Use of large Acacia trees by the cavity dwelling Black-tailed Tree Rat in the Southern Kalahari

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Received 11 July 2003; received in revised form 5 January 2005; accepted 16 June 2005
Available online 8 August 2005

Abstract

Recent extensive harvesting of large, often dead \textit{Acacia} trees in arid savanna of southern Africa is cause for concern about the conservation status of the arid savanna and its animal community. We mapped vegetation and nests of the Black-tailed Tree Rat \textit{Thallicomys nigricauda} to assess the extent to which the rats depend on particular tree species and on the existence of dead, standing trees. The study was conducted in continuous \textit{Acacia} woodland on the southern and eastern edge of the Kalahari, South Africa. Trees in which there were tree rat nests were compared with trees of similar size and vigour to identify the characteristics of nest sites. Spatial analysis of tree rat distribution was conducted using Ripley’s-L function. We found that \textit{T. nigricauda} was able to utilize all available tree species, as long as trees were large and old enough so that cavities were existing inside the stem. The spatial distribution of nest trees did not show clumping at the investigated scale, and we therefore reject the notion of the rats forming colonies when inhabiting continuous woodlands. The selection of a particular tree as a nest site was furthermore depending on the close proximity of the major food plant,
Acacia mellifera. This may limit the choice of suitable nest sites, since A. mellifera was
less likely to grow within a vegetation patch containing a large trees than in patches without
large trees.
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Keywords: Thallomys nigricauda; Nest sites; Acacia erioloba; Acacia mellifera; Boscia albitrunca; Spatial
distribution pattern; Kalahari Savanna Thornveld

1. Introduction

The presence of large trees in savanna woodlands has been shown to be important
determinant of pattern and patch dynamics (Belsky and Canham, 1994). In arid
savannas trees often provides services that are disproportionate to their relative
abundance (Eloff 1959, Milton and Dean, 1995; Dean et al., 1999). The use of large
trees by birds and small mammals in arid savannas differs among species, ranging
from perch sites and foraging sites occupied for a few minutes to permanent nest
sites. For example, in the Kalahari, Southern Africa, scattered large camelthorn trees
Acacia erioloba, can provide shade for a number of terrestrial animals or provide
support structures for the large nests of Sociable Weavers Philetarius socius or
raptors. In at least one animal group (birds), species richness is correlated with plant
height diversity in the Kalahari arid savanna (Pianka and Huey, 1971), and it is
likely that similar patterns are present in other animal groups. Recent extensive
harvesting of large A. erioloba, Acacia haematoxylon and Acacia luederitzii trees in
the arid savanna of the Northern Cape and western Northwest Provinces in South
Africa are cause for concern about the conservation status of the arid savanna in the
Kalahari (Anderson and Anderson, 2001; Liversidge, 2001).

Distribution and abundance of arboreal mammal species, like the Black-tailed
Tree Rat Thallomys nigricauda, may be determined by the structure of the woodland
and the relative abundance of large trees. For many cavity dwelling animals that
cannot excavate their own tree cavities, dead and standing trees may be a critical
habitat component (Muul, 1974; Bendel and Gates, 1987; Rowley and Chapman,
1991; du Plessis, 1995; Gates, 1996; Taulman, 1999). However, little is known about
tree rat’s requirements for nesting trees. Breeding females are using very small home
ranges (<0.25 ha) with a nest and a foraging site, mainly small Acacia trees (Acacia
mellifera, A. luederitzii), close together (Eccard et al., 2004). Nests and food on a
small spatial scale may thus be the limiting factors for the presence of tree rats. Tree
rats are reported to live in groups or colonies (Nel, 1975; Rautenbach, 1982),
however, only solitary nesting females have been observed at the site of our study in
continuous savanna woodland (Eccard et al., 2004). The objectives of the present
study were to investigate the extent to which the Black-tailed Tree Rat is dependant
on vegetation structure and on particular tree species. We also investigated, whether
the social system of tree rats, for example a clumped distribution in colonies, are
creating spatial distribution patterns that may overlay the response to vegetation
parameters.
2. Methods

