



A test of prey-attracting and predator defence functions of prey carcass decorations built by *Cyclosa* spiders

I-CHIA CHOU*, PI-HAN WANG*†, PAO-SHENG SHEN‡ & I-MIN TSO*†

*Department of Life Sciences

†Center for Tropical Ecology and Biodiversity

‡Department of Statistics, Tunghai University

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While decorations of many spiders are made entirely of silk, those built by many *Cyclosa* species are composed of prey carcasses. The functions of prey carcass decorations are unknown. By manipulating their presence on webs of *Cyclosa confusa*, we tested whether they attract prey. Insect interception rates of webs with the decoration removed were significantly higher than those of webs with the decoration present. By monitoring predators' responses to spiders with and without decorations on their webs, we also tested whether prey carcass decorations decreased spiders' mortality. Spiders on undecorated webs experienced fewer attacks from paper wasps, *Vespa affinis*, but these attacks were all directed against the spiders. Although spiders with decorated webs experienced more attacks, wasps usually attacked the decorations rather than the spiders. Finally, we examined how visual signals of prey carcass decorations were perceived by predators. The chromatic colour contrast of the decoration against *C. confusa* was such that hymenopteran predators could not distinguish the chromatic signals of decorations from those of spiders. We conclude that prey carcass decorations do not attract insects, but may redirect the attack of *V. affinis*, and thus enhance the survival of spiders.

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Many animals construct structures composed of various materials in their territories. Such structures are documented from a wide array of organisms and function to increase their performance in, for example, mating (Backwell et al. 1995; Borgia 1995) or predator defence (Stachowicz & Hay 1999). One such structure is the web decoration built by orb web spiders. Many diurnal orb web spiders incorporate various objects called decorations in their webs after they have constructed an orb (Nentwig & Heimer 1987; Herberstein et al. 2000a). Spiders decorating their webs are mostly members of the families Araneidae, Uloboridae and Tetragnathidae (Eberhard 1990; Herberstein et al. 2000a). Most spiders use silk to construct decorations, but many species of the genus *Cyclosa* use prey carcasses (Comstock 1913). After consuming the prey, most orb web spiders drop the carcasses from their webs (Foelix 1996). *Cyclosa* spiders, however, keep prey carcasses more or less permanently and use them to build

a linear decoration (Fig. 1; Rovner 1977; Neet 1990; Rod 1996).

Several functional hypotheses for decorations have been proposed (Herberstein et al. 2000a; Starks 2002). These hypotheses include: (1) avoiding predation by making the spider look bigger (Schoener & Spiller 1992); (2) defence against predators (Blackledge 1998a; Blackledge & Wenzel 2001); (3) warning large flying animals to avoid web destruction (Tolbert 1975; Eisner & Nowicki 1983; Blackledge 1998a, b); (4) serving as a shelter or hideout (Hingston 1927); (5) regulating spider body temperature (Humpreys 1992); (6) attracting prey by reflecting ultraviolet light (Craig & Bernard 1990; Craig 1991; Tso 1996, 1998a, b; Watanabe 1999; Herberstein et al. 2000b; Bruce et al. 2001; Craig et al. 2001); (7) adjusting web tensions (Robinson & Robinson 1970; Watanabe 2000); and (8) reflecting physiological condition under stress (Nentwig & Rogg 1988). Among them, only the prey attraction and predator defence hypotheses have received much empirical support (Herberstein et al. 2000a).

Although the functions of decorations have received much attention, most of the relevant studies have focused on silk decorations built by *Argiope* spiders and only a few

Correspondence: I. M. Tso, Department of Life Sciences, Tunghai University, Taichung 407, Taiwan (email: spider@mail.thu.edu.tw).

