The Condor 98:483–490

INITIAL CHANGES IN HABITAT AND ABUNDANCE OF CAVITY-NESTING BIRDS AND THE NORTHERN PARULA FOLLOWING HURRICANE ANDREW[1]

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Abstract. We examined the initial effects of Hurricane Andrew on nest site availability and abundances of seven species of cavity-nesting birds and the Northern Parula (*Parula americana*) in a large bottomland hardwood forest associated with the Atchafalaya River in Louisiana. As hurricane damage increased, so did the density of understory vegetation and the number of snags, however, the abundance of cavities did not change. None of the abundances of the individual cavity-nesting species were related to hurricane damage or the availability of cavities. Northern Parula abundance was negatively correlated with hurricane damage and density of understory vegetation. The low abundance of this species in forests heavily damaged by the hurricane may be due to loss of canopy foraging habitat or of Spanish moss (*Tillandsia usneoides*), one of its principal nesting sites.

Key words: avian abundance; Spanish moss; snag; cavity; disturbance; woodpecker; bottomland hardwoods.

INTRODUCTION

In many tropical regions, cyclonic storms occur with sufficient frequency to be important factors in determining the structure and species composition of biotic communities (Wiley and Wunderle 1993). Often, bird populations are more adversely affected by habitat changes resulting from cyclonic storms than by the direct effects of high winds and flooding on individual survival (Wunderle et al. 1992, Wiley and Wunderle 1993). An opportunity to examine the effects of a hurricane on avian populations and habitats occurred when Hurricane Andrew made landfall on 25 August 1992 on the Louisiana Gulf Coast. As the storm moved inland maximum sustained winds were 209–217 km per hour, and forests adjacent to and east of the storm track were heavily damaged (Kelly 1993). More than 450 km^2 of cypress (*Taxodium distichum*)-tupelo (*Nyssa sylvatica*) swamps and bottomland hardwood forests in the Atchafalaya River Basin were directly affected (Doyle et al. 1995). These forests constitute one of the largest bottomland hardwood stands in the United States and over 35% of the remaining forest in the Lower Mississippi River Drainage. In some areas of the Atchafalaya Basin over 80% of the trees were damaged by the high winds associated with the hurricane (Kelly 1993).

Birds requiring large mature trees, such as many cavity-nesting species, are particularly susceptible to the effects of cyclonic storms (Wiley and Wunderle 1993). Because many suitable nest cavities are located in snags or in trees weakened by past storms or by disease organisms (Haapanen 1965), it is possible that a large number of cavities were lost in the gale force winds of Hurricane Andrew. Cavities in trees that have been blown to the ground are useless for most cavity-nesting bird species because of ease of access by predators to nest sites < 1 m above the ground (Best and Stauffer 1980). Although the negative effects of hurricanes on cavity-nesting birds have been documented in mature pine forests (Engstrom and Evans 1990, Hooper et al. 1990) and Caribbean rainforests (Varty 1991, Wiley and Wunderle 1993), we are unaware of comparable studies in bottomland hardwood forests like those that experienced the brunt of Hurricane Andrew in Louisiana.

We collected data from bottomland hardwood forests in the Atchafalaya River Basin to determine the initial influence of Hurricane Andrew on cavity nest sites and the bird species that use them. We also evaluated the effects of the hurricane on Northern Parula (*Parula americana*),

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[1] Received 24 July 1995. Accepted 22 March 1996.

