

## An experimental study on the influence of feeding versus predation risk in the habitat choice of juvenile and adult two-spotted goby *Gobiusculus flavescens* (Fabricius)

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### Abstract

The foraging behaviour of juvenile and adult male and female gobies *Gobiusculus flavescens* (Fabricius) were compared. The three groups (juveniles, adult males and females) were tested separately and together for their distribution between two different habitats in an aquarium: One safe habitat with a shelter, and one more risky habitat without a shelter. In half of the trials a predator (cod, *Gadus morhua* L.) was present. Food was added to the two habitats at four different ratios: 1:1, 1:2, 1:5 and 1:8 with the highest food levels on the risky side. When each group was tested separately in the absence of the predator, the distribution between the two habitats was close to that predicted by the Ideal Free Distribution. When juveniles and adults were together without a predator, however, the habitat with the highest food level was under-utilised because the adults showed a strong preference for the shelter-habitat with the lowest food supply. When juveniles and adult males were together in the presence of predator, the juveniles exposed themselves more at the risky side with most food. We conclude that the juveniles give more weight to feeding opportunities than adult males (who give more weight to safety) in their decision where to stay. This interpretation, however, is not straightforward and is discussed in relation to several experimental constraints.

*Key words:* *Gobiusculus flavescens*; Habitat choice; Ideal free distribution predation risk

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### 1. Introduction

It has been demonstrated that male *Gobiusculus flavescens* (Utne et al., 1993) and several other fish species (Milinski, 1979; Gillis & Kramer, 1987; Pitcher et al., 1988)

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distribute themselves according to the Ideal Free Distribution (IFD, Fretwell & Lucas, 1970). When individuals of a species are distributed according to the IFD in the presence of one resource (here food), it is possible to investigate the influence of other factors (e.g. predation risk) by measuring the deviation from the IFD when individuals are exposed to such factors. In such studies male *Gobiusculus flavescens* show a trade-off between predation risk and food availability (Utne et al., 1993). Gilliam (1982) and Werner & Gilliam (1984) introduced the “minimise  $M/f$ ” – theory which simply predicts that an organism should prefer the habitat that minimises the ratio between predation risk ( $M$ ) and food consumption ( $f$ ). Aksnes & Giske (1990) arrived at the same prediction for juveniles that had the possibility of shortening their generation time by increasing their food consumption (see also Giske & Aksnes, 1992). For organisms with a fixed generation time (i.e. organisms that cannot shorten their generation time by increased feeding, such as adults), however, their model predicts that  $M/\ln f$  should be minimised rather than  $M/f$ . This means that habitat value, due to increasing feeding opportunities, is strongly reduced for adults relative to juveniles. Although the models of Gilliam (1982) and Aksnes & Giske (1990) are based on the use of reproductive output ( $R_0$ , being independent of generation time per se) as the fitness measure, the same result is obtained on the basis of a more appropriate fitness measure (see Giske et al., 1993). The experiments of Utne et al. (1993) indicated that adult male gobies gave more weight to an increase in predation risk than to an increase in feeding availability when deciding where to stay. Our hypothesis for the present investigation is that, according to Aksnes & Giske (1990), juvenile gobies should give more weight to an increase in feeding, at the risk of predation, than adult gobies. We tested this hypothesis by elucidating the possible difference in habitat choice of juvenile and adult gobies in relation to predation risk and food availability.

## 2. Material and methods

*Gobiusculus flavescens* was collected over a hard bottom covered with *Fucus* spp. in Raunefjorden close to Bergen (western Norway) with a beach seine. The gobies were acclimatised in the experimental aquarium (80 l) for 3–5 days before the experiments. Live copepods were offered daily. Juveniles, adult males or females were tested separately (10 individuals in each group) and juveniles and adult males together (20 individuals in each group). No feeding was undertaken in the 24 h prior to the experiments. The experiments were done at a temperature of 12–15 °C. The 10 fish within the three different groups were of equal size (juveniles 25 mm and adults 40–45 mm). The aquarium was divided in two equal parts by a net, with one feeding side on each side of the net. During the experimental period (12 min) zooplankton suspended in the water were supplied through two inlets at the opposite sides of the aquarium. This design was also used by Utne et al. (1993). Different feeding ratios at the two sides were achieved by adjusting the zooplankton concentration. The two concentrations were adjusted, however, so that the total number of zooplankton offered was kept at about 60 ind·fish<sup>-1</sup> in all experiments (this number was chosen according to a previous feeding capacity experiment, Utne et al., 1993). *Gobiusculus flavescens* could swim freely through

