Tent Construction and Use by *Uroderma bilobatum* in Coconut Palms (*Cocos nucifera*) in Costa Rica

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ABSTRACT

Tent construction and use, uniformity of tents, and frond selection were studied in a population of *Uroderma bilobatum* roosting in coconut palms (*Cocos nucifera*) in Guanacaste Province of northwestern Costa Rica during July 1988. Palm leaflets were cut at their midribs in a line converging distally with the frond midrib, and the leaflets collapsed downward to form a large enclosed tent. Tent height, number of leaflets cut, and angle between the line of cut leaflets and the midrib of the fronds were measured to assess uniformity of tent construction. To ascertain if bats were selecting specific trees or fronds, we measured the angle of orientation of cut fronds, number of fronds hanging above a tent, and tree height. Bat tents were found in palms with a narrower range of heights than the overall tree population, and trees with tents were taller on average than trees without tents. A single altered frond provides excellent protection from rainfall. Bats do not seem to prefer fronds based on number of overhanging fronds or angle of orientation. The age of the modified frond may be an important factor in roost site selection, as tents in younger fronds were more likely to be occupied than those in older fronds. The number of bats roosting under tents ranged from 1 to 15 adults and subadults. The colony was composed largely of adult females and two age classes of young.

INTRODUCTION

It has been known for over half a century that some bats create their own roosting sites by modifying the shapes of leaves (Barbour, 1932; Chapman, 1932). Bats create these structures by severing the veins and, in some cases, the interconnecting tissues of leaves of various species. The sides of the leaves then collapse downward along the midrib to form a dark, secluded roosting site for the bats. Because some styles of these modified leaves are pyramidal or "tent-shaped," all modified leaves are now called bat tents and the bats that modify them are called tent-making bats.

Fourteen species of New World phyllostomid bats, all in the subfamily Stenodermatinae, are known to construct tents (Timm, 1987). Additionally, two Old World species of flying foxes—*Cynopterus brachyotis* and *C. sphinx* (family Pteropodidae)—have been reported to modify palms to produce diurnal roosting structures (Phillips, 1924; Goodwin, 1979). Reviews of tent construction and use by bats were provided by Kunz (1982) and Timm (1987).

In Costa Rica and elsewhere in the Neotropics we have found that (1) tent bats are often highly localized in occurrence; (2) tent bats seem to be most concentrated in areas that have an abundant supply of the preferred plant species used in tent construction; (3) quite often tents are concentrated in localized areas even though the preferred plant species is more widely distributed; (4) the location of tents within plants varies, as does the shape

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of tents constructed by a given species of bat; and (5) there are often many more tents present in an area than are occupied by bats. These factors suggest that the bats are selecting specific leaves for tents and using only certain tents of those available on a daily basis. Roost site selection in tent bats has been investigated previously for only a few species of the smaller tent-makers: *Artibeus phaeotis* (Timm, 1987), *Artibeus watsoni* (Choe and Timm, 1985), *Ectophylla alba* (Timm and Mortimer, 1976; Brooke, 1990), and *Vampyressa nymphaea* (Brooke, 1987). These studies concluded that bats select specific species of plants for tent construction and that they often select specific ages of leaves. Because of the large size of many altered leaves, especially those of pinnately compound plants, a considerable amount of energy probably is expended by the bat or bats in creating these roost sites. The energetic costs associated with the elaborate nature of many styles of bat tents, especially those constructed by bats of the genus *Uroderma,* suggest that strong selection pressures are involved.

Interestingly, no studies have addressed roost site selection and tent use by Peters's tent-making bat (*Uroderma bilobatum*), the first species of Neotropical bat discovered to modify leaves and one of the largest and most widely distributed of the Neotropical tent-making bats. Our discovery of a sizable population of *U. bilobatum* in the Pacific lowlands of Costa Rica roosting in altered fronds of coconut palms provided an ideal opportunity to explore several aspects of tent construction and use by these bats. The goals of this study were to (1) determine whether *U. bilobatum* chooses specific trees or fronds for tent construction, (2) assess whether they construct tents of a uniform shape or height, (3) determine if tents are effective protection from rain, and (4) evaluate patterns of tent use (including group size, group composition, and movement between tents).

