

# Dispersal-Dependent Oviposition and the Aggregation of Parasitism

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**ABSTRACT:** The prediction that parasitoid foraging effort should increase with distance traversed to reach or to locate hosts has had little experimental attention. Consistent with a number of models of foraging behavior, we found that the per capita number of ovipositions by the minute fairyfly-egg parasitoid *Anagrus sophiae* increased significantly with dispersal distance to planthopper hosts in the field in experimental patches of many host eggs. In large continuous stands of cordgrass host plants, after dispersal of decimeters or less, female wasps laid approximately 18% of their average of 18.6 eggs. After dispersal to plants isolated 10 m from other cordgrass, they laid approximately 84%, and they laid virtually all of their eggs after dispersal of 250 m to experimental floating islands of cordgrass. The increased oviposition following dispersal tripled the  $CV^2$  index of aggregation of parasitism to a level theoretically sufficient to promote locally stable parasitoid-host dynamics in isolated patches. At the same time, the change in wasp behavior did not affect the relationship between parasitism and host density, which was consistently density independent. Our results suggest that increased foraging effort with distance traversed can counter Allee effects in colonization and increase spatial spread of populations of natural enemies.

**Keywords:** aggregation, dispersal distance, host-parasitoid interactions, large-scale experiments, oviposition behavior, spatial population dynamics.

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Most laboratory studies of insect parasitoid foraging behavior have necessarily focused on narrow scales of one or a few host patches in close proximity (e.g., Waage 1979; Galis and van Alphen 1981; Cronin and Strong 1993a,

1993b; but see Thompson 1986; Casas 1989; Driessen and Hemerik 1992; Volkl 1994). In nature, however, at least some hosts are far-flung, and the realistically wide distribution of resources should affect searching behavior. This supposition is well grounded in theory. Foraging models in which optimal behavior is the maximization of the time rate of oviposition predict that residence time and, consequently, number of parasitoid eggs laid in a patch will increase with time spent traveling; distance to the patch correlates with travel time (table 1, models A, B). This prediction also emerges from more realistic models in which foragers are not omniscient and must therefore use simple decision rules for leaving a patch (table 1, model C). When oviposition behavior of parasitoids is linked dynamically to remaining egg load and perceptions of host availability, foraging effort within a patch also is predicted to increase with dispersal distance (table 1, model D).

Dynamics of subdivided populations should also be affected by changes in oviposition following dispersal. First, more parasitoid eggs laid in more distant patches could cause parasitism to be more aggregated in space, and greater aggregation can increase stability of predator-prey interactions (Pacala et al. 1990; Hassell et al. 1991; Reeve et al. 1994a). Second, increased ovipositions following long dispersal could counteract the Allee effect in metapopulations (e.g., Hopper and Roush 1993; Hanski 1994; Amarasekare 1998; Kuussaari et al. 1998) by increasing mate availability, thus enhancing the probability of successful colonization of isolated patches. This, in turn, could increase both the occupation rate of isolated patches and the spatial spread of a population (e.g., Kot et al. 1996). Finally, distance-dependent oviposition could affect parasitism rate as a function of host density, which could in turn influence the stability of the parasitoid-host relationship in isolated populations (Hassell 1978; Murdoch and Stuart-Oaten 1989). Thus, sink populations of long-distance colonists could have quite different dynamics from source populations dominated by nondispersing individuals.

The relationship between dispersal distance and the foraging effort of immigrants has not been studied much in nature (table 2). The majority of studies in this taxonom-

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**Table 1:** Foraging models that include increased foraging activity (e.g., patch time, prey consumed, number of ovipositions) with an increase in dispersal distance or time spent traveling

Model	Optimal solution	Omniscient forager	Ambit of travel	Egg limitation	Source
A	Maximize rate	Yes	Unrestricted	No	Charnov 1976; Parker and Stuart 1976; McNair 1982; Parker and Courtney 1984; Stephens and Krebs 1986
B	Maximize rate	No	Unrestricted	No	Green 1980; Ollason 1980; Janetos and Cole 1981; McNamara 1982; McNamara and Houston 1985; Stephens and Krebs 1986
C	Maximize rate	No	Central place	No	Orians and Pearson 1979; Kacelnik et al. 1986
D	Maximize fitness	No	Unrestricted	Yes	Mangel 1987, 1989 <i>a</i> , 1989 <i>b</i> ; Heard and Remer 1997

Note: Optimal solution is based on whether animals forage to maximize their long-term average rate of oviposition or energy intake or their lifetime reproductive success (fitness). An omniscient forager is one that has complete information about the distribution of resources among patches and ambit of travel relates to whether a forager is free-ranging or forages outward from a nest, burrow or perch (central place). For reference, model categories have been labeled A–D.

ically diverse set found that foraging effort increases following dispersal. To our knowledge, our field study is the first to concern parasitic Hymenoptera (in which “foraging” behavior equates to oviposition behavior). We examine linkages between dispersal, oviposition, and population dynamics of an egg parasitoid and host planthoppers on saltmarsh cordgrass.

#### *Anagrus sophiae* Life History

The minute ( $\approx 0.7$ -mm total body length) fairyfly wasp *Anagrus sophiae* S. Trjapitzin (previously classified as *Anagrus delicatus*; Trjapitzin and Strong 1995) is a solitary parasitoid that attacks the eggs of two congeneric planthoppers, *Prokelisia dolus* Wilson and *Prokelisia marginata* (Van Duzee) (Homoptera: Delphacidae) (Stiling and Strong 1982*a*, 1982*b*; Cronin and Strong 1990*a*). These planthoppers are narrowly oligophagous, feeding on the phloem of the cordgrass *Spartina alterniflora* in intertidal marshes along the Atlantic and Gulf Coasts of the United States and Mexico (Denno and Grissell 1979; McCoy and Rey 1981; Stiling and Strong 1982*b*; Denno et al. 1987; Roderick 1987; Cronin and Strong 1996). Patches of cordgrass can range in size from single plants within mudflats or on isolated oyster bars to relatively pure monocultures that span tens of square kilometers along beach fronts or marshes further inland. *Prokelisia marginata* and *P. dolus* also feed on the closely related *Spartina foliosa* in California (Denno et al. 1996).