the net between the two feeding sites in the aquarium. The predator (when present), however, could not pass this net. The distribution of the gobies was recorded on video tape, and no one was present in the laboratory during the experiments. Artificial light, with day and night simulation, was used. The experiments were always initiated at midday, when the light was at a maximum of  $22 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . Copepods, which were used as prey, were collected with plankton nets and kept alive in containers at low temperature ( $5\text{--}6^\circ\text{C}$ ) for a maximum of 3 days. Zooplankton in the size range 0.5–2 mm were used as food for the gobies. The species composition can be considered to be the same at the two different sides of the aquarium within each experiment, but not among all experiments.

Cod (*Gadus morhua*) of age less than 1 yr, was used in experiments where the effect of predator presence was investigated. This species is a major predator on *Gobiusculus flavescens* (Nordeide & Salvanes, 1991). The cod was introduced at the start of the feeding and was always placed at the side without shelter.

Since introduction of a shelter had little or no effect on the distribution of adult males in absence of a predator, but had a pronounced effect in the presence of a predator (Utne et al., 1993), it was decided to use a shelter at one side of the aquarium in all the present experiments. In this way, the number of predator visits increased and hence the number of zero-observations at the predator side decreased. Simulated macroalgae vegetation was selected in favour of real macroalgae to eliminate possible influence of epizootes and metabolites on the goby behaviour. Furthermore, the synthetic shelter could be used in all experiments to minimise differences between experiments. The position of the predator/shelter (these two were opposite to each other) side were randomised in the different replicates.

The food ratios of 1:1, 1:2, 1:5 and 1:8 were used to see how gobies distributed themselves according to the food, in the absence and presence of a predator (Table 1). In all trials, the numbers of fish located at both sides of the aquarium were recorded every 30 s for 12 min, providing 24 pairs of observations in each trial.

Table 1  
Summary of experiments with *Gobiusculus flavescens*

Factors investigated	No. of fish groups	No. of food levels	<i>n</i> (no. in exp.)	Total
<i>Fish groups tested separately:</i>				
Without predator	3	4	3 (10)	36
With predator	3	4	3 (10)	36
<i>Fish groups tested together:</i>				
Without predator	1	4	3 (20)	12
With predator	1	4	3 (20)	12
Total number of experiments				96

No. of fish groups: 3 indicates that juveniles, adult males and females were tested separately while 1 indicates that juveniles and adult males were tested together. No. of food levels: 4 levels were used for all groups (1:1, 1:2, 1:5 and 1:8). *n*: number of replicates for each experimental set-up. No. in exp.: total number of fish in each experimental set-up. Total: total number of experiments (fish groups  $\times$  combinations  $\times n$ ).

Recording began 2 min after the experiment began as the gobies needed some time to investigate the profitability of the two feeding sites (Utne et al., 1993). The mean of 24 observations was used to characterise the distribution in each of the different trials. Three trials were repeated for each experimental set-up and a new group of gobies was used each time. The mean and standard deviation of these three replicates were then calculated. Comparisons were done using two- and three-way ANOVA with arcsin square root transformed proportions (number of fish present at one side divided by the total number of fish used in the experiment) as the raw data. In the series where each group (male, female and juvenile) was tested separately the main effects in the ANOVA comparison were group membership, food ratio and predator presence. In the second series of experiments where juveniles and adult males were tested together, the observations for the two groups cannot be regarded as being independent. Following Johnson & Abrahams (1991) who employed a similar experimental design, we decided to use the non-parametric Wilcoxon test to compare the two groups.