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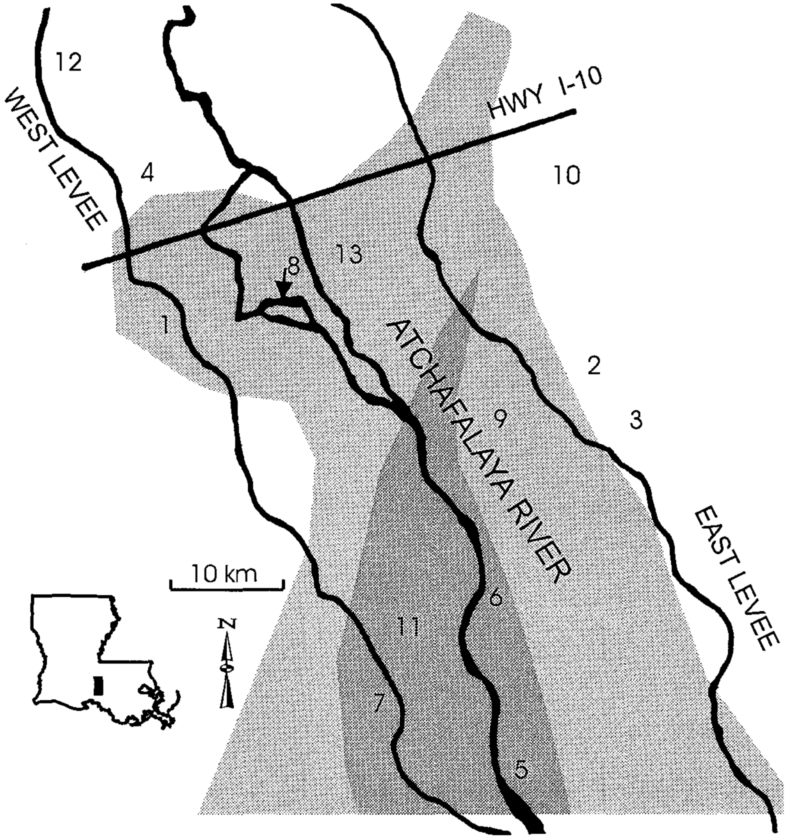

FIGURE 1. Location of transects in areas of light (unshaded), moderate (lightly shaded), and heavy (heavily shaded) hurricane damage within the Atchafalaya River Basin of Louisiana. Locations of damage classes are based on the results of an aerial survey (Kelly 1993). Numbers identify individual transects presented in the text and other figures.

because like the cavity nesters, the abundance of one of its primary nest sites, Spanish moss (*Tillandsia usneoides*), may have been reduced by the hurricane's gale force winds.

MATERIALS AND METHODS

Prior to the hurricane, few data existed on the abundance of either cavities or cavity-nesting birds in the largely roadless Atchafalaya Basin. There were also no truly unaffected sites in close proximity of the basin. Therefore, we compared sites experiencing different degrees of damage to assess the effects of the hurricane on cavity-nesting species. Initial sampling (Fig. 1) was based on an aerial survey of foliar and bole damage to trees resulting from the hurricane (Kelly 1993). We combined several of the survey's damage designations to establish three classes of habitat damage: Light, Moderate, and Heavy damage (Fig. 1). Based on Kelly (1993) the approximate average proportions of hardwood trees that were damaged by the hurricane were 4%, 17% and 80% for our Light, Moderate, and Heavy classes, respectively.

We stratified sampling of bird abundance and habitat by establishing three 500 m transects within each damage class region during 1993. Transects were randomly located in stands of bottomland hardwoods to which we had access (Fig. 1). A vegetation map prepared by the U.S. Fish and Wildlife Service was used to locate stands of bottomland hardwoods. In 1994, three additional transects were established to add a replicate to each damage class. A new transect was also established in 1994 to replace transect 4, which was deemed inappropriate for our study after the first field season due to recent logging of the area. Six points, used as centers of plots described below, were established at equal distances (100 m) along each transect.

In January–February 1994, hurricane damage and the abundance of cavities and snags were assessed at three plots, located 200 m apart, on each transect. Data were collected within a 12.6 m radius circle around the plot center, so a total area of 0.15 ha was sampled for each transect. Standing and fallen trees and snags (standing dead trees) with a diameter at breast height (DBH) ≥ 5 cm were examined. We measured four variables reflecting hurricane damage: BRANCH LOSS, the proportion of standing trees that lost a large limb; SNAPPED OFF, the proportion of standing trees that had bent or snapped off trunks; FALLEN, the proportion of trees characterized as completely fallen; and UPROOTED, the proportion of trees that were partially uprooted, but not fallen. Although these measurements were made approximately 15 months after the hurricane, they reflect damage due to hurricane; the area had experienced no major ice and wind storms within that period that could have caused additional tree damage.

