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Alabama
Author(s): Dilip Mathur

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DILIP MATHUR[1,2]

Alabama Cooperative Fishery Research Unit, Auburn University,
Auburn, Alabama 36830

ABSTRACT: The bandfin shiner (*Notropis zonistius*) showed highest feeding activity between 0300 and 0600 hr and 1400 and 1700 hr in Halawakee Creek. The bulk of the diet over the 24-hr period was composed of terrestrial insects (allochthonous material). Feeding intensity was lowest in winter and highest in summer. Fish less than 35 mm fork length fed mostly on dipteran larvae in spring through autumn. Ephemeropteran nymphs were important in the diet in summer and winter. Collembola were consumed only in winter. The diet was most diverse in summer and winter and least in spring. Fish larger than 35 mm ate mostly terrestrial insects and were more specialized feeders. Dipteran larvae, ephemeropteran nymphs and odonate nymphs were consumed in moderate quantities in some seasons. The diet was most diverse in winter and least in summer. The diet of the bandfin shiner was compared quantitatively with that of the rough shiner (*Notropis baileyi*), a cyprinid recently introduced in Halawakee Creek. Indices of food similarity indicated a significant overlap in their diets in some seasons. Nilsson's hypothesis of interactive segregation and the principle of competitive exclusion are discussed.

INTRODUCTION

One of the fundamental questions in aquatic ecology is the problem of nutrition. Comprehensive data regarding the nutrition of a large share of the consumers of a given aquatic community have not been available, and overall patterns of the trophic relations among consumer species have not been well understood (Darnell, 1961). A complete understanding of community trophic dynamics in the aquatic ecosystem depends upon a thorough knowledge of the food habits of each species present. The objectives of the present study are to provide insight into the trophic dynamics of the bandfin shiner, *Notropis zonistius* (Jordan), and its food relationships with a recently introduced cyprinid, *Notropis baileyi* Suttkus and Raney, in Halawakee Creek, Alabama. Mathur and Ramsey (1974a) concluded that the key to the explosive success of the rough shiner—at least in part—lies in its prolonged successful spawning season, high reproductive potential and opportunistic feeding habits. The feeding dynamics of the black-banded darter (*Percina nigrofasciata*) and rough shiner (*Notropis baileyi*) in Halawakee Creek, two sympatric species, were reported earlier (Mathur, 1973b; Mathur and Ramsey, 1974b). The food

habits of other cohabiting species, the silverjaw minnow (*Ericymba buccata*), stoneroller (*Campostoma anomalum*) and blacktail shiner (*Notropis venustus*) were reported by Mathur (1972).

Halawakee Creek rises in Chambers Co., Alabama, flows SE through Lee Co., and enters Lake Harding (Chattahoochee River), Alabama-Georgia. The creek is about 29 km long and is located in the Piedmont region of E-central Alabama. The creek was described in detail by Mathur (1973a).

METHODS

The method of determination of daily feeding periodicity, seasonal feeding intensity and seasonal food habits was described by Mathur (1973b). The bandfin shiner for the daily feeding periodicity study were captured by seine at 3-hr intervals over two 24-hr periods on 17-18 April and 2-3 September 1970. The specimens were preserved in 10% formalin and later transferred to 40% isopropyl alcohol. Fork length of each specimen was measured to the nearest mm. Fish for the seasonal study were collected by seine once a month during daylight hours from February 1970 to March 1971.

Stomach contents of each fish were removed and identified, and percent volume of each food item was estimated visually (Larimore, 1957). The calculation of the proportion of food eaten by the fish was based on the biomass of the food present in the stomach. This value is given by the expression:

$$P = \sum_{x=1}^{N} P_{ix}/N_j$$

where P_{ix} is the proportion by volume of food that is category i in the stomach of individual x, and N_j is the number of individuals examined. For the sake of convenience and clarity, food data were analyzed seasonally: spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February). Mathur (1972) presented the monthly food data from which the above figures were derived.

