

ARBOREAL DEAD-LEAF-SEARCHING BIRDS OF THE NEOTROPICS

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ABSTRACT.—At least 11 species of birds in northern Bolivia and southern Peru are dead-leaf-searching “specialists”: more than 75% of our foraging observations of these species have been of individuals searching for insects in dead, curled leaves suspended above ground in the vegetation. All known specialists of this kind belong to the families Furnariidae and Formicariidae. An additional six species, here called “regular users,” exhibit dead-leaf-searching behavior in 25% to 75% of our foraging records. The number of specialists and regular users decreases with rising elevation in the Andes. Specialists disappear from the gradient between 2,000 m and 2,575 m, but regular users occur as high as 3,300 m, near timberline. As many as eight species of dead-leaf-searching specialists coexist in western Amazonia.

The degree to which differences in bird species richness between temperate and tropical forests can be explained by increased variety of resources has yet to be adequately quantified (Karr 1975, Terborgh 1980a). Certainly the year-round availability of fruit and nectar (Karr 1971, Morton 1973) and very large insects (Schoener 1971) contributes markedly to the high richness of bird species in the tropics. Other resources and habitats absent from, or with restricted availability in, the Temperate Zone that also contribute to tropical species richness are army ants (Willis and Oniki 1978), oxbow lake edge and permanently flooded forest (Remsen and Parker, in press), bamboo thickets (Parker 1982, Parker and Remsen, unpubl. data), and epiphytic plants (Terborgh 1977, Remsen and Parker, unpubl. data). Our purpose here is to point out the contribution to neotropical bird species richness of the year-round availability of curled dead leaves suspended in vegetation above the forest floor. These dead leaves are searched by a variety of bird species, some of which are highly specialized on this foraging tactic (Terborgh 1980a).

Suspended dead leaves may occur from the top of the canopy to near the ground, especially where vegetation is dense enough to prevent falling leaves from reaching the forest floor. Dead leaves and the birds that search them are most plentiful in vine tangles and dense thickets (Gradwohl and Greenberg 1982), where high foliage density produces greater accumulations of dead leaves than elsewhere in more open vegetation. Birds search leaves of all sizes as long as these are curled to form refugia for insects; we have recorded birds

searching dead leaves ranging in size (uncurled) from 6×4 cm to 45×30 cm.

These dead leaves harbor more insects than do green leaves (data from Panama; Gradwohl and Greenberg 1982; Gradwohl, unpubl. data), and thus potentially provide a high energy yield for those birds that search them. Such birds must expend more time than elsewhere in searching for and handling prey because extracting insects from curled dead leaves often requires probing motions and acrobatics not involved in standard gleaning from green leaves. Dead leaves are also much less abundant, and more patchily distributed than, green leaves, increasing the average travelling time between foraging sites for a specialist.

STUDY AREAS AND METHODS

In the austral winters of 1979, 1980, and 1981, we gathered foraging data on the insectivorous birds at six points (600 m, 1,350 m, 1,650 m, 2,575 m, 3,050 m, and 3,300 m) on an altitudinal transect in the humid Andes of Depto. La Paz, Bolivia. Each time a bird was seen to touch a substrate with its bill while foraging was considered as a single foraging record; no more than three consecutive foraging records were taken for an individual bird. These data allowed us to quantify the degree of specialization on dead-leaf searching by a variety of species in a rich avifauna. We supplemented these data with Parker's foraging information from lowland Peru at the mouth of the Río La Torre on the Río Tambopata, Depto. Madre de Dios, 250 m, Manu National Park, Depto. Madre de Dios, 250 m, and the lower Río Napo area, Depto. Loreto, 125 m., during the austral winter of 1983. Voucher

specimens for all species are deposited at the Museum of Zoology, Louisiana State University (LSUMZ).

We grouped dead-leaf searchers into three categories based on degree of specialization: (A) *Specialists*: species seen searching dead leaves in more than 75% of our observations; we predict that Specialists are obligate dead-leaf searchers. (B) *Regular Users*: species seen searching dead leaves in 25–75% of our observations; for species such as the *Eubucco* barbets that feed on both fruit and insects, over 25% of our non-frugivorous observations were of individuals searching dead leaves. (C) *Occasional Users*: species for which less than 25% of our observations are of dead-leaf searching.

