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A Study of Morphological Character Displacement in the Social Wasp
Polistes fuscatus

A THESIS

The Honors Program

College of St. Benedict / St. John's University

In Partial Fulfillment of the Requirements for Graduation with "Distinction in Biology"

and the Degree Bachelor of Arts

In the Department of Biology

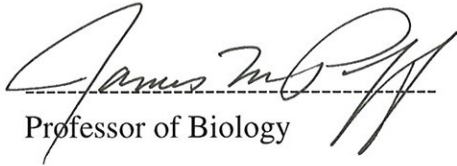
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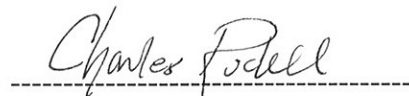
Noah Kerness Whiteman


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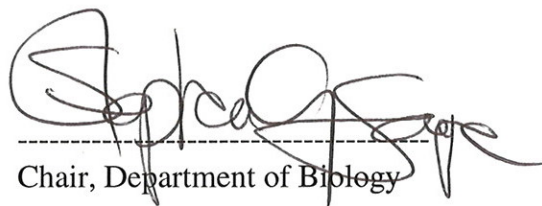
A Study of Morphological Character Displacement in the Social Wasp *Polistes fuscatus*


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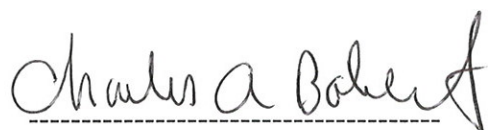

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ABSTRACT

According to competition theory, when a population lives sympatrically with competitor populations, the variation in morphological characteristics within each population should be reduced. In allopatric populations, the variation in these characteristics should increase. I examined morphological character displacement in *Polistes fuscatus* populations in a north-south latitudinal gradient across the United States. *P. fuscatus* is sympatric with at least five other congeneric species in U.S. Gulf Coastal areas. As latitude increases, the number of species is reduced, and only *P. fuscatus* is found in Minnesota. Therefore, body size variation of *P. fuscatus* in Minnesota was predicted to be broader than the body size variation of *P. fuscatus* occurring in the southern U.S. To compare relative body size, I measured each species' forewing length, mesothorax width, and head capsule width from population samples from each of the latitudinal transects.

I found initial indications of character displacement in *P. fuscatus* across latitude, although future studies are needed. In a supplemental study, I found preliminary evidence of character displacement in island and continental populations of *P. exclamans*. An allopatric population of *P. exclamans* from Hatteras Island, North Carolina, had larger ranges of character measurements than one population of *P. exclamans* from continental North Carolina, and another population of *P. exclamans* from Alabama and Texas, where the populations are sympatric with at least four other species of *Polistes*.

INTRODUCTION

According to competition theory, when a population lives sympatrically with competitor populations, there should be some niche reduction as a result of the competition, and the variation in morphological characteristics within each population should be reduced. In areas where the populations are allopatric and inter-specific competition does not exist, the variation in these morphological characteristics should increase. This difference in morphology, due to interspecific competition, is called character displacement. A definition of character displacement by Grant (1972), will be used in this study: “the process by which a morphological character state of a species changes under natural selection arising from the presence, in the same environment, of one or more species to it ecologically and / or reproductively.” More specifically, Brown and Wilson (1956) in their classic paper on character displacement, state that one possible result of this competitive contact between populations occurs when an equilibrium is established via the potential competitors. The competitors, through character displacement, are specialized to split up the exploitable requisites in their environment. The resultant shift in characters is presumed to be of genetic origin, otherwise the phenomenon is due to phenotypic plasticity. “The importance of ecological character displacement lies in what it can tell us about the final stages of speciation, about the manner in which adaptive radiations proceed, and how complex communities develop from simple ones” (Grant 1994).

Schluter and McPhail (1992), who studied character displacement of three-spined sticklebacks (*Gasterosteus aculeatus*) in British Columbia, identify six necessary criteria for demonstrating the occurrence of character displacement in organisms: (1) a statistical null model

of no displacement is easily rejected; (2) variation between and within populations is genetically based; (3) differences in sympatry reflect evolutionary shifts, not use; (4) morphology is closely linked to resource use; (5) evidence of minimal resource differences in sympatric and allopatric species (in their study, minimal resource differences between one- and two-species lakes would fulfill this requirement); and (6) evidence that similar phenotypes compete for resources. We will not attempt to demonstrate all six of these requirements in this study, but we will lay the groundwork for future experimental studies involving the populations studied. Grant (1975), also noted that simply the demonstration of morphological differences between allopatric and sympatric populations of a species, size for example, is not sufficient evidence to deduce that character displacement has occurred.

There have been many studies on character displacement, but good examples of character displacement are lacking in the biological literature (Begon et al. 1996). Usually, studies take the form of 'natural experiments,' observational studies measuring a particular character or group of characters. Begon et al. (1996) identify a key problem with traditional studies of character displacement. If the presence or absence of interspecific competition is causing the observed morphological differences between populations, the only difference between the populations should be the absence or presence of these competitors. This proves very hard to control, and many of these studies should be accepted with caution.

Many studies on character displacement begin initially as 'natural experiments,' which then pave the way for experimental manipulations of the populations of interest (Begon et al. 1996). Indeed experimental/observational studies, such as those done on limnetic and benthic populations of sticklebacks by Schluter and McPhail (1992), show that character displacement

can be seen 'in action.' It should also be noted that the characters in question are not exclusively morphological. As Brown and Wilson (1956) note, behavioral and physiological characters are also prone to character displacement.

E. O. Wilson (1971) also states the need for further study of character displacement, especially within the social insects. Wilson suggests that interspecific competition not only sets constraints on the distribution, ecology, and morphology of certain social insects, but certainly on their social characteristics as well.

One good example of morphological/ecological character displacement within the social insects was a study done on fire ants by Brown and Wilson (1958). Wilson (1971) reported that *Solenopsis saevissima*, native to South America, was first introduced into the United States at Mobile, Alabama in the early part of the twentieth century. Shortly thereafter, the species expanded rapidly (competitive release), into much of the southern U. S. *S. saevissima* apparently only inhabits open terrain, void of woodland. A native species, *S. xyloni*, closely related to the South American invader, also exploited open environments before the arrival of *S. saevissima*. The case for character displacement is as follows. The native species was largely eliminated from its traditional range in a mere twenty years. In addition to this native species being affected by the exotic fire ant, another species, *S. geminata*, has been displaced partially, due to *S. saevissima*. *S. geminata* has been only partially displaced because it traditionally occurred in both woodland and open terrain. After the introduction of the exotic fire ant, *S. geminata* has been largely limited to the woodland habitats, where *S. saevissima* has not invaded. More relevant to this study however, may be the finding by Brown and Wilson that a morphological change has also occurred in the native *S. geminata* population inside the exotic's range. *S.*

geminata populations found largely in the open environments were composed of mainly reddish individuals, and the woodland populations by a darker brown population. However, since the introduction of the exotic species, the reddish form of the open range has been eliminated due to competitive exclusion.

Presence or absence of resource competition is likely to be the ultimate cause of character displacement. A foraging specialization study on a seed-eating harvester ant (*Veromessor pergandei*) in the desert southwestern United States provides us with strong evidence that morphological character displacement is occurring in ant populations between allopatric and sympatric situations (Davidson 1978). Davidson measured mandible lengths of populations of foraging workers in areas of high and low competition. Variation in mandible lengths, and body size in general, decreased in populations, as competition increased. As Begon et al. (1996) note, this study shows that *V. pergandei* becomes more of a seed-size specialist as competition increases. As the number of potential competitors increases, the realized niche is reduced, and resources are partitioned. Competitive release and character displacement are observed when niche expansion occurs in the absence of potential competitors.

Benkman (1993) provides strong evidence that character displacement in northwestern North American crossbills (*Loxia curvirostra*) has occurred. He predicted that four “types” (“types” referring to differing calls of birds that are indeed morphologically distinct) or subspecies of *L. curvirostra* have diversified in their beak morphology as a response to differing peaks presented by their main foraging item, conifer seeds. He identified the major food resource of the crossbill, and predicted that each of the four “types” of birds would be specialists on one of four “key” conifers (*Tsuga heterophylla*, *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Pinus*

contorta var. *latifolia*). He found that two crossbill “types” have bill sizes that match their predicted optimal size for their “preferred” conifer (*Tsuga heterophylla* preferred by crossbill “type” 3, and *P. contorta* var. *latifolia* preferred by the crossbill “type” 5). One of the other crossbill “types” differed only by 0.4 mm from the predicted optimal beak size, and Benkman was unable to predict optimal beak size for the fourth type. He found that the most successful crossbill phenotype for foraging on one of the above conifers, was one-half as efficient on any of the other conifers utilized by crossbills. Highly relevant to our study was that his conclusion that even in environments that are highly variable, optimization of morphological traits still occurs. Finally, he concluded that diversity of cone structure and seed size among identified “key” conifers is responsible ultimately for morphological diversification in these birds.

Darwin’s finches provide one of the best cases for character displacement. Welty (1975) explains that in studies done by Lack (1947), demonstrate that in both the tree finches (*Camarhynchus* spp.) and the ground finches (*Geospiza* spp.), the bills of two species living on the same island are more different than the bills of two species living on different islands. Welty suggests that when the ranges of two closely related birds overlap and both are competing for the same food supply, the situation will likely lead to evolutionary changes in one or both of the species that will lessen the competition, and this is deemed character displacement.

Schluter and McPhail (1992) studied three-spine sticklebacks in small post-glacial lakes. Three populations exist within those lakes. In lakes with two species, some sticklebacks are “limnetic” in morphology and habitat within the lake, and others are “benthic.” In single-species lakes, the third type is morphologically intermediate between the two sympatric species and in habitat. They measured gill-raker size, mouth size, body shape, body size, and collected data on

the feeding behavior. They found that the two species, “limnetic” and “benthic”, differed substantially in these aspects, and in prey selection. Differential prey selection between the species was demonstrated and they found that benthic forms in all lakes consumed most of their prey from substrates (mainly benthic prey items), compared to the limnetic form that consumed mainly plankton. Additionally, they found that morphology affected prey size. The largest bodied populations with the shortest gill rakers consumed the largest prey items. Conversely, the smallest sticklebacks with the longest gill rakers consumed the smallest prey, and allopatric sticklebacks were found to be intermediate in morphology and prey size selection. Schluter and McPhail also showed that the observed differences in morphology and habitat were not due to phenotypic plasticity, but due rather, to genetics. They raised several fish in the same lab, under the same environmental condition, with the same food, and it was shown that all observed differences in morphologies persist under these conditions.