2.1. Study site

We studied vegetation parameters and the Black-tailed Tree Rat at the Molopo Nature Reserve, Northwest Province, South Africa, (25°50'S, 22°55'E) from January to March 2000. We identified an area, study site A, with a high proportion of large *Acacia* trees and abundant tree rat nests for a detailed study of spatial distribution and nest sites. The site was located in the northwest corner of the reserve close to the dry Molopo River on the Botswana border. The site was dominated by large *A. erioloba* trees and contained few *A. luederitzii* and *Boscia albitrunca* trees. The area was connected to continuous woodland, and trees were growing on a slope with sandy soil and extending into a shallow drainage line than ran north–south. The vegetation was markedly patchy, with islands of shrubs and trees interspersed with bare sand, or ground covered after rainfall with the annual grass *Schmidtia kalihariensis*.

At site B, in the central reserve, vegetation was diverse among locations, probably due to a diverse history of land use before establishment of the Nature Reserve in 1988. Ground cover was variable, with disturbance indicators *S. kalihariensis* and *Tribulus terrestris* near houses and former paddocks, and Bushman grasses *Stipagrostis* ssp. further away. In vast stretches, trees were of smaller size than at site A, but tree rats were also abundant in these areas. We investigated many smaller patches (circles of 100 m diameter) distributed within a larger area (approximately 3 × 3 km) by selectively mapping near tree rat nests. Tree species composition of the mapped stands of trees (including smaller trees) was 42% (mostly dead) *A. erioloba*, 25% *B. albitrunca*, and 32% *A. luederitzii*.

2.2. Vegetation structure

We mapped distinct shrub and tree patches. The position of patches was plotted using a compass grid (to ca. 5 m). Patch diameter was estimated by pacing. Species, numbers, and size of shrubs and trees inside the patch were recorded. Most (90%) individual plants were *A. erioloba*, *A. luederitzii*, *A. mellifera*, *A. hebeclada*, *B. albitrunca*, *Ziziphus mucronata*, *Grewia flava* or *Lycium* spp. Plants were considered to be in the same patch if connected by their canopies, or by other woody material that would enable an arboreal mammal to move between trees without descending to the ground. Heights of trees and shrubs were classified into classes: 0–2 m, 2–4 m, 4–6 m, and taller than 6 m. Stem diameters of all tall trees (> 6 m) were measured at breast height, or in cases where there were multiple stems, below their point of branching. Main stems that may have diverged below ground were considered to be two trees. All trees were classified as being alive or dead. Stumps of trees that we could not identify to the tree species were recorded as a separate category. The ground around the main stem of trees was searched for droppings of tree rats. Stems and branches were searched for tree rat nests, and the presence of droppings in fissures and holes in the stem was investigated by climbing.
trees. Nests often emitted a strong, characteristic smell (also reported by B. Lovegrove, personal communication) and were easily identified through piles of old droppings at the base of the stem.

At study site A, we mapped every vegetation patch in a 9 ha grid (Fig. 1). Focussing on nest sites and on food plants (*A. mellifera*, Eccard et al., 2004), we compared among patches with and without large *A. erioloba* trees, and compared patches with trees but with or without the presence of tree rats. Live-trapping confirmed that the identified signs belonged to tree rats. We conducted two series of live trappings: in the first series, we set traps at all large trees (74 locations) in the grid. Medium-sized Sherman traps were tied to horizontal branches, set on the ground and in nearby bushes, pre-baited with oats, peanut butter and jam for two nights to habituate animals to traps before being set for two nights. All subsequent tree rat captures were at trees we had identified as occupied by tree rats prior to the trapping (6 captures at 38 tree rat sites, all on horizontal branches, 0 captures at 36 sites without signs of tree rat presence, see Fig. 1 for capture locations of tree rat females). Captured individuals were marked by fur clipping. We captured one Lesser Savanna Dormouse (*Graphiurus parvus*). Another capture of a Lesser Savanna Dormouse in the following year was at a place where we had captured a tree rat in 2000, indicating that the identified nest sites were potentially used by both species. We conducted a second targeted trapping series 3 weeks after the first, by setting traps at the 38 identified tree rat locations. We re-captured 3 of the marked tree rat individuals and the dormouse, but no additional animals.

