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Long-distance dispersal by a parasitoid (*Anagrus delicatus*, Mymaridae) and its host

M.F. Antolin and D.R. Strong
Department of Biological Science, Florida State University, Tallahassee, FL 32306-2043, USA

Summary. We demonstrate that an egg parasitoid, *Anagrus delicatus* (Mymaridae, Hymenoptera) and its host, *Prokelesia marginata* (Delphacidae, Homoptera) regularly disperse 1 km or more in a north Florida saltmarsh. *Anagrus delicatus* were caught on yellow sticky traps on offshore islets and oyster bars throughout the spring, summer, and fall, whereas *P. marginata* were caught during one pulse in the spring. Parasitism rates were higher on offshore islets than at mainland sites, even though egg densities were higher at the mainland sites. The majority of parasitoids caught offshore were females. Long-distance dispersal by *A. delicatus* may be a cause of inverse density-dependent or density-independent spatial patterns of parasitism and may represent a risk-spreading strategy.

Key words: Dispersal – Parasitoid-host – Insects – Spatial parasitism patterns – *Anagrus*

Dispersal has been implicated as a stabilizing force in the dynamics of many organisms (Strathman 1974; den Boer 1985) and in the interactions of parasitoids with hosts (Huffaker 1958; Pimentel et al. 1963; Crowley 1981). Small arthropods are known to fly long distances (Johnson 1969; Southwood 1962), and movement by insect parasitoids and predators can affect predator-prey dynamics (Kareiva 1984; Murdoch et al. 1984; Chesson and Murdoch 1986). The spatial scales over which both host and parasite move are crucial to dynamics but are unknown for most organisms (Kareiva 1984). Here, we report that parasitoid and host dispersal regularly occurs on the scale of kilometers and mixes individuals among many semi-isolated subpopulations, which exist in patches on a scale of a few meters.

The insect herbivores and predators living on the intertidal saltmarsh cordgrass *Spartina alterniflora* on the Atlantic, Gulf, and Pacific coasts of North America are well studied (Denno 1983; McCoy and Rey 1981; Stiling and Strong 1982a, b; G. Roderick unpublished work). The most common insect herbivore is the planthopper *Prokelesia marginata* (Delphacidae: Homoptera), which feeds on *S. alterniflora* and lays its eggs into slits made on the upper surface of the leaves. It is there that *Prokelesia's* major parasitoid, *Anagrus delicatus* (Mymaridae: Hymenoptera), finds *Prokelesia* eggs and parasitizes them (Stiling and Strong 1982a). *Anagrus* are tiny (1.5 mm) parasitoids that lay one egg per host egg; these wasps live at most a few days and have a total fecundity of twenty to thirty eggs (Ôtake 1969; Stiling and Strong 1982a).

Methods

The study area is in the northeastern Gulf of Mexico, in Oyster Bay, Wakulla County, Florida, about 58 km south of Tallahassee Florida (Fig. 1). Oyster Bay is shallow, and numerous oyster bars and shoals are exposed at low tides. *Spartina alterniflora* is the sole vascular plant growing on these bars; patches of the plant on bars are termed "islets." This study was carried out on the two islets in Oyster Bay that are furthest to sea and most isolated from other *S. alterniflora*. The most seaward of these islets is designated Pluto, and Neptune is about 200 m shoreward. These islets are exposed to the open waters of the Gulf of Mexico. "Islands" are larger, have soil above mean high water, and

Fig. 1. The study area in Oyster Bay, Wakulla County, Florida. Islands have solid outlines; islets are on the oyster bars indicated by stippled areas. Trapping stations were on the outermost islets, Pluto *P* and Neptune *N*, on oyster bars near Pluto *OP* and near Neptune *ON*, on Smith's Island *SI*, and in the small bay *B* behind Smith's Island. Mainland samples were taken at Old Creek *OC*. The nearest large stands of *Spartina* to Pluto and Neptune are 1 km away on Smith's Island and 3/4 km away on the large islands to the west of Pluto and Neptune

Offprint requests to: M.F. Antolin

support plants other than *S. alterniflora*. Islands have continuous outlines on Fig. 1; islets occur on small fractions of the stippled areas. Most of the *S. alterniflora* on these islets dies back to the roots during cold winters, and few leaves are available to the host insect from late December to early March.

To measure movement of the insects, we periodically set six rows of yellow sticky traps in Oyster Bay between June 1985 and July 1986. The traps were 8-x-13-cm file cards sprayed with yellow paint (DAGLO SATURN YELLOW, no 606-16, New York Bronze Powder Co., Elizabeth, NJ 07201). The yellow cards were wrapped with acetate cut from overhead projector film, and the acetate was smeared with Tangle-trap (The Tanglefoot Company, Grand Rapids, MI) to ensnare the insects. The acetate-wrapped cards were clipped onto PVC tubes. A styrofoam float was attached to the bottom of each PVC tube, which was slipped over the top of a metal pole driven into the oyster bar. The yellow cards floated about 1 dm above the water and moved up and down with the tide and waves. There were at least four traps per station, positioned in a row in an east-west direction. The traps were left out in the bay for a week to ten days. Acetate sticky traps were brought back to the laboratory, where all *A. delicatus* and *P. marginata* were counted.