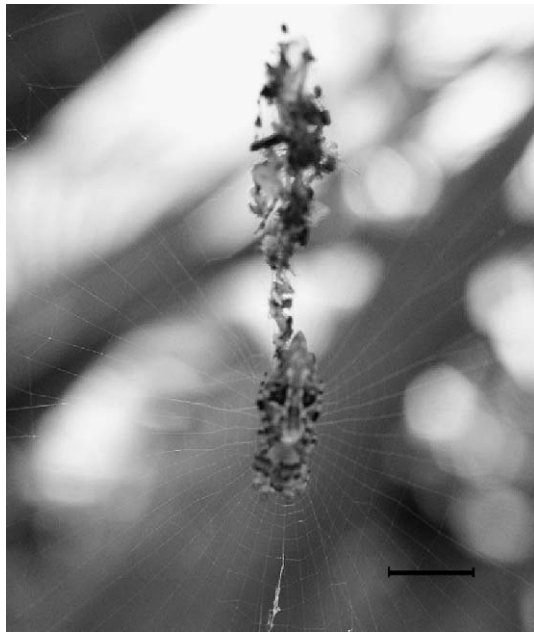


Figure 1. Female *Cyclosa confusa* (below) and its prey carcass decoration (above). The scale bar is 5 mm.

have examined prey carcass decorations built by *Cyclosa* spiders. Neet (1990) found that in calm weather most *C. insulana* built their webs without circular silk decorations and proposed that the type of decoration was determined by weather conditions. However, this hypothesis has not been tested directly. In *C. conica*, decorated webs intercept more insects than undecorated ones, but these are made entirely of silk, not prey carcasses (Tso 1998a). Therefore, the functions of prey carcass decoration remain to be tested empirically.

There is evidence that spiders use prey carcasses to attract prey. Thus, thousands of yeasts growing on the prey carcasses left by *Mallos gregalis* on its communal web produce an odour that is attractive to flies (Tietjen 1986; Tietjen et al. 1987). Although *Cyclosa* rebuilds the web daily, it does not destroy the frame on which prey carcasses are attached (Rovner 1977), so the carcasses are usually kept on the webs for a long time (Neet 1990); these are inhabited by yeasts (I. C. Chou, unpublished data), which might also generate a scent that attracts prey.

Like silk decorations (Craig & Bernard 1990; Zschokke 2002), the prey carcass decorations in *Cyclosa* webs might also create visual signals. The spiders always sit among prey carcasses and the colours of both are similar to human eyes. Because it is not easy for humans to distinguish the spiders from the prey carcasses, arachnologists have long suggested that the prey carcass decorations serve to conceal the spiders from predators (Marson 1947; Eberhard 1990; Foelix 1996). However, the human visual system differs from that of insects (Chittka & Menzel 1992; Vorobyev & Brandt 1997; Briscoe & Chittka 2001), the major prey and predators of most spiders (Coville 1987; Foelix 1996). It is currently not clear whether insects can visually distinguish the *Cyclosa* spider from the prey carcass decoration.

In both field manipulations and laboratory studies, we evaluated the prey-attracting and predator defence functions of prey carcass decorations built by *C. confusa*. First, we manipulated the presence of prey carcasses on webs of *C. confusa* and then compared the prey interception rates. Second, we used video recording to track the behavioural responses of predators to spiders with and without decorations in the field. Finally, we calculated the colour contrasts of decorations against different backgrounds in the colour space of Hymenoptera (Chittka 1992, 1996, 2001) to assess how they are visually perceived by hymenopteran predators.

METHODS

Study Site

We conducted field studies in August 2002 at the Yung-Hsing woodland (area about 6 ha, L. L. Severinghaus, personal communication) on Orchid Island (22°03'N, 121°32'E), Taitung County, Taiwan. Yung-Hsing is a cultivated secondary forest maintained by local people (Chen & Tso 2004). A stable *C. confusa* population occurs in the study site throughout the year (I. M. Tso, personal observations). Dominant tree species in the study site were breadfruits, *Artocarpus communis*, betel palms, *Areca catechu*, Indian almond, *Terminalia catapa*, figi longan, *Pometia pinnata*, and the herbaceous giant elephant ear, *Alocasia odora*.

