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PHENOTYPIC EXPRESSION IN THE PAPER WASP  
*POLISTES FUSCATUS* (HYMENOPTERA: VESPIDAE)<sup>1</sup>

Bonnie K. MacLean<sup>2</sup> Leland Chandler<sup>3</sup> and David B. MacLean<sup>4</sup>

ABSTRACT

Quantification of color/color pattern in *Polistes fuscatus* (Fabricius) revealed that these attributes were the interaction of two antagonistic color sequences; their expression being highly correlated with nest microclimate (relative humidity-temperature). Color/color pattern expressions were modified under experimental conditions to produce forms having natural counterparts in the field.

Principal coordinates analyses and trend surface analyses using specimens collected throughout the United States indicated three color pattern trends, representing three distinct geographic areas, and, when objectively defined, without intergradation between and/or among areas. It was concluded that *fuscatus* should not be considered a widespread, polytypic species; rather, as three discrete species: an eastern, *P. fuscatus* (Fabricius); a western, *P. aurifer* Saussure; and an undescribed "yellow form" from the southwestern United States.

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*Polistes fuscatus* (Fabricius) is a social vespid wasp, widely distributed in North America, and recognized as a polytypic species. It was selected for study because it was available in numbers and suitable for laboratory studies of variation.

The objectives of this research were: (1) to quantify and assess the variation in color and color patterns of *fuscatus*; (2) to determine the distribution of color variation in relation to environmental factors (e.g. temperature and moisture); (3) as a means of subspecific diagnosis, to utilize methodology, classical or numerical, to gain the benefits of each; and, (4) to test, under controlled conditions, the influence of temperature-moisture factors on color expression.

Hayward (1933) stated that it was difficult to divide *fuscatus* into its several color varieties<sup>5</sup> since every color variety intergraded with neighboring ones to the extent that many specimens could never be placed definitely in one variety or another. In some instances two or three of these color forms may occupy the same area and still retain their distinctive characteristics. It is usually the case, however, that as the ranges of the two varieties overlap there is an intergradation in coloration which is often difficult to interpret. In a study of Palearctic *Polistes* and other vespids, Zimmerman (1931) found that color patterns became lighter from north to south, with extremely dark individuals in the mountains.

*P. fuscatus* is an extremely variable species, making taxonomic analysis very difficult (Bequaert, 1940). The variability in coloration even applies to the progeny of a single queen (Rau, 1931). Currently seven subspecies of *fuscatus* are recognized: *P. f. aurifer*

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<sup>5</sup>Historically, in *Polistes* (and other groups), the use of color as a principal means of identification resulted in the use of the category, "variety", to designate "color forms". With the trend toward disuse of "variety", and its subsequent invalidation as a nomenclatorial category, varietal names were often preserved by equating them to subspecies. Hence, the confusion and delay in our understanding.

Saussure, *P. f. centralis* Hayward, *P. f. fuscatus* (Fabricius), *P. f. laurentianus* Bequaert, *P. f. pallipes* Lepeletier, *P. f. utahensis* Hayward, and *P. f. variatus* Cresson (Bohart, 1951; Bequaert, 1940; Snelling, 1954).

The degree of melanism has been correlated with humidity for a number of insect groups including coccinellids (Dobzhansky, 1933; Johnson, 1910), syrphids (Smirnov, 1925), wasps (Bequaert, 1292; Fernald, 1926), bees (Sladen, 1919; Kirkton, 1968; Franklin, 1912) and butterflies (Hovanitz, 1941).

#### CHARACTER SELECTION

The characters most often used in the separation of subspecies of *fuscatus* are the coloration of the antennae, scutellum, legs, wings, the first and second tergites and sternites of the gaster, and total body length (Bequaert, 1940). Analysis of variance based on 15 randomly selected specimens of the subspecies *variatus*, *aurifer*, *pallipes*, *centralis*, *fuscatus*, and *montanus* showed no significant difference ( $P > 0.05$ ) in body length. Wing color varied greatly within subspecies and was not highly correlated with body coloration. Leg color patterns were difficult to record and were not used.

Color patterns were recorded on 12 body areas of 3842 female and 445 male *fuscatus* representing the six subspecies listed above. Eighteen distinct color patterns were recorded for the clypeus, 12 for the vertex and frons, 11 for the mesothorax and post-scutellum, 23 for the scutellum, 14 for the propodeum, 15 for the side of the prothorax, 20 for the first tergite of the gaster, 26 for the second tergite of the gaster, 17 for the first sternite of the gaster, and 29 for the second sternite of the gaster. Based on the date and locality data, each specimen was given a number according to the potential natural vegetation of the region (Kuchler, 1964).