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METHODS

From 16 through 21 July 1988, individuals and groups of *Uroderma bilobatum convexum* and their tents in coconut palms (*Cocos nucifera*) were observed. The planted coconut grove contained 56 trees that varied in height and age, and was located approximately 0.5 km east of the administrative buildings at Refugio Nacional de Fauna Silvestre Dr. Rafael Lucas Rodríguez Caballero (commonly known as Palo Verde) in the Pacific lowlands of northwestern Costa Rica. Palo Verde is a wildlife refuge located approximately 2 km south and 12 km east of Bolsón in Guanacaste Province (10°30'N, 85°20'W; elev. 10 m). The area lies within the Tropical Dry Forest Life Zone (Holdridge, 1967) and is dominated by lowland deciduous and riverine swamp forests and a large seasonal marsh. Rainfall is extremely seasonal, with most of the mean annual precipitation of 1700+ mm falling between April and October. Details of the vegetation, habitat types, and climate of Palo Verde have been described by Slud (1980) and Hartshorn (1983).

All bat tents were surveyed daily, and the number of roosting bats present in each tent was counted. Nursing, nonvolant juvenile offspring (forearm = 32.5 mm [N = 1]) were clearly visible clinging to 23 adult females (forearm $\bar{x}$ = 42.5 mm [N = 2]), enabling us to easily distinguish them from other bats.

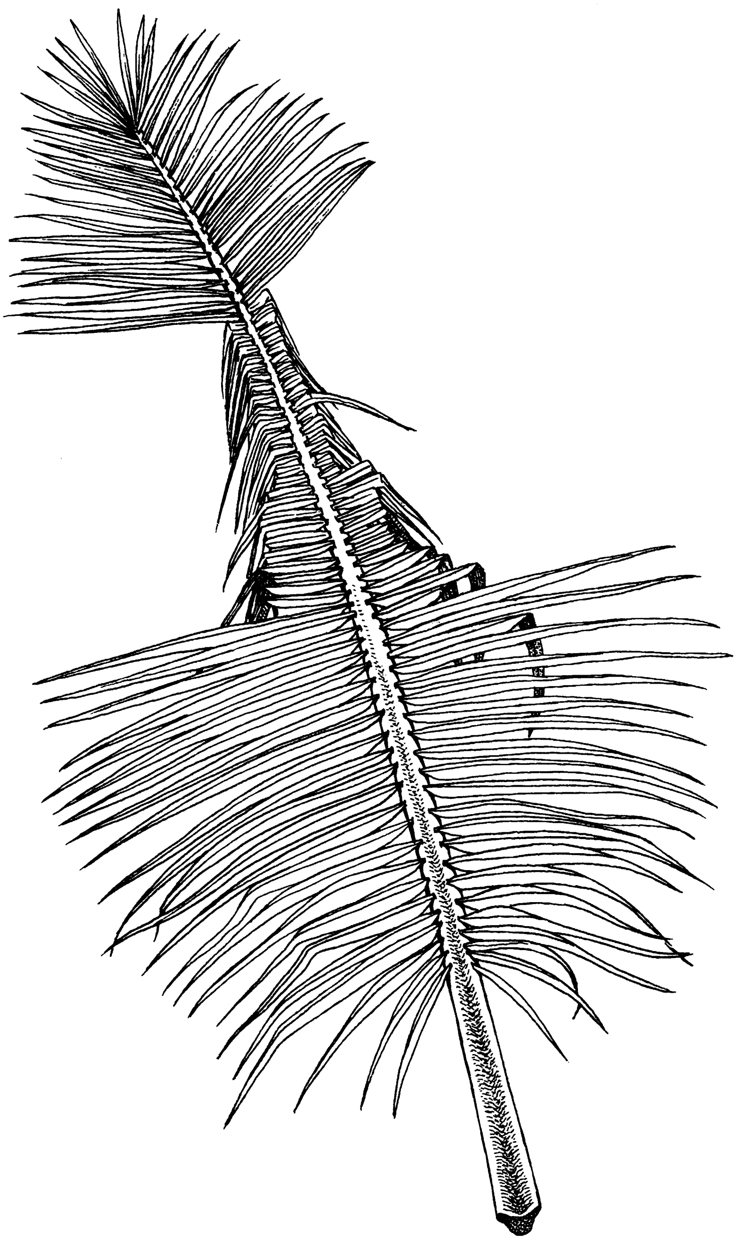

Fig. 1. Dorsal view of a coconut frond showing the leaflets cut by *Uroderma bilobatum* to form a tent.

