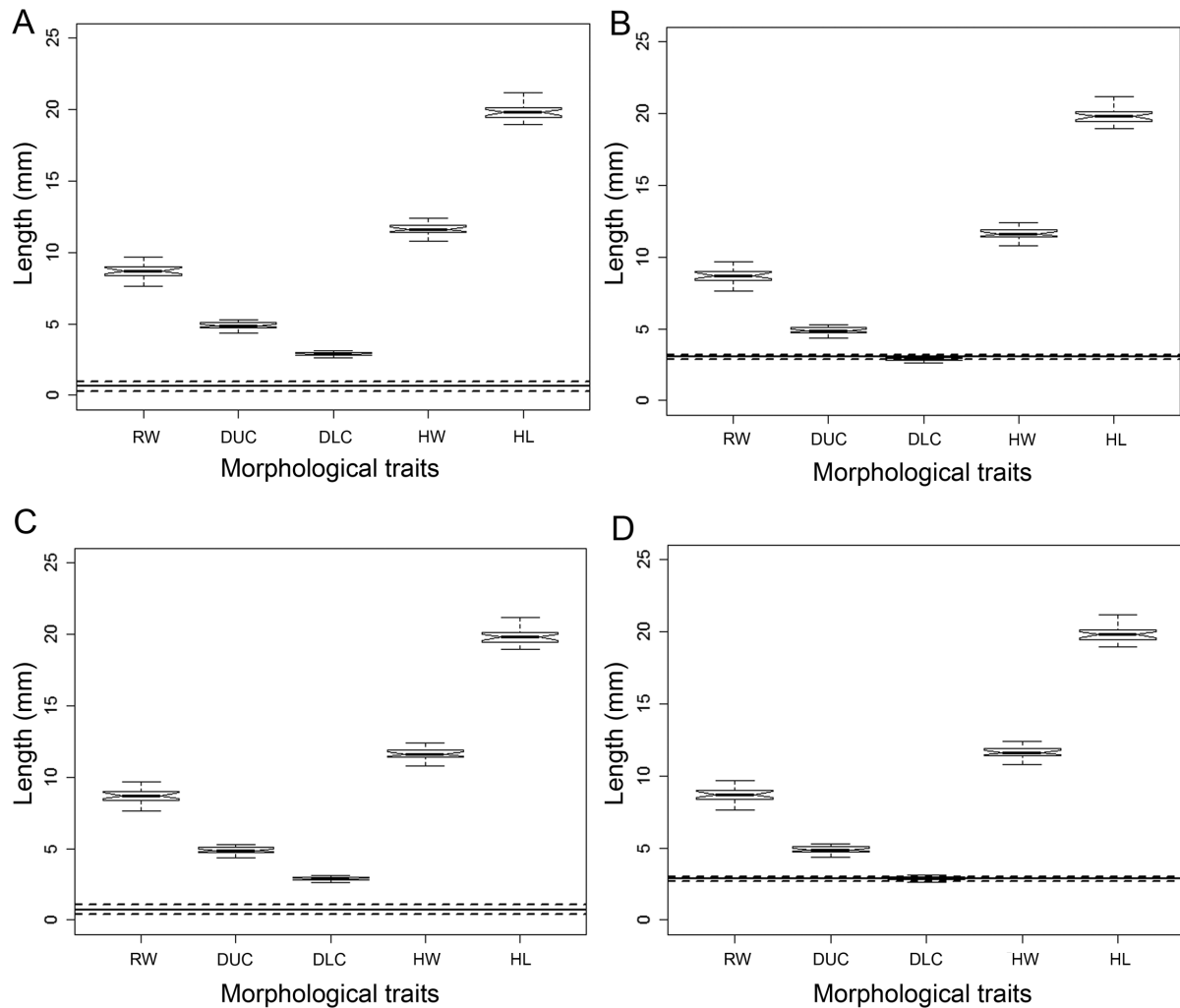


FIG. 5. Median (quartiles and range) of five morphological features of *D. watsoni* (RW — rostrum width, DUC — distance between upper canines, DLC — distance between lower canines, HW — head width, HL — head length). The straight line parallel to the x-axis represents the slopes and confidence limits (dashed lines). A and C show the difference between the first slope and the morphological features of the right and left sides respectively, while B and D the difference of the second slope with the morphological features. Note the overlap of the second slope with the distance of the lower canines

or by weather conditions (e.g., rain or wind) during tent construction. Another possible explanation is that deviations from a strict symmetry in the bifid tents are the result of the inherent variability in many behavioral phenotypes (imprecision hypothesis in Eberhard, 1990b). Although behavioral variation could be advantageous in several contexts (Hansell, 2005), in other cases variation may be the result of imprecision in the execution of some behaviors. However, if the final phenotype is equally functional, despite the imprecision during its construction, natural selection will not suppress such lack of accuracy (Eberhard, 1990b). Thus, deviations from strict symmetry in the bifid tents of *D. watsoni* may not affect the final functionality of the bifid tent.

In contrast to *E. alba*, which only has one tent design, *D. watsoni* possibly produces at least five different tent designs on the leaves of 24 plant genera that have very different shapes (Rodríguez-Herrera *et al.*, 2007). Most of these plants are understory species but others are epiphytes (e.g., *Anthurium*) growing on tree trunks at the subcanopy level. The flexibility in tent building behavior shown by *D. watsoni* is apparently unique in Neotropical bats. Constructing different tent types on leaves with different design, shape and thickness indicates that this bat has an extraordinary perception of the characteristics of each leaf and is capable of adjusting its construction behavior to build functional tents with very different leaf types. This flexibility allows *D. watsoni* to use different strata in mature and old secondary forests.

The evolution of tent construction is far from completely understood. Kunz *et al.* (1994) indicate that within Phyllostomidae tent building/roosting behavior evolved exclusively within the subfamily Stenodermatinae (tribe Stenodermatini). They also suggest that this behavior likely evolved three times within this tribe, without excluding the possibility of a single origin. The phylogeny published by Baker *et al.* (2003) provides us with an evolutionary framework to further evaluate both of these possibilities (one vs. multiple origins). New information on tent-building behavior obtained in the last few decades supports the hypothesis that tent-building behavior evolved within Stenodermatinae and at least three independent times in the genera *Uroderma*, *Ectophylla*, and *Dermanura*, as suggested by Kunz *et al.* (1994). These are, however, tentative hypotheses and more information on roosting and/or tent building behavior is required for all Stenodermatinae species before it will be possible to comprehensively evaluate the evolution of roosting and tent building behavior in Neotropical bats.

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