We surveyed cavities during the winter because of enhanced visibility due to fallen leaves. To determine if visible cavities were suitable for bird use, we examined each of them using a miniature video camera mounted with a small flashlight on an adjustable height aluminum pole (Ouchley et al. 1994). Cavities in the trees and snags ≥5 cm DBH were classified as small or large. Small cavities, suitable for cavity-nesting passerines or small woodpeckers, had an entrance width of 3.2–10 cm (Brawn 1988). Large cavities had a horizontal entrance width > 10 and < 30 cm and a vertical entrance height of 10–60 cm. Such cavities would be suitable for Pileated Woodpeckers, *Drycocopus pileatus* (Bull and Meslow 1977), as well as several cavity-nesting ducks and raptors. Any cavities found in fallen trees were excluded from this analysis because they were assumed to be of little use to birds (Sedgwick and Knopf 1991).

During May 1994, we sampled the density of understory cover vegetation at the six plot centers located along each transect. A density board (Gysel and Lyon 1980) 2 m high and 1 m wide, and divided into 200 cm² squares, was used to measure the density of cover vegetation. Vegetation density was measured by counting the number of squares covered by vegetation when viewed from a distance of 5 m. Estimates of vegetation density were made between 0.1–1.0 m and between 1.1–2.0 m above ground level.

For the purposes of analysis, the following measures of nesting and understory habitat were obtained from the vegetation survey for each transect: SNAG, the number of standing dead trees in three plots; LARGE CAVITIES, the mean number of large cavities in three plots; SMALL CAVITIES, the number of small cavities in three plots; SPANISH MOSS, the proportion of 30 trees that contained Spanish moss; DENSITY 1, the mean density of understory vegetation 0.1–1.0 m from the ground surface in six plots; and DENSITY 2, mean density of understory vegetation 1.1–2.0 m from the ground surface in six plots.

The abundance of cavity-nesting birds was estimated using the fixed-radius point count method (Hutto et al. 1986). For each transect, ten-minute counts were made at each of the six plot centers. Each transect was sampled between 0.5 h before and 2.5 h after sunrise. Birds heard or seen within a 50 m radius of the plot center were identified and counted. Thus, a total area of approximately 4.7 ha was sampled on each transect.

Each of the transects was sampled for bird abundance once a month for two months (May and June) in 1993 and for three months (April, May, and June) in 1994. Thus 54 bird surveys, 18 in each damage class, were conducted. Along with the Northern Parula, seven species of cavity-nesting birds were sampled, including three woodpeckers (Pileated Woodpecker, Downy Woodpecker, *Picoides pubescens,* and Red-bellied Woodpecker, *Melanerpes carolinus* [surveyed only in 1994]), two resident passerines (Carolina Chickadee, *Parus carolinensis,* and Tufted Titmouse, *Parus bicolor*), and two Neotropical migrants (Great Crested Flycatcher, *Myiarchus crinitus,* and Prothonotary Warblers, *Protonataria citrea*). Complete bird abundance and habitat data collected from the plots are presented in Torres (1995).

To minimize pseudoreplication, data from the plots on a transect were averaged, and a transect is the unit of replication in all analyses. The normality of the variables reflecting hurricane damage on vegetation and nest sites was tested using the Wilk-Shapiro test (SAS 1985) to determine if parametric statistical analysis would be appropriate. With the exception of Spanish moss, only three of 33 tests for normality of the variables were rejected at the 0.05 level. This is close to the number of times rejection of the null hypothesis, that the data has a normal distribution, is expected to occur by chance alone. Therefore we used parametric analyses to test hypotheses associated with all of the vegetation variables, except for Spanish moss.

One-way ANOVA (SAS 1985) was used to test the hypothesis that each proposed measure of tree damage did not differ among the hurricane damage classes. Although this analysis is circular, in that our measurements of damage reflected features used to classify hurricane damage in the aerial survey (Kelly 1993), it was necessary to quantify the differences in damage among the transects. Principal component analysis, based on the correlation matrix of BRANCH LOSS, SNAPPED OFF, FALLEN, and UPROOTED, was used to create a composite variable to represent hurricane damage. The relative position of each transect along each component was represented by its component score.

Pearson's correlation (r) analysis was used to test the hypothesis that principal component scores were correlated with the mean numbers of snags, large cavities, small cavities, and understory density. Spearman rank correlation (r_s) analysis was used to test the hypothesis that principal component scores were correlated with the number of trees containing Spanish moss.