### 3. Results

#### 3.1. Experiments without predator

##### 3.1.1. Juveniles, adult males and females tested separately

At food ratios 1:1 and 1:2 the average number of fish at the two sides was close to the prediction from the IFD, except for the juveniles where some over-use of the low food site was indicated (Fig. 1). At high food ratios (1:5 and 1:8) fewer fish than predicted by the IFD were registered at the side with most food. This finding agrees

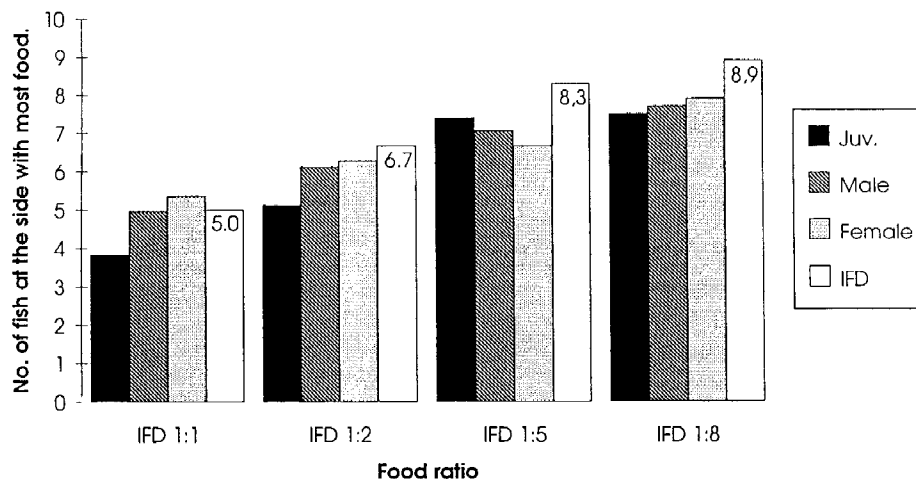


Fig. 1. Average number of juveniles, adult males and adult females *Gobiusculus flavescens* at the side with most food when each group was tested separately. Ten individuals (and three replicates) were used in each experiment and no predator was present. No statistically significant (at  $p = 0.05$ ) difference was found between the three groups (Table 2) and IFD seems to be a reliable approximation for the observed distributions (see text). Mean number of individuals as expected from IFD is added to the IFD bars.

Table 2  
Two-way ANOVA (top, without predator) and three-way ANOVA (bottom, with and without predator) for the experiments where the three groups (female, male, juvenile) were tested separately

Effect	df-effect	df-error	F-value	p-level
<i>Without predator:</i>				
Food ratio	3	24	24.28	0.000
Group	2	24	1.65	0.213
Food ratio/group	6	24	1.19	0.346
<i>With predator:</i>				
Food ratio	3	48	17.52	0.000
Group	2	48	2.94	0.062
Predator	1	48	1564.03	0.000
Food ratio/group	6	48	0.77	0.597
Food ratio/predator	3	48	7.19	0.001
Group/predator	2	48	0.25	0.777
Food ratio/group/predator	6	48	1.76	0.128

Food ratio included the levels 1:1, 1:2, 1:5 and 1:8; group included female, male and juvenile, while predator included presence and absence of predator.

with earlier experiments (Utne et al., 1993). According to the two-way ANOVA (Table 2), food ratio had a significant effect ( $p < 0.001$ ) on fish distribution but there was no significant difference between the groups ( $p = 0.21$ ) (Table 2).

### 3.1.2. Juveniles and adult males together

The combined distribution of juveniles and adult males was not influenced by the food ratio when adult males and juveniles were tested together as the distribution was

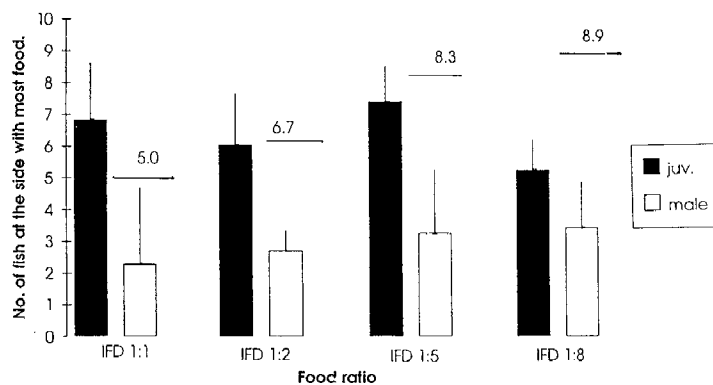


Fig. 2. Average number of juveniles and adult males *Gobiusculus flavescens* at the side with most food when the two groups were tested together. Twenty individuals, 10 of each group, (and three replicates) were used in each experiment and no predator was present. Contrary to the experiments where each group was tested separately (Fig. 1), IFD is not a reliable approximation for the observed distributions. A significantly higher number of juveniles than adults ( $p < 0.005$ ) were present at the side with no shelter and the highest amount of food (Table 3). Mean number of individuals in each group as expected from IFD is indicated. The 95% confidence limits are also shown.