This parasitoid is pro-ovigenic and limited in its lifetime to the average of 33 mature eggs with which it ecloses

(Cronin and Strong 1993*a*). Female wasps search for host eggs that are just beneath the leaf’s upper cuticle and densely aggregated near the base of the linear cordgrass leaf; densities often exceed 300 per patch. Despite the abundance of hosts, *A. sophiae* females normally lay about six (18%) of their eggs in a patch (table 3, row a; Cronin and Strong 1993*a*). Until the current study, the only circumstance under which we had observed a wasp lay her entire clutch of eggs was after she dispersed them among several host patches, each on a different nearby plant (table 3, row b; Cronin and Strong 1993*a*). Roughly the same number of eggs were laid in each plant visited. Short dispersals such as these appear to be common, but *A. sophiae* also disperses several kilometers or more with some regularity (Antolin and Strong 1987). Perhaps as a consequence of this movement-dependent oviposition behavior, parasitism in the field is both spatially and temporally density independent (Stiling and Strong 1982*a*; Roderick 1987; Strong 1989; Cronin and Strong 1990*b*). Overall, the low number of ovipositions in patches of abundant hosts and frequent dispersal by *A. sophiae* is considered sufficiently distinctive to have caused much discussion (Cronin and Strong 1993*a*, 1996; Godfray 1994; Rosenheim and Mangel 1994; Bouskila et al. 1995). Ecologists have argued that this behavior may have evolved to reduce the risk of self superparasitism (ovipositing in hosts previously parasitized by that wasp; Rosenheim and Mangel 1994), spread the risk of offspring mortality in space (Cronin and Strong 1993*a*, 1996), or is simply the consequence of a very discriminating host selection process (Bouskila et al. 1995).

**Table 2:** Experimental studies of dispersal distance or travel time and foraging activity within a patch following dispersal

Predator	Prey patch	Ambit of travel	Supported models	Author
Insects:				
Bumblebees	Plant in flower	U	No	Zimmerman 1981; Hodges 1985
Honey bees	Feeder	CP	Yes	Nuñez 1982
Apple maggot fly	Hawthorn tree	U	Yes	Roitberg and Prokopy 1982
Mushroom flies	Mushroom	U	Yes	Heard 1998
Birds:				
Wheatear	Feeder	CP	Yes	Carlson and Moreno 1981
Starlings	Feeder	CP	Yes	Kacelnik 1984; Cuthill and Kacelnik 1990
Mammals:				
Chipmunks	Feeding station	CP	Yes	Giraldeau and Kramer 1982

Note: Ambit of travel refers to whether the forager is unrestricted in its search (U) or uses a central place (CP) from which to make forays. Support for models indicates that foraging effort increased with dispersal distance.

## Material and Methods

### *Parasitoid Egg Loads*

We counted the eggs carried by *Anagrus sophiae* females captured within large monocultures of cordgrass on shore and by those wasps that had dispersed a minimum of 250 m. A single sticky trap was placed in each of five cordgrass marshes (designated control traps) and on four uninhabited oyster bars (designated the dispersal traps) in Oyster Bay, Wakulla County, Florida. These latter sites were isolated by 250–1,000 m of open water from the nearest cordgrass. The sticky traps were constructed of 8 × 13-cm index cards that were painted fluorescent yellow (Day-glo Saturn Yellow) and wrapped with acetate film smeared with Tanglefoot (Tanglefoot, Grand Rapids, Mich.). Twice-daily high tides flooded the control as well as the dispersal sites, so we designed the traps to float. Traps were attached to a 15-cm length of PVC tubing with a styrofoam float glued to the bottom. The tube was then inserted over a 2-m long steel rod that was driven into the substrate. This design allowed the traps to rise with the tides and remain above the water surface.

Traps were deployed for 3 d and then returned to the laboratory. A maximum of five wasps were removed from each trap and dissected under a stereoscopic microscope at × 50 to determine the number of mature eggs remaining in their ovarioles (egg load). Because *A. sophiae* is pro-ovigenic, this number represents the sum total of eggs remaining for future ovipositions. Egg counts were obtained from wasps on seven separate dates from July 30, 1989, to March 7, 1990. Data from all dates were pooled into either control or dispersal categories, and the difference in egg loads between the two was compared with a *t*-test.

### *Patches of Host Eggs*

Host-egg patches were created following the procedure of Cronin and Strong (1990a). Planthopper adults were collected with a sweep net from cordgrass and returned to the laboratory. Ten female and two male *Prokelisia marginata* were placed in a clip cage that was positioned at the base of a single leaf of a potted cordgrass culm. The cage was constructed of 40-mm long and 18-mm diameter acetate tubing that was inserted over the leaf and capped at either end. Planthoppers laid eggs into the leaves for a 48-h period and were then removed. This resulted in discrete host-egg patches consisting of an average ( $\pm$  SD) of  $79 \pm 49$  eggs (range: 14–200,  $n = 268$ ). Two host-egg patches were established on opposite-facing leaves on each potted plant.

### *Dispersal Experiments*

*10-m Dispersal.* In this experiment, we determined the effect of short-distance dispersal on the per capita number of ovipositions per host-egg patch. This parameter is well correlated with time on a patch (Cronin and Strong 1993a); thus, eggs laid per female also represents a measure of the patch time per wasp. Research was conducted in salt pans surrounded by large stands of pure cordgrass in Oyster Bay. The salt pans were higher than all but the highest tides, so as to avoid the necessity of floating the equipment. We placed 12 potted cordgrass culms, bearing two host patches each, within the open area of the salt pan a minimum of 10 m away from the nearest cordgrass. The pots were placed 2 m apart in a line transect and sunk flush to the mud. At equal distances in between each pot we placed an additional potted cordgrass culm that bore

**Table 3:** Ovipositions per patch of host eggs (mean  $\pm$  SD) by single *Anagrus sophiae* females

Conditions	Eggs laid per wasp	<i>n</i>
Laboratory:		
a. Exposed to single host patch	6.1 $\pm$ 5.7*	33
b. 1-m <sup>2</sup> arena with 81 host patches	5.9 $\pm$ 4.3*	38
Field:		
c. Within cordgrass marsh	3.6 $\pm$ 1.2 <sup>a</sup> *	6
d. Plants isolated by 10 m	15.7 $\pm$ 3.4**	3
e. Plants isolated by $\geq$ 250 m	20.8 $\pm$ 9.6**	3

Source: Cronin and Strong 1993a and this study.

