# The Effect of Floral Nectar Feeding on the Parasitoid *Anagrus* spp. (Hymenoptera: Mymaridae)

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# ABSTRACT

Conventional agricultural systems are characterized by a reduction in non-crop resources, which decreases natural enemy populations and increases pest abundance. Floral resource provisioning (FRP) is one method of increasing natural enemy populations in agricultural systems by providing a non-crop food source. Nectar feeding can increase the longevity, fecundity, and abundance of natural enemies, thus increasing their effectiveness in controlling pest populations. Many studies have examined the effect of FRP on parasitoid natural enemies in the field, but few determine whether the flowers used actually benefit the target wasp in a controlled setting. This study examined whether nectar feeding increases the longevity of Anagrus spp. wasps, which parasitize Western grape leafhoppers (Erythroneura elegantula) in California vineyards. Using wasps obtained from parasitized leafhopper eggs in Davis, CA, I isolated Anagrus spp. in vials with flowers from Ammi majus, Daucus carota, or Phacelia tanacetifolia, 50% honey solution, or just water. I found that wasps in the D. carota and honey treatments, which averaged 1.3 and 1.6 days, lived significantly longer than those in the *P. tanacetifolia* and control treatments, which all died within 24 hours. This confirms that nectar feeding can increase Anagrus spp. lifespan, and that certain flowers have a greater effect on lifespan than others, likely due to differences in morphology, nectar composition, and volatiles. This is important information in choosing flowers to implement and explaining the effectiveness or ineffectiveness of previous FRP designs.

# **KEYWORDS**

floral resource provisioning, conservation biological control, natural enemy, egg parasitoid, western grape leafhopper

## **INTRODUCTION**

The intensification and simplification of conventional agricultural systems have been characterized by a reduction in non-crop habitat, which leads to decreased natural enemy populations and subsequent increases in pest abundance (Miles et al. 2011). Biological control literature offers several hypotheses to explain the lower levels of herbivorous pests in diverse agricultural systems than in monocultures. The natural enemies hypothesis (Fig 1) suggests that predators and parasites of herbivorous pests are more effective in diverse systems than in simple ones (Wratten and van Emden 1995, Miles et al. 2011). By not providing non-crop resources, simplified farming systems, e.g. monocultures, force natural enemies to travel outside of the farm to obtain supplementary resources and shelter. In doing so, natural enemies spend energy on dispersal and searching that could otherwise be spent on predation and parasitism (English-Loeb et al. 2003). A greater diversity of crops and non-crop plants can provide food, overwintering shelter, and alternative hosts/prey for natural enemies, thus increasing their abundance, longevity, and fecundity (Baggen and Gurr 1997, Nicholls et al. 2000, Daane and Costello 2003, Heimpel and Jervis 2005, Vattala et al. 2006, Lee and Heimpel 2007, Sivinski et al. 2011). Conservation biological control (CBC) is a type of biological control that conserves and augments existing natural enemy populations (Ehler 1998, Gurr et al. 2004). Among other practices, CBC employs the introduction of non-crop plants as resources for natural enemies (Gurr et al. 2004).



**Figure 1. Natural enemies hypothesis**. a) Floral nectar increases longevity, fecundity, and abundance of natural enemies. b) Natural enemies predate on/parasitize pest insect. c) Decreased pest densities lead to a reduction in crop damage (Source: Farrell, 2012)

One general form of on-farm diversification to enhance natural enemy populations in CBC is floral resource provisioning (), or the introduction of non-crop flowers into an agricultural system. Floral nectar contains sugars, proteins, amino acids, and lipids, and floral feeding can increase the longevity and fecundity of certain beneficial wasps, including *Anagrus* spp. (Baggen and Gurr 1997, English-Loeb et al. 2003, Winkler et al. 2004, Vattala et al. 2006, Lee and Heimpel 2007, Sivinski et al. 2011, Zhu et al. 2012). Nonetheless, utilization of floral nectar by parasitoids is species specific, and highly dependent on flower and parasitoid morphology, the quality of nectar, and attractants and deterrents such as flower color and volatiles (Landis et al. 2000, Fadamiro and Chen 2005, Wackers 2005, Vattala et al. 2006, Sivinski et al. 2011, Zhu et al. 2015, Wackers 2005, Vattala et al. 2006, Sivinski et al. 2012). Furthermore, FRP must take into account practical considerations of the farmer, such as ease of cultivation and water demands of the non-crop plant. Thus while several flowering species such as buckwheat (Polygonaceae: *Eriogonum* spp.) and alyssum (Brassicaceae: *Alyssum* spp.) are popular cover crops to enhance biological control, the effectiveness of these floral resources varies with the system and species of parasitoid (Heimpel et al. 2005).