For analysis of the effects of hurricane damage on bird abundance, the dependent variable was the mean number of individuals of a species observed per transect. To control for possible temporal shifts in abundance, data for the two years were analyzed separately. To minimize the role of seasonality in estimates of abundances, monthly estimates were averaged to obtain a single measurement for each year. This conservative treatment of the data reduced the number of bird surveys to nine and 12 samples in 1993 and 1994, respectively. Distributions of the number of individuals of each species per transect often differed from normality; attempts to transform abundances to normal distributions were unsuccessful. Therefore, Spearman rank correlations were used to assess relationships of the scores of principal components of hurricane damage and nest site abundance with the abundance of each species. The abundances of most species were compared to the number of small cavities, but the abundances of Pileated Woodpecker and Northern Parula were compared to the number of large cavities and the abundance of Spanish moss, respectively. Significance for all analyses was assessed at the 0.05 level.

RESULTS

The proportions of trees that had branch loss and that were snapped off or uprooted, significantly increased with the hurricane damage designations made during the initial aerial survey (Table 1). In the heavy damage areas, most trees lost major limbs and approximately 38% were uprooted or snapped off. Although tree fall was also highest in the heavy damage class there was no significant difference among damage classes (Table 1). These results indicate that stratification of the sampling locations based on the aerial survey resulted in transects being located in areas experiencing significantly different levels of hurricane damage. Because of the lack of bird abundance data prior to the hurricane, large differences in hurricane damage among transects were necessary to evaluate the relationship between bird abundance and damage.

Correlations among the four variables reflecting hurricane damage were high (r = 0.72–0.87). The first principal component (PCI) of these measures of tree damage explained 86% of the variance among them (eigenvalue = 3.421), while the second principal component explained only an additional 8%. All four variables made similar and positive contributions to PCI (Table 1). The strong relationship of PCI with the four measures of tree damage suggests that this component is a reasonable index of hurricane damage; other components were not compared to bird or cavity abundance.

In general, PCI scores increased with damage class (Fig. 2), but Transect 13 had a much higher score than other moderate damage sites, and Transect 4 had a much higher score than the other light sites. Likewise, Transects 7 and 11 had much lower scores than other heavy damage sites. Inconsistencies between damage classification and PCI are probably due to variation in the effects of the hurricane within each broadly defined damage class. Based on our subjective observations, PCI scores provided a better reflection of hurricane damage than did the damage classes. On this basis we chose PCI as our measure of hurricane damage; however, use of dam-

TABLE 1. Comparisons of the mean proportions (and standard errors) of trees damaged by Hurricane Andrew in bottomland hardwood forests of the Atchafalaya Basin, Louisiana. Hurricane damage classes were based on the results of an aerial survey by Kelly (1993). Means are based on four transects in each damage class. The one-way ANOVAs test the null hypothesis that tree damage did not differ among hurricane damage class. Loadings represent the contributions of each variable to the first principal component of the four measures of habitat damage.

Habitat variables	Mean (SE) of damage class			ANOVA	Principal component
	Light	Moderate	Heavy	$F(P)$	loadings
Branch loss	0.308	0.478	0.740	13.45	0.498
	(0.035)	(0.058)	(0.074)	(0.001)	
Snapped off	0.067	0.124	0.271	6.65	0.524
	(0.016)	(0.042)	(0.062)	(0.015)	
Fallen	0.017	0.024	0.045	2.77	0.456
	(0.008)	(0.009)	(0.008)	(0.110)	
Uprooted	0.004	0.074	0.110	4.35	0.501
	(0.002)	(0.029)	(0.041)	(0.044)	

age class, rather than PCI, as a surrogate for hurricane damage does not change our results.

There was no correlation between PCI and cavity numbers, but there was a positive correlation between PCI and number of snags (Table 2). Additionally, a significant negative correlation was observed between Spanish moss abundance and PCI ($r_s = -0.623$, $P = 0.031$). The understory density from both 0.1–1.0 m and 1.1–2.0 m above the ground increased with hurricane damage (Table 2).

