

IMPACT OF THE THIRD TROPHIC LEVEL IN AN OBLIGATE MUTUALISM: DO YUCCA PLANTS BENEFIT FROM PARASITOIDS OF YUCCA MOTHS?

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In obligate pollination mutualism, selection should favor increased exploitation by either party at the expense of the other. One potential pathway to increase such exploitation at the expense of the mutualist partner is through indirect mutualism across trophic levels, where the natural enemy of a pollinator could reduce pollination costs to the plant. We tested this hypothesis, asking whether a specialized parasitoid wasp that kills yucca moth larvae before they have completed seed feeding will increase the production of intact yucca seeds. In the two years of study in a population of *Yucca treculeana* Carrière (Agavaceae) in west Texas, per capita seed consumption by parasitized larvae of both a pollinator and a nonpollinator yucca moth were significantly reduced when compared to that of nonparasitized conspecific larvae. In one year, fruits that contained at least some parasitized larvae produced significantly more intact seeds than ones with only nonparasitized larvae, whereas the opposite effect was found in the second year. The reason for the latter effect is unclear but is linked with differences in ovule numbers per fruit. The results indicate that natural enemies can benefit *Y. treculeana* indirectly by reducing its cost of pollination.

Keywords: indirect mutualism, *Yucca*, yucca moth, *Tegeticula*, cost of pollination.

Introduction

Plant-herbivore interactions often involve a third trophic level, namely, the natural enemies of the herbivores (Feeny 1975; Price et al. 1980; Godfray 1994). These natural enemies, such as parasitoids, can indirectly benefit the plants by causing the death of herbivores before they have completed feeding and thus reducing the damage inflicted on the plant. This benefit can manifest itself, for example, through increased seed production (Gómez and Zamora 1994; van Loon et al. 2000; Chattopadhyay et al. 2001). Most earlier studies have dealt with antagonistic plant-herbivore interactions, in which the herbivore never provides a benefit to the plant, but the same principle also applies to plant-herbivore mutualisms. In such systems, a parasitoid can potentially serve as an indirect mutualist or antagonist of the plant, thus potentially altering the dynamics and stability of the mutualism. Previous studies that examined how natural enemies of pollinating herbivores affect the dynamics of a mutualism have mostly dealt with figs and fig wasps (Compton et al. 1994; Weiblen et al. 2000; Weiblen 2002). Here we address the same issue in the yucca–yucca moth interaction, which is one of the most extensively studied examples of obligate pollination mutualism (Riley 1892; Rau 1945; Pellmyr and Leebens-Mack 1999; Pellmyr 2003). The female yucca moth serves as the sole pollinator of yuccas. She uses special mouthparts to collect pollen from yucca flowers and then oviposits into floral ovaries and pollinates the flowers with some of the pollen carried. This is critical because her prog-

eny require developing yucca seeds for their development. Each larva consumes only a subset of the available seeds, so the yucca reaps a net benefit from the interaction (Riley 1892). In this interaction, the benefit : cost ratio in terms of intact versus eaten seeds could be improved for the plant if seed consumption by pollinator larvae were reduced by parasitoids (Addicott 1986).

We present results from a 2-yr study testing the hypothesis that parasitic wasps that attack larvae of a pollinating yucca moth species and a coexisting nonpollinating cheater yucca moth species serve as indirect mutualists of the plant by reducing seed consumption such that net production of viable seeds per fruit is increased.

Material and Methods

Study Species

We studied *Yucca treculeana* (= *Yucca torreyi* Shafer; Hess and Robbins 2002), a species with fleshy fruits that is widely distributed throughout the northern Chihuahuan desert and adjacent grasslands and scrub brush in southeastern Texas, southeastern New Mexico, and northern Mexico (McKelvey 1938; Correll and Johnston 1979; Robbins 1983). An individual plant produces one or a few inflorescences, each consisting of several hundred flowers, during a flowering episode. The white, sometimes purple-tinged flowers are open for 1–2 d each, and flowering within an inflorescence is progressive over the course of 1–2 wk. Flowering extends from late February to mid-April in the study area.