Note: Patches were made up of many more host eggs than were ever attacked by a single female and were positioned alone on a cordgrass leaf. Means with different asterisks are significantly different based on individual *t*-tests ( $P < .05$ ). These studies were all located in the field.

<sup>a</sup> Averaged from controls for both experiments combined.

no hosts. These were trap plants that gave estimates of the *A. sophiae* population using the area. The trap plants had a thin layer of Tanglefoot applied to the basal 10 cm of two opposite-facing leaves. *Anagrus sophiae* act as if they do not detect the Tanglefoot and consistently walk onto or alight on the sticky surface and become trapped (Cronin and Strong 1993a).

The within-cordgrass control for the 10-m dispersal experiment consisted of 12 host plants and 12 trap plants deployed simultaneously in the cordgrass surrounding the salt pans. Evidence suggests that the lion's share of dispersal distances within stands of cordgrass are from leaf to leaf and shorter than a decimeter (Cronin and Strong 1993a). From three to 15 leaves occur along decimeter-long transects, and a large fraction of leaves bear parasitized hosts during the growing season from spring through late fall.

Host and trap plants were left in the marsh for 72 h to accumulate parasitoid attacks on experimental host eggs and capture searching wasps on the sticky traps. After this exposure period, we returned the pots to the laboratory and determined the number of planthopper eggs parasitized in each of the 24 host patches ( $p$ ) and the number of adult female wasps captured on each of the 24 sticky leaves ( $w$ ) per transect. Because individual *A. sophiae* are roughly equally likely to disperse between leaves on the same plant, to the adjacent plant, and to a plant about 1 m away, even when other cordgrass plants are in between (Cronin 1991; Cronin and Strong 1993a; J. T. Cronin and D. R. Strong unpublished data), we treated values of  $p$  and  $w$  from each transect as independent measures of the number of hosts parasitized and number of wasps per leaf, respectively. From these independent parameter estimates, we computed the mean number parasitized ( $\bar{p}$ ) and mean

wasps per leaf ( $\bar{w}$ ) for both the control and dispersal transect.

Because  $p$  and  $w$  were obtained from different leaves, we computed an indirect estimate the per capita ovipositions per host patch,  $\bar{o}$ , from the quotient  $\bar{p}/\bar{w}$  (Cronin and Strong 1993a). We used the following bootstrapping method (Efron and Tibshirani 1993) to compute the variance of  $\bar{o}$ . The data set consisting of 24 values of  $p$  was subsampled with replacement to produce 100 bootstrapped samples of 24  $p$ 's each. This was performed in SYSTAT version 7.0 (Wilkinson and Engelman 1997). Each bootstrapped sample was averaged to produce  $\bar{p}_b$  (where  $b$  = bootstrap sample number from 1 to 100). The same was done for the data set on wasps captured per leaf, which produced  $\bar{w}_b$ . For each bootstrap sample  $b$  ( $o_b$ ), the ratio  $\bar{p}_b/\bar{w}_b$  provided an estimate of  $o$ . The standard deviation about the mean of these 100  $o_b$  estimates served as our estimate of the variance in  $\bar{o}$ .

A total of three repetitions of the within-cordgrass control and 10-m dispersal transect were performed. Each control was paired with one dispersal transect and the pairs were run simultaneously: the first pair of transects was run from May 5–7, the second from May 18–21, and the third from October 4–6, 1991. All three replicates were performed within 100 m of each other at Oyster Bay. For the statistical analysis, we used a *t*-test to determine whether the mean number of ovipositions per wasp per leaf differed between each control and its paired dispersal transect.

Two field experiments at Oyster Bay contributed to the data. The first was a short-distance (10 m) dispersal experiment done on the mainland in which wasps had to fly to potted cordgrass plants placed in salt pans where no cordgrass grew; the pots were positioned to be 10 m away from cordgrass growing around the edges of the salt pan.

The control plants for this experiment were placed nearby within the continuous monospecific stand of mainland cordgrass. The second was a long-distance dispersal experiment in which wasps had to fly from 250 to 600 m. Because of the geography of the study area, we set up the long-distance experiment on Smith Island, approximately 9 ha in area and 1.7 km from the mainland in Oyster Bay. Smith Island is effectively a mainland that supports large cordgrass, *A. sophiae*, and planthopper populations. The long-distance dispersing wasps flew to bare oyster bars, devoid of cordgrass, from 250 to 600 m offshore of Smith Island in a direction away from the mainland. The controls for this experiment were placed within the extensive continuous stand of cordgrass on the beach of Smith Island.

*250-m Dispersal.* Around Smith Island in Oyster Bay we performed a second set of experiments in which the wasps had to disperse at least 250 m before finding hosts. Because the oyster bars were completely submerged at high tide, we floated the plants on tiny islands made of plywood ("floating islands"). These islands were constructed of a 60 × 60-cm plywood base (3 mm thick) with two 60 × 10 × 10-cm styrofoam blocks strapped on opposite sides for flotation. Four holes were cut into the plywood 10 cm apart and in a 2 × 2 configuration. Each hole received one potted cordgrass culm; the bottom of the pots reached just below the water surface when the islands were afloat. To stabilize the island during rough weather, a 2-kg lead weight was hung into the water from a 0.5-m length of rope that was tied to the center of the plywood. The islands were able to rise and fall with the tides and remained in place tethered to a storm anchor screwed into the oyster bar.

Two host plants and two trap plants (described in "Patches of Host Eggs" and "10-m Dispersal") were placed on each floating island, and a total of two islands were anchored to each of five different oyster bars. On Smith Island, which was the closest source of insects, we established a control transect on the beach in the cordgrass zone, above the mean high tide level. This transect was identical to the controls in the 10-m dispersal experiment. Experimental islands and the control transect were left in the field for 6 d.

Calculations of the per capita number of oviposition per leaf and variance were the same in the 10-m and 250-m experiments. Each leaf bearing host eggs and each sticky leaf trap were treated as independent sampling units because searching wasps hop among leaves independently of the plant to which the leaves are attached (Cronin 1991; Cronin and Strong 1993a; J. T. Cronin and D. R. Strong, unpublished data). A total of five paired (control transect plus floating islands) experimental replicates were performed, but two sets of floating islands were lost during

storms; consequently, only three replicates will be reported here. These three replicates were performed on October 17–22 and October 28–November 2, 1989, and May 19–24, 1990.