Although our samples for many of the species are small, especially by standards for Temperate Zone studies, we are reasonably confident of our assignments to categories; before formal quantification beginning in 1979, we recorded the foraging behavior of most species discussed below from 1974 to 1978 in conjunction with other studies in Peru and Bolivia.

RESULTS AND DISCUSSION

Eleven species of Specialists and six species of Regular Users were found at our study sites in northern Bolivia and southern Peru (Table 1). Species from these sites that we found to be Occasional Users were: *Piaya cayana* (Cuculidae); *Phaethornis ruber* (Trochilidae); *Capito aurovirens* (Capitonidae); *Sittasomus griseicapillus*, *Dendrocolaptes certhia* (Dendrocolaptidae); *Synallaxis azarae*, *Margarornis squamiger*, *Ancistrops strigilatus*, *Pseudocolaptes boissonneautii*, *Philydor pyrrhodes* (Furnariidae); *Cymbilaimus sanctaemariae*, *Thamnophilus schistaceus*, *T. aroyae*, *Pygiptila stellaris*, *Dysithamnus mentalis*, *Myrmotherula longicauda*, *M. iheringi*, *M. axillaris*, *Terenura humeralis*, *Hypocnemis cantator*, *Myrmeciza hemimelaena* (Formicariidae); *Atlappetes rufinucha* (Emberizinae); *Hemispingus calophrys*, *Thlypopsis ruficeps*, *Habia rubica*, *Tachyphonus luctuosus*, *Buthraupis montana*, *Tangara schrankii*, *T. chrysotis* (Thraupinae); and *Basileuterus luteoviridis* (Parulidae).

All dead-leaf Specialists were furnariids or formicariids, the two largest families of predominately foliage-gleaning birds in the Neotropics; sample sizes, however, were inadequate to test statistically whether or not these families contributed disproportionately, relative to other insectivorous families, to the dead-leaf Specialist category. Regular Users were taxonomically more heterogeneous (Table 1).

We could not find any conspicuous mor-

phological correlates among dead-leaf searchers in comparison to live-leaf searchers. The high frequency of hanging, clinging and probing maneuvers required to reach dead leaves and extract prey from them suggests that subtle morphological differences relative to live-leaf foragers may exist. The only stout-billed dead-leaf searchers, the *Eubucco* barbets, often rip curled leaf clusters open, rather than insert the bill into the leaves as do the more typical, slender-billed species. Thus the barbets, who are Regular Users rather than Specialists, often ruin the dead leaf as a suitable refugium for insects, whereas the obligate Specialists often leave the leaf intact and suitable for new potential prey. Most dead-leaf searchers are dull-colored, primarily shades of brown or buff, but their coloration does not seem to differ in any consistent way from that of non-dead-leaf-searching confamilials. The *Eubucco* barbets, however, are among the gaudiest of tropical birds.

Syntopic dead-leaf Specialists differ in body size, size of leaves examined, and foraging height. The body weights of *Myrmotherula antwreni* (10 g) and small furnariids (15 g for *Cranioleuca* and *Thripophaga*) are approximately one-third to one-quarter that of the larger dead-leaf-searching furnariids (20–40 g for *Philydor*, *Automolus*, *Anabacerthia*, *Thripadectes*), a difference that presumably produces differences in prey sizes taken. The antwrens also search significantly smaller leaves (Mann-Whitney *U*-test, $P < .01$) than the large furnariids; but we do not know whether smaller leaves harbor smaller insects. At Serranía Bellavista, where four furnariids of approximately the same body size coexisted, each Specialist fed at different but overlapping heights above ground (Table 1). All differed significantly from one another ($P < .001$, Mann-Whitney *U*-test) except for *Anabacerthia striatocollis* vs. *Philydor erythrocerus* ($P < .10$).

Examination of the elevational gradient in number of species of Specialists and Regular Users at eight localities in northern Bolivia and extreme southern Peru (Fig. 1) shows that the number of Specialists ranged from 2.5 to 4% of the total resident avifauna up to 2,000 m; Specialists disappeared from the gradient between 2,000 m and 2,575 m. Regular Users comprised 1 to 2% of the total resident avifauna at all elevations except 2,575 m, where no Regular Users were found.