Another well-known, though controversial study on character displacement, was done on mud snails in Denmark and Finland (Fenchel 1975). Fenchel studied populations of allopatrically existing species of hydrobiid snails (four species, three within a single genus) in Scandanavia. He found that when two species, *H. ventrosa*, and *H. ulvae* occur sympatrically, they exhibit character displacement. Especially relevant to our study, Fenchel observed the displacement through body size differences. The average body size of *H. ventrosa* is smaller and the average body size of *H. ulvae* is larger. When the species occur allopatrically, they are roughly the same in average body size. From competition theory, one can deduce that this could be deemed competitive release. In this case of ecological/morphological character displacement, Fenchel deduced that stable coexistence was reached under sympatric conditions due to food

particle selectivity, the “equilibrium” referred to by Brown and Wilson (1956). In other words, *H. ulvae* selected larger food items than *H. ventrosa*. There have been critics of this study. Begon et al. (1996), among others, point out an important problem inherent in all natural experiments. The two species of mud-snails often have differential success in growth in different environments, even when they occur alone. Therefore, they note that “sympatric and allopatric populations can occur in different environmental conditions over which the observer has no control. It may be these environmental differences, rather than competition, that has led to the character displacement.”

Polistes fuscatus, the subject species of the present study, is a species of social paper wasp belonging to the family Vespidae. Its range encompasses almost the entire United States and it is the only species routinely found in Minnesota. Because *P. fuscatus* is sympatric with at least five other species in the Gulf Coastal regions of the U.S; only three other species in northern Missouri; only one other in northern Iowa; and in Minnesota it is allopatric, sharing this northern portion of its range with no other *Polistes* species, it is a logical candidate for such a study. As a result of the decreased number of closely related species, the realized niche of *P. fuscatus* living in Minnesota is expected to be broader than the realized niche of *P. fuscatus* occurring in southern Texas or northern Mexico. Therefore, assuming *P. fuscatus* is genetically variable, we expect to find a broader range of morphological characters as one moves northward in the range of distribution of *P. fuscatus*, going from sympatry with several other species (southern United States) to allopatry (Minnesota). We also expect to find a decrease in variability of morphological characters within the genus *Polistes* as one moves northward, as species diversity decreases.

METHODS

This study focused on six North American species of social wasps within the genus *Polistes*: *P. fuscatus*, *P. metricus*, *P. exclamans*, *P. annularis*, *P. bellicosus*, and *P. dorsalis*. We will only attempt to illuminate a few of the six criteria proposed by Schluter and McPhail (1992) for demonstrating the occurrence of character displacement. (1) We will assume that the variations in body size between and within populations of *Polistes* are genetically based. (2) We will try to show that differences in sympatry reflect evolutionary shifts, not use. (3) We will try to show that the morphological characters we studied are closely linked to resource use and it is known that similar phenotypes compete for resources.

The majority of the data were collected from specimens maintained in the collection at St. John's University in Collegeville, Minnesota. *Polistes bellicosus*, *P. fuscatus* and *P. dorsalis* specimens were obtained from the University of Minnesota, St. Paul, Minnesota campus. Additional *P. fuscatus* and three specimens of *P. dorsalis* were obtained from the University of Missouri, Columbia, Missouri. Some *P. fuscatus* specimens were obtained from Texas A & M University in College Station, Texas. Museum specimens have been used in other studies as well, such as the study done on character displacement in mustelids by Dayan et al. (1989).

Figure 1 shows the geographic distribution of the above *Polistes* species, within 3 degree ranges of latitude across the continental United States. The latitudinal transects were defined at: 45 (+) degrees, 42-45 degrees, 39-42 degrees, 36-39 degrees and 33-36 degrees.

For each species of *Polistes*, female specimens from known localities were measured (Appendix D). Females were chosen for measurement because because it is the females that do all of the foraging and would therefore be subject to competition and because *Polistes* exhibit

haplodiploid reproduction. Males are the product of unfertilized eggs, and females the product of fertilized eggs. Therefore, as a result of polygenic inheritance, it is predicted “that genetic variance in males [is] four times that of their parental sisters. Since most characteristics are under polygenic control, it should, therefore, generally be the case that males are more variable than virgin queens collected from the same colony” (Wilson 1971). Evidence was presented by Eickwort (1969) that this was true of many external morphological characters in one of the polistines measured in my study, *P. exclamans*.

For each specimen, three measurements were made using a dissection microscope and ocular micrometer: 1) the maximum length of the forewing (to the nearest 0.25 mm), 2) the maximum width of the mesothroax (to the nearest 0.12 mm), and 3) the maximum width of the head capsule (to the nearest 0.12 mm). These measurements were chosen due to their correlation with body size in general.

The data sets were combined per species so that the variation in character size was grouped according to 3 degree intervals of latitude. Individual collecting sites within species were generally not measured due to their small sample sizes. One-way ANOVA tests comparing variances between populations were used as described in Rohlf and Sokal (1969). Bartlett’s tests of equal variance were also used to test for differences in measured characters between populations. This test for homogeneity of variances, as described in Rohlf and Sokal (1969), gives the final statistic of significance as a chi-square.

To determine if variances in body size within *P. fuscatus* were different between latitudes, a one-way ANOVA and Bartlett’s test of equal variances were performed on *P. fuscatus* samples along a North-South gradient. Variances of forewing lengths, head capsule

widths, and mesothorax widths between *P. fuscatus* samples were compared from the aforementioned latitudinal transects (Tables 1, 2, and 3).

To further examine differences between allopatric and sympatric populations of *P. fuscatus*, three F-tests comparing variances of *P. fuscatus* measurements between two latitude transects were done. One F-test was done on an allopatric population at 45 (+) degrees latitude and a sympatric population at 36-39 degrees latitude (Table 12). A second F-test was done comparing *P. fuscatus* measurements from another mainly allopatric population at 42-45 degrees latitude and a population sympatric with two other species at 39-42 degrees latitude (Table 15). The third F-test was done comparing *P. fuscatus* measurements between an allopatric population from 45 (+) degrees latitude, and a population sympatric with two other species at 39-42 degrees latitude (Table 16).

To determine if variability in morphological characters decreased in the genus *Polistes* as latitude increases and species diversity decreases, I performed the following tests. From each latitudinal transect where *P. fuscatus* was measured [33-36, 36-39, 39-42, 42-45, and 45 (+)], the entire genus' measurements from each latitudinal transect were pooled together and the variances of each of the three characters measured were compared between transects, using one-way ANOVA and Bartlett's tests of equal variances (Tables 4, 5, and 6).

To further examine differences in body size within the genus *Polistes*, two latitude transects were compared using an F-test. Measurement variances between a population from one transect (45 + degrees latitude) where only one species occurs, were compared to the pooled species' measurement variances at transect (36-39), where at least five congeneric competitors occur together (Table 11). This 36-39 degree transect was chosen due to the presence of local

populations of *P. fuscatus* (collected from the same general area as other species within that transect) which were lacking in the 33-36 degree samples.

To determine if the variances in body size between species in areas of sympatry were different, a one-way ANOVA test and Bartlett's test of equal variances were performed on the five different species at one latitudinal transect, 33-36 degrees. *Polistes fuscatus*, *P. annularis*, *P. dorsalis*, *P. exclamans*, and *P. metricus* forewing length, head capsule width, and mesothorax width variances were compared between each species (Tables 7, 8 and 9). It should be noted however, that the *P. fuscatus* sample used here (33-36) was obtained from southern Nevada, while the majority of the other samples within the genus were collected from sites closer to the central continental United States.

T-tests were used to determine if the means of the measured characters were different at the same latitudes between two polistines of similar size. The means of measured characters of *P. exclamans* and *P. fuscatus* populations were compared at two different latitudinal transects. The two species were compared at 33-36 degrees latitude (Table 13), and at 39-42 degrees latitude (Table 14).

An F-test was used to determine if variances in morphological characters between a sympatric continental population of *P. exclamans* from North Carolina and an allopatric island population of *P. exclamans* from North Carolina were different (Table 10). Due to the small sample size of the continental population of *P. exclamans* from North Carolina (N = 19), the island population of *P. exclamans* was also compared to a sympatric continental population of *P. exclamans* from Alabama and Texas (Table 17) with a larger sample size (N = 70).

RESULTS

I. Forewing length

Of the three characters measured, *P. fuscatus*' forewing length is the most variable between geographic locales and between species. There were significant differences between the means and variances of each *P. fuscatus* population sampled from each of the five three degree transects.

Although not statistically different, a forewing length-species distribution plot (Fig. 2) shows that populations of *P. fuscatus* from the upper latitudes (45 +) appear to have a larger degree of variance in forewing lengths than *P. fuscatus* forewing lengths from lower latitudes (33-36 degrees). Variances in forewing length between *P. fuscatus* population samples from 45+ deg. lat. (allopatric in Minnesota and Wisconsin) and 39-42 degrees latitude (sympatric with *P. metricus* and *P. exclamans*), were significantly different.

Comparisons of the pooled species' forewing length measurements on a north to south gradient (Table 4), show that there were significant differences in the variances between each population from each latitudinal transect tested (45+, 42-45, 39-42, 36-39, and 33-36). Forewing length variance for the pooled species' measurements at two latitude transects (Table 11 and Fig. 5) show that there were significant differences in forewing length variability in *Polistes* between areas of sympatry (36-39 degrees) and allopatry (45 + degrees).

As one moves northward on a latitudinal gradient, the number of species within the genus decreases (Figs. 2, 3, and 4). These plots also show that, although character variability of each species is rather rigid on a north-south gradient, the variability within the genus as a whole

decreases as latitude increases.

Figure 2 shows that the greatest range of variability in forewing length within the species *P. fuscatus* appears to occur at the northern portion of its range from 42-45+ degrees, where it either exists alone (Minnesota), or is sympatric with one other species, *P. metricus*. These populations of *P. fuscatus* have both the longest and the shortest forewing lengths of all latitudinal transects. From 39-42 degrees, where *P. fuscatus* is sympatric with two other species, the range of variation for the species *P. fuscatus* is reduced and shifted up when compared to latitudes above 42 degrees. However, the mean forewing lengths of the other competing species are very similar to the mean forewing length of *P. fuscatus*. From 36-39 degrees, forewing length variability increased slightly from populations measured at 39-42 degrees, and the mean is relatively close. Where competition is greatest within the genus, at 33-36 degrees of latitude, the *P. fuscatus* population from that transect has about the same amount of variation as the population from 39-42 degrees latitude, where there are at least two other congeneric competitors of *P. fuscatus*. For the entire genus, *Polistes annularis* had the longest wings, while *P. dorsalis* had the shortest wings, with *P. fuscatus*, *P. metricus*, *P. bellicosus*, and *P. exclamans* falling somewhere between these two extremes.

The mean forewing lengths between sympatric *P. fuscatus* and *P. exclamans* population samples from 33-36 degrees latitude are not significantly different (Table 13). The mean forewing lengths between sympatric *P. fuscatus* and *P. exclamans* populations from 39-42 degrees latitude were significantly different, however, the probability of accepting the null hypothesis was 0.04 (Table 14).

II. Head Capsule Width

A comparison of *P. fuscatus* head capsule width variances on a North to South gradient (Table 1a), were significantly different for each of the five three degree transects. However, results from a Bartlett's test of equal variances on *P. fuscatus* head capsule width on a North to South gradient (Table 1b) did not reject the null hypothesis that all variances were equal. A head capsule-species distribution plot shows the trend (Fig. 3), and the upper latitudes appear to have a larger degree of variance in *P. fuscatus* head capsule widths compared to *P. fuscatus* head capsule widths in lower latitudes. A comparison of head capsule width variance between an allopatric population (45 + degrees latitude) of *P. fuscatus* and a sympatric population of *P. fuscatus* (36-39 degrees latitude) showed no significant differences between populations (Table 12). However, the result of an F-test (Table 16), on head capsule width variances between *P. fuscatus* population samples from 45 + degrees latitude (allopatric in Minnesota and Wisconsin) and 39-42 degrees latitude (sympatric with *P. metricus* and *P. exclamans*), shows a significant difference between the head capsule variances of these two populations.