One promising opportunity to implement FRP lies in wine grape vineyards. The western grape leafhopper (Hemiptera: Cicadellidae: *Erythroneura elegantula*) is a key pest in northern and central California vineyards. *E. elegantula* nymphs and adults remove the contents of leaf cells, which can lead to loss of leaf efficiency, leaf drop, fruit sunburn, and delayed fruit ripening, and adults are a nuisance to workers during harvest time (UC IPM 2008). Grape-growers generally resort to synthetic pesticides to mediate damage by *E. elegantula* and other pests (CDPR 2009), but there is a growing interest among growers and consumers in alternative methods of pest management (Broome and Warner 2008, Ross and Golino 2008, Brodt and Thrupp 2009). Two key natural enemies of *E. elegantula* in California are *Anagrus daanei* and *Anagrus erythroneurae* (Hymenoptera: Mymaridae), which were both previously classified as *Anagrus epos* (Costello and Daane 2003). These egg parasitoids attack various species of *Erythroneura* leafhoppers (Daane and Costello 1998, Murphy et al. 1998, Nicholls et al. 2000, Daane and Costello 2003, UC IPM 2008). *Anagrus* spp. are proovigenic and thus born with a full

complement of eggs, but still may require carbohydrates for searching and parasitizing host eggs (English-Loeb et al. 2003). Various field scale studies have examined the effects of non-crop resources on *Erythroneura spp.* and the *Anagrus* spp. wasp (Daane and Costello 1998, Daane and Costello 2003), and of FRP on *Erythroneura* spp. and *Anagrus* spp. (Nicholls et al. 2000, English-Loeb et al. 2003). However, these studies have yielded mixed results, and have been unable to draw a clear correlation between introduction of FRP and changes in *Anagrus* spp. densities, parasitism rates, and pest densities. These inconclusive results could be due to inconsistency in the flowering cover crops used, and a poor understanding of how certain introduced flowers benefit *Anagrus* spp. Only two studies have quantified the effect of nectar feeding on *Anagrus* spp. in a controlled lab setting (English-Loeb et al. 2003, Zhu et al. 2012), and buckwheat is the only flower that has been used in both lab and field trials with *Anagrus* spp. In order to explain the variability between different studies' results and tailor on-farm diversification to effectively decrease pest densities, further information is needed on the effects of floral nectar feeding on *Anagrus* spp.

The objective of my study is to quantify the effects of nectar feeding on the longevity of *Anagrus* spp. in a controlled environment. I will be using three flowering species: wild carrot (Apiaciae: *Daucus carota*), bishop's weed (Apiaciae: *Ammi majus*), and lacy phacelia (Boraginaceae: *Phacelia tanacetifolia*). These species are non-native but commonly used as cover crops in California. They were chosen because they are easy for wine grape growers to incorporate in between vine rows, require no additional irrigation, and together provide floral bloom throughout the entire growing season (Miles et al. 2011). These three species are also being used in a field scale study conducted by the UC Berkeley Agroecology lab to observe the effects of flowering cover crops on *Anagrus* spp. and *E. elegantula* in northern California vineyards (Miles et al. 2011). I hypothesize that nectar feeding will increase the longevity of *Anagrus* spp. wasps, and that the effects on longevity will vary between flowers, because they likely have different morphologies and nutritional compositions. Alternatively, *Anagrus* spp. may not require a nectar source to achieve its maximum lifespan, or different flowers may be equally effective as nectar sources.

#### **METHODS**

## **Wasp Collection**

We obtained wasps for the study by collecting grape leaves from three vineyards in Davis, CA (Table 1), which were reported as having high abundance of *Anagrus* spp. Collection occurred several times during *Anagrus* spp. emergence season in late August and early September 2012, and leaves used during the final trial were collected in mid September. We collected during daylight hours, and selected leaves with heavy leafhopper damage (as described by UC IPM), assuming that leaves with high leafhopper incidence would have higher densities of leafhopper eggs and thus higher densities of parasitized eggs. Leaves were placed inside plastic bags to prevent desiccation, and we placed these bags in paper bags to block out light.