![Fig. 1. Map of vegetation and tree rat nests at study site A. Dots (●) indicate vegetation patches, diamonds (◇) patches with a tall tree (>6 m), squares (□) patches with Black-tailed Tree Rat nests, and large circles (○) indicate points of capture of nesting female tree rats. Within the framed area (9 ha) all vegetation patches were mapped. Surrounding this grid, only the large trees were mapped (16 ha). Scale is in meters. Note that the study site was surrounded by continuous woodland.](image-url)
At study site A, we also mapped each large tree (size class > 6 m) in a 16 ha grid that included the 9 ha grid (Fig. 1). The larger grid was used to study the preferences of tree rats for particular nest tree species, and to study the spatial distribution of tree rat nests in relation to the available tree locations. Spatial distribution of tree rat locations was investigated by using Ripley’s L-function as described in Haase (1995). We developed software to conduct Monte Carlo simulations to test for the random distribution of the tree rat nests. In the simulations, selected sites were randomly selected from among potential sites, holding the spatial locations of potential sites fixed in space. The number of sites randomly selected was always equal in number to the number of occupied sites actually observed. These randomly chosen sites were then analysed using Ripley’s L-function as were the observed sites. The maximum and minimum $L$-values obtained from among 19 Monte Carlo simulations were used to construct maximum and minimum values for 95% confidence intervals (Haase, 1995).

At study site B, we identified 10 nest sites of tree rats. For each nest site, we chose a corresponding tree (same size, species, vigour, and stem diameter) within 200 m of the nest-tree. At 7 locations the focal tree was a dead *A. erioloba* tree, and at 3 locations it was a live *Boscia* tree. Since vegetation at different sites was quite dissimilar, we compared within pairs. We mapped the vegetation patch in which the focal tree was growing and the vegetation in all other patches growing within a 20 m radius around the central tree. Larger trees growing in a 50 m radius of the focal tree were identified, and examined for vigour and tree rat occupation. The investigated trees over all circles were summed to calculate if there were preferences of tree rats for certain tree species for nesting. We calculated the preference for tree species separately for each site (two circles with 50 m radius ≈ 1.6 ha). Preference was indicated by a preference index based on the selection ratio (resource selection function of Manly et al., 1993) which represents the percentage of nesting tree by species, divided by the percentage of availability of trees of the species. Selection ratio $< 1.0$ indicates selection against a particular tree species (used less than expected according to availability) whereas $> 1$ indicates selection for a particular tree species (used more frequently than expected upon availability).

3. Results

3.1. Vegetation parameters

At study site A, we identified 1059 vegetation patches within a 9 ha grid (121 patches ha$^{-1}$) with 2797 individual shrubs and trees (Fig. 1). Only 6% of the patches contained trees taller than 6 m, with an average density of 9 tall trees ha$^{-1}$. The average patch size was 4 m in diameter (range 1–20 m) and the average patch contained 2.5 plant individuals (1–25 individuals). The vegetation was dominated by small (<3 m) *A. mellifera* trees (30% of all plant individuals occurring in 41% of the patches), *G. flava* shrubs (23% in 34%) and saplings of *A. erioloba* (21% in 32%).
Tall trees were dominated by *A. erioloba* (92% of tall trees occurring in 5.3% of patches).

*A. mellifera* trees were less likely to grow in a patch containing a large tree of any species (18 out of 73 patches) than in a patch without such a tree (423 out of 986, $\chi^2 = 9.3$, df = 1, $p = 0.002$). Patches with a tall tree were more likely to contain a shrub sized *A. erioloba* (68 out of 73 patches), small *Z. mucronata* (11 out of 73 patches), or shrub-sized *B. albitrunca* tree (18 of 73), than patches without a tall tree (*A. erioloba*: 278 out of 986, $\chi^2 = 130$, df = 1, $p < 0.001$, *Z. mucronata*: 68 out of 986, $\chi^2 = 6.6$, df = 1, $p = 0.010$, *B. albitrunca*: 141 of 986, $\chi^2 = 5.7$, df = 1, $p = 0.017$).