Twenty-three of the 41 adult and subadult bats present were captured in mist nets, and 21 of these were marked for future identification. Volant bats were judged to be adults if the phalangeal epiphyses were fused, and subadults if the epiphyses were not yet fused.

To test whether *Uroderma* selects specific trees or fronds for tent construction, the following measurements were taken. We measured the distance from the ground to the point where the lowest green frond attached to the tree (to the nearest 0.1 m). This provided an estimate of tree height, because coconut trees shed the lowest leaves as they grow taller and leaves are concentrated at the very top of the tree. To assess whether bats were selecting fronds with respect to the direction the fronds hung, we measured the compass direction of each cut frond to the nearest degree. The number of fronds directly above a tent was counted to determine if bats were constructing tents in fronds that had fronds above, possibly providing additional shade or protection from rain.

Two aspects of the coconut trees and altered fronds were measured to assess the degree of uniformity among tents in this area. First, leaflets hanging perpendicularly to the plane of the frond up to the point where the line of cuts converged with the midrib of the frond were counted as cut leaflets that contribute to the tent; any cut leaflets distal to the point of convergence with the midrib were not counted (fig. 1). Second, the angle between the midrib and one of the two rows of cut leaflets was estimated (with a protractor) to the nearest degree.

We also assessed protection from rainfall under tents by measuring water collected over a 4-day period in a 250-ml beaker placed directly under the center of a typical tent, in the position bats normally hang. During the same period, two additional beakers were placed in the open to measure total rainfall.

To evaluate patterns of tent use, we surveyed group size and composition under individual tents throughout the study. Two factors—age of fronds and tent height—were examined to ascertain if bats occupied specific tents of the total tents available. The age of the cut frond (young or old) was estimated by the frond's position on the tree in relation to other fronds. Tent height was measured (to the nearest 0.1 m) as the distance from the ground to the point at which the line of cut leaflets converged with the frond midrib.

A reference specimen of *Uroderma bilobatum* from this population was deposited in the Museo Nacional de Costa Rica in San José; the museum's mammals recently were transferred to INBio (the new National Biodiversity Institute, Santo Domingo, Costa Rica).

RESULTS

At Palo Verde, *Uroderma bilobatum* severs the midrib of leaflets on the large, pinnately compound-leafed coconut palm, *Cocos nucifera,* to form dark, secluded diurnal roosts and maternity sites. The cut leaflets fold downward, perpendicular to the ground, creating large, angular tents (fig. 2). Bats cut the midrib of leaflets but do not appear to sever surrounding tissue, nor do they sever the midrib of the frond. The leaflets closest to the tree trunk are severed at the greatest distance from the midrib of the frond. This distance decreases as the cuts proceed distally to a point at which they converge with the frond midrib (fig. 1). A variable number of leaflets beyond the point of convergence may also be cut. Tent shape is a combination of the number of leaflets cut and the angle at which the line of cuts is made.

Of the 56 trees in the coconut grove, 23 contained tents constructed by *U. bilobatum.* Forty-four tents were located on our first survey. Three additional tents were constructed over the next five nights. Of those trees that had tents, the mean number of tents per tree was 2.0 (range 1–5, SD = 1.2). The road and trails within a 1.5-km radius of the study site were searched for additional tents or large-leafed trees appropriate for tents, but none were found.

Of all the trees in the grove, the range of heights of trees with tents encompassed the taller trees, but excluded the very tallest. The average height of the lowest green frond (our estimate of tree height) of all trees was 1.8 m (range 0.5–5.4 m, SD = 0.96). Bat tents were found in trees that averaged 2.3 m in height to the lowest frond (range 1.6–3.0 m, SD = 0.42). The average height of trees with tents (2.3 m, N = 23) was higher than the average for trees without tents (1.5 m, N = 33, range 0.5–5.4 m, SD = 1.08; Wilcoxon rank sum, $P < 0.001$).