The number of species in both foraging categories decreased in a more or less linear manner with increasing elevation, paralleling the general trend toward decreasing species richness with increasing elevation on the same gradient (Remsen, unpubl. data). The slope for

TABLE 1. Dead-leaf Specialists and Regular Users.

	Percent total foraging maneuvers searching dead leaves (n, total observations)	Localities ¹	Mean foraging height in meters (range)
SPECIALISTS			
Furnariidae			
Speckled Spinetail			
<i>Cranioleuca gutturata</i>	84.6 (26)	5, 6, 7, 9	11.3 (8–15)
Plain Softtail			
<i>Thriphopha fusciceps</i> ²	100.0 (12)	(6), 7	8.4 (6–11)
Montane Foliage-gleaner			
<i>Anabacerthia striaticollis</i>	92.3 (39)	3, 4	9.9 (1.5–26)
Rufous-tailed Foliage-gleaner			
<i>Philydor ruficaudatus</i>	76.9 (39)	5, (6), 7	12.8 (9–21)
Rufous-rumped Foliage-gleaner			
<i>Philydor erythrocercus</i> ³	90.2 (82)	3, 4, 6, 7, 9	12.0 (6–22)
Striped Treehunter			
<i>Thripadectes holostictus</i>	100.0 (9)	3, 4	0.9 (0.2–1)
Buff-throated Foliage-gleaner			
<i>Automolus ochrolaemus</i> ⁴	95.0 (20)	3, 4, 5, 6, 7	3.2 (1.5–8)
Olive-backed Foliage-gleaner			
<i>Automolus infuscatus</i>	86.7 (63)	6, 7, 9	4.7 (0.3–12)
Chestnut-crowned Foliage-gleaner			
<i>Automolus rufipileatus</i>	100.0 (16)	5, 6, 7, 9	4.3 (1.5–9)
Formicariidae			
White-eyed Antwren			
<i>Myrmotherula leucophthalma</i>	95.3 (43)	6, 7	3.6 (1–10)
Ornate Antwren			
<i>Myrmotherula ornata</i>	98.9 (91)	5, 6, 7, 8	5.3 (0.7–18)
REGULAR USERS			
Capitonidae			
Versicolored Barbet			
<i>Eubucco versicolor</i>	100.0 (7) ⁵	3, 4	10.0 (1–20)
Lemon-throated Barbet			
<i>Eubucco richardsoni</i>	86.4 (22) ⁵	5, 6, 7, 9	14.2 (12–24)
Scarlet-hooded Barbet			
<i>Eubucco tucinkae</i>	100.0 (12) ⁵	(6), 7	6.6 (2–11)
Dendrocolaptidae			
Buff-throated Woodcreeper			
<i>Xiphorhynchus guttatus</i>	34.4 (32)	5, 6, 7, 9	10.8 (1–21)
Furnariidae			
Light-crowned Spinetail			
<i>Cranioleuca albiceps</i>	25.0 (36)	1, 2	2.5 (1.5–3)
Troglodytidae			
Moustached Wren			
<i>Thryothorus genibarbis</i>	73.3 (15)	3, 4, 5, 6	5.3 (1–12)

¹ Localities: Those in parentheses are those from the elevational transect (Fig. 1) where the species was found but where no foraging data for the species was obtained at that locality. The localities, with code numbers, are: (1) Cotapata, 4.5 km WNW Chuspipata, 3,300 m; (2) ca. 1 km S Chuspipata, 3,050 m; (3) Serranía Bellavista, 35 km by road N Caranavi, 1,650 m; (4) Serranía Bellavista, 47 km by road N Caranavi, 1,350 m; (5) Río Beni, ca. 20 km by river N Puerto Linare, 600 m; (6) mouth of Río La Torre on Río Tambopata, 250 m; (7) Manú National Park, 250 m; (8) Pilcopata, Río Madre de Dios; (9) lower Río Napo area, 125 m. Localities 1 through 5 are in Depto. La Paz, Bolivia, 6 through 8 in Depto. Madre de Dios, Peru, and 9 in Depto. Loreto, Peru.

² Assignment to Specialist category tentative because all observations came from only one individual observed intermittently for over an hour.

³ Includes data from two distinct races, *P. e. subfulvus* and *P. e. ochrogaster*, which may prove to be separate species. Ridgely (1976) noted for a third race, in Panama, "often probing dead leaf clusters."