### Population Dynamics

In this section, we determine whether control and isolated transects differed in the relationship between host density per leaf and parasitism rate and the degree of parasitoid aggregation among leaves. Only data from the 10-m dispersal experiment were used because insufficient numbers of parasitized host eggs were obtained from the 250-m floating islands for reliable estimates of the density relationship and aggregation (Reeve et al. 1994b).

To determine whether dispersal altered the relationship between density and parasitism rate, we performed an analysis of covariance. Comparison of control and 10-m dispersal transects was the treatment effect and host density per leaf was the covariate. The dependent variable, proportion parasitized per leaf, was converted into a normally distributed variable by the angular transformation (Sokal and Rohlf 1981). In the analysis, we were mainly interested in the interaction between treatments and host density, which would indicate that the control and 10-m treatments differed in their density-parasitism relationship. We also performed a separate regression analysis on each of the six transects to determine how parasitism rate varied within a transect.

Parasitoid aggregation was estimated indirectly from the distribution of parasitized hosts among leaves (see Pacala et al. 1990; Hassell et al. 1991; Pacala and Hassell 1991). Here, we used the maximum likelihood method of Reeve et al. (1994b), which assumes that parasitoids aggregate independently of host density. In light of the evidence from several studies that shows density-independent patterns of parasitism for *A. sophiae* (Stiling and Strong 1982a; Strong 1989; Cronin and Strong 1990b; Roderick 1987), this assumption seems valid. The log-likelihood function of aggregation used is

$$L = \sum_{i=1}^M \ln \left[ \binom{n_{2i}}{n_{1i}} \frac{k^k}{\Gamma(k)} \int_0^{\infty} (e^{-aPu})^{n_{2i}-n_{1i}} (1 - e^{-aPu})^{n_{1i}} u^{k-1} e^{-ku} du \right],$$

where  $M$  is the number of patches,  $n_{1i}$  and  $n_{2i}$  are the number of individuals parasitized and hosts, respectively, in the  $i$ th patch,  $P_i$  is the number of searching parasitoids

in patch  $i$ , and  $a$  is the attack rate of the parasitoid. The variable  $u_i$  is a  $\gamma$  random variable with a mean of 1 and shape parameter  $k$ . Parasitoid aggregation is controlled by  $k$ , where  $k < 1$  indicates a highly aggregated distribution of parasitoids across patches and  $k > 1$  indicates a more even distribution. In this model,  $1/k$  is equal to the coefficient of variation squared ( $CV^2$ ). For a broad class of models, parasitoid-host stability is achieved when  $CV^2 > 1$  (Pacala et al. 1990; Hassell et al. 1991; Pacala and Hassell 1991). The maximum likelihood estimates of  $k$  and  $aP$  (a measure of parasitoid density) were found by maximizing  $L$  with respect to the above parameters. Finally, asymptotic 95% confidence intervals for  $k$  were calculated by inverting the likelihood ratio test (Reeve et al. 1994b).

For this model, the number of parasitoids visiting a patch is assumed to be enough that their distribution can be approximated by a continuous (i.e.,  $\gamma$ ) random variable. Low parasitoid densities can bias the estimates of  $k$  to smaller values, and so cause an overestimate of  $CV^2$  (Hassell et al. 1991). Reeve et al. (1994b) have empirically demonstrated that values of  $aP \geq 0.1$  are sufficient to meet this assumption for *A. sophiae*.

We estimated  $k$ ,  $aP$ , and  $CV^2$  for each of the six transects. Within an experimental replicate ( $n = 3$ ), we tested whether the distribution of *A. sophiae* differed significantly between the control and dispersal transects by comparing 95% confidence intervals around  $k$ .

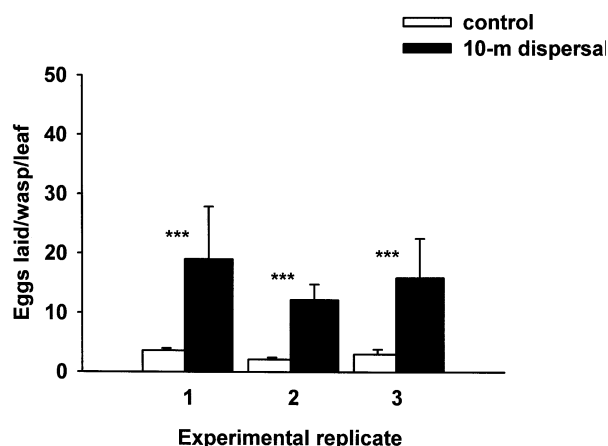
## Results

### Parasitoid Egg Loads

The number of eggs did not differ between wasps captured on the sticky traps in the mainland continuous cordgrass ( $\bar{X} = 18.8 \pm \text{SD}, 10.2, n = 100$ ) and on the floating islands 250–1,000 m offshore ( $18.4 \pm 10.5, n = 95; t = 0.319, \text{df} = 193, P = .750$ ). This suggests that dispersal distance is independent of egg load.

### Dispersal Experiments

**10-m Dispersal.** Wasps dispersing 10 m laid substantially more eggs per capita than mainland control wasps in each of the three replicate experiments (fig. 1). Dispersing wasps laid an average of 15.7 eggs ( $\pm 3.4 \text{ SD}, n = 3$  transects) per leaf and per patch of host eggs while nondispersing, control wasps laid 2.9 ( $\pm 0.8, n = 3$ ; table 3, rows c and d). Thus, the dispersers laid 84% of the eggs that they carried to 10 m, while the wasps remaining in the continuous stand of cordgrass laid only 16% of their eggs. The difference between these treatments is statistically significant ( $t = 6.294, \text{df} = 4, P = .019$ ). Number of hosts per host patch (i.e., per leaf) did not differ between the