Prey Interception Rates

We marked web sites of *C. confusa* (Fig. 1) by fastening green tapes with identification numbers on nearby vegetation. We chose spiders with decorations of similar size as the study subjects (decoration area $\bar{X} \pm \text{SE} = 97.5 \pm 4.8 \text{ mm}^2$). The spiders were then randomly assigned to two groups, experimental and control. In the experimental group, we carefully removed all prey carcasses without damaging the web and in the control group the decorations were left intact. Each day before 0900 hours, we used forceps to remove new prey carcasses incorporated by spiders of the experimental group. Horizontal and vertical web diameters were measured to calculate orb area. Since the orbs constructed by *C. confusa* were nearly symmetrical (vertical diameter: $\bar{X} \pm \text{SE} = 57.1 \pm 0.1 \text{ mm}$; horizontal diameter: $69.7 \pm 0.1 \text{ mm}$), we simply averaged the two diameters and used the πr^2 approximation. Spider body length and the length and width of decorations on all webs were measured to the nearest millimetre with a digital calliper. The prey interception data were retrieved from video-taped recordings made on four video recorders set up in the study site. Two were placed in front of two experimental webs and the others in front of two control webs. We placed the video cameras 2 m away and made recordings at an angle of 45° to the left or right side of the webs (depending on the microhabitat nearby). The recordings were conducted daily from 1000 to 1800 hours between 8 and 17 August 2002 (except 14 August because of bad weather), resulting in 288 spider-hours (144 for

each group). We estimated prey interception data by averaging the number of prey intercepted by webs per h recorded on the videotapes.

The prey interception data set fitted well with the Poisson distribution (Pearson χ^2 test: $P < 0.05$; Steel et al. 1997, pp. 558–561). Therefore, we used the Poisson regression to examine the relation between prey interception rate, orb area and presence of prey carcass decorations. The web area was designated as a categorical variable owing to a small sample size. We ranked web areas into the following categories: <100, 100–200, 200–300, 300–400, 400–500, 500–600, 600–700, 700–800 and >800 cm². The Poisson log-linear model with explanatory variable X is:

$$\log \mu_N = \log N(X_i) + X_i\beta$$

where $\mu(X)$ is the expected value, X is the explanatory variable (decoration, weather and web area), β is the unknown parameter and $N(X)$ is the total number of individuals.

Predation Events

The same video recording was also used to identify the predators of *C. confusa* and the behavioural interactions between them. We noted type of predator, number of attacks, duration of attack, behaviours of predators and responses of *C. confusa* from the videotapes. Attack behaviours were classified into two categories: attack on a spider and attack on a decoration. An attack was defined as a wasp bumping into an object on a web. A chi-square test was performed using SYSTAT 5.2 (Wilkinson et al. 1992) to compare the number of attacks between two groups and the frequencies of the two attack behaviours recorded from the control group.

Colour Contrasts

We collected *C. confusa* spiders and their decorations from the study site. We also collected leaves and barks of betel palm, Indian almond, figi longan, breadfruit, and the giant elephant ear. The reflectance spectra of the spiders, decorations and different vegetations were measured with a spectrometer (S2000, Ocean Optics, Inc., Dunedin, Florida, U.S.A.) in the laboratory. For each measurement, the illumination leg of the reflection probe (with six illumination fibres) was attached to a light source (450-W, Xenon arc lamp) and the read leg (with one read fibre) to the spectrometer. The tip of the probe was placed vertically 5 mm above the sample. Four measurements of reflectance spectra were made on each decoration and the dorsum and ventrum of each *C. confusa*. We used the means in the subsequent calculations of colour contrasts. Those of barks and leaves were obtained in a similar way. Because these objects were larger, we took six measurements from each of them. The fraction of the light reflected by the surface is the surface reflectance function. Colour signals could be generated when the surface reflectance function was multiplied by the illumination

function of the habitat (Wandell 1995). The daylight illumination function of the forest understory on Orchid Island was obtained from Tso et al. (2004).

Since the paper wasp, *Vespa affinis*, was the only predator appearing in all recorded attacks, we chose the spectral sensitivity functions of the genus *Vespa* to determine the photoreceptor excitation for each measured spectra (Peitsch et al. 1992). The calculations of colour contrasts of decorations against various vegetation backgrounds followed Chittka (1992, 1996, 2001). We used two-tailed t tests to compare the colour contrasts of decorations against different backgrounds with the discrimination threshold value of 0.05 estimated for hymenopteran insects (Théry & Casas 2002). We used the Bonferroni method to control for experiment-wise type 1 error. The P values were obtained by the Bonferroni t statistics given by Kuehl (2000). Hymenopterans use achromatic vision when searching for objects far ahead and chromatic vision when approaching the object (Giurfa et al. 1997; Spaethe et al. 2001; Heiling et al. 2003). We thus calculated the colour contrasts under these two conditions to examine how predators view the spiders and decorations under different chromatic systems.