Tegeticula treculeanella Pellmyr (Lepidoptera: Prodoxidae) is the only documented pollinator of *Y. treculeana* (Pellmyr 1999). The female lays her eggs inside the ovaries of yucca

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flowers, in a cavity above the topmost ovule in a locule. After oviposition, she uses specialized mouthparts to deliberately pollinate the flower with pollen gathered from flowers. The larva feeds on a portion of the developing seeds inside the fruit, generally starting at the top of locules and feeding downward. Upon completion of development, the larva chews its way out of the fruit and drops to the ground, where it burrows in to diapause in a dense cocoon. The adult emerges during a subsequent flowering period one or a few years later (Riley 1892; O. Pellmyr, unpublished data).

Tegeticula corruptrix Pellmyr (Lepidoptera: Prodoxidae) is a nonpollinating yucca moth that oviposits directly into well-developed fruits a few weeks after pollination (Pellmyr et al. 1996; Pellmyr 1999). Eggs are laid directly inside large developing seeds, or occasionally in the fleshy mesocarp, and the larva consumes yucca seeds side by side with pollinator larvae. Subsequent life history is similar to that of the pollinator species. In contrast to *T. treculeanella*, *T. corruptrix* thus does not provide a benefit to *Y. treculeana* through pollination, only inflicting a cost on the plant through seed consumption.

The parasitoid of the moth larvae is *Digonogastra* Viereck n.sp. (Hymenoptera: Braconidae, Braconinae), an undescribed member of a large genus of parasitic wasps that mostly attack concealed beetle and moth larvae (Force and Thompson 1984; Powell 1984; Quicke 1988, 1997). *Digonogastra* n.sp. has been reported previously from yucca moths under the name of *Iphiaulax* Foerster n.sp. (Force and Thompson 1984; Powell 1984). Adults have been observed on numerous fleshy-fruited yucca species (*Y. treculeana*, *Y. carnerosana* [Trelease] McKelvey, *Y. periculosa* Baker, *Y. schidigera* Roetzl ex Ortgies, and *Y. schottii* Engelmann), two capsular-fruited species (*Y. elata* Engelmann and *Y. rostrata* Engelmann ex Trelease), and the spongy-fruited *Y. brevifolia* Engelmann (Force and Thompson 1984; Powell 1984; B. A. Crabb and O. Pellmyr, unpublished data); thus, they are present on perhaps most yucca species in the southern portion of the combined range of all yuccas. The female wasp bores into yucca fruit with her long ovipositor, permanently paralyzes the moth larva with venom, and then lays an egg on the outside of it. *Digonogastra* n.sp. appears to be almost exclusively solitary, since 187 out of 189 parasitized moth larvae in this study hosted one wasp larva each. The remaining two moth larvae hosted two wasp larvae each. The wasp larva feeds until fully developed on the paralyzed moth larva and then pupates inside the larval feeding gallery in the yucca fruit. Adults are found on *Y. treculeana* throughout the fruiting period. There appear to be two generations per year, since wasp larvae are found on first- and second-instar moth larvae as well as on final-instar moth larvae but rarely on intermediate-size larvae. Further evidence that the wasps develop on host larvae of different size is the marked difference in adult body size between the wasps present early and late in the season; the later wasps are noticeably bigger. Such strong positive correlation between host and wasp size is a particularly evident pattern in idiobiont, i.e., host-paralyzing, parasitoid wasps (Godfray 1994).

Sample Collection

Samples were collected in Big Bend National Park, Texas (29°15'N, 103°15'W), in May 2000 and March–May 2001.

Some observations were made in the adjacent Black Gap Wildlife Management Area. In each year, 100 flowering plants were located during the flowering season and then used for fruit collection. To assure that seed consumption had ceased, we monitored the study plants daily for larval exit holes. When most fruits on a given plant had exit holes, we haphazardly harvested five fruits that were distributed within the infructescence from each plant. Larvae continue to feed inside the harvested fruit and eventually exit, so per capita seed consumption is not affected by this protocol.

The 500 harvested fruits were dissected, and the number of parasitized and nonparasitized larvae was determined in each fruit. Parasitized larvae were identified by the presence of a *Digonogastra* larva actively feeding on the moth larva or by a *Digonogastra* pupa or pupal exuviae in the moth feeding gallery. Finally, we counted the number of seeds consumed by each larva and the total number of intact viable seeds remaining in each fruit; the edge of each eaten seed is left behind by the larva, making it easy to determine the exact number of eaten seeds. Fruits at maturity contain a mixture of filled black seeds and empty yellow seeds (unfertilized ovules or prematurely dead seeds), so for this purpose only undamaged black seeds were counted as viable.

