Interspecific variation in behavior and its role in thrips ecology

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Abstract: Southeastern USA is home to a complex of native and adventive *Frankliniella* species, as well as the thrips predator *Orius insidiosus.* The primary *Frankliniella* species present in this region are *F. occidentalis, F. tritici, F. bispinosa,* and *F. fusca.* This diversity presents a model system for examining how species-specific behavioral attributes affect large-scale spatial and temporal population dynamics and predator-prey interactions. Here we discuss how interspecific variation in behavior of thrips can produce different spatial and temporal dynamics for populations of these species, and how variation in thrips behavior could impact regulation of thrips populations by the predator *O. insidiosus*. We examined interspecific differences in development, fecundity, activity, and susceptibility to predation. We found that *O. insidiosus* is able to prey effectively on *F. occidentalis, F. tritici and F. bispinosa*. However, less mobile prey, such as larvae and adults of *F. occidentalis,* tend to be more vulnerable to predation than are more mobile prey, such as adults of *F. bispinosa.* Previous research has demonstrated, both theoretically and empirically, that the predator *O. insidiosus* has the capacity to regulate populations of thrips, but our results indicate that the regulatory ability of *O. insidiosus* will be mediated by species-specific behavioral differences of their thrips prey.

Introduction

The population dynamics and ecology of thrips have been enduring sources of fascination for ecologists and entomologists alike. Since the classic studies on *Thrips imaginis* in Australia (e.g., Davidson and Andrewartha, 1948a, b) and before, researchers have looked for biotic and abiotic factors that would account for the large-scale spatial and temporal patterns displayed by populations of thrips. Here, we use a comparative approach to suggest how small scale events, specifically differences in behavioral events, can mediate large-scale population dynamics of *Frankliniella* species.

A complex of *Frankliniella* species occurs throughout northern Florida and the southeastern USA (Salguero-Navas et al., 1991; Chellemi et al., 1994; Puche et al., 1995; Eckel et al., 1996). The primary species that we address are *Frankliniella bispinosa*, *F. occidentalis*, and *F. tritici*. All of these species are highly anthophilic (Cho et al., 2000; Hansen, 2000) and inhabit flowers of a variety of cultivated and uncultivated plants (Chellemi et al., 1994). *F. bispinosa* and *F. tritici* are native to this region, whereas *F. occidentalis* is an invasive species that has been present in the southeastern USA for just over 20 years (Beshear, 1983). Despite their similarity in appearance and their overlapping host ranges, these species display radically different population dynamics (Cho et al., 2000; Hansen, 2000; Ramachandran et al., 2001; Baez, 2002; Reitz, 2002). For example, in northern Florida, *F. occidentalis* populations typically peak earlier in the spring than those of *F. tritici* (Fig. 1). In addition, proportionately more adults of *F. bispinosa* and *F. tritici* are found in tomato (*Lycopersicon esculentum*) than are found in pepper (*Capsicum anuum*), whereas the opposite is true of adults of *F. occidentalis.*

Several factors could contribute to these interspecific differences in population dynamics. The species could differ in such intrinsic traits as developmental rates and female fecundity. In addition, differences in host plant use and activity patterns could further influence population dynamics. Variation in these characteristics then can have profound consequences for interactions of thrips with their natural enemies. Extensive

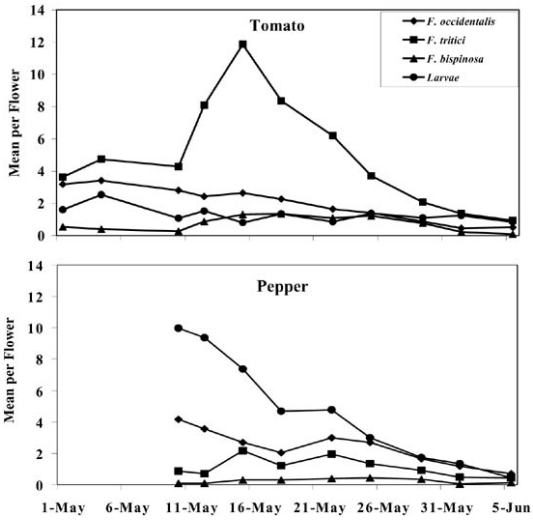

Figure 1. Representative seasonal dynamics of *Frankliniella occidentalis* and *F. tritici* in tomato and pepper in north Florida. Data are from the spring 2000 growing season. (Modified from Baez 2002).