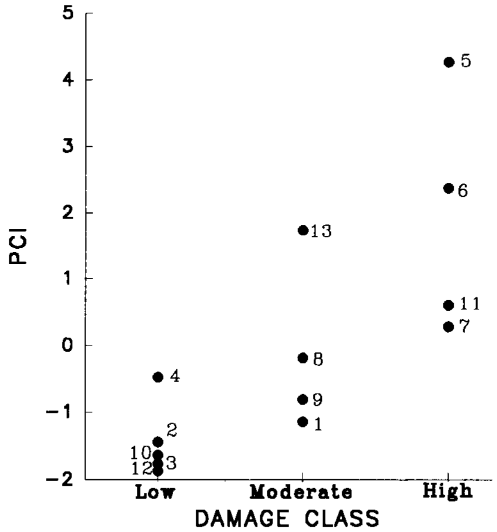

FIGURE 2. Relationship of scores of the first principal component (PCI) of variables reflecting hurricane damage to damage categories based on an aerial survey of the Atchafalaya Basin in Louisiana. Numbers refer to individual transects identified on Fig. 1.

None of the abundances of cavity-nesting species in 1993 or 1994 were correlated with PCI ($P > 0.05$). Additionally, the abundances of these species were not correlated with understory density, number of cavities, or number of snags per transect. However, the abundance of Northern Parula was found to be negatively correlated with hurricane damage for both the 1993 and 1994 data (Fig. 3). The abundance of *Parula* was also negatively correlated with understory density from 1–2 m ($r_s = -0.81$, $P = 0.02$) in 1993 and 0.1–1.0 m ($r_s = -0.64$, $P = 0.03$) and 1.1–2.0 m ($r_s = -0.65$, $P = 0.02$) in 1994. However, there was no significant relationship between the abundance of *Parula* and Spanish moss ($r_s = 0.21$, $P = 0.59$).

DISCUSSION

Tree damage in bottomland hardwood forests affected by Hurricane Andrew was high, however, few trees fell to the ground. Although the number of snags increased with hurricane dam-

TABLE 2. Pearson correlations (r) of PCI with numbers of cavities and snags, as well as the density of understory vegetation, measured at 12 transects in bottomland hardwood forest of the Atchafalaya Basin, Louisiana.

Habitat variables	r	P
Large cavities	−0.143	0.642
Small cavities	−0.255	0.397
Snags	0.724	0.008
Density 0.1–1.0 m	0.678	0.015
Density 1.1–2.0 m	0.724	0.008

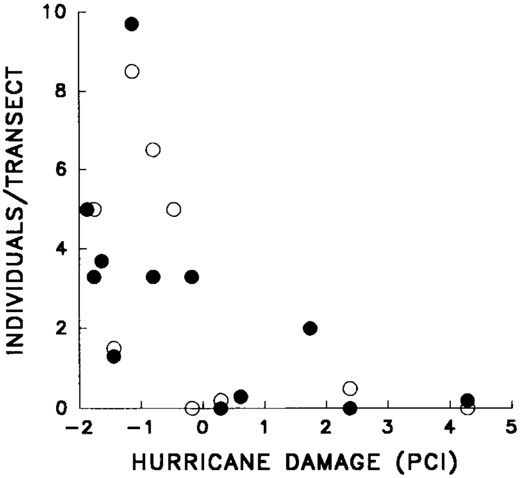

FIGURE 3. Relationship of the abundance of Northern Parula to hurricane damage as measured by PCI. Survey results are represented by open and closed circles for the springs of 1993 and 1994, respectively.

age, the actual percentage of trees killed on any transect was low (<10%). Resprouting was evident even in trees snapped off at 2 m. The low rates of tree mortality in the Atchafalaya Basin indicate that forest composition may change little as a result of Hurricane Andrew. However, the loss of major limbs, broken trunks and uprooting of trees from Hurricane Andrew are expected to produce lasting changes because many years of regrowth will be necessary to reconstruct lost canopy (Loope et al. 1994). Loss of the forest canopy also led to a large increase in the density of understory plants in areas of heavy hurricane damage; the positive association of hurricane damage and understory growth has been noted in other ecosystems (Loope et al. 1994).