A comparison of the pooled species' head capsule width measurements on a north to south gradient (Table 5), show significant differences in the variances between each population at each latitude transect sampled. Generally, the mean head capsule width increases as latitude decreases (as one moves north to south). The variance in head width of *Polistes* above 45 degrees latitude, where the genus is represented by only one species, was less than that of the genus' head pooled head width variance in the adjacent more southern latitudinal transect, with at least two congeneric species. This pattern is consistent as one moves further south, with each transect of increasing latitude showing greater variance in head widths than norther latitudes.

There were significant differences in head capsule width variances between the pooled species' measurements at two specific latitudinal transects (Table 11 and Fig. 5) where the genus is represented by one species (45+ degrees latitude) compared to samples with at least four members of the genus represented (36-39 degrees latitude).

Figure 3 shows that variability in head capsule width within the species *P. fuscatus* appears to be relatively uniform throughout the distribution of the species. The greatest range of variability in head capsule width appears to be from the population samples at 42-45 degrees latitude. From 39-42 degrees, where *fuscatus* is sympatric with two other species, the low-end of the range of variation for the species, *P. fuscatus* appears to be shifted-up when compared to latitudes above 42 degrees. From 36-39 degrees, head capsule width variability increases slightly from populations measured at 39-42 degrees, and the mean is relatively close. The amount of variation in *P. fuscatus* from 33-36 degrees latitude, where competition is at its greatest, had about the same amount of variability as the population from 39-42 degrees latitude, where there are at least two other congeneric competitors of *P. fuscatus*. For the entire genus, *Polistes annularis* had the widest head capsules, while *P. dorsalis* had the narrowest head capsules (except in the transect from 27-30 degrees, where *P. exclamans* had the narrowest head capsule, however, only one specimen of *P. dorsalis* was measured here), with *P. fuscatus*, *P. metricus*, *P. bellicosus*, and *P. exclamans* falling between these two extremes. A comparison of the mean head capsule widths between sympatric *P. fuscatus* and *P. exclamans* population samples from 33-36 degrees latitude shows that the means of the two populations are significantly different (Table 13). A comparison of the mean forewing lengths between sympatric *P. fuscatus* and *P. exclamans* population samples from 39-42 degrees latitude show significant difference between

the two populations (Table 14).

III. Mesothorax Width

Mesothorax width was the most stable character of the three measured in this study. There were, however, subtle differences found between populations of *P. fuscatus*. Table 1 shows that there are significant differences between the means and variances of each *P. fuscatus* population sampled from each of the five three degree transects on a North to South gradient. A mesothorax width-species distribution plot shows this trend (Fig. 4), and the upper latitudes appear to have a larger degree of variance in *P. fuscatus* mesothorax widths than *P. fuscatus* mesothorax widths at lower latitudes. A comparison of mesothorax variance between an allopatric population (45+ degrees latitude) of *P. fuscatus* and a sympatric population of *P. fuscatus* (36-39 degrees latitude) shows that there is no significant difference in mesothorax width variation between these populations (Table 12). However, the result of an F-test (Table 16), on variances in mesothorax widths between *P. fuscatus* population samples from 45 deg. lat. (allopatric in Minnesota and Wisconsin) and 39-42 degrees latitude (sympatric with *P. metricus* and *P. exclamans*), shows a significant difference between the mesothorax width variances of these two populations.

A comparison of the pooled species' mesothorax measurements on a north to south gradient (Table 6), shows that there were significant differences in the variances between each population from each latitude transect sampled. Generally, the mean mesothorax width increases as latitude decreases (as one moves north to south). The variance in mesothorax width of *Polistes* above 45 degrees latitude, where the genus is represented by only one species, was less than that of the genus' pooled head width variance in the adjacent more southern latitudinal

transect, with at least two congeneric species. This pattern is fairly consistent (with the exception of latitudinal transect 36-39) as one moves further south, with each transect of increasing latitude showing greater variance in mesothorax width as one moves further south.

A comparison of variances in mesothorax widths for the pooled species' measurements at two latitude transects shows significant differences in mesothorax width variability in samples (Table 11 and Fig. 5) where the genus is represented by only one species (45+ degrees latitude) compared to samples with at least four members of the genus represented (36-39 degrees latitude).

Figure 4 shows that, although not significantly different than southern populations, the greatest range of variability in mesothorax width within the species *P. fuscatus* occurs at the northern portion of its range from 42-45+ degrees, where it is either allopatric (Minnesota) or sympatric with one other species, *P. metricus*. This is the same trend seen in forewing length variation. These populations of *P. fuscatus* had both the widest and the narrowest mesothoraxes of all latitude transects. From 39-42 degrees, where *fuscatus* is sympatric with two other species, the range of variation for the species *P. fuscatus* is reduced and shifted up when compared to latitudes above 42 degrees. However, the mean mesothorax widths of all *P. fuscatus* populations from each transect measured are similar to each other. From 36-39 degrees, mesothorax width variability increased slightly from populations measured at 39-42 degrees. For the entire genus, the widest mesothoraxes were measured in *P. annularis*, while *P. dorsalis* has the narrowest mesothoraxes (except in the transect from 27-30 degrees, where *P. exclamans* was recorded as having the narrowest head capsule, however, only one specimen of *P. dorsalis* was measured here), with *P. fuscatus*, *P. metricus*, *P. bellicosus*, and *P. exclamans* falling between these two

extremes.

The mean mesothorax widths between sympatric *P. fuscatus* and *P. exclamans* population samples from 33-36 degrees latitude were significantly different (Table 13). The mean mesothorax widths between sympatric *P. fuscatus* and *P. exclamans* population samples from 39-42 degrees latitude (t-test used: one-tailed, unequal variances) are significantly different (Table 14).

Supplemental Study Results: Morphological Character Displacement in Continental and Island populations of *P. exclamans*

I found preliminary evidence of character displacement in island and continental populations of *P. exclamans*. An allopatric population of *P. exclamans* from Hatteras Island, North Carolina, has larger ranges of character measurements than a population of *P. exclamans* from continental North Carolina, where it is sympatric with four species of *Polistes*. An F-test (Table 10) shows no significant difference in the variability between forewing lengths measured from the continental population and the island population. However, Fig. 6 shows that the range of forewing length is much larger in the allopatric island population, than in the sympatric continental population of *P. exclamans*. F-tests were also performed on head capsule width and mesothorax width variation between the two populations, and like the analysis of variance in forewing length, the null hypothesis was not rejected for either character.

Due to the small sample size of the continental population, another continental population that is sympatric with at least five other congeneric species was compared to the island population (Fig. 7). This population sample (N = 70) of *P. exclamans* from Texas and Alabama (latitude transect 30-33), has a range of variability that is even narrower than the continental

population from North Carolina. The shortest forewing length from this population sample was 13 mm, (which is 2 mm longer than the shortest forewing length from Hatteras island, and 1.25 mm shorter than the shortest continental populations' forewing measured), and the longest wing length was 16.25 mm. This is the *same* maximum forewing length as the continental population of *P. exclamans* from North Carolina, and .50 mm less than the maximum island population from Hatteras, where allopatry is occurring. The result of an F-test (Table 17) comparing the variances in the population of *P. exclamans* from Hatteras Island to the continental population from Alabama and Texas shows that the range of variation for all three characters measured of the two populations is not equal, with probabilities less than 0.05 for all characters.

Table 1: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on *P. fuscatus* forewing length (mm) on a North to South gradient.

| a. | | | b. | | |
|-------------------------|-------|--------|------------|------|--------|
| Degrees of freedom (DF) | F | p | Chi-square | D.F. | p |
| 4 | 55.48 | 0.0000 | 44.66 | 4 | 0.0000 |

| Degree Transect | Mean | Sample Size | Group Standard Deviation (G.S.D.) |
|-----------------|--------|-------------|-----------------------------------|
| 45+ | 14.746 | 251 | 1.2209 |
| 42-45 | 14.924 | 174 | 1.1783 |
| 39-42 | 16.298 | 131 | 0.7240 |
| 36-39 | 15.623 | 75 | 1.2216 |
| 33-36 | 14.221 | 43 | 0.9958 |

Table 2: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on *P. fuscatus* head capsule width (mm) on a North to South gradient.

| a. | | | b. | | |
|------|------|--------|------------|------|--------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 2.11 | 0.0770 | 2015.42 | 4 | 0.0000 |

| Degree Transect | Mean | Sample Size | (G.S.D.) |
|-----------------|--------|-------------|----------|
| 45+ | 3.8685 | 251 | 0.1917 |
| 42-45 | 3.9055 | 172 | 0.1997 |
| 39-42 | 4.3386 | 129 | 3.5442 |
| 36-39 | 3.9721 | 75 | 0.1904 |
| 33-36 | 3.9467 | 42 | 0.2034 |

Table 3: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on *P. fuscatus* mesothorax width (mm) on a North to South gradient.

| a. | | | b. | | |
|------|-------|--------|------------|------|--------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 18.01 | 0.0000 | 24.95 | 4 | 0.0001 |

| Degree Transect | Mean | Sample Size | (G.S.D.) |
|-----------------|--------|-------------|----------|
| 45+ | 3.6232 | 240 | 0.2496 |
| 42-45 | 3.6448 | 172 | 0.2666 |
| 39-42 | 3.8252 | 133 | 0.1780 |
| 36-39 | 3.7412 | 77 | 0.2559 |
| 33-36 | 3.6167 | 43 | 0.2538 |

Table 4: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on pooled data for the entire genus' forewing length (mm) on a North to South gradient.

| a. | | | b. | | |
|------|-------|--------|------------|------|--------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 65.01 | 0.0000 | 555.47 | 4 | 0.0000 |

| Degree Transect | Mean | Sample Size | G.S.D. |
|-----------------|--------|-------------|--------|
| 45+ | 14.746 | 251 | 1.2209 |
| 42-45 | 14.828 | 200 | 1.1698 |
| 39-42 | 16.400 | 232 | 0.9333 |
| 36-39 | 16.926 | 287 | 2.6544 |
| 33-36 | 17.014 | 180 | 3.4646 |

Table 5: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on pooled data for the entire genus' head capsule width (mm) on a North to South gradient.

| a. | | | b. | | |
|------|------|--------|------------|------|--------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 5.39 | 0.0003 | 2375.13 | 4 | 0.0000 |

| Degree Transect | Mean | Sample Size | G.S.D. |
|--------------------|--------|-------------|--------|
| 45+ | 3.8685 | 251 | 0.1917 |
| 42-45 | 3.8835 | 198 | 0.2052 |
| 39-42 | 4.2159 | 230 | 2.6614 |
| 36-39 | 4.2152 | 283 | 0.3322 |
| 33-36 | 4.2316 | 178 | 0.4345 |