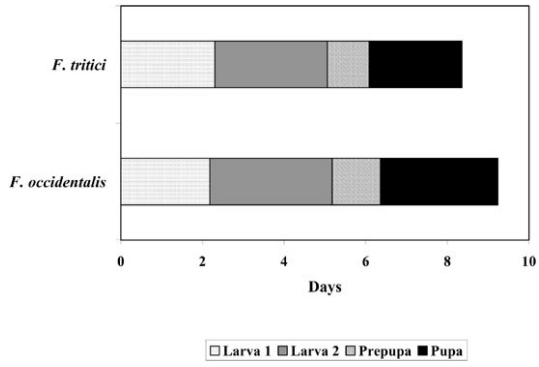

Fig. 2. Comparative development times for life stages of *Frankliniella occidentalis* (n = 40) and *F. tritici* (n = 37) females reared on green bean pods. The total development time is significantly less for *F. tritici* than for *F. occidentalis* ($F_{1, 41}$ = 7.33, P < 0.01, one way ANOVA), with the primary difference being the duration of the pupal stage.

research has documented the capacity of natural enemies, such as species of *Orius* (Heteroptera: Anthocoridae), to suppress populations of *F. occidentalis* (Higgins, 1992; Chambers et al., 1993; Nicoli, 1997; Funderburk et al., 2000; Ramachandran et al., 2001). The impact of this predator on other species of thrips is less well understood (but see Funderburk et al., 2000; Ramachandran et al., 2001). A better understanding of how behavioral variation among thrips affects such predator-prey dynamics will improve the understanding of thrips population dynamics.

Intrinsic differences in development and fecundity

Longer development time will result in a slower intrinsic rate of population increase. Likewise, lower individual female fecundity will produce slower rates of population increase. The typical seasonal data for *Frankliniella* spp. in north Florida shown in Fig. 1 suggest that *F. tritici* is more abundant than *F. occidentalis* in the north Florida region, but the lag in the population peak of *F. tritici,* compared with that of *F. occidentalis,* suggests that *F. tritici* may have either slower developmental rates and / or lower fecundity than *F. occidentalis*.

To determine if such interspecific differences exist, we conducted laboratory experiments to compare the developmental time and fecundity of individual females of *F. occidentalis* and *F. tritici.* For the development study, neonate larvae (< 6 hrs old) were transferred individually to 4cm sections of green bean pods (*Phaseolus vulgaris* L.) contained in 31 ml plastic cups, and these were kept in an environmental chamber (26C, 14:10 L: D). The cups were inspected every 12 hrs, and the life stage of each individual was recorded until the individual died or had eclosed as an adult. Only those progeny that survived to adulthood were included in the analysis. Data were analyzed as a repeated measure analysis of variance (ANOVA).

To compare fecundities of *F. occidentalis* and *F. tritici,* newly eclosed (< 6 h old), unmated females were transferred to 4cm sections of green bean pods, and these were kept individually in 31-ml plastic containers in an environmental chamber (26 C, 14:10 L:D). Females were provisioned with fresh green bean sections every two days. The numbers of progeny for each female were recorded. Data were analyzed by one-way ANOVA.

Despite our prediction that *F. tritici* would have a slower developmental time than *F. occidentalis,* our laboratory data show that the development time of *F. tritici* is approximately one day shorter than that of *F. occidentalis* ($F_{1, 40}$ = 7.33, P < 0.01, Fig. 2), with the primary

difference occurring in the pupal stage ($F_{1, 40}$ = 8.49, P < 0.006). In addition, we did not find a difference in oviposition rates over the course of a female's lifetime ($F_{1, 53}$ = 1.03, P = 0.31, Fig. 3). Nor did we find a difference in the mean number of progeny produced per day by these two species (4.12 ± 0.24 and 4.08 ± 0.21, for *F. occidentalis* and *F. tritici,* respectively, $F_{1, 53}$ = 0.02, P = 0.90). In fact, *F. tritici* females produce a higher proportion of their total progeny earlier than do *F. occidentalis* females (Fig. 3). Based on these results, *F. tritici* should have a greater rate of increase than *F. occidentalis,* but this difference is not apparent based on field sampling. Given our laboratory findings, these intrinsic differences in development rate or fecundity, by themselves, would not account for differences in the population dynamics of *F. occidentalis* and *F. tritici.* However, other behavioral factors that affect the realized fecundity and development could affect the population dynamics of these species.