To determine the intra- and interspecific relationships, I calculated a numerical value to estimate the degree of food similarity (overlap). I used the overlap measure of Morisita (1959) as modified by Horn (1966). The overlap coefficient C_λ ranges from 0 when the samples are completely distinct (containing no food category in common) to 1 when the samples are identical with respect to proportional food categories. The overlap coefficient was calculated from the formula:

$$C_\lambda = \frac{2 \sum_{i=1}^{S} X_i\, Y_i}{\sum_{i=1}^{S} X_i^2 + \sum_{i=1}^{S} Y_i^2}$$

where S is the total number of food categories, X_i is that proportion of total diet of species (or size) X taken from a given category of food i, and Y_i is the proportion of the total diet of species (or size) Y taken from a given food category i.

To investigate the seasonal diversity in the diet of the bandfin shiner, diversity indices ($D = - \sum\limits_{i=1}^{N} p_i \log_2 p_i$, where p_i is the proportion of the ith taxon in the stomach contents) were calculated for each size group.

Results and Discussion

The daily feeding cycle.—Changes in feeding activity of the bandfin shiner over the 24-hr period were reflected by changes in the ratio of the weight of the stomach contents to fish body weight. The daily feeding pattern differed slightly between April and September. Three feeding peaks were observed in April, while only two were distinct in September (Fig. 1). In April, the high feeding peak was observed at 0600 hr, a lower one at 1100 hr and an intermediate one at 1700 hr. In September, a high feeding peak occurred at 1700 hr and a lower one at 0600 hr. On both dates, feeding probably started in midevening, continued until dawn, and decreased through midmorning. Except for the small feeding peak which was observed at 1100 hr in April, feeding activity did not recommence until sometime in the late afternoon. There was no indication that feeding activity ceased completely at any
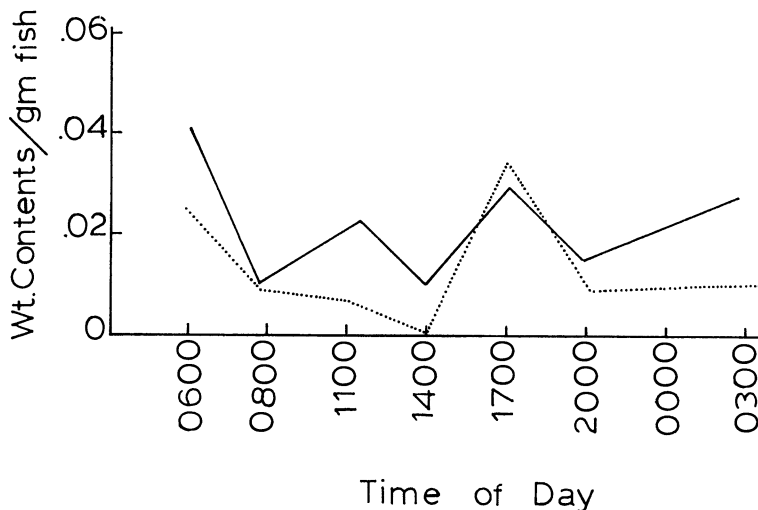

Fig. 1.—Feeding periodicity of the bandfin shiner (*Notropis zonistius*) expressed as the weight of stomach contents per gram of fish on 17-18 April (solid line) and 2-3 September 1970 (dotted line)

one time period. The latter was supported by the presence of freshly eaten items at most time periods.

The amount of food present in the stomachs in September at most time periods was generally lower than in April (Fig. 1). This difference was probably due to higher water temperatures in September. The water temperature ranged from 21.1 to 22.8 C in September and 15 to 17.2 C in April. The high temperature either increased the digestive rates, which resulted in less food remaining in the stomachs at each time period, or caused a reduction in food intake as has been noted in other species (Mathur, 1972).

Daily ration.—The cyclical nature of the feeding in fishes provides a basis for calculation of the daily ration according to the method used by Keast and Welsh (1968). This method involves determination of the differences between the mean weights of stomach contents per gram of fish weight at the peaks and for succeeding low points (troughs). For the bandfin shiner data shown in Figure 1, the resultant values were: April, 0.059 (5.9%) g per g of fish body weight; September, 0.048 (4.8%). These values may be considered minimal because some digestion must take place during the feeding periods (*i.e.*, from preceding low to the high). Mathur and Ramsey (1974b) provided the corresponding daily ration values for the introduced species, the rough shiner, as follows: April, 0.065 (6.5%) g per g of fish body weight; September, 0.059 (5.9%). This analysis indicates that the rough shiner, the introduced species, feeds more extensively on the available food resources than the long-established native species, the bandfin shiner. Thus, the population of the rough shiner may offer competition not only by feeding on the same resources but also exploiting more of the food resources, thereby reducing the resources that might otherwise be available for other native species.