There was no relationship between hurricane damage and the abundance of cavities. Although many trees were damaged in the hurricane, most did not fall flat or die. Thus, most cavities available before the hurricane were also available after the storm. We found no correlations between the abundances of cavities and any species of cavity-nesting birds, suggesting that nest sites are not limited in bottomland hardwood forests of the Atchafalaya Basin. This explanation is supported by the high density of potentially habitable cavities (≈260/ha). It is possible that insufficient time has occurred to detect the response of cavity-nesting species to the storm damage. However, if cavities are not limited, and if hurricane damage was not related to decreased cavity availability, it is not surprising that the abundance of cavity-nesters was not correlated with hurricane damage.

The future abundance of cavities may increase as a result of the large number of limbs lost in the storm. These wounds provide disease organisms access to trees as well as a place for primary cavity nesters to start new excavations. Additionally, cavity nesters will often select trees with broken tops (Mannan et al. 1980). The increase in the number of snags as a result of the storm may also provide additional nest sites in the future. Population densities of cavity nesters are often positively related to snag density (O'Meara 1984, Raphael and White 1984).

Red-cockaded Woodpeckers (*Picoides borealis*) provide an example of the large negative effects that hurricanes can have on mainland populations of cavity-nesting species (Engstrom and Evans 1990, Hooper et al. 1990, Hooper and McAdie 1995). This species excavates cavities for roosting and nesting in mature, living pine trees (Jackson et al. 1979). Thus, pine trees killed by hurricanes, including standing dead trees, are of little use to this species. Unlike the Red-cockaded Woodpecker, most of the species we studied will use a wide variety of nest sites and can nest in snags as well as in living trees. Therefore, our results are not contradictory to previous work done on species that have more specialized habitat requirements.

In both years of our survey Northern Parula abundance decreased with hurricane damage. This association may be due to reduced abundance of Spanish moss, a preferred nesting substrate, in areas of heavy hurricane damage. Bent (1937) mentions a report of Swallow-tailed Kites (*Eanoides forficatus*), which often line nests with Spanish moss, abandoning an area after hurricanes reduced moss abundance. In our study, however, it is not clear if a reduction of nesting habitat was responsible for the relationship between hurricane damage and Northern Parula abundance. Spanish moss abundance was significantly correlated with hurricane damage, but its correlation with Northern Parula abundance was weak. It is possible that some other factor associated with hurricane damage may be responsible for the decrease of Northern Parula abundance in areas of heavy damage. The Northern Parula forages by gleaning insects off leaves at the ends of branches, often high in the canopy

(Morse 1970). Perhaps the widespread defoliation of the canopy in hurricane-damaged areas affected the foraging habitat of this species to the extent that its abundance declined. The strong negative correlation between the abundance of Northern Parula and the understory vegetation might also reflect the decreased abundance of the species in areas where the canopy was removed by the hurricane. Declines of populations of Northern Parula wintering in the Virgin Islands were attributed to loss of canopy foraging habitat resulting from Hurricane Hugo (Askins and Ewert 1991). The other species we studied forage closer to the ground or on tree trunks and thus did not experience a decrease in foraging sites.

In summary, the abundance of cavity-nesting birds in bottomland hardwood forests we studied were not affected by Hurricane Andrew. This is probably due to the limited loss of trees (and thus cavities) as a result of the hurricane. Limb damage and greater numbers of snags in damaged areas may provide increased excavation opportunities and food resources for primary cavity-nesters. Increased understory could provide increased foraging habitat and food resources for some of these species, although habitat of species that nest and forage in the canopy, such as the Northern Parula, certainly decreased. Unlike the case of the Red-cockaded Woodpecker in pine forests, the abundances of cavity-nesting species in bottomland hardwood forests seem to be relatively unaffected by the ecological disturbance of hurricanes. It is certainly possible that a stronger hurricane would produce greater damage to bottomland hardwoods, leading to similar reductions in the abundances of cavity-nesting species that have occurred in tropical forests (Wiley and Wunderle 1993), however, hurricanes that are substantially stronger than Andrew are relatively rare events.

ACKNOWLEDGMENTS

We thank R. Conner, C. Jeske, P. Klerks, C. Lance, T. Mallach, S. Pius, R. Twilley, J. Wiley, and J. Wunderle for commenting on earlier drafts of this manuscript. Valuable assistance was provided by P. Almond, B. Keeland, B. McHugh, C. Morgan, R. Taylor, S. Wilson T. Torres, and especially S. Matt. This work was funded by the Southern Science Center of the National Biological Service and by NSF Grant DEB-9123943.

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