Table 3

Comparison (Wilcoxon rank sum test) of the numbers of juvenile and adult male *Gobiusculus flavescens* at the side with most food in the experiments where they were together in the absence (Fig. 2) and presence (Fig. 4) of predator (cod)

Between:	No predator Juvenile–adult male	Predator Juvenile–adult male
<i>Wilcoxon rank sum test:</i>		
<i>n</i>	12	12
<i>T</i>	0	5
<i>P</i>	<0.005	= 0.005

close to 1:1 for all food ratios (Fig. 2). The Wilcoxon test showed that a significantly higher number of juveniles relative to adults was observed at the high food site without shelter ( $p = 0.005$ , Table 3). Hence, the presence of juveniles seemed to induce a marked adult over-use of the site with the shelter, but with the lowest amount of food.

### 3.2. Experiments with a predator

#### 3.2.1. Juveniles, adult males and females tested separately

Introduction of a predator (cod) at the site with most food had a significant effect ( $p < 0.001$ ) on distribution for all three groups (Fig. 3 and Table 2). In contrast to the experiments without a predator, the food-ratio had little or no effect (see Fig. 3) on the distribution of gobies when a predator was present, and this is reflected in the highly significant food-ratio/predator interaction effect ( $p = 0.001$ , Table 2). There was a higher

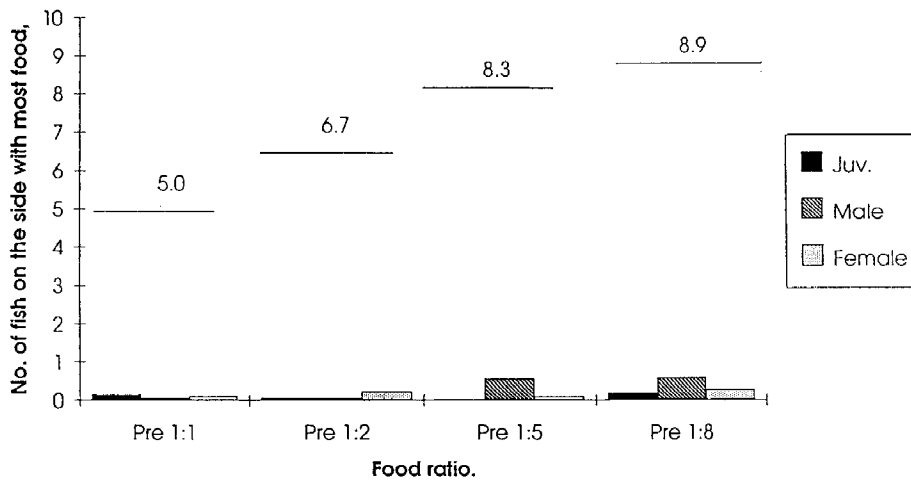


Fig. 3. Average number of juveniles, adult males and adult females *Gobiusculus flavescens* at the side with most food when each group was tested separately with a predator present. Ten individuals (and three replicates) were used in each experiment. Mean number of individuals as expected from IFD is indicated.