Islets Pluto and Neptune (P, N) each received a row of traps, as did the bare oyster bars nearest them (about 100 m away; OP and ON on Fig. 1). For comparison to the outer islets, a row of traps was set up in a meadow of *S. alterniflora* on Smith's Island and monitored from November 1985 to July 1986, when islet samples were taken. This meadow is similar to marshes on the mainland and has mud that is higher in elevation than that of the oyster bars. *Spartina alterniflora* survives most winters in the rosette stage in these habitats, providing year-round habitat for *P. marginata* and *A. delicatus*. Both insects overwinter on Smith's Island in most winters, but they do not overwinter on Pluto, Neptune, or many other islets. For another comparison to both Smith's Island and the outer stations, a line of traps was placed on a reef of oysters 200 meters inshore from the meadow in the bay between Smith's Island and the shoreline (SI and B on Fig. 1).

Between November 1984 and July 1986, levels of parasitism were determined on Pluto and Neptune in samples of 25 to 100 *S. alterniflora* leaves (depending upon availability). In the laboratory leaves were dissected and the numbers of parasitized and non-parasitized eggs were counted. Unparasitized eggs are pale yellow, eventually developing red eye spots. Parasitized eggs are initially milky white or clear, then change from pink to red within the first few days of development of the parasite (Ôtake 1969; Stiling and Strong 1982a). Beginning in November 1985, leaf samples were also taken from Smith's Island. Egg densities and parasitism rates from a mainland marsh meadow on Old Creek are included (OC on Fig. 1). Parasitism rates estimated in this fashion are accurate because most host eggs are layed in clutches and are thus synchronous in vulnerability to parasitism. We disregard data from clutches so old that eggs are hatching and, thus, biasing parasitism rates.

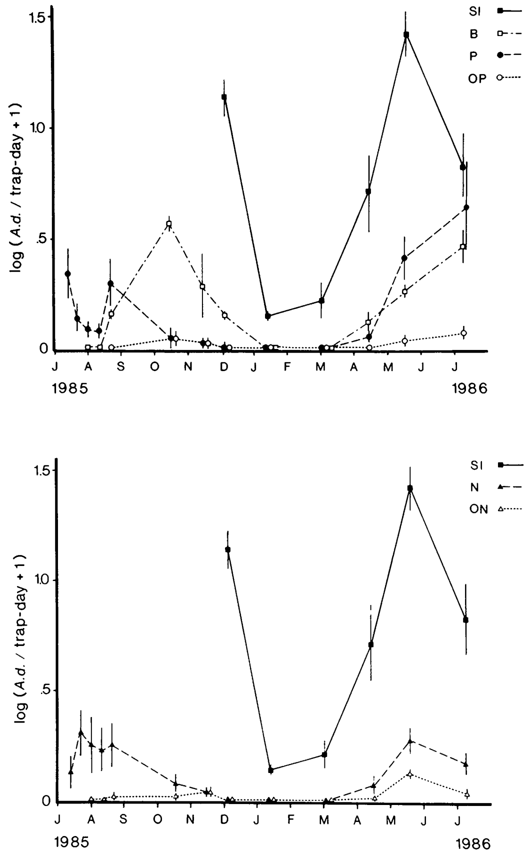

Fig. 2. The numbers of *Anagrus delicatus* per trap-day plotted on a log scale. The bars are ± 1 s.e. For comparison, the data for Smith's Island *SI* appear on both plots. See Table 1 legend for other abbreviations

Table 1. Captures on yellow sticky traps of the parasitoid *Anagrus delicatus*

	Females	Males
Pluto (P)	304	26
Outside near Pluto (OP)	10	0
Neptune (N)	171	78
Outside near Neptune (ON)	19	0
Smith's Island (SI)	1096	333
Bay (B)	122	3

Results

The host insect became extinct on Pluto and Neptune Islets between December of 1985 and March of 1986, as revealed by the absence of nymphs and adults from sweep samples and the absence of eggs from host plant leaves on the islets. Host eggs appeared in leaves on the islets between April and May of the intervening summers. Some nymphs and brachypters, which probably hatched on the islets, were found on traps on the islets in spring (Fig. 4).