To collect emerging wasps from the leaves, we brought the leaves back to a windowless lab in the UC Berkeley greenhouse and put them in plastic bags inside dark containers, about 20 leaves to a bag. Each container had one clear vial attached to the top, and as wasps emerged from parasitized leafhopper eggs they moved to the vial, attracted by the light (English-Loeb et al. 2003). We set up three temperature and humidity loggers in the room, and one light meter, and collected readings from the time we put the leaves in the emergence containers to the end of the trials (Table 2). The light was on from 6:30am-10:00pm every day.

We moved wasps by chilling the vials so that they were mildly stunned, emptying them out onto a petri dish under a dissecting microscope, and using a size 0 camel hair paintbrush to transfer them to the study chambers. Wasps were not fed anything prior to being moved to the study chambers. Based on our observations of the wasps, we assumed that *Anagrus* spp. wasps did not live more than a day in the emergence vials without food or water, thus any wasps we used in our study were no more than 24 hours old.

Wasps were not identified to species due to time constraints, but it was assumed that wasps were *A. daanei* and *A. erythroneura* (Costello and Daane 2003).

#### **Table 1. Vineyard locations**

Vineyard	Location (in Davis, CA 95616)	
Beth Flory's Vineyard	Near the intersection of County Rd 104 and	
	Tremont Rd	
Village Homes Vineyard	2657 Portage Bay East	
Tyree Vineyard	UC Davis Dept of Viticulture and Enology	

#### Table 2: Temperature and humidity data from leaf collection until trial completion

Average Temperature (F)	Standard Error	Average Humidity (%)	Standard Error
76.23	0.0094	46.42	0.0166

# **Flower Cultivation**

I sowed *Ammi majus, Daucus carota*, and *Phacelia tanacetifolia* in the UC Berkeley greenhouse between March and June, 2012. I transplanted them into the UC Berkeley Student Organic Garden in July. I did not apply chemicals to the plants at any point in their development. *D. carota* seeds were collected from untreated plants in Napa county in Fall 2011, and *A. majus* and *P. tanacetifolia* seeds were purchased from Peaceful Valley Organics the same Fall.

# **Study Setup**

In order to monitor the longevity of the *Anagrus* spp. wasps, we isolated each wasp in a clear plastic vial. We inserted a plastic micropipette tip filled with distilled water in the top of each vial. Each of the three flower treatments contained a cluster of *A. majus, D. carota,* or *P. tanacetifolia* flowers in a glass vial filled with tap water. The honey treatment had a second micropipette tip containing a 50% organic honey solution. The flower clusters were roughly one centimeter in diameter. A fifth set of vials contained only a micropipette tip with distilled water, and served as the control. Each vial contained one wasp, and there were ten reps of each treatment and the control, for a total of 50 wasps. I monitored the wasps daily, allowing 30 seconds of search time for each chamber, and recorded whether or not each wasp was alive. Flowers were replaced every three days, and water and honey solution were replenished as needed. The trial ran for six days, until the last wasp died.

#### **Data Analysis**

I ran a Shapiro-Wilkes test for normality on my data from each treatment (Table 3). Because all but the *D. carota* treatment were non-normally distributed, I ran a Kruskal-Wallis rank sum test to compare all of the treatments at once, and I ran Wilcox rank sum tests to compare each treatment to the control. I modeled my data using Kaplan-Meier survival curves, and ran Log-Rank tests with a Bonferroni correction to test for significant differences between curves. I ran all of my tests using R 2.15.1 GUI 1.52, and considered p-values of 0.05 or less significant.