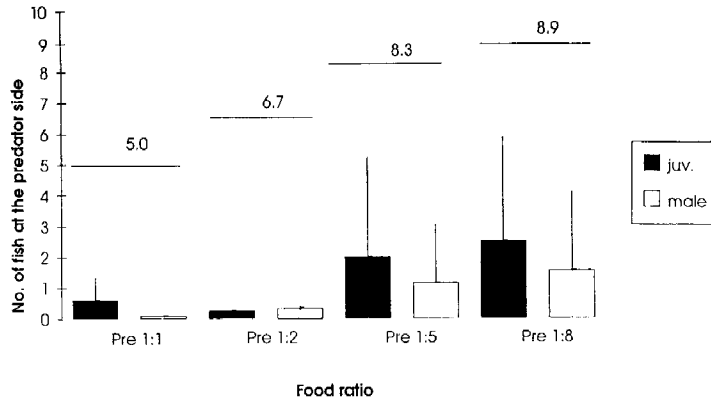


Fig. 4. Average number of juveniles and adult males *Gobiusculus flavescens* at the side with most food when the two groups were tested together with a predator present. Twenty individuals, 10 of each group (and three replicates), were used in each experiment. More fish, especially juveniles, visited the predator when juveniles and adults were together compared with when they were alone (see Fig. 3). Mean number of individuals in each group as expected from IFD is indicated. The 95% confidence limits are also indicated.

number of adult males than juveniles and females on the predator side, which suggests that adult males took a higher risk (Fig. 3). This difference, however, was not statistically significant ( $p = 0.06$ ) according to the three-way ANOVA (Table 2).

### 3.2.2. Juveniles and adult males together

When males and juveniles were together each individual spent, on average, more time with the predator than in the experiments where each group was alone with the predator (Fig. 4 versus Fig. 3). Although not significant, there was a tendency for both juveniles and adults to increase their time on the predator side when the food availability increased on this side (Fig. 4). As in the experiments without a predator (juveniles and adults together) a significantly higher number ( $p = 0.005$ ) of juveniles than adults was present at the side with a predator (high food site) (Table 3).

## 4. Discussion

Fewer fish than predicted by the IFD were found on the side of the tank with most food. This deviation from the IFD increased with the degree of inequality in the food ratio between the two sides and corresponds with earlier results obtained by Sutherland et al., (1988) and Utne et al., (1993). The tendency for over-use of the poorer side was largest for the juveniles (although not significant) and could have been due to overfeeding. The same amount of food was fed to both juvenile and adult fish, while the juveniles probably required less food than the adults. Studies on crucian carp (*Carassius carassius*) showed that a large carp has a foraging rate nearly twice that of a small individual (Paszkowski et al., 1989), and studies on sticklebacks showed that feeding rate was positively correlated with size (Ranta & Lindström, 1990). This can

be attributed to increased encounter rates and handling efficiencies. A larger body size gives increased swimming capacity (Yates, 1983), better vision (Fernald, 1988; Wanzenböck & Scheimer, 1989) and a larger mouth (Wankowski, 1979). As will be discussed later on, such possible differences in the capacities of juveniles and adults introduce some difficulties in the interpretation of the habitat choice of juveniles versus adults in the present experiments.

#### 4.1. Juveniles and adults together

When juveniles and adults were tested together they did not distribute according to the IFD, but close to 1:1 for all feeding ratios. A difference was observed between adults and juveniles, however, as significantly more adults were located on the shelter side (having a lower amount of food), indicating a preference for shelter rather than for food (Fig. 2). Numerical deviation from the IFD is to be expected in the case of unequal competitors. According to Sutherland & Parker (1985) it is not the number of individuals, but rather the competitive weights that should match prey input rates. In this case, a lower competitive weight is indicated for the adults in the present experiments (as the adults were located at the site with the lowest feeding rate). This seems unlikely and we believe that the violation of the IFD is due to other factors. Our field observations (unpublished) have revealed a tendency for the adults to shoal closer to the kelp and rocky shoreline than the juveniles. This corresponds with the observation by Potts & McGuigan (1986) of a gradient in *Gobiusculus flavescens* schools, where the larger/older individuals were closer to focal rocks while the smaller individuals were located towards the periphery of the school away from the rock. Grant & Noakes (1987) study on young-of-the-year brook trout showed that "risky foraging" decreased with increasing body size. And that fish older than 1 yr occupied foraging sites under cover while young-of-the-year were foraging out in the open. They concluded their observations by suggesting that the salmonids become more wary with increasing size because the relative benefits of growing quickly, and hence taking risks while foraging, decreased with increasing body size. Hamner et al., (1988) propose that planktivorous fishes at the windward side of a reef form a "wall of mouths", and zooplankton concentrations diminish inwards towards the reef as a result of zooplanktivorous feeding. By analogy, there will be more food available away from the kelp, which seems to be the place favoured by juvenile *Gobiusculus flavescens*. Hence our experimental results, indicating a higher juvenile preference for food (relative to the adults), and a higher adult preference for shelter, seems reliable. On this basis it may be concluded that the observed difference between adults and juveniles are reflecting different habitat choices, in which adults give more weight to shelter (i.e. less predation risk) than increased feeding opportunities. It is striking, however, that such behaviour is induced (at least in the experimental situation) only when adults are together with juveniles. Indicating that habitat choice in both groups is modified by the presence of conspecifics.