Table 6: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on pooled data for the entire genus' mesothorax width (mm) on a North to South gradient.

| a. | | | b. | | |
|------|-------|--------|------------|------|--------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 83.74 | 0.0000 | 253.8 | 4 | 0.0000 |

| Degree Transect | Mean | Sample Size | G.S.D. |
|--------------------|--------|-------------|--------|
| 45+ | 3.6232 | 240 | 0.2496 |
| 42-45 | 3.6312 | 197 | 0.2669 |
| 39-42 | 3.8945 | 232 | 0.2784 |
| 36-39 | 4.1109 | 284 | 0.4587 |
| 33-36 | 4.0720 | 179 | 0.5859 |

Table 7: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on pooled data for the each species' forewing length (mm) at one latitude sector (33-36 degrees).

| a. | | | b. | | |
|------|--------|--------|------------|------|--------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 363.43 | 0.0000 | 10.20 | 3 | 0.0169 |

| Degree Transect | Mean | Sample Size | G.S.D. |
|---------------------|--------|-------------|--------|
| <i>P. fuscatus</i> | 14.221 | 43 | 0.9958 |
| <i>P. metricus</i> | 16.771 | 84 | 1.0195 |
| <i>P. exclamans</i> | 14.037 | 20 | 1.3136 |
| <i>P. annularis</i> | 23.758 | 30 | 1.5306 |
| <i>P. dorsalis</i> | 10.750 | 1 | 1.496 |

Table 8: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on pooled data for the each species' head capsule width (mm) at one latitude sector (33-36 degrees).

| a. | | | b. | | |
|------|--------|--------|------------|------|-------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 164.01 | 0.0000 | 8.95 | 3 | 0.029 |

| Degree Transect | Mean | Sample Size | G.S.D. |
|---------------------|--------|-------------|--------|
| <i>P. fuscatus</i> | 3.9467 | 42 | 0.2034 |
| <i>P. metricus</i> | 4.2854 | 87 | 0.1777 |
| <i>P. exclamans</i> | 3.5790 | 20 | 0.1821 |
| <i>P. annularis</i> | 4.9183 | 30 | 0.2706 |
| <i>P. dorsalis</i> | 3.5000 | 1 | ----- |

Table 9: Results of a one-way ANOVA (a) and Bartlett's test of equal variances (b) on pooled data for the each species' thorax width (mm) at one latitude sector (33-36 degrees).

| a. | | | b. | | |
|------|--------|-------|------------|------|-------|
| D.F. | F | p | Chi-square | D.F. | p |
| 4 | 140.11 | 0.000 | 12.37 | 3 | .0062 |

| Degree Transect | Mean | Sample Size | Group Std.. Dev. |
|---------------------|--------|-------------|------------------|
| <i>P. fuscatus</i> | 3.6167 | 43 | 0.2538 |
| <i>P. metricus</i> | 4.2194 | 87 | 0.2663 |
| <i>P. exclamans</i> | 3.1850 | 20 | 0.2518 |
| <i>P. annularis</i> | 4.8813 | 30 | 0.4130 |
| <i>P. dorsalis</i> | 2.8700 | 1 | ----- |

Table 10: F-test results on island and continental populations of *P. exclamans* from North Carolina comparing variances (mm) of forewing length (a), head width (b), and mesothorax width (c) between the two populations.

| | |
|--|--------------|
| Island population of <i>P. exclamans</i> (N = 91) | a. p = 0.714 |
| Continental population of <i>P. exclamans</i> (N = 19) | b. p = 0.950 |
| | c. p = 0.976 |

Table 11: F-test results on the pooled genus' mean forewing length (a), mean head width (b), and mean mesothorax width (c) between samples from 45+ degrees latitude and 36-39 degrees latitude.

| | |
|-----------------|---------------|
| 45+ (N = 250) | a. p = 0.0000 |
| 36-39 (N = 285) | b. p = 0.0000 |
| | c. p = 0.0000 |

Table 12: F-test results on mean forewing length (a), mean head width (b), and mean mesothorax width (c) between *P. fuscatus* samples from 45+ deg. lat. and 36-39 degrees latitude.

| | |
|----------------|------------------------------|
| 45+ (N = 250) | a. p = 0.350 |
| 36-39 (N = 74) | b. p = 0.582 c. p = 0.550 |

Table 13: Student's T-test results on mean forewing length (a), mean head width (b), and mean mesothorax width (c) between sympatric *P. fuscatus* and *P. exclamans* population samples from 33-36 degrees latitude (t-test used: one-tailed, unequal variances).

| | |
|------------------------------|--------------------------------|
| <i>P. fuscatus</i> (N = 42) | a. p = 0.2916 |
| <i>P. exclamans</i> (N = 19) | b. p = 0.0000 c. p = 0.0000 |

Table 14: Student's T-test results on mean forewing length (a), mean head width (b), and mean mesothorax width (c) between sympatric *P. fuscatus* and *P. exclamans* population samples from 39-42 degrees latitude (t-test used: one-tailed, unequal variances).

| | |
|------------------------------|------------------------------|
| <i>P. fuscatus</i> (N = 134) | a. p = 0.047 |
| <i>P. exclamans</i> (N = 41) | b. p = 0.000 c. p = 0.000 |

Table 15: F-test results on mean forewing length (a), mean head width (b), and mean mesothorax width (c) between *P. fuscatus* samples from 42-45 deg. lat. (allopatric in Idaho) and 33-36 degrees latitude (all from southern Nevada, and sympatric with at least five other species).

| | |
|-----------------|------------------------------|
| 42-45 (N = 173) | a. p = 0.200 |
| 33-36 (N = 42) | b. p = 0.842 c. p = 0.716 |

Table 16: F-test results on mean forewing length (a), mean head width (b), and mean mesothorax width (c) between *P. fuscatus* population samples from 45 deg. lat. (allopatric in Minnesota and Wisconsin) and 39-42 degrees latitude (sympatric with *P. metricus* and *P. exclamans*)

| | |
|-----------------|------------------------------|
| 42-45 (N = 250) | a. p = 0.000 |
| 39-42 (N = 130) | b. p = 0.000 c. p = 0.000 |

Table 17: F-test results comparing variances of an island population of *P. exclamans* from North Carolina to a continental population of *P. exclamans* from Alabama and Texas for forewing length (a), head width (b), and mesothorax width (c).

| | |
|--|--------------|
| Island population of <i>P. exclamans</i> (N = 91) | a. p = 0.000 |
| Continental population of <i>P. exclamans</i> (N = 70) | b. p = 0.007 |
| | c. p = 0.000 |

DISCUSSION

Resource competition is the underlying cause of character displacement (Brown and Wilson 1956). Therefore, if character displacement does occur in the genus *Polistes*, and specifically in *P. fuscatus* that occurs both allopatrically and sympatrically with one to five congeneric species in the lower latitudes of the U.S., these species are likely to be competing for a variety of resources. Competition for food and nesting sites between the sympatric species is likely because it is known that the main prey item of all the species within the genus are lepidopteran larvae and it is also known that all members of the genus choose similar nesting sites.

Of the three characters in this study, it was predicted that forewing length, and possibly mesothorax width would show the most character displacement. We predicted this due to the nature of the major prey item within the genus. Larger prey items require larger wings and more lifting power, which is why I measured the length of forewing and width of the mesothorax, where the flight muscles are located. So, if *P. fuscatus* gets displaced by either a larger or smaller member of the genus, then the range of variation of the selected trait should be shifted accordingly, so that the variabilities/means do not overlap. So, for example, if *P. dorsalis* is placing competitive pressure on *P. fuscatus* by competing with that species for smaller caterpillars, the low end of variation in body size of *P. fuscatus* should be shifted up.

Brown and Wilson (1956) cite the study done by Bourne (1955) on two shearwaters of the Cape Verde Islands as an example of an example of food size as an example of resource partitioning and resultant character displacement: "It would appear that the bill-size and the breeding seasons of these shearwaters vary with the amount of competition occurring between

different species breeding at the same site.” In other words, the birds eat the same types of foods, but their breeding seasons have been displaced, their breeding behaviors become divergent. So it is not unreasonable to imagine a different sort of divergence, a morphological one. As Fenchel (1975) noted, “body size is probably quickly changed by selection (*cf.* domestic animals),” making it a logical candidate for a study on morphological character displacement on *Polistes*. So, it was predicted that in Minnesota, the allopatric species *P. fuscatus*, would be more of a generalist predator of lepidopteran larvae, consuming a wide variety of sizes (competitive release). As latitude decreases (as one moves farther south), *P. fuscatus* will become more of a specialist predator, consuming prey of a more uniform size, due to the presence of other polistines that are larger and smaller (ecological character displacement) that are also consuming lepidopterous caterpillars. As previously stated, competition for nesting sites may also be a contributing, if not predominating factor in resource competition among the polistines. In fact these competitions for food and nesting sites are intimately related. As Wilson (1971) noted in the social insects, “the productivity of the colony will probably depend on the food yield of the territory.” But the amount of food available to a colony is dependent on nesting factors. Wilson notes that Brian (1956a,b) showed that in Scotland, colony densities are controlled by the availability of nesting sites. In Scotland the ants that he studied were in heavy competition for nesting sites due to high vegetation of the land. In the polistines, this may be not as much of a problem, but these social insects, especially at northern latitudes only have a certain “window” of time within which the foundresses can start and therefore have successful colonies during the growing season (Poff 1998). Nesting sites must be void of water, out of direct sunlight and reasonably accessible to foraging workers, yet far enough away from other colonies. Indeed,

“The abundance of nest sites appears to be a common primary control of colony density throughout the social insects” (Wilson 1971). So where other species drop out at northern latitudes, *P. fuscatus* does not experience either food competition or nest site competition by other member of the genus, the shorter growing season is an ecological tradeoff that the species has made, in order to have no interspecific competition.

It was then hypothesized that these competitive pressures would “displace” *P. fuscatus*, from above by the comparatively large *P. annularis* and from below by the smaller *P. dorsalis*, among others, so that a reduced amount of character variability would be seen as resource competition increases.

I have shown that the means of the measured characters of most of the species do differ within a latitudinal transect (Figs. 2, 3, and 4), and that species drop out as latitude increases, to a point where the genus *Polistes* is represented by a single species, *P. fuscatus*, whose body size is intermediate when compared with the smallest and largest members of the genus.

At a latitude of 33-36 degrees, the mean forewing lengths of *P. fuscatus* and *P. exclamans* are not significantly different, so it would seem that they are competing for the same resources at many levels. However, the mean mesothorax and head capsule widths of both species are significantly different (Table 13). This may be explained not by competition theory, but by the fact that the *P. fuscatus* population measured here was collected in Nevada, and not in a local area where the other congeneric species were taken at that latitude. If this phenomenon was due to resource competition, then *P. exclamans* with less powerful wings and smaller heads were selected for when in the presence of *P. fuscatus*. Or *P. fuscatus* with more powerful flight muscles and larger heads were selected for in the presence of *P. exclamans*. A similar pattern is

seen in this relationship at latitudes 39-42, where both *P. fuscatus* and *P. exclamans* occur sympatrically, and both of these samples were collected in areas much closer to each other than the samples of *P. fuscatus* and *P. exclamans* collected at a latitude of 33-36 degrees. The means of the two species' head widths and mesothorax widths are significantly different within this latitude transect, and the forewing length means are significant to a probability of 0.047 (Table 13). This data then may then support the resource competition model above. As stated, the means of these characters for each species remain relatively stable across latitude, but for at least some characters and some species, the effects of resource competition may be illuminated here.