The presence of *G. flava* shrubs and of other shrub species was not related to the presence of a tall *A. erioloba* tree in a patch ($\chi^2 = 0.1$, df = 1, $p = 0.804$; and $\chi^2 = 0.6$, df = 1, $p = 0.409$).

If a tall tree was present in a patch, we found more signs of the presence of tree rats as indicated by their droppings (27 out of 73 patches) or nests (17 out of 73 patches) than in the absence of such trees (droppings: 8 out of 986 patches, $\chi^2 = 278.3$, df = 1, $p < 0.001$, nests: 4 out of 986, $\chi^2 = 125$, df = 1, $p < 0.001$). Most nests were situated in tall *A. erioloba* trees. The remaining nests were situated in large specimens of other tree species (3 nests) and in a smaller *A. erioloba* tree that was <6 m in height.

If the large tree was an *A. erioloba* ($n = 70$), the patches with a tree rat nest more often had shrub-sized *Boscia* trees growing in the patch (6 of 14) than patches without tree rat nests (10 of 56; $\chi^2 = 3.9$, df = 1, $p = 0.046$). The occurrence of *Ziziphus* trees in a patch was more frequent in patches with tree rat droppings (7 of 24) than in patches without tree rat droppings (3 of 46, $\chi^2 = 6.6$, df = 1, $p = 0.010$), but their occurrence was not related to either the presence (4 of 14 patches) or absence of tree rat nests (6 of 56, $\chi^2 = 2.9$, df = 1, $p = 0.088$). There was neither correlation between the occurrence of other species of plants in a patch and the presence of tree rat droppings, nor did the occurrence of these plants appear to be associated with the nest tree.

In the 16 ha grid, we measured the stem diameter of 64 large *A. erioloba* trees. Nests were always in cavities or hollows in the main stem, occasionally with a nest of twigs in a fork above the entrance of the hollow. *A. erioloba* trees with signs of tree rat occupation were larger (stem diameter $45 \pm 15$ cm, crown diameter $9 \pm 3.7$ m, $n = 47$) than trees without tree rats ($n = 64$ measured trees; stem $37 \pm 13$ cm, student’s $t = 3.2$, df = 109, $p = 0.002$; crown: $7 \pm 4.5$ m, student’s $t = 2.0$, df = 75, $p = 0.046$). The wider the stem diameter, the more stems were hollow (binary logistic regression, Walds statistic: 10.3, df = 1, $p = 0.001$, based on 64 large trees, 42 with hollows).

### 3.2. Spatial distribution of tree rat patches

Taking into account that Black-tailed Tree Rats seem to be restricted to large trees, we tested the distribution of tree rats with respect to large trees (>6 m) on the 16 ha grid in site A. The distribution of Black-tailed Tree Rats, indicated by
droppings or nests in large trees was not different from random at the investigated scale (Fig. 2).

3.3. Nest-trees versus other trees

At site B, we found that the control trees without tree rat nests were less likely to have hollows (2 hollow trees out of 20), whereas all nest-trees were hollow (Fisher’s exact, \( p < 0.001 \)). The numbers of vegetation patches growing in a 20 m radius around the tree was higher around nest trees than around control trees in eight of the tree pairs (Wilcoxon signed rank test, \( Z = -2.1, p = 0.038 \)). In seven of the pairs, more A. mellifera shrubs were growing within 20 m radius of the nest tree than of the control tree and in two of the pairs numbers were even (Wilcoxon signed rank test, \( Z = -2.3, p = 0.021 \)). There were no differences in the number of other species of shrubs or trees within the patch surrounding the focal tree \((-0.2 > Z > -1.0, P > 0.317)\) or within the 20 m radius around the tree \((-0.3 > Z > -0.8, P > 0.437)\). The number of large trees and of large trees occupied by other tree rats within a 50 m radius also did not differ among trees of a pair \((-0.7 > Z > -0.9, P > 0.340)\).
Table 1

Number of trees by species and vigour, number of nests in these tree types, and selection ratios of tree rat nests in available trees of the Black tailed Tree Rat in Molopo Nature Reserve, Southern Kalahari