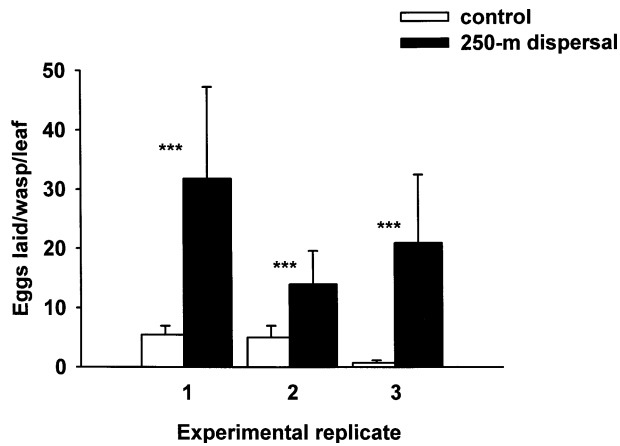


**Figure 1:** The mean ( $\pm 1 \text{ SD}$ ) per capita number of eggs laid for *Anagrus sophiae* per host patch within a cordgrass marsh where typical dispersal distance was about less than a decimeter (control) and on isolated plants to which dispersal distances were at least 10 m (10-m dispersal). Significantly more eggs were laid in dispersal patches (dark bars) than in control patches (open bars) in all three experimental replicates (replicate 1:  $t = 36.20, P < .001$ ; replicate 2:  $t = 64.38, P < .001$ ; replicate 3:  $t = 34.88, P < .001$ ) and is denoted by three asterisks.

control and dispersal treatments in any of the three experimental replicates (replicate 1:  $t = 1.24, \text{df} = 48, P = .219$ ; replicate 2:  $t = 1.69, \text{df} = 36, P = .095$ ; replicate 3:  $t = 0.28, \text{df} = 29, P = .780$ ).

The number of wasps captured on the 10-m dispersal plants was much lower than on mainland control plants. An average of  $0.6 \pm 0.3$  ( $n = 3$ ) wasps were caught per sticky leaf on the dispersal plants versus  $9.1 \pm 3.3$  per leaf in the controls (for means of the three replicates,  $t = 8.56, \text{df} = 4, P = .011$ ). Only  $6.2\% \pm 3.1\%$  of the total number of wasps captured in the experiment (control and dispersal wasps combined) were on the dispersal plants. Because the closest surrounding cordgrass is the source of most wasps, the 6.2% is a good estimate of the dispersal rate of *Anagrus sophiae* from the mainland to distances of 10 m. Finally, parasitism rate at 10 m was less than that in the continuous cordgrass controls ( $0.16 \pm 0.11$  vs.  $0.34 \pm 0.06$ , respectively;  $t = 2.60, \text{df} = 4, P = .060$ ).

**250-m Dispersal.** Wasps laid an average of  $20.8 \pm 9.6$  eggs/leaf after dispersal of  $\geq 250$  m to the floating islands, compared with only  $3.7 \pm 2.6$  eggs/leaf in the controls for this experiment (fig. 2), and this oviposition number was even higher than after dispersal of 10 m (table 3, rows d and e). Based on an average of 18.8 eggs carried to the floating islands, the number of ovipositions after  $\geq 250$ -m dispersal equates to 112% of the average egg load. There was no difference in host density per leaf between dispersal and control treatments in the first and third replicates (replicate



**Figure 2:** The per capita number of ovipositions per leaf in cordgrass onshore (control) and on floating islands  $\geq 250$  m offshore. Mean ( $\pm 1$  SD) is reported for each replicate experiment. Significantly more eggs were laid in dispersal patches (dark bars) than in control patches (open bars) in all three experimental replicates (replicate 1:  $t = 26.50$ ;  $P < .001$ , replicate 2:  $t = 19.24$ ,  $P < .001$ ; replicate 3:  $t = 11.51$ ,  $P < .001$ ).

1:  $t = 0.88$ ,  $df = 48$ ,  $P = .384$ ; replicate 3:  $t = 1.83$ ,  $df = 36$ ,  $P = .076$ ), while the control had a higher density than the dispersal in the second replicate ( $t = 2.85$ ,  $df = 43$ ,  $P = .028$ ). This significant difference is not unexpected by chance, given experiment-wise error brought about by the use of three separate  $t$ -tests (Sokal and Rohlf 1981).

The number of wasps reaching the floating islands was significantly lower than the number on control plants in the  $\geq 250$  m experiments:  $0.14 \pm 0.07$  versus  $3.08 \pm 0.47$  per leaf, respectively (based on replicate means;  $t = 10.63$ ,  $df = 4$ ,  $P < .001$ ). Thus,  $4.4\% \pm 1.9\%$  of the total number of wasps captured in this experiment (control and floating islands combined) were on the floating islands, giving an estimate of the dispersal rate of the *A. sophiae* population to  $\geq 250$  m. There was no significant difference between the dispersal rates to 10 m and  $\geq 250$  ( $t = 0.83$ ,  $df = 4$ ,  $P = .45$ ). Mean parasitism rates did not differ significantly between the control and  $\geq 250$  m dispersal ( $t = 1.37$ ,  $df = 4$ ,  $P = .24$ ), even though control and floating islands did differ in replicate 1 (0.13 and 0.07 for control and floating islands, respectively;  $t = 2.40$ ,  $df = 49$ ,  $P = .025$ ) and replicate 2 (0.13 and 0.02;  $t = 6.62$ ,  $df = 44$ ,  $P < .001$ ), but not replicate 3 (0.03 and 0.04;  $t = 0.56$ ,  $df = 45$ ,  $P = .543$ ) of this experiment.

Although mean per capita ovipositions was greater after dispersal of  $\geq 250$  m (20.8) than of 10 m (15.7), this difference was not statistically significant ( $t = 0.88$ ,  $df = 4$ ,  $P = .43$ ; table 3). Given the low number of wasps dispersing to  $\geq 250$  in our experiment and the low number

of replications, this test had low power ( $1 - \beta = 0.11$ ). However, only one of the dispersal replicates in the 250-m experiment had a higher number of ovipositions than the mean for all three replicates in the 10-m experiment (figs. 1, 2).

### Population Dynamics

There was no evidence of local density dependence in the rate of parasitism in any of the replicates of the 10-m experiment in either dispersal or control plants (all values,  $P > .05$ ). Neither was there evidence that the relationship between host density and parasitism per leaf differed between control and 10-m dispersal treatments. ANCOVA indicated significantly higher rates of parasitism in control transects, but there were no cases where the covariate, host density, or the interaction term (transect  $\times$  host density) were statistically significant (table 4; fig. 3).