Time Budgets of Thrips

Although we found no differences in fecundity between *F. occidentalis* and *F. tritici,* variation in how species allocate their time and activity on host plants could contribute to interspecific variation in spatial and temporal dynamics. To determine if time budgets and activity patterns differ between species, we compared the time spent by adult female *F. occidentalis* and *F. tritici* in different activities on either tomato or pepper plant parts. Individual female thrips were placed in Plexiglas arenas (75 mm diameter) with a flower bud, flower bloom and leaf of either tomato ("Florida 47") or pepper ("Camelot"), and their behaviors recorded for one-hour intervals. All observations were made with the assistance of a video camera mounted on a stereomicroscope. Behavioral states and durations were recorded with the use of the Observer software (Noldus Information Technology, Sterling, VA). A two-factor multivariate ANOVA was used to compare time budgets for the two species on the two host plants (Aitchison 1986).

We found that *F. occidentalis* and *F. tritici* females have significantly different time budgets and host use patterns ($F_{8, 31}$ =2.34, P = 0.01). For both species, over 77% of the time spent on the plant parts was spent in the flowers. However, female *F. occidentalis* spent significantly more time on, and fed over three times longer on pepper than on tomato (Fig. 4). Female *F.*

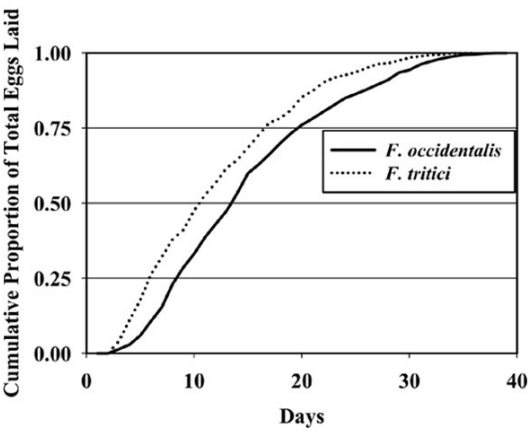

Fig. 3. Cumulative proportion of progeny produced over female lifetime for *F. occidentalis* and *F. tritici* maintained on green bean pods. Mean daily fecundity ($F_{1, 46}$ = 0.02, P = 0.89) and longevity ($F_{1, 54}$ = 1.49, P = 0.23) did not differ between species.

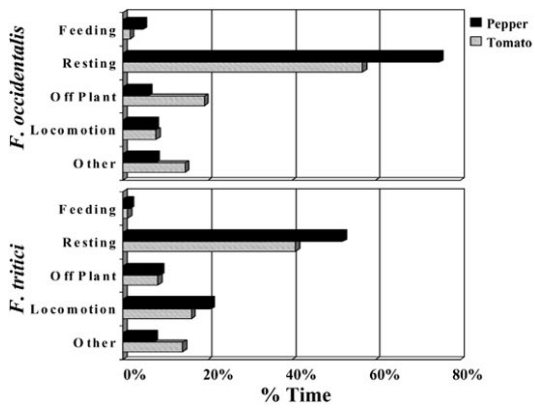

Fig. 4. Time budgets recorded for females of F. occidentalis and F. tritici on either tomato or pepper. Arenas contained a flower, flower bud and leaf of one of the host plant species. Over 95% of time spent on plant parts was spent on the flowers. Therefore, the behaviors on the three different plant parts have been summed. Only the percent of time spent in the predominant behaviors of feeding, resting on plant parts and moving, and percent of time spent not moving but off of any plant part are shown. Percent of time spent in all other behaviors are grouped as "other."