<table>
<thead>
<tr>
<th>Area size (ha)</th>
<th>Nests</th>
<th>Trees size class &gt; 6 m</th>
<th>Selection ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site A</td>
<td>16</td>
<td>17</td>
<td>16</td>
</tr>
<tr>
<td>Site B Focal tree: size class</td>
<td></td>
<td></td>
<td>Trees size class &gt; 4 m</td>
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<tr>
<td></td>
<td></td>
<td>Dead A.e. &gt; 6 m</td>
<td>B.a.</td>
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<td></td>
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<td>B.a. &gt; 6 m</td>
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<td>Dead A.e. &gt; 6 m</td>
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<td>Dead A.e. 4–6 m</td>
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<td>Dead A.e. 4–6 m</td>
<td>1.6</td>
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<tr>
<td></td>
<td></td>
<td>Stump 4–6 m</td>
<td>1.6</td>
</tr>
</tbody>
</table>

Site A was a rather homogenous block of woodland dominated by large, old *Acacia* trees. Site B was a large less homogenous area and was investigated in many small locations. A.: *Acacia* (can be either *erioloba* or *luederitzii*), e.: *erioloba*, B.a.: *Boscia albitrunca*, selection ratio was calculated by dividing the percentage of nests in the respective tree species by the availability of the respective tree species.
3.4. Preference of tree species

At site A, a total of 151 large trees in 16 ha were examined (Table 1). The proportion of alive and dead A. erioloba trees was 52% and 28%, respectively, of stumps was 13%, and of A. luederitzii and B. albitrunca was 5% each. A total of 36 Black-tailed Tree Rat nests were found. Most (30) nests were in A. erioloba trees, 13 in dead trees, and 3 in stumps. There was no significant preference of dead A. erioloba over other trees for nesting (preference index 1.4, $\chi^2 = 1.1$, df = 1, $p = 0.303$). Tree rats did not prefer A. erioloba trees (either dead, alive or stumps, $n = 33$ nests and 137 trees) over other tree species ($n = 3$ nests and 14 other trees) for nesting ($\chi^2 = 0.04$, df = 1, $p = 0.850$). Selection ratio was near 1 (selected as expected from availability of trees) for all tree types (Table 1).

In the total mapped area at site B of 15.8 ha (10 locations with 2 circles each of 50 m radius) large trees were scarce ($n = 42$) compared to site A. We therefore took into account also the next smaller size class of trees $>$4 m. Dead trees accounted for 34% of trees, 42% were live Acacia trees (A. erioloba and A. luederitzii together), and 25% were live B. albitrunca trees. We found a total of 14 tree rat nests, of which 8 were situated in dead trees and the others in alive B. albitrunca. No tree rat nest was found in live Acacia trees. Selection ratio for or against B. albitrunca and for or against dead trees varied between locations (Table 1).

4. Discussion

All nests of the Black-tailed Tree Rat in Molopo Nature Reserve were situated in cracks and crevices of tree stems. Many cavity dwelling animals depend on dead and standing trees for nesting as reported e.g. for the flying squirrel Glaucomys volans (Muul, 1974; Bendel and Gates, 1987; Taulman, 1999), the Major Mitchell Cockatoo Cacatua leadbeateri (Rowley and Chapman, 1991) and Green Wood-hoopoe Phoeniculus purpureus (du Plessis, 1995). At study site A, many large and alive A. erioloba trees were available for nesting, with sufficient hollows inside the stems. No preference for dead trees was observed. At study site B, all available trees were smaller and we found no tree rat nests in alive Acacia trees. Nests were inside main stems of dead trees or stumps, or in main stems of live, large B. albitrunca trees. Preference for either tree type varied between sites and among locations. Our results suggest, that trees with hollows were the critical habitat element for the nesting of tree rats, but that the tree species or tree vigour was less critical.

The spatial distribution of tree rats at site A was at random, when taking vegetation parameters into account (Fig. 2). Nest sites were not distributed in colonies, since we did not observe clumping of nest sites in our spatial statistics. However, the scale of our study may have been too small to detect an even distribution of occupied nests. Plenty of empty nest sites were available in the area. The abundance of empty nest sites might have been due to the fact that male tree rats use several trees for daytime roosts within their home range (Eccard et al., 2004), and our study did not separate breeding nests from daytime roosts. It could also be
possible, that nests are regularly abandoned by breeding females. Reasons for this could be a high parasite load in nests used for an extended period, the strong smell of the old nest attracting predators, or the temporary depletion of nearby food shrubs.