Table 3. Results of Shapiro-Wilkes test for normality (p-values greater than 0.05 indicate normality)

Treatment	P-value
A. majus	0.00022
D. carota	0.06683
P. tanacetifolia	NA*
Honey	0.008776
Control	NA*

\*All values in P. tanacetifolia treatment were zero

## RESULTS

Based on the results of my longevity study, I found that the honey and *D. carota* treatments significantly increased *Anagrus* spp. lifespans. The mean lifespan for the honey and *D. carota* treatments were 1.6 days and 1.3 days, respectively, while all of the wasps in the control vials died within the first day of the trial (Fig 2, Fig 3). The Kruskal-Wallis test showed a significant difference across the treatments (p<0.001). The Wilcox rank sum test showed significant differences between the honey and control (p=0.002) and the *D. carota* and control (p=0.002). Log-rank tests showed significant differences between the honey and control (p=0.00138). Neither of the other treatments was significantly different than the control (Table 4). There were also significant differences between the honey and *D. carota* treatments and the *P. tanacetifolia* treatment, which, like the control, exhibited 100% mortality within the first 24 hours.

Although there were no significant differences between the *A. majus* treatment and the other treatments or the control, *A. majus* did exhibit a positive effect on wasp longevity. Wasps

in the *A. majus* treatment lived on average 0.4 days, compared to zero days in the control and *P. tanacetifolia* treatment (Fig 2).





Figure 2. Anagrus spp. lifespan by treatment



Figure 3. Kaplan-Meier survival curves by treatment

Table 4. Comparisons across treatments an	nd between treatments and	d control (significa	nt values in italics
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Test Used	Treatment Being Compared to Control	P-value
Kruskal-Wallis	NA	0.00030
Wilcox	A. majus	0.07758
	D. carota	0.00210
	P. tanacetifolia	NA*
	Honey	0.00210
Log-rank	A. majus	0.06710
	D. carota	0.00138
	P. tanacetifolia	NA*
	Honey	0.00138

\*All values in *P. tanacetifolia* treatment were zero

#### DISCUSSION

Though *Anagrus* spp. are proovigenic and do not require food resources to produce eggs, they still require a source of carbohydrates to achieve their maximum lifespan. My findings agree with previous research (Baggen and Gurr 1997, English-Loeb et al. 2003, Winkler et al. 2004, Vattala et al. 2006, Lee and Heimpel 2007, Zhu et al. 2012), and support my hypotheses that *Anagrus* spp. lives longer with access to honey or floral nectar, and that different nectar sources vary in their effect on *Anagrus* spp. lifespan. This variation can likely be explained by differences in flower morphology, nectar quality, or plant volatiles. Variability in field scale studies suggests that additional factors are at play that may affect *Anagrus* spp. utilization of nectar sources, such as movement between grape vines and flowers and proximity of off-farm source populations of *Anagrus* spp. (Murphy et al. 1998). However, my findings, by identifying flowers that have a positive impact on *Anagrus* spp. longevity, could make future field scale studies more effective.

## Need for carbohydrate source

While *Anagrus* spp. are born with a full complement of eggs, they still may require food energy for searching and parasitizing host eggs (English-Loeb et al. 2003). Zhu et al. (2012) even suggest that proovigenic parasitoids may resorb eggs in a food shortage. Various lab studies confirm that access to flowers or a similar sugar source increases the lifespan of hymenopteran parasitoids (Baggen and Gurr 1997, Winkler et al. 2004, Vattala et al. 2006, Lee and Heimpel 2007), while English-Loeb et al. (2003) and Zhu et al. (2012) found that access to a nectar source increased longevity of *Anagrus* spp. in New York and eastern China, respectively. My study also showed a significant increase in *Anagrus* spp. lifespan with access to honey and certain flower nectar, compared to wasps that lived less than 24 hours with only water, or apparently unsuitable flowers.

### Suitability of flowers

Differences between flower treatments may be attributable to flower morphology and accessibility of nectaries to wasps (Fadamiro and Chen 2005, Wackers 2005). Sivinski et al. found that different species of flowering plants were associated with different families of hymenopteran parasitoids, though some attracted multiple families, while others attracted none (2011). This suggests that certain flowering plants are suitable to parasitoid feeding, and that within these plants there is variability in attractiveness and suitability depending on the species of parasitoid. The most important morphological factor in the suitability of flowers is corolla width and depth, in relation to parasitoid head width and mouthpart structure (Fadamiro and Chen 2005, Vattala et al. 2006, Sivinski et al. 2011). In my study, P. tanacetifolia may have had no effect on *Anagrus* spp. lifespan because the wasps could not access its nectaries; Vattala et al. (2006) found that access to *P. tanacetifolia* significantly lowered the lifespan of a hymenopteran parasitoid compared with those with access to water, concluding that, though the corolla was wider than the wasp's head, it may have been too deep to access. Sivinski et al. (2011) speculated that for very small insects, like Anagrus spp., corolla width may not matter, but it is still possible that the nectaries of *P. tanacetifolia* are too deep within the corolla to be attractive or accessible to Anagrus spp. A. majus and D. carota nectaries, which are wide and shallow (Sivinski et al. 2011), may have been more easily accessible to Anagrus spp., thus allowing for feeding. It is worth noting that honey, the most readily accessible nectar in my study, had the greatest positive impact on lifespan, which supports accessibility as an important factor in nectar utilization.