occidentalis exposed to tomato also spent a substantial proportion of time completely off any of those plant parts (19.1 ± 0.06%). These results suggest that tomatoes elicit an avoidance response by *F. occidentalis.* In contrast, *F. tritici* had similar time budgets on tomato and pepper, and fed on both plant types for similar amounts of time. Another important interspecific difference is that *F. tritici* are significantly more active than *F. occidentalis.* Therefore, both pepper and tomato may be suitable hosts for adult females of *F. tritici*, and that *F. tritici* females could move readily between the two host plants. In contrast, our results indicate that *F. occidentalis* females prefer pepper to tomato.

Additional data indicate that the time budget for *F. bispinosa* is similar to that for *F. tritici* (EAH and SRR, unpubl.). Like *F. tritici*, *F. bispinosa* are relatively more active than *F. occidentalis.* These results support the conclusions of Ramachandran et al. (2001). They measured colonization of peppers over time when placed in different insecticide treatment plots that were designed to include or exclude different species of thrips and natural enemies. They found that *F. tritici* and *F. bispinosa* will move rapidly among plants, and this rapid movement may assist these species in avoiding predation. In contrast they found *F. occidentalis* slower at colonizing newly available resources. Ramachandran et al. (2001) also demonstrated that *O. insidiosus* is able to rapidly colonize newly available host plant resources, and hence *O. insidiosus* should be able to track available prey in time and space. However, this supposition is dependent on the ability of *O. insidiosus* to capture and consume various thrips prey.

Behavioral Effects on Predator-Prey Interactions

Our results demonstrating behavioral differences among these species of thrips allow us to formulate hypotheses regarding the manner in which these species interact with natural enemies, such as the generalist predator *O. insidiosus.* Generalist predators may display a preference for certain prey because those prey occur in the preferred habitat of the predator (Cloutier and Johnson, 1993). Generalist predators also may select prey based on vulnerability of the prey (Lang and Gsödl, 2001), with more vulnerable prey being taken disproportionately in mixed species assemblages.

The extent of predation on *Frankliniella* spp. by *Orius* spp. (Salas-Aguilar and Ehler, 1977, Van den Meiracker and Ramakers 1991, Funderburk et al. 2000, Ramachandran et al. 2001) could be a function of habitat preference, because both predator and prey prefer flowers (Cloutier and Johnson 1993, Hansen 2000). Also, because the larvae and adults of different species of *Frankliniella* occur together in flowers, *O. insidiosus* may selectively capture prey based on their vulnerability. Less mobile prey should be more vulnerable to predation because they cannot escape predators as well as faster moving prey. Therefore when given both larvae and adults as potential prey, *O. insidiosus* should take proportionately greater numbers of the less mobile larval stage than the more mobile adult stage. Furthermore, when exposed to adults of two species, we would expect *O. insidiosus* to capture more of the relatively sedentary *F. occidentalis* than the more active *F. tritici* or *F. bispinosa.* To determine if *O. insidiosus* preferentially takes less mobile prey, we conducted a series of laboratory experiments with various combinations of thrips exposed to *O. insidiosus* in pepper flowers.

Predation on F. occidentalis larvae and adults

In the first experiment, we released ten 2nd instar and ten adult female *F. occidentalis* onto a pepper flower ("Yolo Wonder"). The pepper flower was held in a small, water-filled vase in the bottom of plastic petri dish (150 mm diameter). Two hours after the thrips were placed in the flower, an adult female *O. insidiosus* was released onto the flower. In one half of the replicates (n = 10), we counted the number of larvae and adults that were consumed by *O. insidiosus* after 10 hours. In the other half of the replicates (n = 10) we counted the number of larvae and adults that were consumed by *O. insidiosus* after 34 hours. Data were analyzed by fitting log linear models to determine if there was a significant difference in the proportion of each type of thrips consumed by *O. insidiosus* (Sokal and Rohlf 1995)