Forewing length variation in *P. fuscatus* populations appears to be the greatest in the northern United States (42+ degrees latitude), where there exists no, or one congeneric competitor(s). There were significant differences in forewing length variation between populations of *P. fuscatus* on a north-south gradient, but this may or may not support my initial hypothesis that the characters will exhibit a greater degree of variation in Minnesota where *P. fuscatus* is allopatric compared to populations where sympatry exists further south. The null hypothesis of the F-test was rejected and thus the variances between an allopatric and sympatric population of *P. fuscatus* are not significantly different, but this aside, there does seem to be some support of our initial hypotheses. It should be noted however, that sample sizes for the data from the northern U.S. are much larger than sample sizes from the southern U.S. (Tables 1-9).

Mean head-capsule widths have the greatest variability at a latitude of 42-45 degrees, excluding the widest head capsule measurements from transect 39-42, *P. fuscatus* head capsule widths are smallest and equal to *P. fuscatus* from latitude transect 36-39, to make up the widest head capsules here when compared to the other transects.

Mesothorax widths have the greatest variability at sector 42-45 as well, having the narrowest mesothorax widths, although all populations of *P. fuscatus* have equal maximum mesothorax widths except for sector 33-36, which has narrower mesothorax widths than all other population samples.

It should be noted that the majority of the populations sampled from 42-45 degrees latitude were collected from locations in Idaho and Washington, where *P. metricus* does not occur at all (Poff, personal communication). The *P. metricus* population sample were collected at locations in Iowa, but only a small number of *P. fuscatus* specimens were taken in Iowa and southern Minnesota. So, it could be that indeed *P. fuscatus* from Idaho, where they occur sympatrically are exhibiting competitive release. When compared to another western population of *P. fuscatus*, a sample collected from latitude transect 33-36, at roughly the same longitude, there appears to be a substantial difference in variability of all three measures, between the two populations. Figs. 2, 3 and 4 show this trend. F-tests show that there was no significant difference between variances of the two populations of *P. fuscatus* however.

In another latitudinal comparison of an allopatric population and a sympatric population, there may be evidence of morphological character displacement. When comparing the variances of the allopatric population of *P. fuscatus* from 45+ degrees latitude to the population at 39-42 degrees which is sympatric with *P. exclamans*, a smaller species and *P. metricus*, a larger species, it appears that the allopatric population has a larger range of variation than the sympatric population, of all three characters measured. Indeed, the results of an F-test (Table 16) show that the differences in the variances between the populations were significant at the 0.05 level. The selective pressure on *P. fuscatus* body size may have been resultant from competition with *P.*

exclamans at the low end, and the larger *P. metricus* at the high end of variation. So if character displacement has occurred where there are only three sympatric polistines, should this also be seen when competition is even greater?

Supplemental Study Discussion: Morphological Character Displacement in Continental and Island Populations of *P. exclamans*

Mac Arthur and Wilson (1967) proposed the theory of island biogeography. Their main thesis concerned predicting the diversity of the flora and fauna of an island. Islands are have biotas that are predictively less diverse than continental biotas. It should not be much of a surprise then, that only one polistine has been documented on Hatteras Island, North Carolina. The island is a barrier island, very thin and long, separated from the mainland by 20 miles of water. On the mainland at least five species occur, and *P. exclamans* is a very common one. *P. exclamans* has no other congeneric competitors on that island, so it should exhibit a broader range of variability than the continental population that is sympatric with a number of competitors. So, did we find evidence of character displacement? Although no significant difference in forewing variability was found between the two populations of *P. exclamans*, the trend seen in fig. 5, seems to support the competitive release model. Where *P. exclamans* is allopatric (on the island) the variability in forewing length is larger than the variability (from 11 mm-16.75 mm) of forewing length from mainland North Carolina (from 11.75-16.25). The sympatric populations' forewing variability on the short end started was .75 mm longer than the island populations' shortest forewing length. The longest forewing length on the mainland was .50 mm shorter than the longest forewing length on the island. This difference may explained by sample size differences. Only 19 individuals were measured from the mainland and 91 were

measured from the island population. However, a larger population sample (N = 70) of *P. exclamans* from Texas and Alabama (latitude transect 30-33), where the species is sympatric with at least five others, similar conditions to continental North Carolina, the range of variability is narrower yet (Fig. 7). The shortest forewing length from this population sample was 13 mm, (which is 2 mm longer than the shortest forewing length from Hatteras island, and 1.25 mm shorter than the shortest continental populations' forewing measured), and the longest wing length was 16.25 mm, the *same* maximum length as the continental population of *P. exclamans* from North Carolina, and .50 mm less than the maximum island population from Hatteras, where allopatry is occurring. The fact that the longest maximum forewing lengths are the same for these two sympatric populations (the continental population from North Carolina and the continental population from Texas and Alabama) suggests that the larger species, *P. fuscatus*, *P. metricus* and *P. annularis* are placing selective pressure on *P. exclamans* in areas of sympatry so that there is a maximum forewing length that this species is able to achieve. On the island these larger species are not present, so the species is not subject to this selective pressure, and its maximum wing length increases. It may seem like 0.50 mm is not a large difference, but we must remember that these insects are small. This 0.5 mm difference represents approximately 10% of the total variation present in the species.

Alternative Explanations

Simberloff (1983) notes that "simply observing greater difference in sympatry than between allopatric populations need not implicate character shift, because independent clinal variation in two or more species could produce the same pattern. . .the difference in sympatry could merely be a clinal response to gradients in the physical environment" (after Grant 1972).

So, it could be that the subtle differences observed in *P. fuscatus* populations across latitude are merely resultant from clinal responses to different weather patterns, nesting sites, nutritional differences in the prey items, etc. However, a closer look at two allopatric populations may illuminate an important point. The allopatric populations of *P. fuscatus* from Minnesota and Idaho both occur at about the same latitude (42-45+ degrees). Both of these populations also exhibit the most variation in forewing length when compared to the other populations of *P. fuscatus* that I measured. The physical features of the two locations are quite different, one population occurs in a mountainous region (Idaho), while the other occurs in a relatively flat region.

Yet another possible explanation for the differences observed between species and within the species *P. fuscatus* at different latitudinal transects is related to the social behavior (specifically the caste structure) and resultant physiological and morphological consequences. As Wilson (1971) states,

Workers of this genus are subordinate individuals who must commit relatively large fractions of their time on foraging trips. When they return to the nests, the food they have collected is transferred in disproportionate amounts to the dominant females, who use the energy to make more eggs. . .evidence also exists to suggest that differential larval growth leading to morphological caste differences among the adults has a relatively direct origin in larval nutrition. . .

So, if a sample consisted wholly of one colony, the size variation could be a phenotypic response to the environment induced by the behavioral ecology of the wasps. Intimately associated with nutritional factors, colony cycling could also control the body sizes of colony members. In *P. fuscatus* colonies, Wilson (1971) points out that Eberhard (1969) observed that “. . .from June to

August there is a gradual increment in the percentage of loads brought back by *Polistes* workers consisting of food opposed to building materials. The average size of newly emerging females also increases gradually until finally, in August and September, many individuals are produced that are as large as the foundress queen." So, body size may be a phenologically related response to colony growth peaks and food delivery rates. If some of the populations I compared were collected at opposite points on the colony-life cycle, any observed differences or similarities could theoretically be explained by the above.

CONCLUSIONS

There does seem to be some evidence that when *Polistes fuscatus* occurs allopatrically, the amount of variation in body size increases relative to that in areas where the wasp occurs sympatrically with other congeneric species. This is possibly due to competitive release. An alternative explanation for these subtle differences in variability is given by Grant (1972) who stated that the differences could be clinal responses by these populations to differences in the physical environment between locations, and not because of interspecific competition. As Schluter states, "The debate mirrors a long-standing issue in ecological research: whether differences between coexisting species are commonly the outcome of ecological character displacement (evolutionary change resulting from interspecific competition)" (1994). It seems however, that because two allopatric populations of *P. fuscatus* from Idaho and from Minnesota, living in two distinctly different physical environments, had a larger variability in forewing length, head capsule width, and mesothorax width than the sympatric populations of *P. fuscatus* in lower latitudes, that effects other than competitive release caused these two very similar trends seems suspect to me.

As a whole, there is a reduction in variability and diversity as one moves northward, with the largest and smallest members of the genus dropping out first. The larger member (*P. annularis*) drops out probably due to developmental constraints caused by the combination of large size and shorter growing season in the north. The smallest member (*P. dorsalis*) drops out first perhaps due to competition with *P. fuscatus*. Presumably, there are a more limited number of food items (lepidopterous caterpillars) as one moves northward, both actual numbers and different species, so *P. fuscatus*, being mid-range in body size, can exploit a larger range of

resources than *P. dorsalis* individuals, that are restricted to smaller caterpillars. In addition, competition for nesting sites is presumably a primary control factor of colony densities in the social insects (Wilson 1971), so resource partitioning may occur here as well, which is probably a selective pressure that determines body size variations between species within a particular geographic locale, shown in this study (Figs. 2, 3, and 4) by the varying means of measured characters within a latitudinal transect where sympatry exists.

There does seem to be evidence that character displacement has occurred between a sympatric continental and an allopatric island population of *P. exclamans* in North Carolina. Although the differences in variability between these two population were not significant, the results of a subsequent comparison between the same island population and a continental population from Alabama and Texas (with a larger sample size than the original continental population) , along with the observation that both continental populations showed the same maximum forewing length (0.50 mm shorter than the maximum forewing length of the island population of *P. exclamans*) suggests that indeed competitive release may have occurred in *P. exclamans* from Hatteras Island, North Carolina.

Possible Confounding Variables

This study was dependent upon accurate identification of each population, to the species level. To address problems dealing with the taxonomic judgement of specimens, as Mayr stated (in Brown and Wilson, 1956), “the decision as whether to call such forms species or subspecies is often entirely arbitrary and subjective. This is only natural, since we cannot accurately measure to what extent reproductive isolation has already evolved.” It appeared that in some populations, *P. fuscatus* and *P. metricus* were very similar, and in addition to this, some museum

specimens on loan may have been misidentified as *P. fuscatus*, but they appeared to be *P. metricus*.

Since this study was done on the species level, we are in essence “standardizing” our measurements or at least being consistent, as no one population of a species was classified further as a subspecies. We did not key the specimens to the sub-specific level because there is considerable taxonomic disagreement. As Wilson and Brown (1956) note, in fact, subspecies are “usually no more than arbitrary units drawn for curatorial convenience.”

Samples of *P. fuscatus* from latitude transects 27-30 and 30-33 were not available for measurement. These are both regions where heavy interspecific competition is likely to exist, and measurements of individuals from these regions is necessary before any broad-based conclusions can be solidified on character displacement in *Polistes fuscatus*. In addition, larger sample sizes of *P. exclamans* from the continental population in North Carolina may also be necessary before a conclusion that character displacement did occur in the species between these two populations on the island and mainland.