Food composition during the 24-hr period.—The bandfin shiner was quite selective in its feeding habits as only 2-5 types of items were present in the stomachs at any time period (Table 1). The relative importance of these items differed over the 24-hr period. Dipteran larvae were important items in the diet only at 1400 and 1700 hr and were absent from the diet at four time periods. However, the bulk of

TABLE 1.—Food composition of *Notropis zonistius*, expressed as percent volume over the 24-hr period

Item	Time of Day							
	0800	1100	1400	1700	2000	2400	0300	0600
Diptera	....	8	15	24	4	....	....	....
Ephemeroptera	....	....	....	....	6	....	....	6
Trichoptera	....	4	8	....	8	5	....	16
Odonata	....	....	....	....	6	....	....	....
Terrestrial insects	98	80	77	63	77	91	95	78
Diatoms	2	3	....	tr	....	1	1	....
Algae	....	5	....	....	....	2	3	....
Detritus	....	....	....	13	....	2	tr	....

tr = less than 0.5%

the diet was composed of terrestrial insects (allochthonous material) throughout the 24-hr period. At three time periods the diet was composed exclusively of terrestrial insects. Presence of high amounts of terrestrial insects in the diet suggests that the bandfin shiner feeds almost exclusively on the surface with little bottom feeding. Drift studies (Mathur, 1973a; Mathur and Ramsey, 1974b) showed that the times of peak feeding of the bandfin shiner were mostly at times of peak terrestrial insect drift. Ephemeropteran nymphs, trichopteran larvae and odonate nymphs were eaten in negligible quantities and only at certain hours. It is conjectural whether or not the low quantities of diatoms, algae and detritus were eaten directly or ingested incidentally along with the prey.

Seasonal feeding intensity.—Seasonal feeding intensity was determined by the percent fullness of stomachs and percentage of empty stomachs (Table 2). The proportion of empty stomachs in winter as measured by t-test was significantly greater (P < 0.01) than in other seasons, and in this season the stomachs contained the least amount of food. A significantly higher (P < 0.01) proportion of empty stomachs was observed in summer than in spring. The proportion of empty stomachs in autumn was higher (P < 0.01) than in spring or summer. In summer and autumn, both the percentage of empty stomachs and mean percent fullness were high. Although the reasons for this discrepancy are not known, it is known that the mean value of percent fullness is considerably lower than that for the individual with the fullest stomach. This indicates that the "average" stomach in the population is far from filled to its capacity during a feeding period. There may be several reasons for this. An individual that "overeats" during one feeding period may consume correspondingly less at the next one. Alternatively, metabolic needs may be met adequately by less than the maximum intake of food; feeding may be rhythmic, or the amount of food in a given time may be limited (Keast and Welsh, 1968).

Change in food with fish size.—Food habits varied considerably with fish size (Table 3). The food of small fish (16-35 mm) consisted of dipteran and trichopteran larvae, Collembola and some terrestrial insects. In contrast, the diet of the larger fish (> 35 mm) was dominated by terrestrial insects, immature forms of Odonata and Ephemeroptera and detritus. The most distinct shift in the diet was the increased consumption of terrestrial insects by the larger fish. They

TABLE 2.—Seasonal feeding intensity of *Notropis zonistius,* expressed as mean percent fullness and percentage of empty stomachs

Season	No. stomachs examined	Stomachs empty (%)	Percent fullness	
			Range	Mean
Spring	198	17	10- 80	28
Summer	212	29	10-100	37
Autumn	289	40	10- 90	34
Winter	196	52	10- 60	21

comprised only about one-fourth of the total diet of smaller fish but formed more than one-half of the diet of larger fish. Trichopteran and dipteran larvae were considerably less important in the diet of larger fish. Also notable was the absence of large-sized odonate nymphs in the diet of smaller fish. They were eaten in moderate amounts by the larger fish. Detritus was taken in moderate quantities only by the larger fish.