Species Determination of the Host Larvae

Because the host larva generally had departed, it was necessary to develop a means to infer what species of larva had created a given feeding path. Since *T. treculeanella* oviposits only at the top of the ovary, we predicted that for this species, larval feeding paths should start in the top third of locules. *Tegeticula corruptrix* can oviposit anywhere on the fruit surface, but its oviposition takes place several weeks after pollinator oviposition. Eggs laid in the top third run the risk that seeds already may have been eaten by pollinator larvae. For this reason, we predicted that *T. corruptrix* larvae would inhabit the lower two-thirds of yucca locules. To test these predictions, we used 82 final-instar larvae that exited from fruits immediately after harvest and recorded their feeding location. Whereas the adults are readily distinguished, there are no known diagnostic morphological traits for distinguishing between the species, so we used a mitochondrial sequence marker.

Larvae exiting from fruit were preserved in a -70°C freezer. Genomic DNA was extracted using a modified version of the protocol described by Harrison et al. (1987). We amplified a 662-bp segment at the 5' end of the cytochrome oxidase I region for each individual in 30 μL reaction volume for PCR (1X Promega buffer, 50 mM KCl, 10 mM Tris [pH 9.0], 1.67 mM MgCl_2 , 0.2 mM dNTPs, 0.25 mM of each primer, 0.033 units Promega B *Taq* polymerase [Promega, Madison, WI], and 100 ng of genomic DNA). Primer sequences were 1461F (5'-ACAATTTATCGCCTAAACTTCA-GCC-3') and 2302R (5'-CAATTGGATTATTAGGATTTGT-AG-3'), where numbers refer to the nucleotide positions in the *Drosophila yakuba* mtDNA sequence (Clary and Wolstenholme 1985). Thirty-five amplification cycles were performed (60 s at 95°C , 60 s at 52°C , 90 s at 72°C). PCR products were cleaned using QIAquick (Qiagen, Valencia, CA). Sequencing products were generated with cleaned PCR product, BigDye terminator cycle sequencing mix (PE Applied Biosystems,

Foster City, CA), and 4 pmol of the 2302R primer. Thermal cycling was programmed for 25 cycles of 30 s at 96°C, 30 s at 50°C, and 4 min at 60°C. Products were cleaned using Centri-sep Sephadex columns (Princeton Separations, Adelphia, NJ). Because the two species show about 2.5% sequence difference in this region (Pellmyr and Leebens-Mack 1999), we sequenced only the reverse strand, using an ABI 377 automated DNA sequencer (PE Applied Biosystems). Sequences were checked with Sequencher 3.1 (Gene Codes, Ann Arbor, MI). Sequence data were analyzed in PAUP* version 4.0b5 (Swofford 2000). In addition to the study samples, we added published sequences for the two *Tegeticula* species (Genbank AY004292, AY004301) as references and used *Parategeticula pollenifera* Davis (Genbank AF150921) as outgroup in a neighbor-joining analysis.

Sequences grouped around the reference sequences with 2.25% divergence (14 steps) or more between samples in the two groups. Seventy-three of the sequenced moths had feeding paths that began feeding in the top third of the fruit. Sixty-three were *T. treculeanella* as predicted, while 10 were *T. corruptrix*. Nine sequenced individuals fed in the middle or bottom third of the fruit; eight of them were *T. corruptrix*, and one was *T. treculeanella*. These data imply that species identification based on feeding path, as used in this study, carried an error rate of 11%–13% for both species. This is sufficiently small to be unlikely to have any qualitative effect on the results.

Statistical Analyses

Data on per capita seed consumption by the two moth species could not be normalized, so we used a Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Sokal and Rohlf 1994) to determine whether parasitization reduced per capita seed consumption. Parasitization status was the treatment effect and year was the block effect in this test.