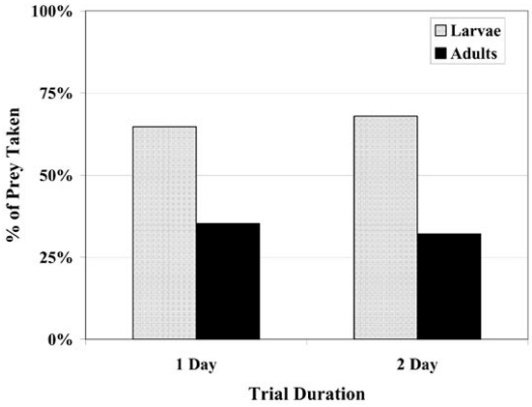

Fig. 5. Proportion of adult and larvae captured as prey by female *O. insidiosus.* In one-day trials, 10 2nd instar and 10 adult female *F. occidentalis* were exposed to a predator for 10 hours. In the two-day trials, the same number of thrips were exposed to a predator for 34 hours. *O. insidiosus* captured significantly more larvae than adults of *F. occidentalis.*

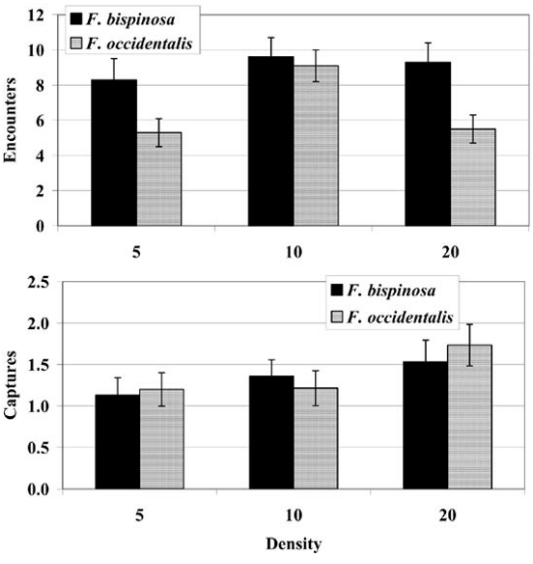

Fig. 6. Predatory behavior of *O. insidiosus* when exposed to different densities of either *F. bispinosa* or *F. occidentalis* adults. *O. insidiosus* had significantly more encounters with *F. bispinosa* than *F. occidentalis,* but there was no significant difference in the mean number of prey captured. Bars above columns represent the standard error of the means.

We found that larvae of *F. occidentalis* are significantly more vulnerable to predation by *O. insidiosus* than are adults. Regardless of the length of the trials, approximately two-thirds of the prey consumed by *O. insidiosus* were larvae (Fig. 5). Somewhat surprisingly, the proportion of larvae in the diet of *O. insidiosus* did not change over time, even though the population demographic would have changed as the proportion of larvae decreased with predation. These results support the hypotheses that larvae are more vulnerable to predation because they are less mobile than adults and that *O. insidiosus* captures less mobile prey more frequently than they capture more mobile prey.

Predation on F. bispinosa and F. occidentalis adults

We examined the behavioral variation in predation by examining short-term predation on *F. bispinosa* and *F. occidentalis* adults in single pepper flowers. In these experiments, we used an arena similar to those used in the predation trials with larvae and adults of *F. occidentalis.* In the first of these experiments, we observed predation by *O. insidiosus* for one hour on groups of adult *F. bispinosa* or *F. occidentalis.* As before, thrips were released onto a pepper flower, and one hour later, an adult female *O. insidiosus* was released. We used three densities of thrips, five, ten, or 20 individuals per replicate. The number of encounters and captures were recorded. Data were analyzed by a two factor ANOVA. We then observed predation by *O. insidiosus* for one hour on mixed groups of adult *F. bispinosa* and *F. occidentalis* (n = 10 for each species). The number of encounters and prey captures were recorded for each species. Data were analyzed with paired t-tests to determine if *O. insidiosus* encountered or captured one species more than another.