TABLE 3.—Food composition of various sizes of *Notropis zonistius*, expressed as percent volume. N represents the number of fish with food in each length group

	Length group (mm)			
N =	16-25 30	26-35 106	36-45 113	46-55 119
Diptera	27	18	17	12
Ephemeroptera	5	15	12	9
Trichoptera	11	7	3	3
Coleoptera	3	1	1	1
Odonata	....	....	....	1
Collembola	22	17	1	....
Terrestrial	12	28	41	59
Unidentified	13	9	16	10
Hydracarina	....	....	tr	tr
Cladocera	tr	....	....	....
Oligochaeta	3	1	1	....
Detritus	2	2	5	2
Algae	1	tr	tr	tr
Diatoms	....	tr	tr	1
Plant seeds	....	....	....	1
Eggs	....	....	2	....
Fish	....	....	....	....

tr = less than 0.5 %

TABLE 3.—(continued)

	Length group (mm)			
	56-65 128	66-75 59	76-85 29	86-95 7
Diptera	6	8	11	17
Ephemeroptera	5	7	13	4
Trichoptera	5	3	2	....
Coleoptera	1	3	....	....
Odonata	2	2	....	22
Collembola	....	....	....	....
Terrestrial	63	45	57	47
Unidentified	14	14	2	10
Hydracarina	....	....	....	....
Cladocera	....	....	....	....
Oligochaeta	....	....	....	....
Detritus	3	15	14	....
Algae	3	1	1	....
Diatoms	1	1	tr	....
Plant seeds	....	....	....	....
Eggs	....	....	....	....
Fish	....	2	....	....

The data indicate some size-related food selection. The larger fish preferred large-sized organisms such as the odonate nymphs and terrestrial insects. In contrast, the smaller fish tended to feed on small-size dipteran and trichopteran larvae and ephemeropteran nymphs.

On a qualitative basis, some differences between the diets of the smaller and larger fish were apparent. The diet of the two largest size groups (76-85 and 86-95 mm) was least diverse (D = 1.89); only 5-8 items were consumed. The diversity was highest for small fish (D = 2.64 to 2.79); some 10-13 items were consumed. The differences in the diversity values indicate that the smaller fish are generalized feeders, whereas the larger fish may be more specialized.

Seasonal food of 16-35 mm fish.—Considerable seasonal variations in the food habits were noted (Fig. 2). Dipteran larvae formed the bulk of the diet in spring through autumn and were eaten in low quantities in winter. Ephemeropteran nymphs were important in the
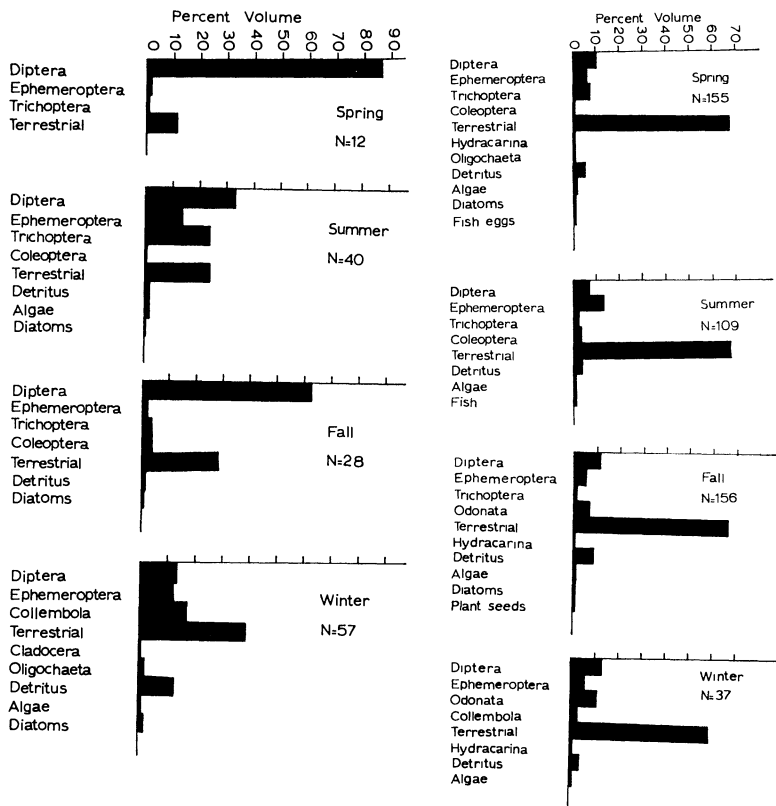