Future Studies

If character displacement has occurred in *P. fuscatus* and *P. exclamans* there should be genetic evidence. Breeding experiments between allopatric individuals and sympatric individuals of the same species would be ideal, but perhaps not pragmatically feasible.

Grant (1994), states that because patterns which suggest character displacement are subject to explanation by alternative hypotheses, “measurement [s] of food supply and diets of the presumed competitors with displaced characters”, are necessary. There have been measurements of the main food items of *Polistes* in North America, which indicate that indeed

all of these species are competing for food resources. However, measurements of the sympatric species' prey selection (type and physical measurements) have not been done. If in one sympatric locale there is indeed resource partitioning, and if *Polistes* are more generalists as sympatry decreases, this would suggest that character displacement is at least a feasible explanation for the observed variation in morphological characters.

Due to time restrictions we were forced to measure museum specimens almost exclusively. The dates of collection varied dramatically in some cases, but the majority were collected in the 1980's. A careful analysis of character displacement resultant from resource competition necessitates that population samples be collected both at the same time, and at the same geographic locale (population samples should be collected at sites of local competition). We did have some population samples collected from the same location at the same time (different species), but getting a better sample distribution would have been more ideal.

In addition, if truly accurate studies in character displacement are to occur, precise identifications of the specimens at the species level are extremely important, and future studies in *Polistes* may be refined by a careful molecular phylogenetic study to determine precise specific and sub-specific bounds, such as the study done on Caribbean *Anolis* lizards by Losos (1990). Specimens identified by some taxonomists as *P. fuscatus* appeared to be in fact *P. metricus*, and these two species are very closely related, as they occur within the same sub-genus.

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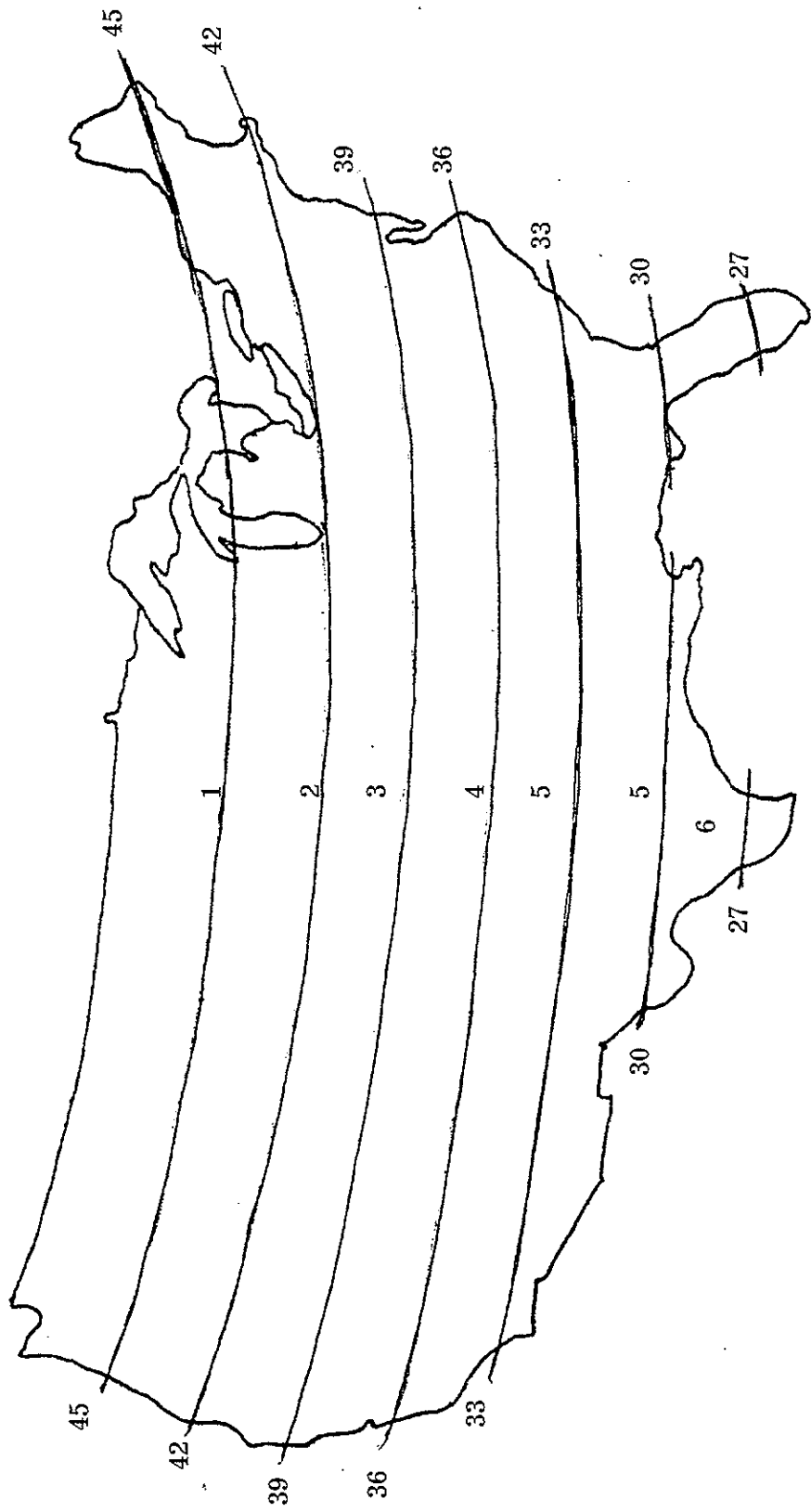


Figure 1. Schematic representation of the latitudinal transects. The number of species of *Polistes* known to occur in each transect is indicated by the number located within each transect.

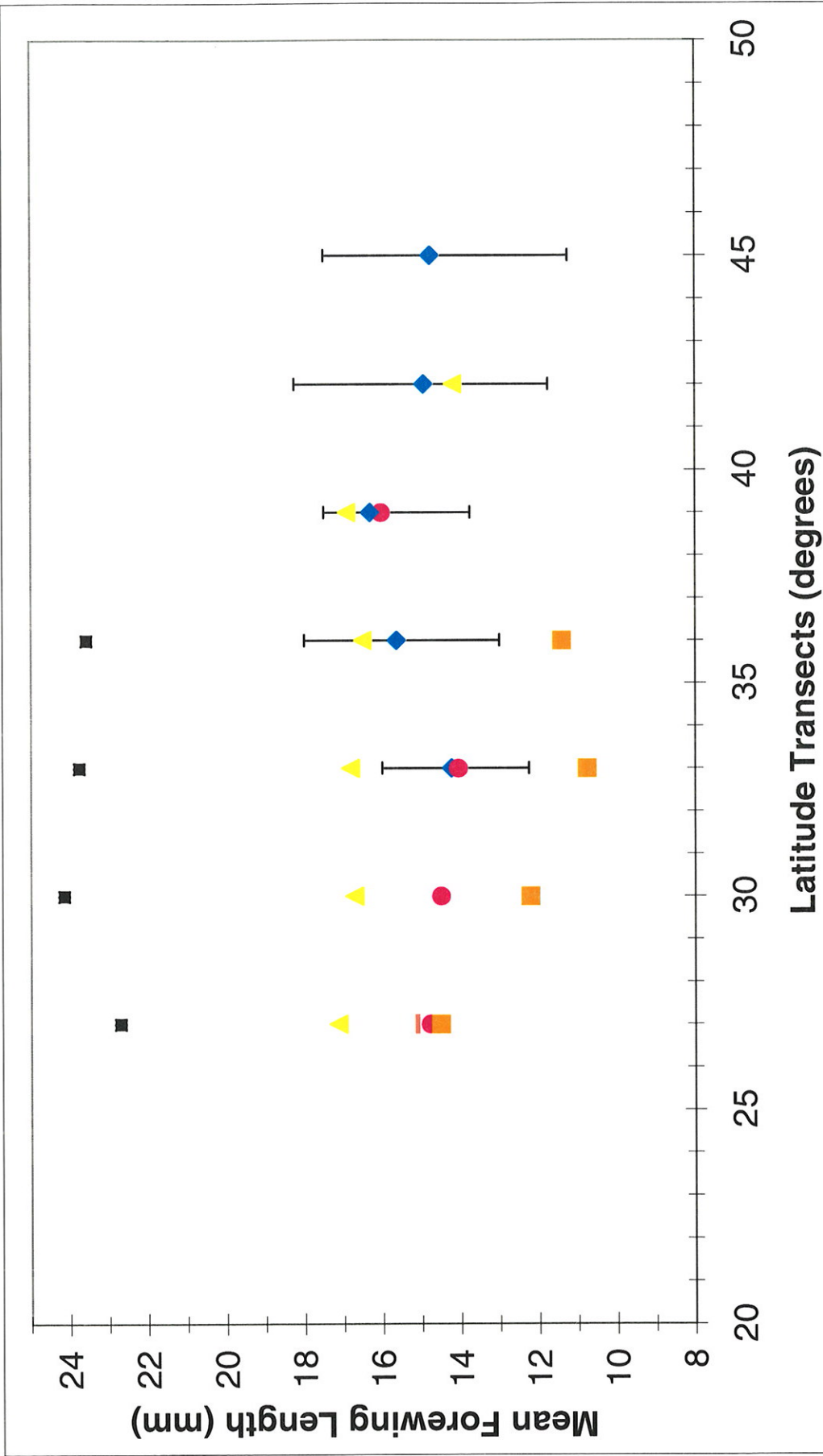


Fig. 2. Plot shows mean forewing lengths of all species per three degrees (N) latitudinal transect. Northern latitudes are on the right side of the X-axis, and the measure in millimeters is on the Y-axis. Symbols represent: blue diamonds = *Polistes fuscatus*, yellow triangles = *P. metricus*, pink circles = *P. exclamans*, black boxes = *P. annularis*, orange boxes = *P. dorsalis*, coral dash = *P. belllicosus*. The Y-bars indicate the range of variation of *P. fuscatus* forewing length, with the ends of the whiskers indicating the extremes.