Parasitism tended to be more aggregated after 10 m of dispersal than after the decimeter-scale of dispersal among the control plants (table 5). Although  $k$  was consistently lower among host patches at 10 m than among control patches, the difference was statistically greater only for the first experimental replicate. In two of the three dispersal transects, both bounds of the 95% confidence intervals for  $k$  fell below one, indicating that the  $CV^2$  ( $1/k$ ) was significantly greater than one. This was not the case for any of the control transects. Parasitism rates ( $aP$ ) were suffi-

**Table 4:** ANCOVA of parasitism rate (angular transformed) for the effect of treatment (control or 10-m dispersal), and host density (covariate)

Replicate and source of variation	df	$\bar{X}^2$	F	P
<b>1:</b>				
Treatment	1	.237	7.482	.009
Host density	1	.001	.032	.858
Treatment $\times$ density	1	.003	.090	.766
Error	48	.032		
<b>2:</b>				
Treatment	1	.001	.012	.912
Host density	1	.006	.150	.701
Treatment $\times$ density	1	.076	1.786	.189
Error	38	.042		
<b>3:</b>				
Treatment	1	.451	6.139	.020
Host density	1	.262	3.569	.069
Treatment $\times$ density	1	.200	2.720	.110
Error	28	.074		

Note: Separate tests are given for each of the three replicates. The test of whether the treatment (control vs. 10-m dispersal) affects density dependence of parasitism rate is given by the term for the interaction of treatment and density. To better normalize the distribution of parasitism rates among leaves, zeros were omitted before the analysis. We note, however, that their inclusion did not alter the results.

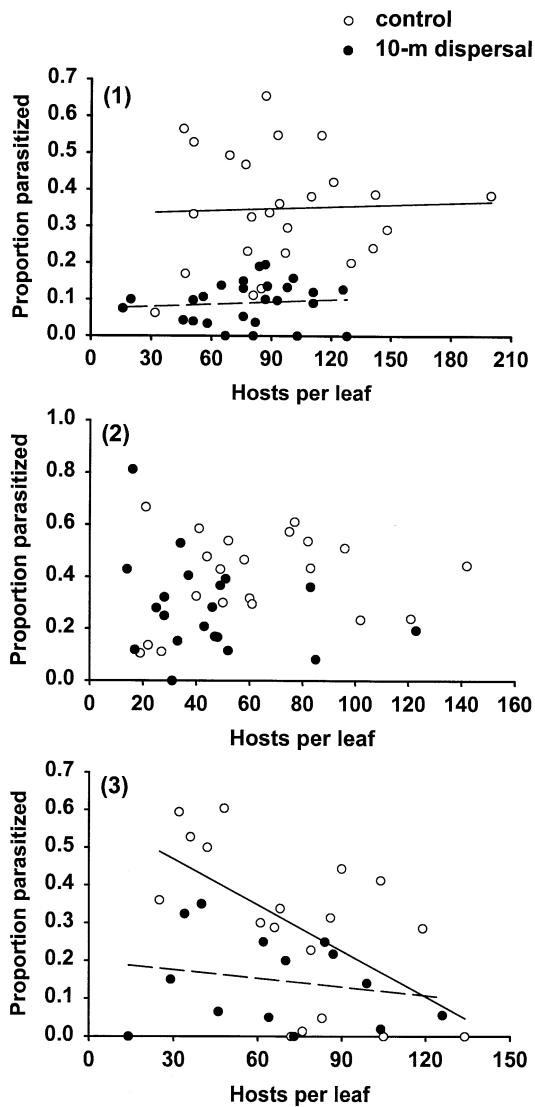


Figure 3: Relationship between host density (number of planthopper eggs per leaf) and proportion parasitized for control (*open circles*) and 10-m dispersal transects (*filled circles*). ANCOVA was used to determine whether there was an effect of dispersal treatment or host density on parasitism among cordgrass leaves (see table 4). Least-squares regression lines (solid for controls, dashed for 10-m dispersal) are reported for those experimental replicates (1–3) where either treatment or host density were significant factors in the analysis.

ciently high in all but one case to produce unbiased estimates of  $k$  and  $CV^2$ ; the only exception (10-m replicate 1) had an estimated  $aP$  of only slightly less than the 0.10 cut-off (table 5).

### Discussion

*Anagrus sophiae* is not unusual in living in a subdivided habitat. Cordgrass and host insects are separated among

many patches in marshes, on beaches, and on bars, just as the host habitats of most if not virtually all other species of parasitoids are discontinuous. Consequently, the role played by dispersal in population dynamics of this insect should not be considered extraordinary. Though minute, *A. sophiae* is vagile and disperses more than a kilometer from the mainland to find hosts on oyster bars (Antolin and Strong 1987). In this study, approximately 5% of foraging *A. sophiae* dispersed away from continuous stands of cordgrass to isolated plants in salt pans or on our experimental floating islands off shore. Other species of *Anagrus* also disperse long distances (Doutt et al. 1966; Ôtake 1970, 1976; McKenzie and Beirne 1972; Doutt and Nakata 1973; Williams 1984; Corbett and Rosenheim 1996; Corbett et al. 1996).

Our data show a substantial difference in oviposition behavior between wasps within the continuous mainland stand and those that have discovered isolated patches of cordgrass. Wasps that traveled only 10 m laid more than five times as many eggs per host patch than wasps moving on the decimeter scale through continuous cordgrass, which amounted to 84% of the average egg load. The additional 30% increase in mean ovipositions between 10 m and the floating islands anchored  $\geq 250$  m from shore was not statistically significant, and the asymptote in oviposition number as a function of distance could not be estimated accurately in our study. Because we did not observe the oviposition behavior of *A. sophiae* in these experiments, we do not have direct evidence about what caused the increased oviposition on plants isolated 10 and  $\geq 250$  m from the mainland. Is this a consequence of the direct effects of dispersal, the direct effects of isolation that are brought about indirectly by dispersal, or both? Certainly, wasps that immigrated to isolated patches may be subsequently reluctant to disperse from those patches (see Roitberg and Prokopy 1982), more likely to return to the isolated patches, or relatively free of competition with other conspecifics (reduced parasitoid interference). Our previous experiments with *A. sophiae* support the dispersal hypothesis more than the isolation hypothesis.