⁴ In Central America, this species is also specialized on searching dead leaves, as noted by Skutch (1952, 1969), Slud (1964), Orians (1969) and Ridgely (1976).

⁵ Sample size does not include observations of frugivory.

the Specialist's regression (Fig. 1) was nearly identical to that of all bird species combined (-0.0030 vs. -0.0031). The slope for Regular Users was much lower, but with so few Regular User species, the difference means little.

The number of species in both foraging categories was slightly inflated at the 250-m and 600-m localities by greater habitat heterogeneity. At both localities, *Automolus rufipileatus* was separated by habitat differences from

the other *Automolus* species ("terra firme" vs. river edge forest), as were the two antwrens at 250 m (*M. leucophthalma* in forest and *M. ornata* in bamboo thickets). At the 600-m site, where *leucophthalma* was absent, *ornata* occurred in all types of forest as well as in bamboo thickets; this seems to be an excellent example of a "niche shift" and "ecological release." At the 250 m site, *Eubucco tucinkae* was a scarce inhabitant of forest at oxbow lake

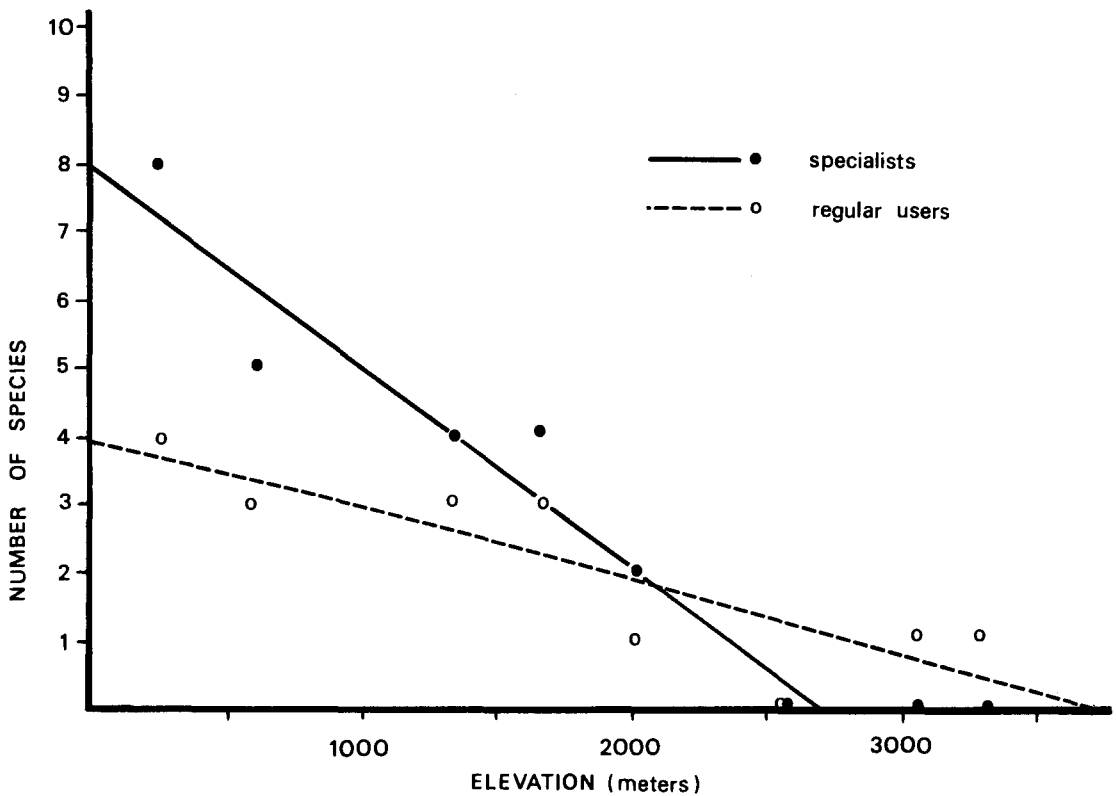


FIGURE 1. Number of species of dead-leaf-searching Specialists and Regular Users at various elevations in humid forest in northern Bolivia and southern Peru. The solid line ($y = -.00300x + 8.0$) represents that produced by a linear regression of elevation against number of species of Specialists ($r = -.96$, $P < .01$) between 250 m and the lowest elevation, 2,575 m, at which Specialists disappear. The dotted line ($y = -.00111x + 4.0$) represents that produced by a linear regression of elevation against number of species of Regular Users for all eight localities ($r = -.86$, $P < .01$). The data for the 2,000-m site come from an LSUMZ collecting locality a few kilometers from the Bolivian border in extreme southeastern Peru (Abra de Maruncunca, 10 km SW San Juan del Oro, Depto. Puno; courtesy T. S. Schulenberg); the two Specialists there are *Anabacerthia striaticollis* and *Thripadectes holostictus* and the Regular User is *Eubucco versicolor*. The number of resident forest species at each site is: 48 at 3,300 m, 72 at 3,050 m, 79 at 2,575 m, 99 at 1,650 m, 116 at 1,350 m, 138 at 600 m, and approximately 300 at 250 m (the latter is the Río Tambopata site; see footnotes of Table 1 for precise localities).

edges and *E. richardsoni* was found in other types of forest. We found no such habitat division from 1,350 m to 3,330 m; at these montane localities the river-created habitats responsible for a high degree of habitat partitioning in the lowlands (Remsen and Parker, in press) were absent.