We used ANCOVA to determine whether fruits that contained at least one parasitized larva produced more viable in-

Table 1

Number of Seeds Consumed by Parasitized and Nonparasitized *Tegeticula treculeanella* and *Tegeticula corruptrix* Larvae in 2000 and 2001

Year	Number of larvae	Mean seeds consumed per capita
<i>T. treculeanella</i> :		
Nonparasitized:		
2000	545	13.5 ± 0.18
2001	415	7.69 ± 0.61
Parasitized:		
2000	100	5.99 ± 0.37
2001	67	4.20 ± 0.20
<i>T. corruptrix</i> :		
Nonparasitized:		
2000	28	9.57 ± 1.07
2001	76	7.67 ± 0.35
Parasitized:		
2000	8	3.00 ± 0.60
2001	14	6.00 ± 0.75

Note. Values for mean seeds consumed are given ± 1 SEM.

Table 2

Results of the Scheirer-Ray-Hare Rank Test Comparing the Total Number of Seeds Consumed by Parasitized and Nonparasitized *Tegeticula treculeanella* and *Tegeticula corruptrix* Larvae, Total Number of Seeds Consumed in Each Year, and the Interaction Effect

Source	<i>H</i>	<i>P</i>
<i>T. treculeanella</i> :		
Parasitized?	228.11	<0.001
Year	6.34	<0.025
Year × parasitized?	1.05	>0.25
<i>T. corruptrix</i> :		
Parasitized?	19.16	<0.001
Year	2.18	>0.1
Year × parasitized?	5.04	<0.025

Note. For all tests, *df* = 1.

tact seeds than did fruits that did not contain any parasitized larvae. The number of intact viable seeds produced was used as the effect, and the number of larvae in the fruit was the cofactor. The criterion of categorizing fruits based on presence or absence of a single parasitized larva, when several larvae often coexist in a fruit, was chosen because it is the most conservative test of possible effects of parasitization on intact seed production.

Results

Parasitism Rates and Effects on Seed Consumption

Among the 645 *Tegeticula treculeanella* larvae analyzed in 2000, 15.5% were parasitized, whereas the parasitism rate in 2001 was 13.9% in 482 checked larvae (table 1). The corresponding figures for *Tegeticula corruptrix* were 22.2% parasitization among 36 larvae in 2000 and 15.6% of 90 larvae in 2001. In both years and in both *Tegeticula* species, parasitized larvae consumed significantly fewer seeds than nonparasitized larvae (table 1). Examination of larval head capsules found in galleries with parasitoids indicated that many larvae died during the second or third instar. In *T. treculeanella*, parasitized larvae consumed 45.4% and 55.6% fewer seeds than nonparasitized larvae in 2000 and 2001, respectively. In *T. corruptrix*, reduction in seed consumption with parasitization was 68.7% and 21.8% in 2000 and 2001, respectively. In *T. treculeanella*, there was also a significant effect of year in that more seeds were consumed per larva in 2000 than in 2001 (table 2). In contrast, *T. corruptrix* showed no effect of year but a significant interaction between year and parasitization in that the magnitude of the parasitization effect was larger in 2000 than in 2001.

Effects of Parasitism on Net Viable Seed Production

In both 2000 and 2001, there were significant differences in viable seed counts between fruits with and without parasitized larvae, but the effects were opposite in the two years. In 2000, fruits that contained at least one parasitized larva produced significantly more intact viable seeds than fruits that did not contain any parasitized larvae. In contrast, fruits with parasitized larvae in 2001 produced significantly fewer

Table 3
Results of ANCOVA of Data by Year to Test Whether
Fruits That Contained Parasitized Larvae Produced
More Intact Viable Seeds than Fruits That Did
Not Contain Parasitized Larvae

Source	SS	F	P
2000:			
Parasitized?	7867.0	12.17	0.0006
Number of larvae	24,235.8	37.48	<0.0001
2001:			
Parasitized?	5023.9	8.40	0.0042
Number of larvae	15,184.7	25.39	<0.0001

Note. For all tests, $df = 1$.

intact viable seeds than those without parasitized larvae (table 3; fig. 1).

Discussion

The importance of the third trophic level in interactions between plants and herbivores has long been appreciated (Price et al. 1980; Godfray 1994; Abrahamson and Weis 1997; van Loon et al. 2000; Kessler and Baldwin 2001; Thaler et al. 2002). These studies have addressed purely antagonistic interactions, where the net outcome of the interaction with the herbivore invariably is negative to the plant. In contrast, some mutualistic or near-mutualistic associations between plants and herbivores, such as those between pollinating seed parasites and plants, have not been considered. They may show different dynamics in that parasitoids may increase the benefit : cost ratio of the plant by reducing seed destruction, even to the point of tipping a slightly antagonistic interaction so that benefits exceed granivore damage.