Differences between flower treatments could also be explained by differences in nectar quality and composition. Vattala et al. (2006) found that, in flowers with accessible nectaries, those that increased parasitoid longevity the most had the highest ratio of sucrose to glucose and fructose, and Zhu et al. (2012) identified nectar odor as an important factor in floral attractiveness. The composition of *P. tanacetifolia* nectar may not be suitable to the nutritional requirements of *Anagrus* spp. However, even unsuitable nectar would provide additional carbohydrates, and given that the longevity of wasps in the *P. tanacetifolia* treatment was identical to those in the control treatment, it is more likely that the flower was inaccessible or produced repellent volatiles (Vattala et al. 2006, Sivinski et al. 2011) that restricted *Anagrus* spp.

from feeding. Variation in nectar composition and volatiles may be a better explanation for the higher average lifespan of wasps in the *D. carota* treatment versus those in the *A. majus* treatment, though this may also be attributable to differences in flower morphology.

#### Variation in field scale studies

While my results agree with other laboratory studies (English-Loeb et al. 2003, Zhu et al. 2012), field scale studies on the effect of non-crop resources on Anagrus spp. have variable results (Table 5). In a 1998 study in California grape vineyards, Daane and Costello found no differences in Anagrus spp. abundance between control rows and rows sown with different combinations of ten flowering and non-flowering cover crops, but did not report whether there were significant differences between the different combinations of cover crops. In a similar study in 2003, Costello and Daane saw no differences in Anagrus erythroneurae and Anagrus daanei egg parasitism rates between control rows and rows sown with purple vetch, barley, and resident grasses, though leafhopper abundance was lower in ground cover treatments. The cover crops used in these studies were mostly non-flowering grasses, and those that did flower are not commonly used as nectar resources. Very few field scale studies on the effect of nectar resources on Anagrus spp. have been done, and these also have variable results. Nicholls et al. (2000) found lower leafhopper abundance in rows sown with buckwheat and sunflower, but no difference in Anagrus spp. abundance or parasitism rates between treatments. English-Loeb et al. (2003) did find significantly higher Anagrus spp. abundance in plots sown with buckwheat versus plots sown with clover or with no cover, but only late in the season at the edge of the vineyard, suggesting that the effectiveness of cover crops may be dependent on proximity to source habitats off the vineyard. One explanation offered by Costello and Daane (2003) for similar parasitoid abundance between treatments is that higher leafhopper abundance in control plots elicited a functional response by *Anagrus* spp., masking any increase in *Anagrus* spp. abundance in cover plots. Another possible reason for discrepancies is inconsistency in the species of cover crop used. Buckwheat increased Anagrus spp. parasitism rates and other hymenopteran parasitoids' longevity in lab studies (English-Loeb et al. 2003, Vattala et al. 2006), and also increased Anagrus spp. abundance in the field in one study (English-Loeb et al. 2003), though it had no effect in another (Nicholls et al. 2000). None of the other flower species

used in these field studies have been used in lab studies with *Anagrus* spp., and it is probable that they are unsuitable as nectar resources. Additionally, there are a variety of factors at play in the field that may affect *Anagrus* spp. utilization of nectar resources, such as distance between vines and ground cover, and distance between the vineyard and *Anagrus* spp. source populations.