RESULTS

Prey Interception Rates

Prey interception rates differed significantly between the two groups (Table 1). In contrast to the predictions of the prey attraction hypothesis, spiders in the experimental group (with the decoration removed) caught significantly more prey than the spiders in the control group (with the decoration intact; Fig. 2). Compared with *C. confusa* with decorations, those without decorations on average caught 30% more insects.

Predation Events

During the 8 days of monitoring by video recording, *V. affinis* was the only predator that attacked *C. confusa*. A total of 15 attacks were recorded from 288 spider-hours: 13 from the control and two from the experimental group

Table 1. Results of Poisson regression comparing prey interception rates of *Cyclosa confusa* webs estimated by video recordings between experimental (decoration removed) and control groups (decoration intact)

Parameter	Estimate	SE	χ^2	P
Intercept	-4.474	0.328	185.90	<0.0001
Web 200–300	-1.158	0.641	3.27	0.071
Web 300–400	-0.217	0.353	0.38	0.539
Web 400–500	0.253	0.338	0.56	0.453
Web 500–600	0.493	0.306	2.60	0.107
Web 600–700	0.057	0.354	0.03	0.873
Web 700+	<0.001	<0.001	—	—
No decoration	0.347	0.175	3.91	0.048
Decoration	<0.001	<0.001	—	—

Web 200–300 to web 700+ indicates the area of the web.

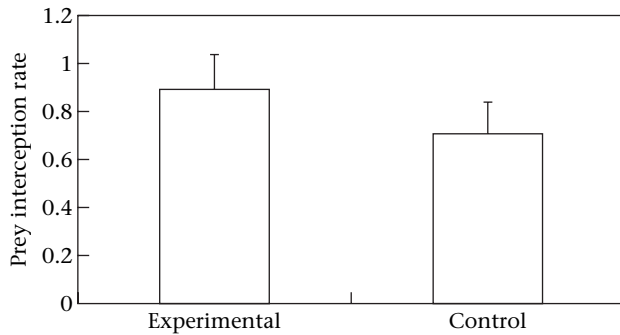


Figure 2. Mean \pm SE prey interception rates (number of insects per 400 mm² orb area) of *Cyclosa confusa* in the experimental (decoration removed) and control (decoration intact) groups estimated from video recording.

($\chi^2_1 = 8.06$, $P < 0.05$). On average, each attack lasted about 4 s ($\bar{X} \pm SE = 3.5 \pm 0.5$ s). In the two observed attacks in the experimental group, *V. affinis* directly attacked the spider, which seemed to have been caught or forced to abandon the web, because after the attacks both spiders dropped from the web and did not return for the rest of the day. Among the 13 observed attacks in the control group, two were directed at the spiders and 11 at decorations ($\chi^2_1 = 6.23$, $P < 0.05$). Whereas *C. confusa* in the experimental group quickly dropped from the web after an attack, most individuals in the control group remained on the web during the initial stage of an attack on the decoration. Only when the attacks on the decoration were prolonged and intensified did *C. confusa* in the control group jump away. In most cases the wasp kept attacking the decorations even after the spiders had jumped away. None of the spiders in the control group disappeared during the 8 days of recording. Spiders that jumped away because of an attack usually returned to the webs after about 30 s.

Calculation of Colour Contrasts

Prey carcass decorations and *C. confusa* had similar chromatic properties (Fig. 3). Both had low reflectance at short wavelengths and slightly higher reflectance at long wavelengths. Colour contrasts of decorations against *C. confusa* (both dorsum and ventrum) when viewed under chromatic vision were not significantly greater than the discrimination threshold (Fig. 3, Table 2). This result indicates that hymenopteran predators could not distinguish between the colour signals of prey carcass decorations and spiders from a short distance. Under chromatic vision, colour contrasts of prey carcass decorations against barks of *A. communis*, *P. pinnata*, *T. catapa* and leaves of *P. pinnata* and *A. odora* were not significantly higher than the threshold (Fig. 3, Table 2). However, prey carcass decorations showed strong colour contrast against the bark of *A. catechu* and the leaves of all plants except *P. pinnata* and *A. odora* (Fig. 3, Table 2). When viewed under achromatic vision, the colour contrasts of decorations against most backgrounds were significantly higher than the threshold (Fig. 3, Table 2). Only those against spider dorsum and ventrum, bark of *A. communis* and