However, parasitoids may also negatively affect the plant by suppressing pollinator populations if occurring at higher densities, or, as in the case of a koinobiont (which permits completion of feeding by the herbivore larva), they may tip a weakly mutualistic interaction to antagonism by increasing host damage on the plant. Here we took a first step in addressing third-trophic-level dynamics in the obligate yucca-yucca moth mutualism by measuring the impact of a braconid wasp on the exclusive pollinator and a coexisting nonpollinator species on *Yucca treculeana*. Such coexistence of a pollinator and a nonpollinator is common in yuccas (Addicott 1996; Pellmyr et al. 1996), so the results may be widely applicable. It should be noted that optimal suppression of moth populations by the parasitoid in terms of intact seed yield differs between the cheaters and the pollinators, with optimal suppression of cheater moth larvae being parasitization of all larvae.

The two components that determine the possible indirect effects of the parasitoid on the plant are the mortality rates of the moth larvae and possible reduced feeding by the hosts before death. Mortality rate in *Tegeticula treculeanella* and *Tegeticula corruptrix* from *Digonogastra* was on average 14.8% and 17.5%, respectively, during the two years of the study. By comparison, Force and Thompson (1984) reported 4% mortality from *Digonogastra* and a eurytomid parasitic wasp in *Tegeticula mojavelle* Pellmyr larvae and an estimated 35% mortality from *Digonogastra* in *Tegeticula maderae* Pellmyr and 11% in *Parategeticula pollenifera* that coexist on *Yucca schottii*. This attack rate is lower than rates reported in some other studies of tritrophic interactions (e.g., Abrahamson and Weis 1997) but within a range where other studies have demonstrated indirect positive effects on seed production. For example, Gómez and Zamora (1994) reported that a 9%–20% mortality rate from parasitic wasps in a granivorous weevil significantly increased seed production in the weevil host plant.