Study	Type of Study	Flowers Used	Anagrus spp response	Erythroneura spp. response
Daane and Costello 1998	field	purple vetch, common vetch, Australian winter pea, fava bean	no reponse	decreased abundance
Nicholls et al. 2000	field	buckwheat, sunflower	no response	decreased abundance
Daane and Costello 2003	field	purple vetch	no response	decreased abundance
English-Loeb et al. 2003	field	buckwheat	increased abundance	no response
		clover	no response	no response
English-Loeb et al.	lab	Buckwheat	increased parasitism rates	NA
Zhu et al.	lab	Sesame	increased longevity and parasitism rates	NA

Table 5. The effect of flowers on Anagrus spp. and Erythroneura spp. in previous lab and field studies

# Limitations

Thus while my study showed increased *Anagrus* spp. longevity in the presence of certain flowers, these flowers may not produce the same results in the field. Very little is known about *Anagrus* spp. dispersal within vineyards and between vineyards and edge habitats (Miles et al. 2011), though one study found increased *Anagrus epos* (now *A. erythroneurae* and *A. daanei*) incidence in central and northern California vineyards adjacent to *Prunus* spp. overwintering habitats (Murphy et al. 1998). It could be that *Anagrus* spp. do not typically move between vines and ground cover, or that FRP is only effective in increasing parasitoid abundance if there is adequate habitat for a source population of *Anagrus* spp. near the vineyard. In addition, my study does not take into account unintended effects of ground cover, such as benefits to herbivorous pests and other non-target species. In a field study of potato crops, Baggen and Gurr found that pest populations and crop damage were higher next to flowering plants, though access to flowers increased parasitism of the pest in a lab setting (1998), and Zhu et al. notes the importance of

denying benefits to herbivores when selecting a cover crop species (2012). There are also potential benefits of cover crops that my study did not take into account. Of two studies that found reduced leafhopper populations in vineyards with ground cover, one attributed the result to reduced vine vigor caused by resource competition with the cover crop (Daane and Costello 1998), and the other to increased predation by spiders (Nicholls et al. 2000). While *D. carota* increases *Anagrus* spp. lifespan, it may not be the most effective cover crop to utilize other factors that play a role in pest reduction, such as generalist predators and vine vigor.

Finally, I collected wasps in northern California, where *Anagrus* spp. populations consist of *A. daanei* and *A. erythroneurae* (Costello and Daane 2003). It is possible that different species of *Anagrus* respond differently to floral resources (English-Loeb et al. 2003); Zhu et al. found differences in floral odor preferences between *Anagrus nilaparvatae* and *Anagrus optabilis*, though the longevity of both species was increased by sesame nectar (2012). Regional differences in vegetation may play a role in floral preference by native parasitoids; though none of the flowers used in my study are native to northern California, *D. carota* occurs frequently in the wild, and it is possible that *Anagrus* spp. respond more positively to flowers that occur naturally in their region. Given the potential variation in floral preferences between different species of *Anagrus*, my results may not apply to regions outside of California, where *Anagrus* populations are composed of different species.

# **Future directions**

While my findings suggest that floral resources can be used to increase *Anagrus* spp. longevity, it is still unclear whether increased wasp longevity will lead to higher parasitism rates and lower pest densities. Studies show that access to floral nectar increased parasitism rates of *Anagrus* spp. (English-Loeb et al. 2003, Zhu et al. 2012) and other hymenopteran parasitoids (Baggen and Gurr 1998) in a lab setting, but it is unclear whether floral resources will increase *Anagrus* spp. abundance and parasitism rates in the field, and whether this will lead to an economically significant reduction in pest populations and crop damage. Future research can determine whether the flowers used in my study increase *Anagrus* spp. parasitism rates in a controlled setting, and if so, whether the use of these flowers as ground cover in vineyards

increases *Anagrus* spp. abundance and parasitism rates, and reduces leafhopper densities and crop damage.

#### **Broader significance and conclusions**

The results of my study can be used to more effectively tailor CBC efforts to increase *Anagrus* spp. abundance and parasitism of grape leafhoppers. *Anagrus* spp. is an important natural enemy in central and northern California vineyards (UC IPM 2008). Very little is known about *Anagrus* spp. habitat, dispersal, and utilization of non-host resources, and this information is important in designing and implementing biological control to reduce crop damage by grape leafhoppers. Increased *Anagrus* spp. longevity and abundance in the field may lead to increased parasitism rates, lower pest densities, and lower crop damage, decreasing the now-prevalent use of harmful synthetic pesticides in vineyards (Miles et al. 2011).

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