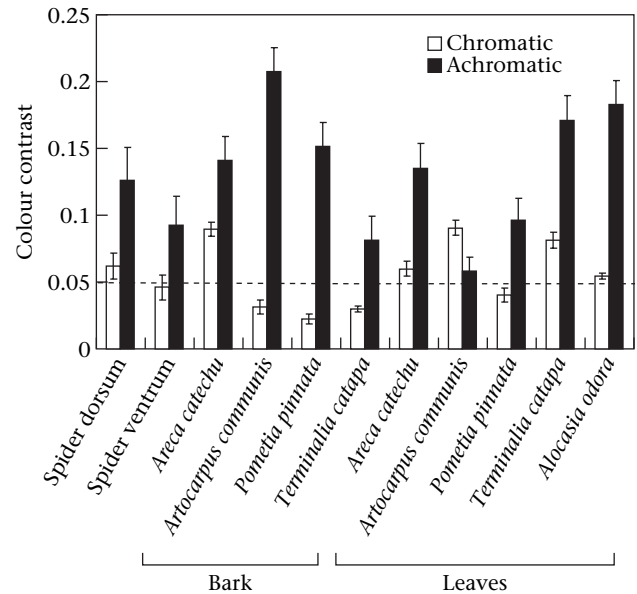


Figure 3. Mean \pm SE colour contrasts of prey carcass decorations built by *Cyclosa confusa* against different background types viewed by *Vespa* sp. by chromatic and achromatic vision. Dashed line represents the threshold for colour contrast discrimination calculated for Hymenoptera.

T. catapa and leaves of *P. pinnata* were not significantly larger than the discrimination threshold (Table 2).

DISCUSSION

Our study shows that the prey carcass decorations of *C. confusa* do not function as a prey attractant. In contrast

Table 2. Results of two-tailed *t* tests (with the Bonferroni method implemented) comparing the colour contrasts of prey carcass decorations built by *Cyclosa confusa* against different backgrounds viewed by *Vespa* sp. by chromatic and achromatic vision with the discrimination threshold of 0.05

	Chromatic		Achromatic	
	t_{12}	<i>P</i>	t_{12}	<i>P</i>
Spider				
Spider dorsum	2.062	0.062	3.047	0.010
Spider ventrum	-0.224	0.827	1.600	0.138
Bark				
<i>Areca catechu</i>	7.166	<0.001**	5.042	<0.001**
<i>Artocarpus communis</i>	-1.916	0.079	0.759	0.463
<i>Pometia pinnata</i>	-5.676	<0.001**	5.612	<0.001**
<i>Terminalia catapa</i>	-5.222	<0.001**	1.755	0.105
Leaves				
<i>Areca catechu</i>	3.708	0.003*	4.729	<0.001**
<i>Artocarpus communis</i>	7.340	<0.001**	8.725	<0.001**
<i>Pometia pinnata</i>	-0.013	0.990	2.843	0.015
<i>Terminalia catapa</i>	6.882	<0.001**	6.712	<0.001**
<i>Alocasia odora</i>	2.790	0.016	7.345	<0.001**

The Bonferroni $t_{\alpha/2, k, v}$ (k = number of comparisons = 11, $v = df = 12$) is 3.48 for $\alpha = 0.05$ and 4.27 for $\alpha = 0.01$. * $P < 0.05$; ** $P < 0.01$; at $\alpha = 0.05$ level.

to the predictions of the prey attraction hypothesis, decorated webs did not intercept more insects than undecorated ones. On the contrary, video recordings showed a significantly lower foraging success for spiders with decorated webs. There may be two explanations for this result. First, the reflectance spectrum of prey carcass decorations was rather low across a wide range of wavelengths, lacking the insect-attractive chromatic properties of many diurnal orb-weaving spiders (Craig & Ebert 1994; Hauber 2002; Tso et al. 2002). Second, compared with the prey carcass masses deposited by *M. gregalis* (see Introduction), those accumulated by *C. confusa* were rather small (less than 10 mm long) and thus the intensity of any olfactory signal produced by yeasts might be too small to be attractive. Therefore, lack of both visual and olfactory attractiveness might be responsible for the control groups' low foraging success.