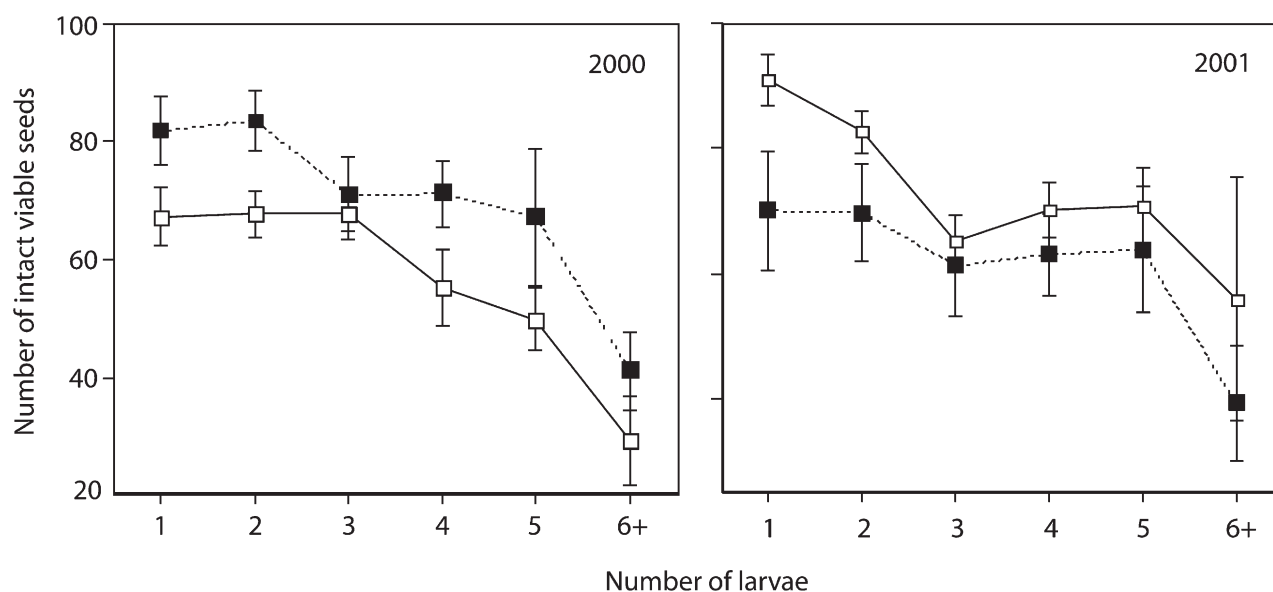


Fig. 1 Number of intact black seeds (\pm SE) produced in fruits that contained parasitized larvae (filled squares) and nonparasitized larvae (open squares) during the two years of study.

Table 4

Mean Number of Ovules of Fruits with and without Parasitized Larvae during the Two Years of Study

Year	Fruits with parasitized larvae	Fruits without parasitized larvae	<i>t</i>	df	<i>P</i>
2000	132 ± 3.25	129.00 ± 2.43	-0.724	232	0.4699
2001	137.67 ± 5.32	148.58 ± 2.30	2.122	206	0.035

Note. Means are given ±1 SEM.

Digonogastra, which paralyzes the host larva during oviposition, was predicted to have an indirect positive effect on *Y. treculeana* because it paralyzes both *T. treculeanella* and *T. corruptrix* larvae when they had consumed only about half as many seeds as nonparasitized larvae that completed development. As a result, in the year 2000, fruits that contained one or more parasitized larvae indeed produced more intact viable seeds at maturity than fruits that contained only nonparasitized larvae, when the number of larvae was taken into account. Interestingly, this result was reversed in 2001.

Why would the indirect benefit caused by *Digonogastra* be reversed in 2001? One intriguing pattern is that there were differences in the total number of ovules in fruits with and without a parasitized larva (table 4), and this difference masked any increase in seed production caused by *Digonogastra*. In 2000, there was no significant difference in the total number of ovules in fruits with and without parasitized larvae, and the increase in intact viable seeds caused by *Digonogastra* attack resulted in a significant difference between fruits containing parasitized as opposed to nonparasitized larvae. In 2001, fruits without a parasitized larva contained significantly more ovules than those with a parasitized larva. This can explain the lack of indirect benefit for *Y. treculeana* caused by *Digonogastra* in 2001, but this raises the question of why ovule number affects larval parasitization probability, especially only in some years.

In the underlying evolutionary conflict between obligate partners, such as seed-eating pollinators and their hosts, the attraction of indirect mutualists can potentially alter the dynamics of the relationship (Bronstein 2001). Although natural enemies of such pollinators have been documented before, their effects on the mutualism have not been considered. For example, only attack frequencies of *Digonogastra* on yucca moths were reported in prior reports (Force and Thompson 1984). In the recently described mutualism between senita cacti (*Lophocereus schottii* [Engelmann] Britton and Rose; Cactaceae) and seed-parasitic senita moths (*Upiga virescens* Hulst; Lepidoptera, Pyralidae), Holland and Fleming

(1999) documented 12%–17% parasitization of the moth by an unidentified parasitic wasp. It affected moth pupae and could thus not provide benefits to the host cactus by reducing damage but could possibly lower pollinator density in subsequent generations. The impact of parasitoids on fig pollinators and their fig hosts is poorly known, in large part because of the complexity of fig wasp communities (Weiblen et al. 2000; Weiblen 2002). Further, the fig–fig wasp pollination mutualism differs from the other pollination systems based on seed parasitism in that fig wasps provide additional benefits to the fig tree after pollination, and the emerging brood provides all pollen dispersal. For this reason, mortality of fig wasps resulting from a parasitoid has a direct negative effect on the host fig through reduced male fitness. Yuccas receive no benefits from the yucca moth after pollination, so any mortality of pollinator yucca moth larvae in the fruit could in principle increase plant fitness. This could hypothetically lead to selection for attraction of pollinator parasitoids by the plant. Our results, with opposite net outcomes to the plant of parasitoids in the two years of study, indicate that the three-way dynamics between plant, pollinator, and parasitoid may be influenced by several factors and thus subject to spatiotemporally variable outcomes. To further understand obligate mutualism in a community context, it will be important to identify the critical factors that determine the outcomes of interactions between these three trophic levels.

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