Fig. 2.—Seasonal food composition of the small (≤ 35 mm, left) and large (> 35 mm, right) bandfin shiner (*Notropis zonistius*) expressed as percent volume. N represents the number of fish with food

diet in summer and winter. Trichopteran larvae comprised an im-
portant segment of the diet only in summer. Collembola were con-
sumed only in winter. Terrestrial insects comprised an important
component of the diet in summer through winter. Detritus was rarely
taken but, when present, formed an important portion of the stomach
contents in winter.

The diet was most diverse in summer and winter (D = 2.14 to
2.39) and least in spring (D = 0.64). The low diversity values may
indicate selective feeding while the high values indicate generalized
feeding. The seasonal change in feeding probably is in response to
the differential availability of the food resources.

Seasonal food of 36-95 mm fish.—Quantitatively, the diet of these
fish was dominated by terrestrial insects (Fig. 2). They comprised 59
to 67% of the total food in various seasons. However, dipteran larvae,
ephemeropteran nymphs, odonate nymphs and detritus were also taken
in moderate quantities. Other items which were eaten in low quantities
in some seasons included trichopteran larvae, coleopteran larvae,
Collembola, Hydracarina, oligochaetes, algae, diatoms, plant seeds,
eggs and fish.

Qualitatively, the diet was most diverse in winter (D = 1.83) and
least in summer (D = 1.62). This is in contrast to that of the smaller
fish whose diet was most diverse in summer and least in spring. How-
ever, the D values for larger fish were generally lower than those for
the smaller fish. This indicates that food selectivity increases with
size. The nature of the foods consumed suggests that the larger feed
almost exclusively on surface-drifting terrestrial organisms. This is also
supported by the low proportion of bottom-dwelling organisms in the
diet.

Interrelationships of food and feeding.—Results from this exten-
sive analysis of food habits of cohabiting species provide evidence to
support Nilsson's (1965) hypothesis of "interactive segregation."
Interactive segregation means that the ecological differences between
species in food and/or habitat are often magnified through interaction,
i.e., the species segregate into different niches through competition
and/or predation. Nilsson (1967) suggested that the study of the
food habits of the two closely related species of dace (*Rhinichthys
cataractae* and *R. falcatus*) in the Fraser River System by Gee and
Northcote (1963) is an example of interactive segregation. Nilsson
(1967) stated that food segregation in fishes is interactive and is due to
one or more mechanisms such as food competition (exploitation) and
interference, territoriality and predation. Clearly then, interactive
segregation is not a description of the mechanisms involved in popula-
tion interactions, but rather it describes the results of these mecha-
nisms (Andrusak and Northcote, 1971).

I examined the C_λ values (Table 4) in view of the above hypothe-
sis; the feeding data on the silverjaw minnow (*Ericymba buccata*),

rough shiner (*Notropis baileyi*) and blackbanded darter (*Percina nigro-fasciata*) are taken from Mathur (1972; 1973a) and Mathur and Ramsey (1974b). The overlap in the daily feeding chronology was examined first. It was assumed that any food overlap that might occur between species must be over 50% in order to be biologically significant. Thus, a C_λ value of 0.60 or greater was chosen to depict significant food overlaps. Only one high overlap is observed between the rough shiner and bandfin shiner over the 24-hr period. Also notable is the fact that the introduced rough shiner showed a greater overlap than did the bandfin shiner with the other native species. Although the overlaps are not significant, they do indicate the versatility in feeding of the rough shiner. The ecological effect of the significant overlap between the rough shiner and bandfin shiner may be further increased because both of these species show maximal feeding peaks generally at similar time periods (Mathur and Ramsey, 1974b). The high overlap probably occurred when the surface-drifting organisms became abundant. The similarity in diets of cohabiting species may be attributed to a superabundance of common food resources (Keast, 1965; Nilsson, 1967).