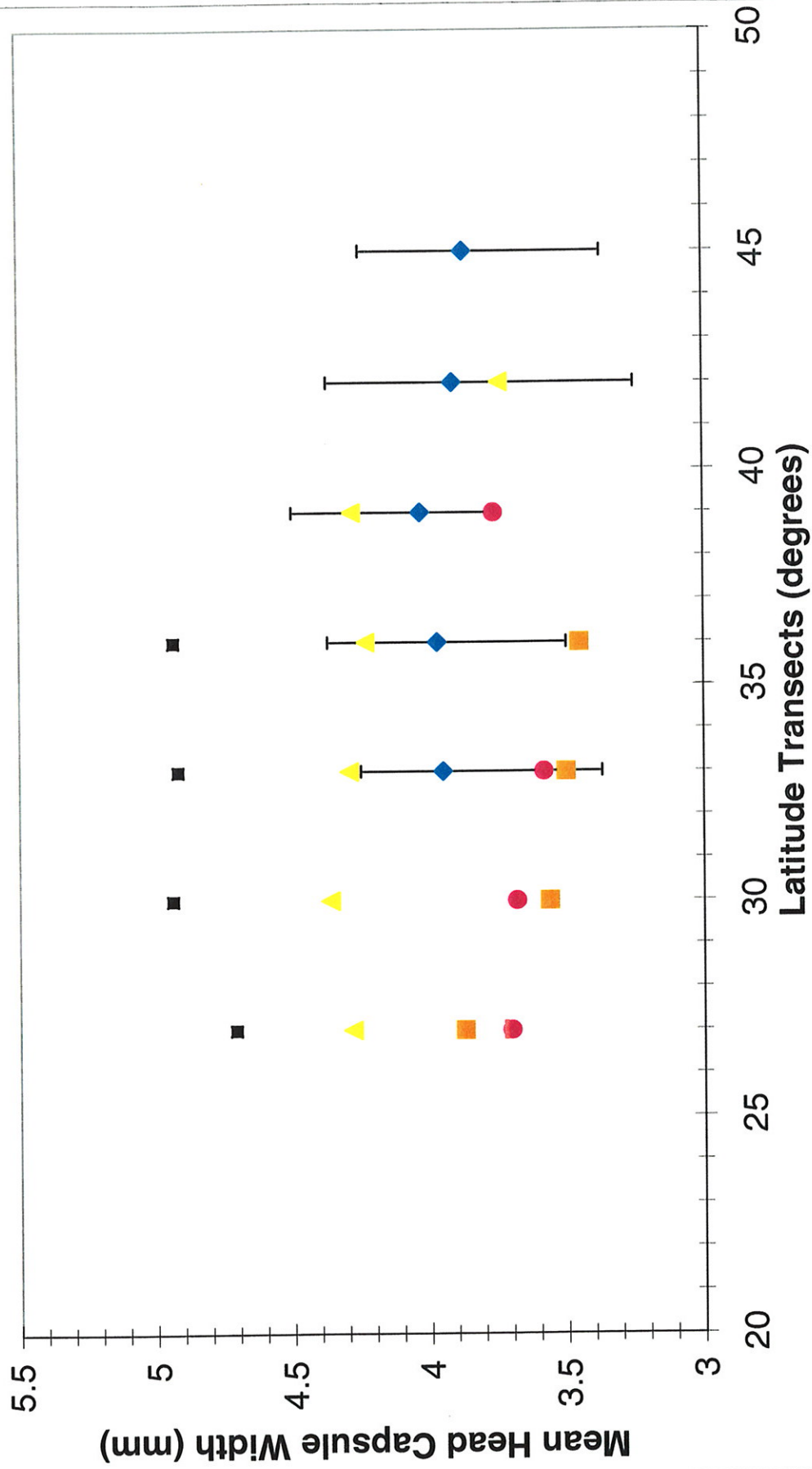


Fig. 3. Plot shows mean head capsule widths of all species per three degrees (N) latitudinal transect. Northern latitudes are on the right side of the X-axis, and the measure in millimeters is on the Y-axis. Symbols represent: blue diamonds = *Polistes fuscatus*, yellow triangles = *P. metricus*, pink circles = *P. exclamans*, black boxes = *P. annularis*, orange boxes = *P. dorsalis*, coral dash = *P. belllicosus*. The Y bars indicate the range of variation of *P. fuscatus* head capsule width, with the ends of the whiskers indicating the extremes.

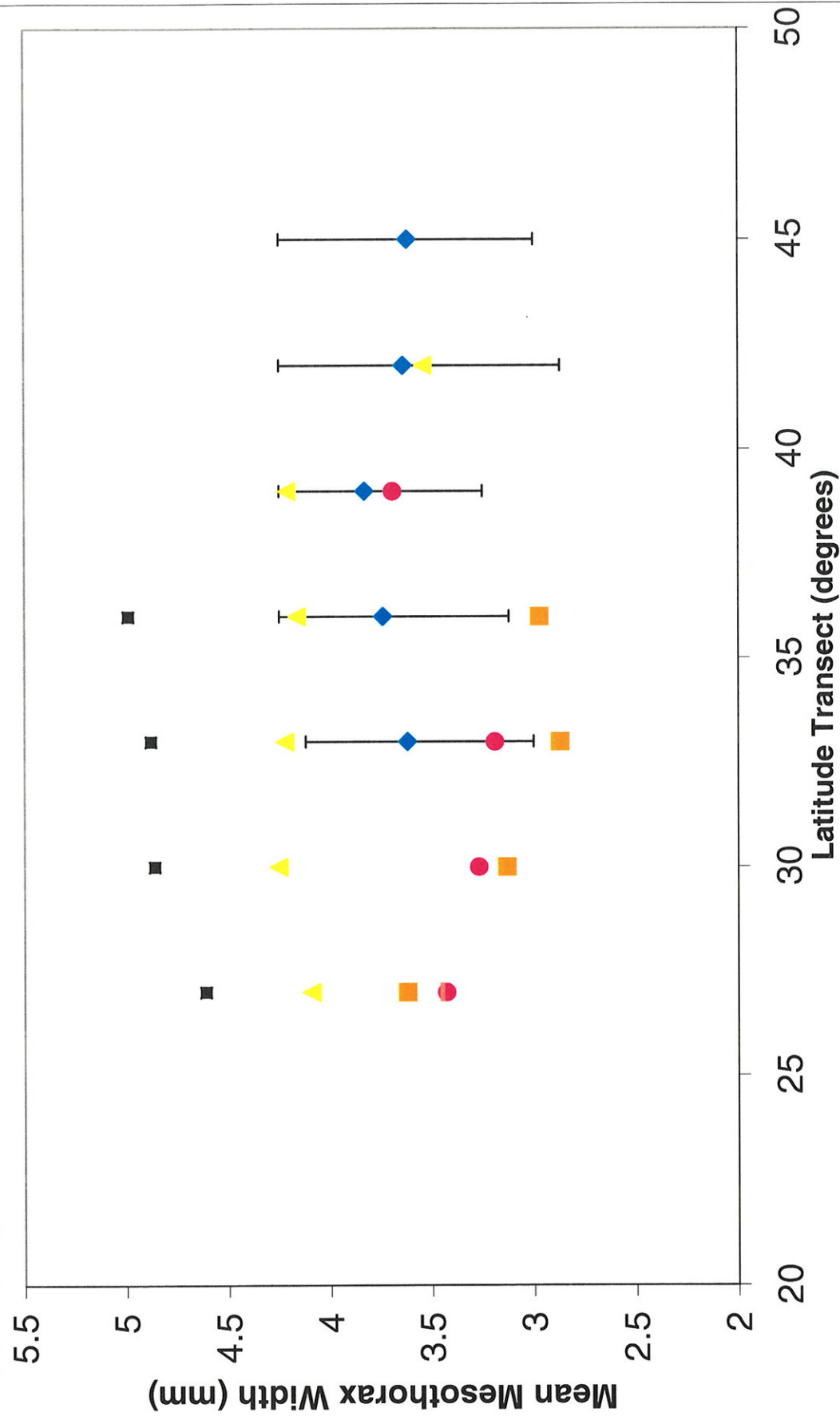


Fig. 4. Plot shows mean mesothorax widths of all species per three degrees (N) latitudinal transect. Northern latitudes are on the right side of the X-axis, and the measure in millimeters is on the Y-axis. Symbols represent: blue diamonds = *P. olistes fuscatus*, yellow triangles = *P. metricus*, pink circles = *P. exclamans*, black boxes = *P. annularis*, orange boxes = *P. dorsalis*, coral dash = *P. bellicosus*. The Y bars indicate the range of variation of *P. fuscatus* mesothorax width, with the ends of the whiskers indicating the extremes.

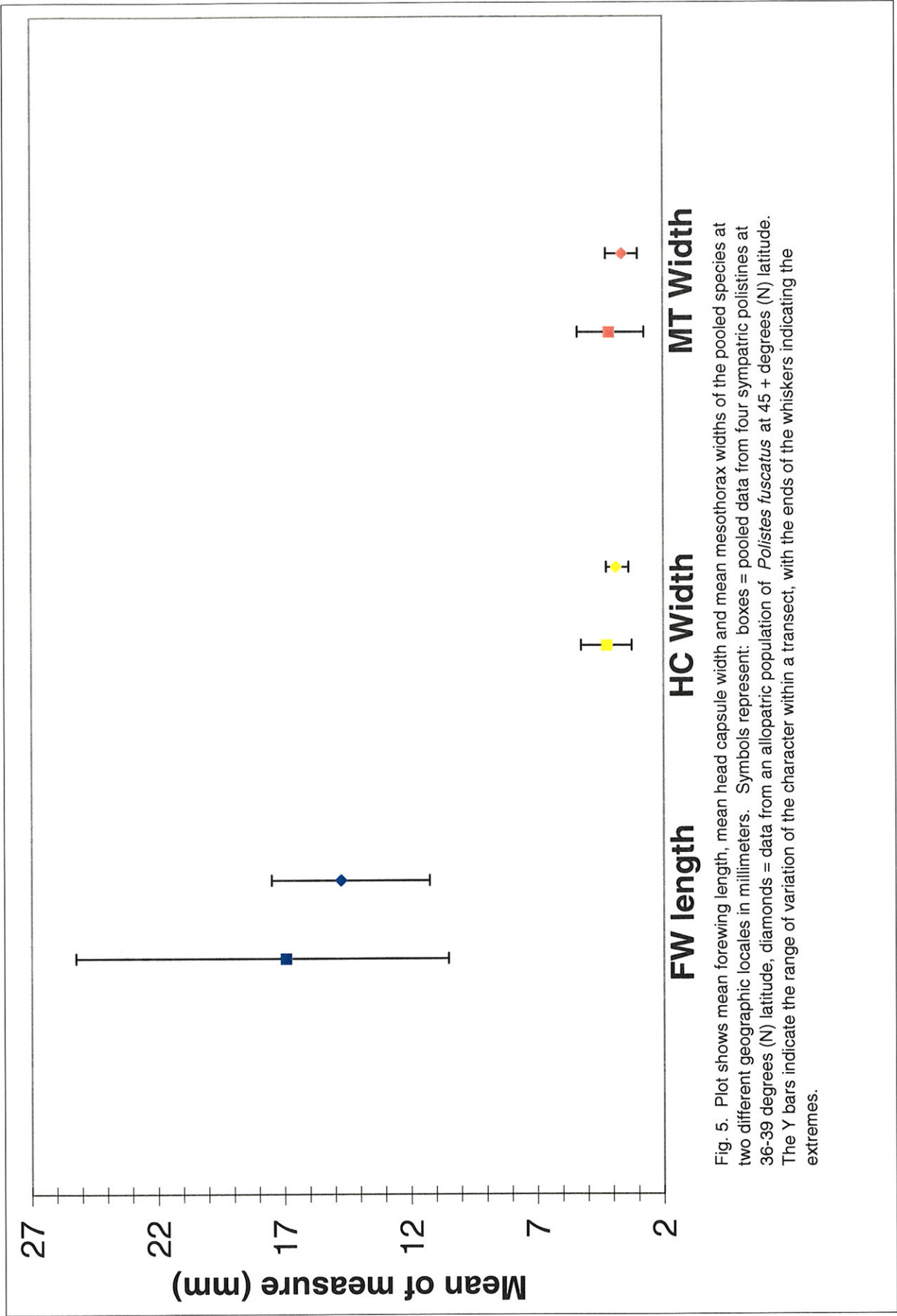


Fig. 5. Plot shows mean forewing length, mean head capsule width and mean mesothorax widths of the pooled species at two different geographic locales in millimeters. Symbols represent: boxes = pooled data from four sympatric polistines at 36-39 degrees (N) latitude, diamonds = data from an allopatric population of *Polistes fusca* at 45 + degrees (N) latitude. The Y bars indicate the range of variation of the character within a transect, with the ends of the whiskers indicating the extremes.