Numbers of trapped *A. delicatus* are shown in Fig. 2. The most striking pattern for *A. delicatus* is that, during spring, summer, and fall, at least a few parasitoids were caught at every station, all of which are more than a kilometer away from any other *S. alterniflora*. More *Anagrus* were caught on Pluto and Neptune Islets than on the traps on the adjacent oyster bars, but more were caught on the reef inshore from Smith's Island than on the offshore reefs (Table 1). The lowest non-zero values on the islets represent

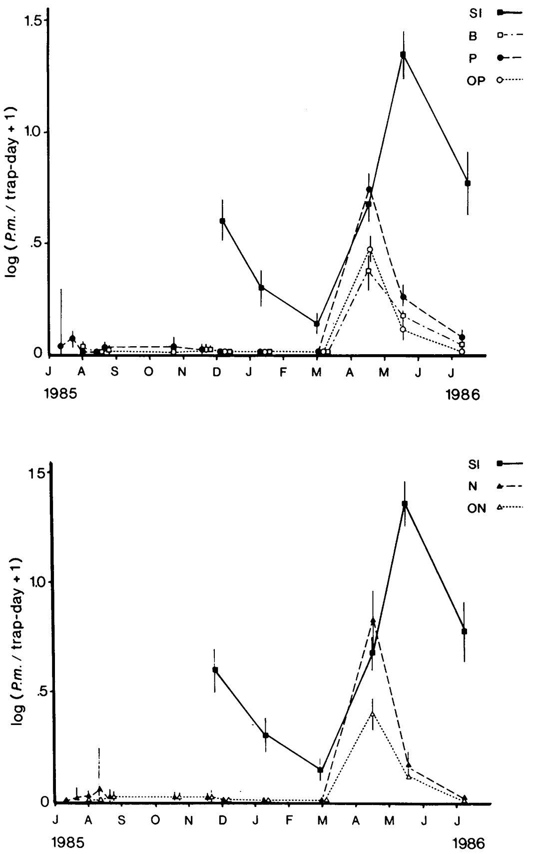

Fig. 3. The numbers of *Prokelesia marginata* per trap-day plotted on a log scale. the bars are ± 1 s.e. For comparison, the data for Smith's Island *SI* appear on both plots. See Fig. 1 legend for other abbreviations

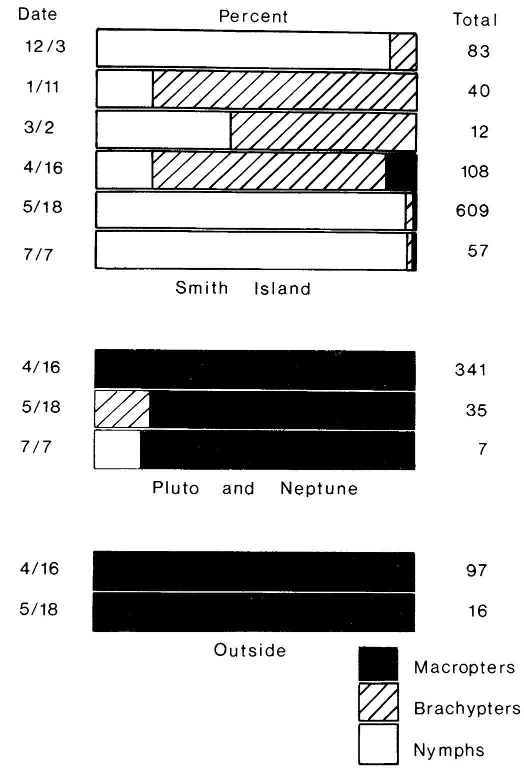

Fig. 4. The percentage of each morph of *Prokelesia marginata* caught on Smith's Island, on Pluto and Neptune, and on the two outside stations near Pluto and Neptune. Total is the number of *P. marginata* caught on all the traps combined for the sampling period

1–5 parasites per trap for a week's trapping period. The highest values for Smith's Island are in the range of 90–250 *A. delicatus* per trap. Parasitoids dispersed to the islets seasonally, and islet trap catches were zero in the winter between December and March. *Anagrus delicatus* were trapped in all months on Smith's Island, but only between April and December on the offshore islets and on the adjacent oyster bars. The majority of *A. delicatus* caught were females, and proportionately more females were caught at trapping stations on oyster bars than on Smith's Island (Table 1).

The host insect, *P. marginata,* appeared on the traps in a more seasonal pattern than that of the wasp (Fig. 3). Almost no *P. marginata* were caught away from Smith's Island except in April and May 1986, and then equal numbers were caught at all stations. By July there were still large numbers trapped on Smith's Island, but few were caught anywhere else.