Seasonal food overlap values were also calculated to determine the intra- and interspecific differences in utilization of the food resources (Table 5). The overlaps are shown only for the bandfin shiner and

TABLE 4.—Food overlap calculations (C_λ) comparing differences among species over the 24-hr period

	E. buccata	N. baileyi	N. zonistius
Notropis baileyi	0.34	..	..
N. zonistius	0.07	0.73	..
P. nigrofasciata	0.47	0.33	0.02

TABLE 5.—Seasonal overlap (C_λ) calculations comparing food similarities among various sizes of *Notropis baileyi* and *N. zonistius*. Code to sizes and species is as follows: A — *N. baileyi* (16-35 mm); B — *N. baileyi* (36-75 mm); C — *N. zonistius* (16-35 mm); D — *N. zonistius* (36-95 mm)

	..	..	0.40	B		0.72	..	..	
Autumn	..	0.61	0.85	C		0.55	0.85	..	Winter
	0.53	0.79	0.37	D		0.26	0.57	0.77	
	C	B	A			A	B	C	
	0.56	0.77	0.67	D		0.47	0.62	0.26	
Summer	..	0.65	0.93	C		0.70	0.54	..	Spring
	..	..	0.74	B		0.71	..	..	

Annual unweighted means

	B	C	D
A	0.64	0.76	0.44
B	..	0.66	0.69
C	..	..	0.53

rough shiner. These data indicate marked seasonal intra- and inter-specific overlaps. On an interspecific basis, the large rough shiner and large bandfin shiner showed significant food overlaps in all seasons except winter. The small rough shiner and bandfin shiner showed high overlaps in all seasons except spring. The small rough shiner also showed high overlap with large bandfin shiner, but only in the summer. The significance of this overlap may be further increased because small fish are generally more abundant than larger fish in the population.

Although the quantitative data on the microdistributions of the two species are not available, field observations indicated substantial overlap in the habitats of the two species. Both the rough shiner and bandfin shiner occur sympatrically, particularly in tributaries char-acterized by shallow sand- and gravel-bottomed pools and riffles with slow to moderate current. Thus, the competitive relationship between the two species is increased by a high degree of homogeneity in habitat preference. The rough shiner was generally more abundant in most collections.

When cohabiting species are similar in food and habitat preference, the question arises as to whether they are in competition. Larkin (1956) defined interspecific competition as "the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply." But as Northcote (1954) and others have pointed out, it is extremely difficult to measure whether the demand is greater than the supply. As a result, it is rarely possible to demonstrate directly from field studies that food competition occurs between fish species. Results from this study are no exception, and at best only inferences of ecological importance can be made re-garding food competition among fish species in Halawakee Creek. The great overlap in the diets of the rough shiner and bandfin shiner is noteworthy because *Notropis baileyi* is a recently (1968) introduced species in Halawakee Creek and has become one of the dominant species (Mathur and Ramsey, 1974b).

It is not known from this study whether the two species have reached a stable coexistence. If the two species are assumed to be in a stable equilibrium, then such a coexistence is at variance with the principle of competitive exclusion which states that two species competing for the same limiting resources cannot stably coexist in the same habitat. In other words, no two species can be identical in their ecological properties or in the efficiency with which they exploit any particular resources. However, the two species may coexist in a similar niche without effective competition in the presence of a temporarily super-abundant resource (Keast, 1965). I believe the latter may also be true of the fish community in Halawakee Creek, because these species are abundant in the creek. Ayala (1972) stated that although two species may be in competition with each other for the same food resources, they can stably coexist in equilibrium. In nature, the physical and biotic environments are extremely heterogeneous and the

principle of competitive exclusion is based on an argument which ignores the complexities of the biological world.

It must also be pointed out that the significance of overlap of the diets can be judged only on the basis of the effects rough shiners will have on the mortality, natality, survival and growth of the native species. At present, I do not have distributional and abundance data on the native species prior to the introduction of rough shiner, so it is difficult to say what effects it has had on the native fauna. However, observations (J. S. Ramsey, pers. comm.) indicate that the bandfin shiner is also an aggressive species. It became locally dominant when introduced into the Coosawattee, Little Tallapoosa, Oconee and Tallulah river basins in northern Georgia. Thus, it is difficult to imagine that the rough shiner could possibly displace the bandfin shiner completely from the Halawakee Creek ecosystem.

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