The orientation of the frond and the number of fronds above a tent did not affect which fronds the bats selected for tent construction. There was no pattern to the orientation of cut fronds; the compass direction ranged from 0 to 352° ($\bar{x}$ = 191°, SD = 101°). The number of fronds above a given tent ranged from 0 to 3 ($\bar{x}$ = 0.7, SD = 0.85).

Although there was a definite inverted V-shaped pattern to the general form of tents constructed, actual tent shape was variable. Of 26 tents we were able to measure and count, 17 had leaflets cut on both sides and

Fig. 2. Tent of *Uroderma bilobatum* in the pinnately leafed coconut palm *Cocos nucifera*.

9 had leaflets cut on only one side. The mean number of leaflets cut per side was 12.8 (range 0–36, SD = 7.9). The angle formed by the frond midrib and the line of cut leaflets averaged 32.3° (range 20–46°, SD = 7.7°).

Two beakers placed in the open each collected approximately 90 ml of rainfall during a 4-day period. The beaker placed under a bat tent during the same period collected only 2 ml of rain.

Although 44–47 tents (3 tents were constructed during our study) were available to the roosting bats, only 9–11 were occupied on any given day during the study. Sixty-nine percent of the occupied tents were in use 4 or more days. Thirty-four tents were never occupied during the study. Occupied tents appeared to be spatially clumped within the coconut grove.

Occupied and unoccupied tents differed in frond age and height. Occupied tents tended to be in younger fronds (fronds higher in the tree) than did unoccupied tents ($\chi^2 = 10.9$, $P < 0.05$). Sixty-seven percent of occupied tents were found in young fronds, whereas 84 percent of unoccupied tents were in old fronds. Accordingly, tent height differed significantly between occupied ($\bar{x}$ = 4.6 m, SD = 0.8) and unoccupied tents ($\bar{x}$ = 3.8 m, SD = 0.7 m; Wilcoxon rank sum = 2.3, $P < 0.05$).

Fourteen trees had two or more tents, but in only one instance was more than one tent occupied in a single tree. That tree had five tents, one of which was occupied on 5 of the 6 days by a large cluster of bats. On one of those days, an additional tent was occupied by a single bat. The other three tents in this tree were never occupied.

On three occasions we observed *U. bilobatum* roosting under coconut fronds that clearly had not been altered to form a tent. The leaflets of each of these fronds drooped naturally perpendicular to the ground, similar to the pattern seen in cut leaflets. Two of these fronds were occupied by single bats for 1 day only. The third was used by three, two, and four bats on consecutive days.

Of the 13 different tents used by bats (and 3 unaltered fronds), 8 were occupied by single bats and 8 by groups of two or more bats. The average group size was 5.2 (range 1–15, SD = 3.3). Twenty-three of the 34 groups (68%) were composed primarily of females with nursing offspring.

Forty-one adult or volant subadult *U. bilobatum* were observed in the coconut grove on the first day, and of these 23 were adult females that had nutritionally dependent, juvenile offspring. We captured 16 adult females, 1 adult male, 5 subadult males, and 1 subadult female. Fourteen of the adult females were lactating, one was visibly pregnant, and one was postlactating. Six females were captured while carrying their offspring within the first 30 minutes after sunset. Females that were lactating but not carrying their offspring were captured later in the evening. The single adult male observed had fully scrotal testes. No other species of bats were found roosting under the coconut fronds.

Over the 6-day period when bats were marked, the lactating females with nursing young roosted in six of the tents (table 1). Not all of these six tents were continuously occupied over the 6-day period. Of our 28 observations of tents occupied by lactating females, on 10 occasions the groups included only the mother/offspring pair(s) and on 18 occasions included mother/offspring pair(s) and 1–9 ($\bar{x}$ = 1.9) other nonlactating bats. On three occasions we observed single, lactating females roosting alone with their offspring. Each of these females roosted in a different tent, and each mother/offspring pair was found alone only for 1 day. Three of the marked subadults roosted singly, one roosted with an adult female and her offspring, one roosted with one to three other bats, and one roosted in a large cluster of bats that included lactating adult females and their nursing offspring.