Why do dead-leaf-searching species become fewer at higher elevations? Although we lack direct data concerning productivity, our qualitative impressions agree with those of Terborgh (1977) for Andean elevational transects: overall productivity declines markedly with increasing elevation, as would be expected with the decline in air temperatures. Janzen (1973) has documented an overall decline in numbers and species of insects (above intermediate elevations) with increasing elevation in Costa Rica. Thus, available insect biomass, presumably including that harbored by dead leaves, should decrease with increasing elevation.

Furthermore, as canopy height decreases with rising elevation, opportunities for vertical stratification by the dead-leaf searchers decrease. In the low-stature forests at the 3,050-m and 3,300-m sites, no potentially competing bird species segregate by differences in foraging heights, other than by the broad categories, *undergrowth* vs. *trees* (Remsen, unpubl.). This contrasts with the vertical stratification of four species of dead-leaf searchers at 1,650 m (see above) and numerous examples among live-leaf searchers at low elevations (Pearson 1971, 1977; Terborgh 1980b).

Does insect density in dead-leaf clusters (and/or density of dead leaves) above 2,000 m elevation decline below some threshold value that prevents specialization on dead-leaf searching? Gradwohl and Greenberg (1982, unpubl. data) have demonstrated how amenable the dead-leaf system is to quantification of the variables needed to answer such a question.

With most critical parameters so readily measurable (dead-leaf density, distance between leaves, prey density) and with a spectrum of degrees of specialization by the predators, this system would be nearly ideal for testing models of optimal foraging (e.g., MacArthur and Pianka 1966, Pulliam 1974).

Our study areas contained very many species, yet several Neotropical species that are Specialists were absent from our Bolivian-Peruvian study sites: *Philydor atricapillus* and *Thripophaga macroura* (Parker, pers. observ.), *Myrmotherula fulviventris* (Orians 1969, Wiley 1971, Willis 1972, Gradwohl and Greenberg 1980, 1982), *M. haematonota* (Willis 1972; 100% of 27 observations searching dead leaves, Parker, pers. observ.), *M. erythrura* (Willis 1972; Pearson 1977; Parker, pers. observ.), and *M. gutturalis* (Willis 1972). (We suspect that the remaining *Myrmotherula* with a spotted throat, *M. gularis*, will also be found to be a Specialist when its foraging behavior is studied.)