Prokelesia has a wing dimorphism; long-winged macropters are the dispersal morph, and short-winged brachypters generally do not move far (Denno et al. 1985; McCoy and Rey 1981). Only macropters were trapped at any time on the oyster bars and reefs away from the host plant. On Pluto and Neptune only macropters were trapped in the spring, but sparse populations did become established on the islets, and brachypters and nymphs were trapped as well (Fig. 4). It can be seen that on Smith's Island no

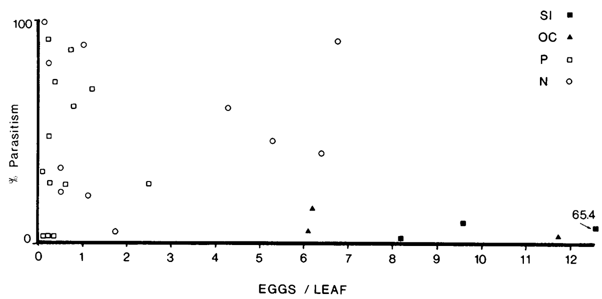

Fig. 5. Plot of the percent parasitism versus the numbers of eggs per leaf, calculated from samples of 25–200 leaves for each point. Note that open symbols are for offshore islets and closed symbols are for mainland-like sites

macropters were produced until April, when they appeared on the oyster bars and islets.

Parasitism rates are shown in Fig. 5. Egg densities were much higher on the mainland-like Smith's Island and at Old Creek on the mainland than on the islets (t-test on log-transformed data: $t = 5.49$, 30 *d.f.*, $P < 0.001$). The percentage of eggs that were parasitized was higher on the outer islets than on Smith's Island and at Old Creek (t-test on arcsin-square-root-transformed data: $t = 2.34$, 30 *d.f.*, $P < 0.05$), yielding a spatial pattern of vaguely inverse density dependence. However, the correlation between egg density per leaf and parasitism was not significant when all leaves were considered together ($r = -0.218$).

Discussion

Colonization of the offshore islets demonstrates that both the planthopper *P. marginata* and its egg parasitoid, *A. delicatus*, regularly disperse on the scale of kilometers to host plants and subpopulations quite distant and separate from those upon which they matured. Adults of both of these species are the winged stage and do the dispersing. *Anagrus delicatus* arrives at the islets throughout the warm months, and its planthopper host has a pulse of dispersal in the spring, when macropterous individuals are most numerous in the population (Strong and Stiling 1983).

Adult *P. marginata* have been trapped on oil platforms as far as 160 km offshore in the Gulf of Mexico (Sparks et al. 1986), and dispersal is a major facet of life history of *P. marginata* in marshes of New Jersey (Denno 1983; Denno et al. 1985). In New Jersey, the planthopper colonizes stands of cordgrass on creek banks in the spring and overwinters mostly in the back marsh away from creeks. In North Florida seasonal population fluctuation between areas in the marsh is not as evident. As well, the frequency of macropters, which disperse great distances, is much lower during most of the year (about 10%) at Oyster Bay than in New Jersey (McCoy and Rey 1981; Strong and Stiling 1983). However, neither the lesser seasonal/spatial dichotomy in population nor the low macropter frequency has caused the elimination of dispersal and immigration as substantial demographic factors in the host at Oyster Bay.

Species of *Anagrus* other than *A. delicatus* disperse long distances and seasonally colonize new sites. *Anagrus epos* disperses from watercourses in California and British Columbia to serve as a biological control organism in vinyards several kilometers away from the overwintering sites (McKenzie and Bierne 1972; Doutt and Nakata 1973; Williams 1984). *Anagrus flaveolus* parasitized the eggs of the brown rice planthopper in experimental plants placed in wheat plots, and away from the plots on bare ground. Parasitism rates were not different in these two apparently alien habitats from those in control rice plants placed in rice plots (Ôtake 1970, 1976). Likewise, the results of Murdoch et al. (1984) indicate that dispersal of parasitoids among habitats plays a large role in the interactions between parasitoids and their host populations.

Population dynamics are likely to be substantially affected by dispersal (Kareiva 1984). Van Lenteren and Bakker (1976) have shown how the artefactual prevention of dispersal in laboratory studies of parasitoids can bias the spatial pattern of parasitism. Dispersal by parasitoids may be a cause of the high incidences of inverse density-dependent and density-independent parasitism in parasitoid-host systems (Morrison and Strong 1980; Stiling 1987) and will have to be studied carefully before parasitoid-host dynamics will be understood. Dispersal by *A. delicatus* away from areas with relatively high egg densities may cause the parasitism rates and inverse spatial density dependence found in this system (Stiling and Strong 1982a, b).

One profound implication of frequent dispersal over fairly great distances is "risk spreading" in population dynamics and evolutionary influences (den Boer 1968, 1985; Roff 1974; Levin et al. 1984). With haphazard dispersal among semi-isolated subpopulations, the mechanisms maintaining populations need not be seen in the local density relationships and behavior within subpopulations. Thus, the standard view of parasitoid-host mathematical stability, based upon "aggregative responses" among patches within subpopulations, may be wide of the mark (Murdoch et al. 1984; Chesson and Murdoch 1986).

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