A different habitat preference of juveniles and adults was also indicated in the experiments when the predator (cod) was present. The juveniles spent significantly more time at the side with the highest amount of food (and predator) than the adults (Table 3).



Increased predator exposure, as observed in the present experiments with juveniles and adults together (Fig. 4 versus Fig. 3), may have been caused by the dilution effect resulting from being part of a larger group (20 versus 10 individuals). Such possible dilution applies to both juveniles and adults, however, and does not explain differences between the two groups.

The experiments of Utne et al., (1993) indicated that adult male gobies gave more weight to an increase in predation risk than an increase in feeding availability when the decision on where to stay was taken. This is in accordance with the “clutch-manipulator” strategy that should be expected from adults (Aksnes & Giske, 1990; Giske & Aksnes 1992). Here, the ratio between predation risk and the logarithm of expected feeding rate ( $M/\ln f$ ) should be minimised or kept constant in order to induce a habitat shift. For juvenile “time manipulators” more weight should be put on feeding and this is expressed in the “minimise  $M/f$  rule” (Werner & Gilliam 1984; Aksnes & Giske 1990). The present experiments have shown that when juveniles and adults were together, more juveniles relative to adults preferred the side with the highest amount of food (both with and without predator), while more adults preferred the side with shelter and lowest amount of food; a behaviour pattern that seems to correspond with the field situation. Thus, concerning habitat choice, a decision rule that gives more relative weight to feeding opportunities (and hence growth), such as expressed in the minimise  $M/f$ -rule, seems to apply the juveniles.

This interpretation, however, is not straightforward because the true risk associated with predator exposure may be different for the two age groups. Kotler (1984) demonstrated that species of desert rodents least vulnerable to predation tend to forage in open areas, whereas the most vulnerable species were restricted to the areas under the bushes. Adults represent a larger piece of “meat” and being larger makes them also easier to spot, and adults may therefore be more vulnerable to predation. Hence, several variables preclude us from drawing definitive conclusions about habitat preference of juvenile versus adult gobies in relation to food and predation risk. This is also evident in the following section, where the results from the “alone”-experiments on juveniles and adults are discussed.

#### 4.2. *Juveniles and adults alone*

The “alone”-experiments indicated that adult males visited the predator and the site with highest feeding rate more than the juveniles. Although this result was not significant, it should not be overlooked as it is in conflict with the results from the “together”-experiments where the juveniles apparently had the highest risk exposure (Figs. 3 and 4). The low predator exposure of the juveniles in the alone-experiments, however, may have been caused by a relatively higher food availability at the safe side for the juveniles. As mentioned earlier, adults and juveniles were offered the same amount of food, while the juveniles probably needed less food because of their much smaller size. Since the value of additional food gained by taking a risk depends on the absolute amount of food that can be obtained in safety (Sih, 1982), fewer juveniles than adults may have decided to leave the safe side. Thus, the present alone-experiments involving different size-groups are hardly comparable with respect to risk-taking versus food gain. Males

and females, however, were of the same size and comparisons are more valid. There was a tendency for the males to take a higher risk than the females (Fig. 3). The experiments were conducted in August and all females contained a large amount of eggs. They had already fully invested in eggs and almost reached the goal of their life (reproduction), and presumably in this situation predation risk should be minimised as much as possible. The males on the other hand, had not invested fully yet (the energy content of the male goby (*Pomatoschistus microps*) gonad is <3.7% of the females (Rogers, 1988). The male *Gobiusculus flavescens* invest heavily in nest guarding and maintenance behaviour, which is energetic costly and almost no time is available for feeding during this period (Gordon, 1983). The accumulation of energy before this nest guarding period is therefore important, and the need to do so may provide a possible explanation for the observed tendency for males to risk greater exposure.

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