In the single species trials, *O. insidiosus* females had significantly more encounters with *F. bispinosa* than with *F. occidentalis* ($F_{1, 82}$ = 8.42, P = 0.005, Fig. 6a). Density also had a significant effect on the number of encounters ($F_{2, 82}$ = 4.04, P = 0.021), although not in a consistent manner. At the highest and lowest densities, *O. insidiosus* had more encounters with *F. bispinosa* than with *F. occidentalis.* However, at the intermediate density of 10 thrips per

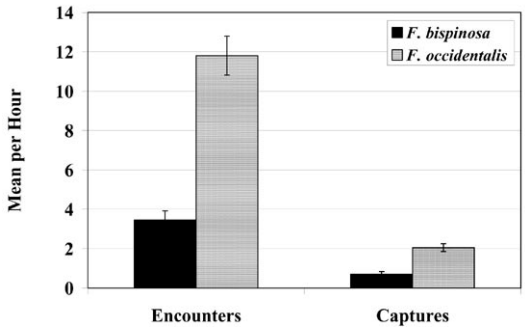

Fig. 7. Predatory behavior of *O. insidiosus* when exposed to mixed groups of *F. bispinosa* or *F. occidentalis* adults. *O. insidiosus* had significantly more encounters with *F. occidentalis* than *F. bispinosa,* and captured significantly more *F. occidentalis*. Bars above columns represent the standard error of the means.

arena, there was no significant difference in the number of encounters *O. insidiosus* had with the two species of thrips. Despite differences in the numbers of encounters, the number of captures made by *O. insidiosus* did not differ for the two species of thrips ($F_{1, 82} = 0.05$, $P = 0.83$, Fig. 6b).

In contrast to the single species trials, *O. insidiosus* females had significantly more encounters with *F. occidentalis* than with *F. bispinosa* in the mixed species trials ($t = 8.15$, $df = 19$, $P < 0.0001$, Fig. 7). In this case, the greater number of encounters with *F. occidentalis* resulted in significantly more captures of that species than of *F. bispinosa* ($t = 5.54$, $df = 19$, $P < 0.0001$). Again differential movement appears to play an important role in this phenomenon. We observed that *F. bispinosa* moved more and displayed escape behaviors more than did *F. occidentalis*. An actively hunting predator would be more likely to encounter sedentary prey than prey that disperse more readily from a habitat.

Predation on F. occidentalis and F. tritici adults

In a separate experiment, we used an arena similar to those above, but with four pepper flowers. Three flowers were placed individually in water-filled vials that were spaced equidistant from a centrally located flower. Ten female *F. occidentalis* and 10 female *F. tritici* were released on the center flower. Two hours later an adult female *O. insidiosus* was released into the arena. As with the test with *F. occidentalis* larvae and adults, we evaluated predation after 10 or 34 hours, and analyzed the data by fitting log-linear models to determine if prey species, distribution and probability of being preyed upon were associated (Sokal and Rohlf, 1995).

In these longer-term trials in more complex environments, the two species of thrips showed different distribution patterns. In the 10-hour trials, significantly more *F. tritici* dispersed to the outer flowers or into the arena than *F. occidentalis,* the majority of which remained in the central flower where they were released (Fig. 8). In this case, virtually all of the predation occurred in the flowers, although there was no significant difference in the proportion of each species taken as prey by *O. insidiosus.* In the longer trials (34 hour exposure to *O. insidiosus)*, an even greater proportion of *F. tritici* dispersed from the central release flower to the outer flowers and into the arena. The risk of predation was highest in the central flower, which had the greatest mean density of thrips of the four flowers in the arena. However, the overall risk of predation was not related to the species of thrips. These results showing that proportionately more *F. tritici* moved from the central release flower indicate that *F. tritici* is a more active species than *F. occidentalis.* Despite these differences in activity, *O. insidiosus* is capable of preying on both the more sedentary *F. occidentalis* and the more active *F. tritici*. *O. insidiosus* was able to successfully locate and capture prey in different flowers as well as outside of pepper flowers. However with the two time intervals that we used, we were unable to establish if *O. insidiosus* also selects prey in a frequency dependent manner, or to what extent if it does. *O. insidiosus* could take more vulnerable prey selectively until the proportion of vulnerable prey is reduced sufficiently to make pursuit of less vulnerable, but more common prey profitable. Over time, *O. insidiosus* should continue to change its prey selection as the frequencies of available prey types continue to change.