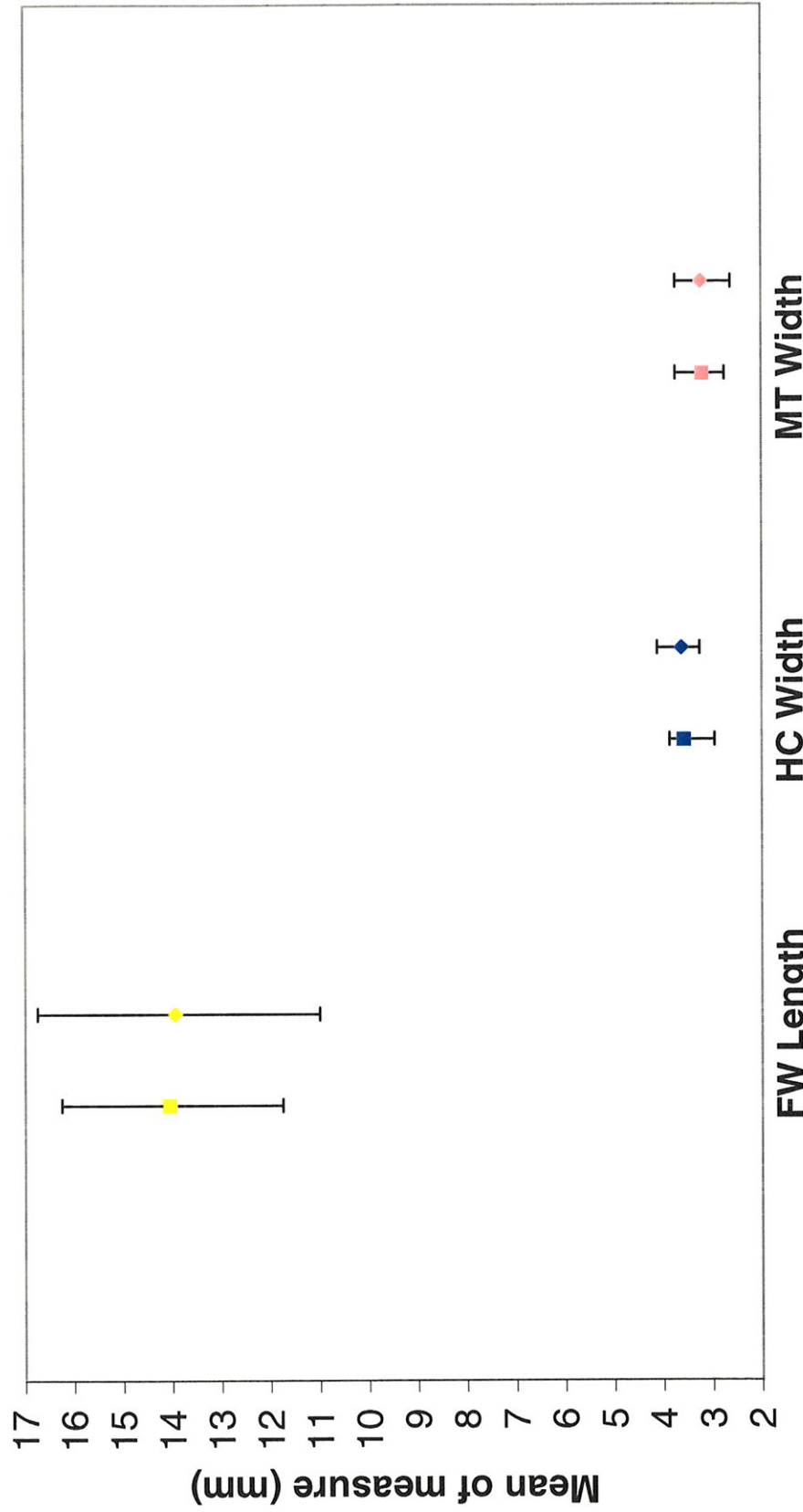


Fig. 6. Plot shows mean forewing length, head capsule width and mesothorax width of a continental population (N = 19) of *Polistes exclamans* from North Carolina and the mean forewing length of an island population of *P. exclamans* (N = 91) from Hatteras Island, North Carolina. Symbols represent: boxes = continental population that is sympatric with at least four other *Polistes*, and diamonds = allopatric island population. The Y bars indicate the range of variation of *P. exclamans*, with the ends of the whiskers indicating the extremes.

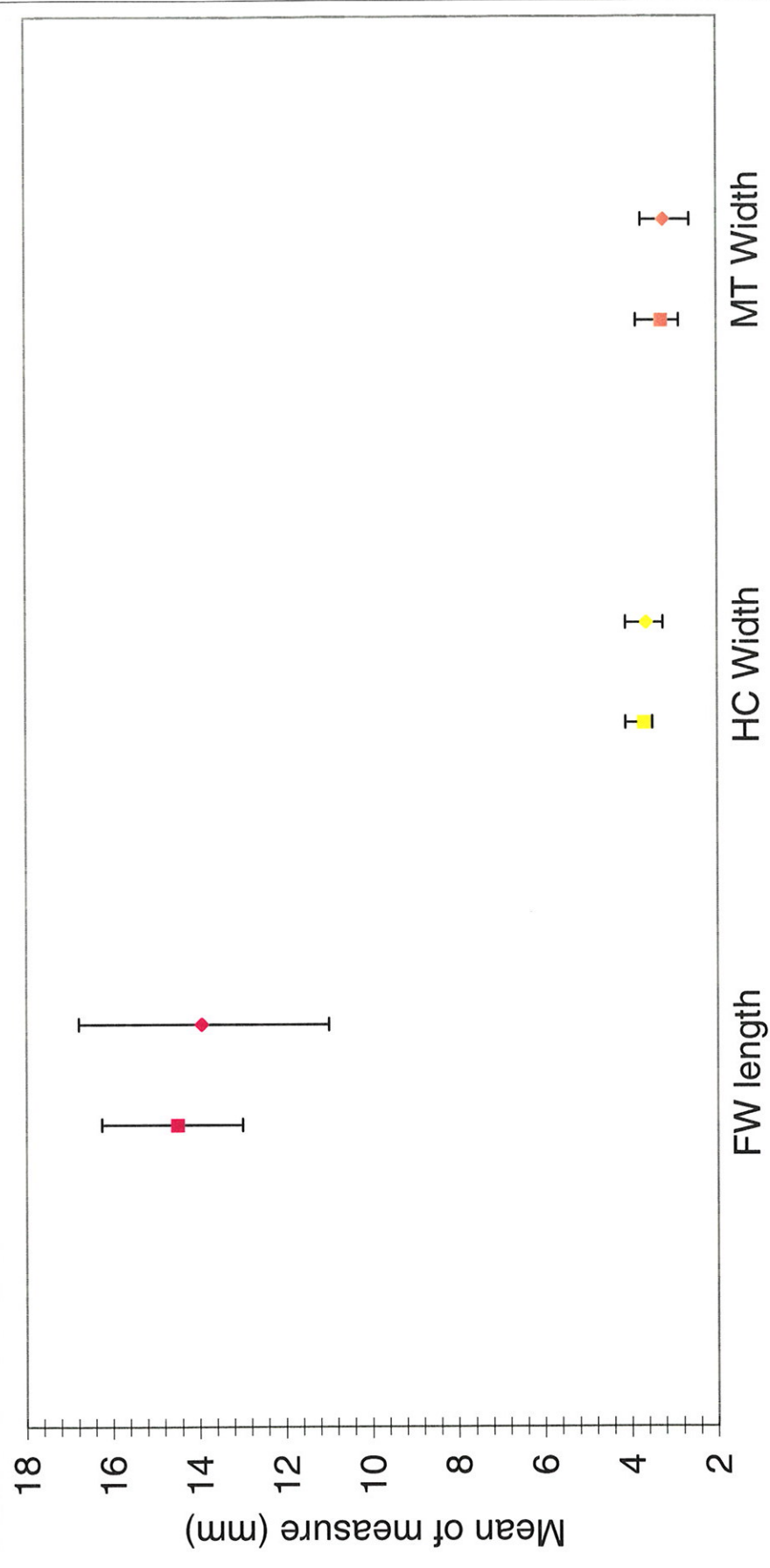


Fig. 7. Plot shows mean forewing length, head capsule width and mesothorax width of a continental population (N = 70) of *Polistes exclamans* from Alabama and Texas, and the means of the same measures of an island population of *P. exclamans* (N = 91) from Hatteras Island, North Carolina, in millimeters. Symbols represent: boxes = continental population that is sympatric with at least four other polistines, and diamonds = allopatric island population. The Y bars indicate the range of variation of *P. exclamans* with the ends of the whiskers indicating the extremes.

Appendix I

Specimens were measured from the following collecting sites:

Polistes fuscatus

Minnesota, Stearns Co, Brown Co, Taylors Falls, Chisago Co, Pine Co. ar
Minnesota, Brown Co, Idaho, Washington and Adams Co, Iowa, Bremer
Iowa, Boone, Monona, Lee Co
Washington, D.C.
Nevada, Clark Co
Ohio, Brown Co

P. metricus

Massachusetts, Hampshire Co
Kansas, Cloud Co and Iowa, Monona Co
Ohio, Brown Co
Missouri, St. Francois Co
Missouri, Lincoln Co
Missouri, Washington Co
Kentucky, McCracken Co
Kansas, Cowley Co
Kansas, Saline Co
Tennessee, Putnam Co
Tennessee, Cumberland Co
Georgia, Morgan Co
Texas, Cherokee Co
Alabama, Clay Co
Louisiana, Iberville Parish
Louisiana, Ascension Parish

P. bellicosus

Texas, San Antonio--Medina/Atascosa/Wilson/Guadalupe

P. dorsalis

Arizona, Pinal Co
Texas, Collin Co
Louisiana, New Orleans
California, Sacramento
California, Morgan Hill
Arizona, St. Cruz Co

P. annularis

Missouri, St. Francois Co
Georgia, Morgan Co
Texas, Cherokee Co
Texas, Sabine Co
Alabama, Clay Co
Louisiana, Iberville Parish

P. exclamans

Kansas, Cloud Co
North Carolina, Jackson Co
North Carolina, Buxton
Texas, Nacodoches Co
Alabama, Clay Co
Louisiana, Jefferson Davis Parish
Louisiana, St. Martin Parish