TABLE 1

Distribution and Numbers of *Uroderma bilobatum* Roosting in 13 Tents and 3 Unaltered Fronds (indicated by *) in Coconut Palms (*Cocos nucifera*) at Palo Verde in 1988[a]

Tent no.	16 July	17 July	18 July	19 July	20 July	21 July
1	15/6	13/10	9/6	3/3	0	1/1
2	6/5	4/4	8/8	7/6	10/7	9/6
3	6/5	6/5	6/5	5/4	5/4	5/4
4	7/7	4/4	0	3/3	1/1	4
5	1	2/2	2/1	2/1	2/1	2/1
6	0	2	3	4	3	4
7	1	2	1	1	1	1
8	1	1	1	1	1	1
9	1	1	1	1	0	0
10	1	1	0	0	1	1
11	1	0	0	0	0	0
12	1	0	0	0	0	0
13	0	0	0	0	1	1
14*	0	0	1	3	3/1	1/1
15*	0	2	0	0	0	0
16*	0	0	0	0	0	1

[a] The numerator (or single number in a column) is the number of adults and/or volant subadults; the denominator is the number of juveniles (nonvolant) observed. 0 = no bats present in tent that day.

DISCUSSION

The species of bats that use modified leaves as diurnal roost sites face both advantages and disadvantages due to this roosting strategy. Potential advantages of roosting in tents include the ability to change roost sites as food availability or weather conditions change or as ectoparasite infestations increase, as well as protection from predators that specialize on more traditional bat roosts such as caves or hollow trees. Disadvantages include the energetic costs of modifying the leaf; the ephemerality of the leaf, causing the need for construction of new roosts every few months; vulnerability of bats roosting under leaves to rain, heat, and wind; and vulnerability to certain arboreal predators. Depending on the habitat, suitable roost sites may or may not be readily available. These and other costs and benefits are likely to affect roost site selection by tent-making bats.

At Palo Verde, *Uroderma bilobatum* constructs tents in coconut palms by partially cutting leaflets along a line tapering distally toward the midrib (fig. 1). The pattern of leaf modification is similar to that in tents cut by *U. bilobatum* in the palm *Scheelea rostrata,* as well as in a variety of other large-leafed plants (Timm, 1987). Both the angular cut and the selection of large-leafed plants seem characteristic of this species. Although the inverted V-shaped tent style is characteristic and easily recognizable, we observed considerable variability among individual tents. Some tents were cut only on one side, varying numbers of leaflets were cut, and the angle at which the line of cut leaflets converged toward the midrib varied.

The most important factor we studied regarding frond selection for tent construction was the height of the tree. Bats construct tents in trees in only a narrow range of the total available tree heights. Trees taller than average, but not the tallest, are used. Taller trees may provide increased protection from climbing predators, but very tall trees may be more exposed to high-velocity wind. Bats did not select fronds on the basis of their angle of orientation or on whether or not the frond was overhung by one or more other fronds.

At first glance, pinnately compound palm leaves, with their gaps between leaflets, might not seem to provide adequate protection from the torrential rain showers of the lowland tropics. However, the results of our simple test, measuring rainfall under a tent versus in the open, strongly suggest that tents provide roosting bats with excellent protection from rain. During our study, 90 ml of rain fell in this area, but the beaker placed under a bat tent in the position where bats roost collected only 2 ml of water.

Age of the frond may also be an important factor in the selection of a specific tent as a roost site. Tents in younger fronds are more likely to be occupied than those in older fronds. It is likely that tents in more mature fronds represent older, previously occupied tents constructed when the leaf was younger. Young fronds are more tender and probably easier to modify than older fronds. Tents constructed in young fronds will be available as roosting sites for a longer period of time than those in older fronds. Younger fronds are farther from the ground and may be more difficult for predators to reach. These young fronds also have more pliable rachises, which may provide a more "sensitive" early warning of the approach of a climbing predator. Because fronds are present on coconut trees for 2.5–3 years (Vandermeer, 1983), tents constructed in these fronds are potentially available to bats for many months. As tents age, they are increasingly damaged by wind and other environmental factors and become less suitable as roost sites. While this provides a partial explanation for the observation that there were many more tents in the area than were in use at any one time, extra tents may also provide an alternate roost site for bats that have been disturbed in their tents. We observed single bats flying from one tent to another during our census on three occasions; these were bats that we accidentally disturbed.