#### ANALYTICAL METHODS

In order to analyze the data objectively it was necessary first to recode specimens by means of an additive procedure (Sneath and Sokal, 1973). Color patterns were numbered from 1 to n for each of the 12 body areas (n represents the last pattern number for a specimen). Since the patterns were arranged in order of increasing melanism it was possible to code each pattern as the additive result of all preceding color states. Thus the color patterns for each specimen were replaced by ones and zeros. Data in this form were next subjected to a principal coordinates analysis. Because of the large number of characters (color patterns) it was necessary to limit the number of specimens analyzed by one particular computer run to 70. Two groups of 70 specimens each were selected which represented 31 geographic areas (Table 1). Specimens representing each area were randomly selected. More specimens were selected from areas that either covered large geographic regions or included a wide range of color variations than from smaller more homogeneous areas. A principal coordinates analysis was performed on the transformed matrix of association coefficients (Rogers and Tanimoto coefficient) for 95 coded color states from seven body areas: (1) head: vertex and clypeus; (2) alitrunk: postscutellum, dorsal surface of the mesothorax, and propodeum; and, (3) the gaster: first and second sternites. These seven areas were selected due to their more definitive attributes; thus, as being most objectively quantified.

In order to evaluate any geographical distribution of color patterns, a trend surface analysis (Fisher, 1968; Gittins, 1968) was carried out on the factor loadings of all principal coordinates with eigen values larger than 1.0 Longitude and latitude were determined from the date locality data. To compare any geographical trends in color patterns with climate, separate analyses were carried out using temperature and rainfall data (monthly averages for May through September) based on meteorological records from specific sites within the 31 different areas.

A second factor analysis was run on females using the coefficient of similarity  $C = 2w/(A + B)$  where A equaled the total samples containing pattern A, B equaled the

Table 1. Geographic areas based on potential natural vegetation (Kuchler, 1964).

Area	Reference site <sup>a</sup>	Area	Reference site <sup>a</sup>
2	Medford, OR	66	Redig, SD
5	Ashland, OR	74	Brookings, SD
6	Tustin, CA	76	Dallas, TX
11	Lonepine, MT	77	Houston, TX
23	Albuquerque, NM	82	Urbana, IL
28	Corvallis, OR	98	Medora, ND
31	Alpine, TX	100	Lafayette, IN
33	Palm Springs, CA	102	Columbus, OH
35	Riverside, CA	104	Marietta, OH
38	Tuba City, AZ	106	Ithaca, NY
41	Needles, CA	109	—
42	Yuma, AZ	110	Freehold, NJ
48	Willows, CA	111	Raleigh, NC
49	Danair, CA	112	Orlando, FL
51	Richland, OR	113	Shreveport, LA
55	Burns, OR		

<sup>a</sup>Source of meteorological data

total samples containing pattern B, and w, the total of samples containing both patterns A and B. Coefficients of association were calculated for 41 geographic areas.

#### EXPERIMENTAL REARINGS

In order to determine what effect environmental conditions may have on wasp coloration, wasp pupae were maintained in 125 mm desiccators at three temperatures: 22.2°, 26.6°, and 35° C, and five humidities (concentrated salt solutions): 33, 44, 54, 65, and 76 percent. Excessive mold growth prevented successful pupal development at humidities higher than 76 percent. Adult wasps collected from nests were preserved for comparison with the laboratory reared material. Pupae and late instar larvae were placed in paper straws cut into 31.75 mm (1 1/4 inch) lengths that had been plugged on one end with cotton and individually placed in zipper cases. Inhabitants of a single nest were distributed as evenly as possible among the five humidities and three temperatures. One day after emergence, each wasp was killed, pinned and labeled for examination.

#### PRINCIPAL COORDINATES ANALYSIS

The results of the principal coordinates analysis are presented in Table 2. Only the first 10 principal coordinates are given in the table. Five principal coordinates were extracted from group one which accounted for a combined 66 percent of the total variation in color patterns. The first coordinate accounted for 36.69 percent while coordinates two, three, four and five accounted for 12.58, 7.89, 5.12, and 3.82 percent, respectively. Analysis of group two resulted in only four principal coordinates which accounted for 38.38, 17.69, 8.85 and 4.91 percent for a combined total of 70 percent of the variation in color patterns. The correlation between the association matrix and an euclidian distance matrix was very high in both cases (-0.976 and -0.977). Factor scores from the analysis of both groups one and two were combined for the trend surface analysis.

Analysis of the association coefficient,  $C = 2w/(A + B)$ , gave similar results. Three factors accounted for a combined 78 percent of the variation in color patterns. The

Table 2. Principal coordinates analysis of an association matrix (Rogers and Tanimoto coefficient) based on 95 color states from two groups of 70 adult female *Polistes fuscatus*.