Other Neotropical species absent from our sites, or for which we have few observations, that should be found to be Regular Users are: *Eubucco bourcierii* (Slud 1964, Orians 1969, Ridgely 1976, Parker, pers. observ.), *Craniouca erythrops* (Skutch 1969), *Thripophaga berlepschi*, *Anabazenops fuscus*, *Philydor lichtensteini*, *Thryothorus longirostris* (Parker, pers. observ.), *T. coraya* (100% of 10 observations searching dead leaves; S. W. Cardiff, T. S. Schulenberg, and A. P. Capparella, pers. comms.), *T. nigrogularis* (78% observations searching dead leaves; $n = 18$; Parker, pers. observ.), and *T. rutilus* (Slud 1964, Morton 1980). Descriptions of the foraging behavior of *Cacicus* [*Amblycercus*] *holosericeus* by Skutch (1954) and Slud (1964), combined with our own limited observations on this species in Bolivia, indicate that this species may be a Regular User. Willis (1960, 1966) indicated that the ant-tanagers *Habia rubica*, *H. gutturalis*, and *H. cristata* may be Regular Users; our limited data for *rubica* also support this. We suspect that when studied thoroughly many or most species of *Craniouca*, *Philydor*, *Automolus*, *Hylocistetes*, and *Thripadectes* (see Slud 1964 for *T. rufobrunneus*) will be classified as Regular Users or Specialists. Our limited observations for *Automolus dorsalis* and *A. melanopezus* indicate that they are probably Specialists. Parker's foraging data from lowland Peru in 1983 indicate that *Capito niger* (Capitonidae) is a Regular User of dead leaves: of 24 foraging observations (not including those feeding on fruit), 20 (83.3%) were of individuals searching dead leaves. This species occurs at the 250-m point on the transect in Figure

1. *Pygiptila stellaris* may also be a Regular User, but our sample size of observations is insufficient at present.

Skutch (1954, 1960, 1967, 1969, 1972, 1982) mentioned dead-leaf searching for the following Central American species, most of which, when studied in detail, should prove to be only Occasional Users: *Synallaxis brachyura*, *Xenops minutus* (Furnariidae); *Taraba major*, *Myrmotherula schisticolor*, *Myrmeciza exsul* (Formicariidae); *Caryothraustes poliogaster* (Cardinalinae); *Mitrospingus cassinii*, *Euphonia imitans*, *Cyanerpes lucidus* (Thraupinae); *Hylophilus decurtatus* (Vireonidae); *Cacicus uropygialis* (Icteridae); and *Psilorhinus mexicanus* (Corvidae). To this list of Occasional Users should be added *Xiphorhynchus flavigaster* (Dendrocolaptidae; Willis 1960); *Margarornis rubiginosus* and *Syndactyla subalaris* (Furnariidae; Ridgely 1976); *Thamnophilus punctatus* (Formicariidae; 9% of 165 foraging records, Oniki 1975; Gradwohl and Greenberg 1982); *Craniouca pallida*, *Philydor rufus*, *Thamnophilus cryptoleucus*, *Dysithamnus stictothorax* and *Perenostola schistacea* (Parker, pers. observ.); and *Piezorhina cinerea* (Emberizinae; 3.6% of 55 observations, S. W. Cardiff, unpubl. data). We suspect that virtually every Neotropical foliage-gleaning bird investigates curled dead leaves occasionally. We encourage all investigators who study the foraging behavior of forest birds to present their results in such a way that the degree of specialization on dead leaves can be quantified.

Forests of temperate latitudes of course also have dead leaves suspended above ground, and these are searched for insects by some bird species to varying degrees. In particular, the Worm-eating Warbler (*Helmitheros vermivorus*) seems to use dead leaves heavily; even vagrant individuals in California 3,000 km west of their normal migration route search dead leaves (Remsen, pers. observ.). Perhaps it is not coincidental that in coloration and bill-size the Worm-eating Warbler resembles furnariids more than most parulids. Other North American species that we have observed foraging regularly in dead-leaf clusters are the Carolina Chickadee (*Parus carolinensis*), Northern Oriole (*Icterus galbula*), and Golden-winged Warbler (*Vermivora chrysoptera*); the latter also feeds this way frequently on the wintering grounds in the Neotropics (Slud 1964, Willis 1972:129, Ridgely 1976, Morton 1980), as do the Blue-winged Warbler (*V. pinus*), Prothonotary Warbler (*Protonotaria citrea*) (Morton 1980), and the Worm-eating Warbler (Willis 1960, Lack and Lack 1972).

At temperate latitudes, the strong season-

ality in leaf-fall limits the degree to which birds may specialize on searching dead leaves, and perhaps the degree to which insects specialize on them for refugia. At tropical latitudes, leaf-fall is presumably much less seasonal, and dead leaves suspended in the vegetation appear to be available year-round in most areas. Thus, as our data from Bolivia and Peru show, as many as eight dead-leaf-searching Specialists may be added to Neotropical forest communities by the continuous availability of this resource.

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