Tents in general, as well as occupied tents, appeared to be clumped within the coconut grove. This clumped distribution could be due to the social organization of the bats, but more likely is due to the clumped distribution of preferred trees. Taller trees tended to be clumped in this area. The relative importance of these factors could best be studied in an area where tree heights are randomly distributed or where palms are all of equal height.

The range of *Uroderma bilobatum* extends throughout Central America and northern South America, and the bats are found in a variety of habitats. In tropical dry forests such as at Palo Verde, bats seem to be limited in available roost sites because the large-leafed plants they prefer are uncommon or absent. A search of the trails at the wildlife refuge produced no plants that seemed suitable for tent construction by this species, other than the planted coconut palms. This suggests that the bats may be locally limited by the number of available roost sites. However, the number of bats roosting in the coconut grove diminished throughout the 6 days of our study, perhaps because they were sensitive to our disturbance, so alternative roost sites may be available in the area.

Bats roosted alone or in groups of up to 15 adults or subadults in the coconut grove. Females with nursing young were most likely to be found with at least one other bat (other than their offspring), and most groups were composed of lactating females. Maternity roost formation is a common phenomenon in many species of bats. It seems likely that during the period of parturition and lactation, the tents in this area are used by *Uroderma bilobatum* as maternity roosts. The dynamics of maternity roost formation and group composition will be addressed in a future paper. Our observations of females with nutritionally dependent juveniles and volant subadults that appeared to be of uniform age support the classification of *U. bilobatum* as being bimodally polyestrous, as suggested by previous studies of this species (Fleming et al., 1972; Wilson, 1979; Baker, 1981; Baker and Clark, 1987).

Our observations, and those of previous workers (summarized by Timm, 1987), show that groups of *Uroderma bilobatum* roost under leaves that have been altered by the bats to form tents. *Uroderma* selects large leaves that may be in a variety of shapes; however, the tents constructed are characteristically created with a large, inverted V-shaped pattern in the cut leaf or leaflets. Considerable energy is expended by the bats to create these roosts, as evidenced by the large size of the cut area made by *Uroderma* and by our observations that a period of several nights is required for the creation of a new tent. Lactating females at Palo Verde usually roosted in groups containing more than one bat. Volant, nonreproductive subadults may roost singly or with groups of adult females. Tent roosts provide the bats with excellent protection from rain. Although tents probably require considerable effort to construct, in coconut palms they remain available to the bats for a period of at least several months, providing the bats with protection from the elements and undoubtedly from predators as well.

ADDENDUM

Lewis returned to Palo Verde during June and July of 1989 and surveyed the numbers of *Uroderma bilobatum* roosting under the fronds of this same grove of coconut palms as part of a study on the population dynamics of these bats. She found 54 tents in 26 of the 54 coconut trees in the area. In early June, from 6 to 10 *U. bilobatum* were using the palm tents. As the study progressed, the greatest number of bats observed roosting in the palm grove on one day was 35. Both male and female bats were observed roosting under tents.

During early February 1990, Kathryn E. Stoner visited Palo Verde and surveyed the numbers of *U. bilobatum* for us at this same grove. Of the 42 tallest trees in the coconut grove, 21 contained one or more tents. The bat tents were checked for occupancy during four consecutive days. On 2 February, three bats were observed in this grove, each roosting singly under tents in separate trees. On 3 February, two bats were observed roosting together in a fourth tent in another tree (fig. 3); no other bats were observed. On 4 February, there were no bats roosting under any of the tents. On 5 February, only one bat was found; it was roosting under the same tent that contained two bats on 3 February.

On 2 February 1991, Timm returned to this site to survey the numbers of *U. bilobatum* in this coconut grove. He found a total of 41 tents in 29 of the 54 trees. Only three *U. bilobatum* were found, each roosting singly under fronds that had been altered to form tents.

These additional observations emphasize the flexibility of tent-making bats regarding roost sites. *U. bilobatum* appears to use this grove seasonally. It is possible that some bats move into or out of the area to track changing food resources (Kunz, 1982); movement back to the grove might revolve around colonial

Fig. 3. Two *Uroderma bilobatum* roosting in a coconut palm tent. Photograph courtesy of Kathryn E. Stoner.

maternity roosting and/or mating. Additional research, especially following marked bats throughout the year, would be extremely valuable in determining the factors affecting movements and choice of roosts by these bats.

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