In laboratory studies we have consistently found these wasps to leave patches definitively, without small excursions or hanging around; they fly away and do not return. In one study, recently eclosed *A. sophiae* females that had been prevented from flying more than a few centimeters were placed on single patches of host eggs on isolated plants; they remained for an average of an hour and laid approximately six eggs, 18% of their average total egg load (Cronin and Strong 1993a, 1993b, 1996). Wasps returned to these patches extremely infrequently after dispersing away. We have found this behavior for host patches on excised leaves, for two patches on different leaves of the same whole plant, and on different plants placed close to



**Table 5:** Maximum likelihood estimates of  $k$ ,  $aP$ , and  $CV^2$  for control and 10-m dispersal transects in each of the three replicate experiments

Replicate and treatment	$k$	95% CI for $k$	$aP$	$CV^2$	$n$
1:					
Control	3.803*	1.99, 6.96	.454	.263	26
10-m	.403*	.19, .81	.090	2.481	26
2:					
Control	4.627 NS	2.06, 10.38	.542	.216	21
10-m	2.304 NS	1.04, 5.17	.342	.434	21
3:					
Control	.607 NS	.30, 1.17	.372	1.647	18
10-m	.382 NS	.14, .93	.178	2.618	13
Mean:					
Control	3.012 NS	-2.26, 8.28	.456	.332	3
10-m	1.030 NS	-1.71, 3.77	.197	.971	3

Note:  $k$  is a measure of the degree of parasitoid aggregation,  $aP$ , parasitoid density, and  $CV^2$ , the coefficient of variation squared ( $1/k$ ). Treatment comparisons have overlapping (NS) or nonoverlapping (asterisk) 95% confidence intervals.

one another. For example, in a study in which no other host patches were available (Cronin and Strong 1993b; J. T. Cronin D. R. Strong, unpublished data), only one of 68 wasps revisited the only host patch in the laboratory. The same results were observed in experiments with multiple host patches, with *A. sophiae* foraging among patches of host eggs on cordgrass leaves in areas of 81 potted cordgrass plants in a 1 m × 1 m array. Patch residence times and oviposition rates were similar for the first and all subsequent host patches visited by a single wasp and were no different from those of wasps ovipositing on isolated host patches (Cronin and Strong 1993a, 1993b, 1996). Only one out of 40 total patches encountered were revisited in this experiment (J. T. Cronin and D. R. Strong, unpublished data). In sum, these laboratory data suggest that isolation does not increase patch philopatry or patch revisitation by *A. sophiae*, nor does isolation cause higher rates of oviposition. These observations, however, do not address potential interactions between dispersal and isolation on parasitoid oviposition behavior. Any such response, however, would be an effect of dispersal.

Because fewer wasps are likely to disperse to isolated sites, the rate of parasitism would be expected to be much lower offshore than on the mainland. This would be an indirect effect of dispersal. We did not, nor do we see how it would be possible to, maintain similar wasp densities in the different habitats. The density of wasps and parasitism rate per leaf were much lower on dispersal than on control plants in both experiments, and interference among parasitoids or superparasitism could have differed as a result (van Lenteren 1976, 1981; Hassell 1978; van Alphen and Visser 1990; Visser and Driessen 1991). However, neither of these factors could have accounted for the high number of per capita ovipositions on the dispersal

plants. Direct interference does occur among searching *A. sophiae*; there is a linear decrease in the per capita number of ovipositions per host patch as wasp density increases ( $\ln$  number of hosts parasitized per patch =  $-0.77 \times [\ln$  wasp density] + 0.37,  $r^2 = 0.47$ ,  $P = .001$ ; Cronin and Strong 1993a, 1993b). We used this interference equation to calculate the expected per capita number of ovipositions in the high wasp-density controls and the low wasp-density 10-m transects and  $\geq 250$ -m floating islands. The difference between the control and dispersal treatments was used as a measure of the loss of ovipositions in the control transects caused by parasitoid interference. Accounting for eggs lost caused by this form of interference among wasps would have increased the number of eggs laid by only two in the 10-m and five in the 250-m controls; this is insufficient to explain the much larger difference between control and dispersal transects.

Only a single *A. sophiae* can develop in a host, and this wasp does superparasitize. We have found no indication that this parasitoid discriminates between parasitized and unparasitized hosts (Cronin and Strong 1993b). As a consequence, host patches with high rates of parasitism are expected to have a higher incidence of superparasitism; which in turn would translate into higher mortality rates of wasp eggs. Superparasitism leads to underestimates of per capita ovipositions. While parasitism rates were significantly higher on control plants than on dispersal plants (0.34 vs. 0.16 at 10 m, and 0.10 vs. 0.04 at 250 m), the rates on both were low and the differences small. Using a Poisson process to determine the distribution of wasp eggs among hosts in each transect (Cronin and Strong 1993b), we estimated the frequency of superparasitism to be low in this study. Adjusting for the loss of wasp eggs caused by superparasitism would increase the per capita ovipo-

sitions in controls by 0.2–0.5 eggs. Overall, any greater parasitoid interference and superparasitism in the control plants could not account for the number of ovipositions being five to six times greater in the dispersal treatment.

There remain two possibilities to explain the dispersal-dependent oviposition observed in this study. The first, most consistent with the evidence, is a homogeneous population in which oviposition rate increases with dispersal distance. This is consistent with optimality models (table 1). Several other species of insects have behavior consistent with this possibility (table 2); our study is the first demonstration for parasitic Hymenoptera. Oviposition rate of *A. sophiae* is probably more closely linked to caloric expenditures than to absolute time because, all else being equal, females of this species do not have a greater propensity to lay eggs later in life. *Anagrus sophiae* that were provisioned with food and held for 1 d of the average 2.0 d (maximum, 3 d; Cronin and Strong 1990a) adult lifetime did not lay more eggs per patch than females mated and eclosed within the hour (J. T. Cronin and D. R. Strong, unpublished data).