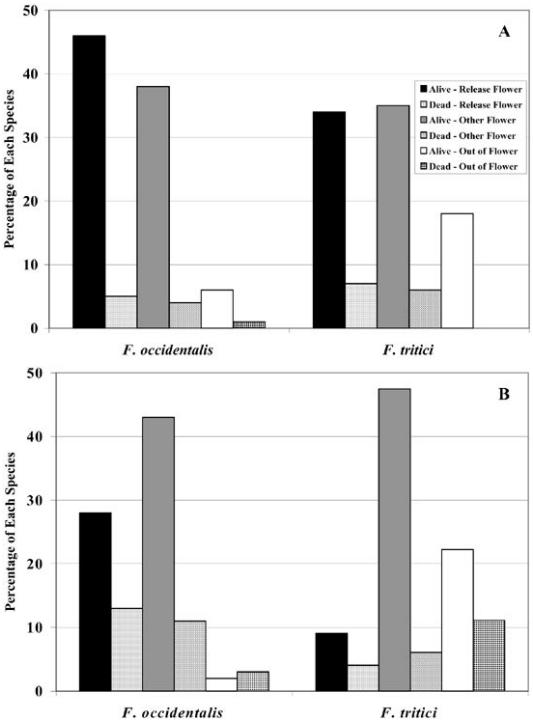

Fig. 8. Distribution and status of *F. occidentalis* and *F. tritici* when exposed to *O. insidiosus* for 10 hours (A) and 34 hours (B) in arenas containing four pepper flowers. Thrips were released on the center flower. The outer flower categories represent the cumulative proportion of thrips that had moved to the outer flowers at the conclusion of each trial. For the 10 hour trials, significantly more *F. tritici* dispersed to the outer flowers. In the 34 hour trials, significantly more *F. tritici* than *F. occidentalis* dispersed to the outer flowers and to the arena. Although most predation occurred in the flowers, the risk of predation was greatest for thrips outside of the flowers.

Conclusions

Our results show that small-scale behavioral differences exist among *F. bispinosa, F. tritici* and *F. occidentalis*. Females of *F. bispinosa* and *F. tritici* are significantly more active and mobile than females of *F. occidentalis*. Also females of *F. tritici* are able to better exploit certain hosts (e.g. tomato) than are females of *F. occidentalis*. Although tomato may not be as suitable a reproductive host as pepper for *Frankliniella* species, adults of certain species, such as *F. bispinosa* and *F. tritici,* can readily disperse to and inhabit tomato (Greenough et al., 1990, Baez, 2002). In addition these species may use plants such as tomato as a refuge to escape from predation (Coll and Ridgway, 1995).

More sedentary, less mobile individuals appear to be more vulnerable than more mobile individuals to predation by *O. insidiosus*, and *O. insidiosus* does prey selectively on the more vulnerable prey. In situations with mixed prey types, *O. insidiosus* attacked and captured significantly more of the less mobile prey. This bias probably reflects the greater cost for *O. insidiosus* in attacking more mobile prey, as shown in our trials with a single species of prey. However, *O. insidiosus* is capable of capturing the various thrips prey that we tested. Our results also suggest that when exposed to mixed groups of prey in the field this predator adjusts its prey selection in a frequency dependent manner.

Given these results, the ability of *O. insidiosus* to suppress populations of these *Frankliniella* species should vary. If *F. tritici* and *F. bispinosa* move readily to hosts that are not suitable for the predator, it should take *O. insidiosus* longer to suppress their populations than to suppress populations of *F. occidentalis.* Although plants such as tomato may provide some degree of enemy free space for adult thrips, the females must locate suitable hosts for reproduction. As this movement occurs, *O. insidiosus* is able to prey on these thrips and reduce the populations of those species. In general, understanding behavioral differences among thrips species can contribute to understanding mechanisms that mediate predator – prey interactions. Consequently, understanding the behavior of thrips can provide insight into understanding their spatial and temporal population dynamics (see Sabelis and Van Rijn 1997). The differential use of host plants, both for reproduction and enemy free space, and how these types of behavior affect predator – prey interactions and population dynamics need to be explored further.

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