Although prey carcass decorations might generate a foraging cost, this study provided evidence that they could help defend the spiders by redirecting *V. affinis* into attacking the wrong target. There were fewer recorded attacks in the experimental group than in the control group. Such a result may be interpreted as spiders without decorations actually enjoying lower predation pressure than those incorporating prey carcasses into their webs. The cues used by *V. affinis* to locate *C. confusa* are not clear. However, studies on vespid wasps show that members of this family use both visual and olfactory cues to detect their prey (Richter 2000). Spiders without decorations on their webs might have a lower probability of being seen because of a smaller visual or olfactory cue. However, once they were detected by the hymenopteran predators, they were much more likely to be attacked than spiders incorporating carcasses into their webs, because, in the absence of decorations, *V. affinis* aimed their attacks directly at the spiders. Spiders in the experimental group that were attacked also did not return to the web after they dropped from the webs. However, in most of the recorded attacks in the control group, *V. affinis* were misled into attacking the prey carcass decorations. In many recorded attacks even though *C. confusa* had dropped from the web, *V. affinis* still vigorously attacked the decoration. Several studies have reported that the wasp usually forces the spider to drop from the orb, then descends to the ground to catch it (Eberhard 1970; Coville 1987; Blackledge & Pickett 2000; Blackledge & Wenzel 2001). In the case of *C. confusa*, prey carcass decorations may draw the attention of predators, giving the spider an opportunity to escape unnoticed. In contrast to the inconsistent decoration building of *Argiope* spiders (Seah & Li 2002), *C. confusa* always incorporate a linear string of prey carcasses on their webs. This phenomenon suggests that the benefit of reducing detectability by removing prey carcasses seems to be outweighed by the risk of being accurately attacked once they are found by the predator.

Colour signals are important for Hymenoptera when they are foraging or avoiding a predator (Craig 1990, 1994; Craig & Ebert 1994; Blackledge 1998b). The prey carcass decoration had lower-than-threshold colour contrasts against a spider when viewed by achromatic or chromatic vision. This result suggests that when *V. affinis* was

searching for prey, it could not distinguish the colour of *C. confusa* from that of the prey carcass decoration. However, since *V. affinis* has compound eyes, when viewed from a long distance the image of the spider-decoration combination may be blurred (Wehner 1997). As *V. affinis* approaches the spider and switches to chromatic vision, although the resolution of images is improved, the chromatic signal of the spider remains indistinguishable from the prey carcass decoration. Therefore, *V. affinis* cannot successfully target the real prey when it gets close.

Our study shows that video recording is useful in studying the behaviours of stationary predators, such as orb-weaving spiders. The traditional monitoring method may underestimate the foraging success of spiders, because, during the interval between successive visits, spiders may have caught and consumed small soft-bodied prey. In some studies, investigators improved the accuracy of estimation by shortening the intervals between successive visits (e.g. 30-min interval: Blackledge & Wenzel 1999; Herberstein 2000) or by mapping the web damage to trace the predation events that occurred during the intervals (Craig & Bernard 1990; Tso 1996; Hauber 1998, 2002). However, no matter how frequently the marked webs are visited, one can never ascertain what might have happened during the intervals. In addition, although web damage mapping is able to trace the number of prey intercepted by the web, this method cannot provide an exact estimate of number of prey consumed by spiders. Studies have found a low and inconsistent catching success of prey intercepted by the webs (17–53%, Olive 1980; 25%, Pasquet & Leborgne 1990). Video recording monitors the web continuously and so can accurately measure prey interception rate, capture success and foraging intake. Another advantage of video recording is that it is able to record predation events, which are relatively rare and brief. Before this study we had conducted two field trips to Orchid Island. From a total of 16 days of observation in the same study site using hourly monitoring in February and March 2002, no single predation event was identified (unpublished data). However, in the August 2002 field trip using video recording, a total of 15 attacks were recorded from 8 days. On average, the duration of a single attack usually lasted less than 5 s and in almost all cases *V. affinis* left no damage on the webs. Data of such nature can be successfully obtained only by continuous monitoring of the web. Therefore, future studies on various behaviours of orb-weaving spiders should consider using video recording to enhance the quantity and ensure the accuracy of the data.

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