The selection of a nest site for tree rats seemed to be limited to trees with *A. mellifera* nearby. This plant was an important food plant for tree rats (Eccard et al., 2004). Meanwhile in the larger data set of site A, *A. mellifera* trees were less frequently found in patches with (or under) a large trees, which may have been due to plant–plant competition, or even through a selective foraging pressure by herbivorous tree rats. The demands for both a safe nest site and nearby foraging sites may restrict the number of potential nesting places, especially when the additional resources required for raising a litter are taken into account. Nest sites for this purpose must have an appropriate cavity size and sufficient food for the lactation period very near. During winter, females were more mobile and the nest only needed to house one animal (Eccard et al., 2004). Thus, the requirements for a suitable habitat and nesting sites may differ among seasons.

No droppings of tree rats were found in *A. mellifera* on foraging sites, whereas trees in patches used by Black-tailed Tree Rats as nest sites typically had scattered droppings in crevices in the bark and in junctions between the main stem and branches. Possibly, the Black-tailed Tree Rats may use the relative safety of hollow trees for defecation and may not advertise their presence in the open bush. It may also be possible that the tree rats digest mainly during daytime when they are resting inside a hollow tree. Since tree rats deposit large amounts of faeces and urea inside the trees, we may further speculate that tree rat nesting could contribute to the decay and death of old trees.

*Z. mucronata* and shrub-sized *B. albitrunca* were more abundant in a patch in the presence of both large *A. erioloba* and tree rat nests. However, total prevalence of these shrubs was very low, and both the association of shrubs and of tree rats may well depend on the age or size of the major tree in the patch, rather than depending on each other. On one occasion during mapping at site B, we had observed twigs of both plant species in an occupied Black-tailed Tree Rat nest, but we hardly encountered tree rats foraging in these plants when following them by radio-tracking the following year (Eccard et al., 2004). It may be, that *Ziziphus* and *Boscia* are only occasionally used as nesting material, but not preferred food plants. In this case, other more preferred plants may experience selective grazing pressure by tree rats, and that would give the not-preferred plants a competitive advantage near tree rat nests. As another possibility, the tree rats may utilize fruits and seeds of *Ziziphus* and *Boscia* and could actively contribute to their distribution.

In conclusion, we show that Black-tailed Tree Rats in the dry savanna woodland on the fringe of the Kalahari did not depend on specific tree species. All nests were situated inside stems of trees; therefore the presence of hollow trees for nesting is a critical habitat element for tree rats. Hollows were more prevalent in larger and probably older trees than in smaller trees. The spatial distribution of nest trees did not show clumping on any investigated scale, and we therefore reject the notion of Black-tailed Tree Rats forming colonies when inhabiting continuous woodlands. Instead the choice of nest locations seems to depend on the prevalence of the
appropriate cavity for nesting but also on the availability of food plants nearby. Thus, nesting locations for tree rats are limited, and the extensive harvesting of large trees in the Kalahari may pose a threat to the arboreal tree rat *T. nigricauda*.

**Acknowledgements**

This study was financed by the German Environmental Research Center, the UFZ Halle-Leipzig. We thank Jork Meyer and and two anonymous referees for comments on earlier versions of this manuscript. Our rangers in Molopo, Steven and Perry Dell, are thanked for help and friendship, music and water. We also want to thank Rich Newberry, the North-west Park Conservation and Tourism Board, Mark Anderson and the Northern Cape Department of Agriculture, Land Reform, Environment and Conservation, PC Anderson of the McGregor Museum in Kimberley, and Hennie Erasmus for their support in the planning stages of the study. Spatial analyses were conducted while MCW held a fellowship of the DAAD (German Academic Exchange Service). JAE and SMH were supported by the Academy of Finland and by the project of Hannu Ylönen (Mammalian Ecology, Jyväskylä, Finland), who kindly tolerated some tree rats among his voles.

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