The second possibility is a heterogeneous population of wasps with a propensity for higher rates of oviposition, correlated with a propensity to disperse. *Anagrus sophiae* populations from the study area in Oyster Bay, Florida, do contain substantial phenotypic variation in oviposition behavior (Cronin and Strong 1993a; J. T. Cronin and D. R. Strong, unpublished data). Also, California populations have significant genetic variability in egg loads, patch time, number of ovipositions, and oviposition rate (Cronin and Strong 1996). However, in no experiment with either Florida or California *A. sophiae* did we find per capita ovipositions per patch nearly as high as those found on our off-shore plants. In our laboratory work, only two of the 210 Florida wasps examined (<1%) laid a greater number of eggs per patch than the mean for the floating islands 250 m offshore (fig. 4). Furthermore, in an examination of 41 different *A. sophiae* isolines from California, none showed an average number of ovipositions that equaled the number found on the offshore islands of the Florida study (Cronin and Strong 1996). We interpret the data, then, as showing that the increased oviposition rate after dispersal is a behavioral change. Thus, it is not unreasonable to suggest that the foraging behavior of more animal species varies with dispersal on the scale of the natural ambit of the organism in question.

The meaning of the patch-level oviposition behavior of *A. sophiae* has been debated (Cronin and Strong 1993a, 1996; Godfray 1994; Rosenheim and Mangel 1994; Bouskila et al. 1995). Under a variety of laboratory conditions, wasps lay only  $\approx 18\%$  of their available eggs in host patches bearing an abundance of planthopper eggs (Cronin and Strong 1993a, 1993b, 1996). This corresponds very closely

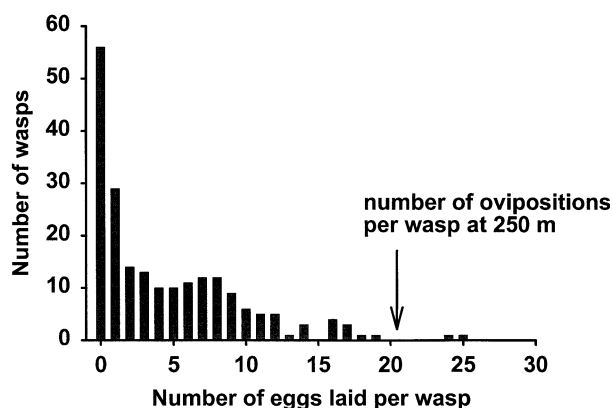


Figure 4: Frequency distribution of the per capita number of ovipositions by *Anagrus sophiae* per patch of host eggs in the laboratory. Wasps were left uncaged on host patches. Arrow, mean number of ovipositions per wasp per leaf found in the present field study on floating islands  $\geq 250$  m off shore.

with the 11%–20% eggs laid per wasp in expansive monocultures of cordgrass in the field (Cronin and Strong 1993a; and control transects in this study). Close inspection of the behavior of wasps has revealed that they are fastidious in host choice, probing many more hosts than they eventually parasitize (Cronin and Strong 1993a). *Anagrus sophiae* can be reared from probed and rejected hosts that were accepted for oviposition by searching wasps that visited the host subsequently. One possibility for this high rejection rate, and consequently the low ovipositions per patch, is that wasps discriminate a quality of hosts unknown to us (Bouskila et al. 1995). Alternatively, the low number of ovipositions per host patch could be an evolved response either to aid in the avoidance of self superparasitism (Rosenheim and Mangel 1994) or to spread the risk of mortality to parasitoid offspring in space (Cronin and Strong 1993a, 1996). The change in oviposition behavior following dispersal can be consistent with the first hypotheses. Here, we might expect that the mechanism by which ovipositions increase with dispersal distance is that wasps become less discriminating with time lost in dispersal. This, however, remains an open question. For the latter two hypotheses, we would not necessarily expect increased oviposition with dispersal distance.

Small isolated cordgrass patches are likely to be populated by a higher proportion of immigrant wasps than are larger patches of cordgrass. This result is expected because *A. sophiae* adults rarely remain on their natal plant long enough to oviposit (Cronin 1991; J. T. Cronin and D. R. Strong, unpublished data). As the size of the cordgrass patch decreases, the probability increases that it is a population sink; the ratio of immigrant to resident ovi-

positions increases. This means that the changes in oviposition behavior observed in this study could influence population dynamics, with fewer immigrant wasps sufficient to initiate a population. *Anagrus sophiae* in California are female-only parthenogens (Cronin and Strong 1996). Therefore, a single immigrating female can initiate a population there with no constraint from the availability of mates. The changed oviposition behavior with dispersal in *A. sophiae* can counter the Allee effect in metapopulations by increasing the initial number of colonists within an isolated, and previously vacant, patch. Without the effects seen in this study, colonization success would rise more slowly with the numbers of immigrants. Increased oviposition rate with dispersal could also lead to a greater rate of patch occupation in metapopulations than in the absence of this behavior (Hanski 1994). Moreover, attenuation of the Allee effect could lead to more rapid spatial spread (Kot et al. 1996; Amarasekare 1998; Kuussaari et al. 1998). With dispersal-dependent oviposition, immigrant *A. sophiae* play a role in population dynamics that increases more rapidly as the size of the patch decreases than do animals without this behavior.

This behavior also increased aggregation of parasitism. In two of three dispersal transects,  $CV^2$  was greater than one and, therefore, met the criterion necessary to stabilize a broad class of discrete host-parasitoid models (Pacala et al. 1990; Hassell et al. 1991; Pacala and Hassell 1991). In an age-structured model tailored for this system, these levels of aggregation are stabilizing (Reeve et al. 1994a). Because aggregation will increase in cordgrass patches with an increasing fraction of immigrants, the interaction between parasitoid and hosts will be more stable than one with only residents.

Given the predictions of foraging models and the empirical evidence presented in this article and table 2, a positive correlation between dispersal distance and subsequent foraging effort within a patch may be common in nature. The ramifications of this behavioral response extend to issues of biological control (e.g., the colonization and spread of introduced natural enemies), conservation (e.g., persistence and stability of endangered populations within an "island" refuge), and evolution (e.g., founder events and genetic structure of subdivided populations). Finally, we suggest that future population-dynamic modeling efforts (particularly for metapopulations) and experiments would be improved by considering this link between an animal's foraging behavior and its population dynamics.

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## QUERIES TO THE AUTHOR

1 Between this equation and the definitions following it, there are at least two inconsistencies: In the equation there is a "P" but no "Pi" and a "u" but no "ui," as given in the following definitions. Please clarify and make consistent.

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