Coordinate no.	Eigen value	Percent variation	Accumulated Percent
Group 1			
1	10.76	36.69	36.69
2	3.69	12.58	49.26
3	2.31	7.89	57.15
4	1.50	5.12	62.27
5	1.12	3.82	66.09
6	0.91	3.11	69.21
7	0.79	2.71	71.92
8	0.73	2.49	74.41
9	0.59	2.03	76.43
10	0.54	1.85	78.25
Group 2			
1	11.78	38.88	38.88
2	5.35	17.68	56.56
3	2.68	8.85	65.41
4	1.49	4.91	70.31
5	0.89	2.95	73.26
6	0.79	2.64	75.90
7	0.75	2.48	78.38
8	0.53	1.76	80.14
9	0.48	1.58	81.72
10	0.42	1.37	83.09

factor loadings of factor I were highest west of the 100th meridian, exclusive of the southwest. Factor II had its highest values throughout the eastern U.S. and southeastern Canada. The third factor was restricted to the arid southwest.

#### TREND SURFACE ANALYSIS

The results of the trend surface analysis are given in Table 3 for the first four principal coordinates. The highly significant F values for the first three principal components revealed a geographic trend of the color patterns represented by these components. The first two regression equations accounted for 65 and 68 percent of the variation of coordinates one and two while the third regression accounted for 41 percent of the variation of coordinate three.

Trend surface maps were prepared by plotting trend lines with longitude and latitude (Figures 1, 2, and 3). These maps provided a visual interpretation of the trend surface analysis and represented three major geographic color trends of *fuscatus*.

Figure 1 depicted a highly significant geographic trend in color pattern from the northeast to the southwestern United States. The contour lines represented areas of equal factor scores. The zero line showed the average value for a coordinate and separated a trend into its two extremes as measured by increasing positive or negative scores. The zero line for coordinate one was narrow which indicated an abrupt transition in color patterns. The highest positive scores occurred in the northeast and also in the southeast. Negative scores occurred in the southwest with the highest values in the arid desert regions of Arizona and California. Zero and low positive values were found in the northwest. Based on typical specimens in these regions, coordinate one represented a

Table 3. Summary of trend surface analysis (5th degree polynomial) of the first four principal coordinates with longitude and latitude.

Principal coordinate	R	R <sup>2</sup>	s	F(21, 118 d.f.)
1	0.808	0.653	0.236	10.56 <sup>a</sup>
2	0.825	0.681	0.144	11.99 <sup>a</sup>
3	0.641	0.411	0.142	3.92 <sup>a</sup>
4	0.238	0.056	0.142	0.34

<sup>a</sup>P 0.001

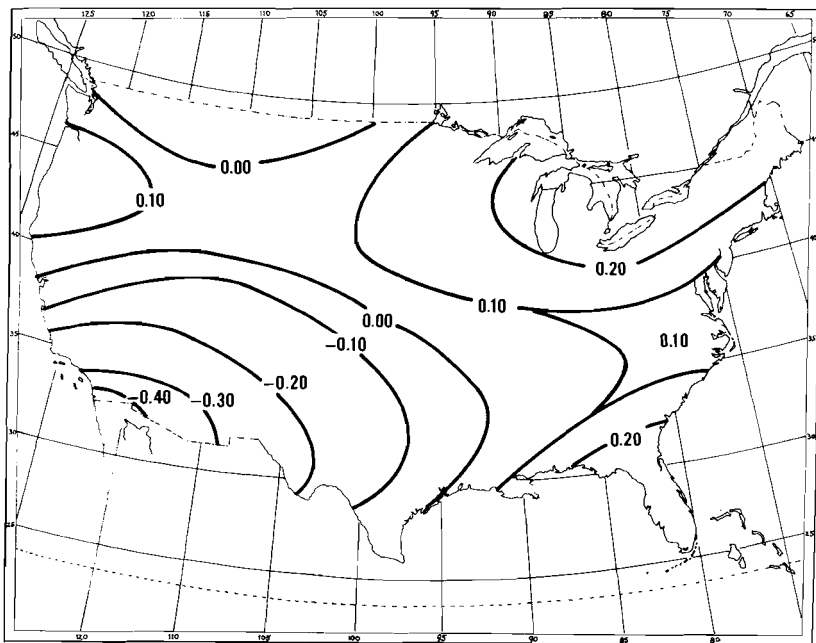


Fig. 1. Trend surface map (5th degree fit) of coordinate one with longitude and latitude.

trend in color from dark, highly melanic browns and blacks plus yellows in the east, to decreasing melanism in the southwest dominated by pale ferruginous and yellow markings. The extremes of trend 1 occurred in the humid east and the extremely arid southwest.

The second trend (Figure 2) showed another east-west progression of changes in color patterns of *fuscatus*. Unlike the first trend, the zero line in Figure 2 was wide which indicated that there was a gradual transition for this trend throughout the central United States. Positive scores increased slowly toward the east coast while negative scores increased more rapidly and reached their values in the Pacific Northwest. The extremes of this trend were yellows and blacks in the northwest and browns, blacks, and yellows in

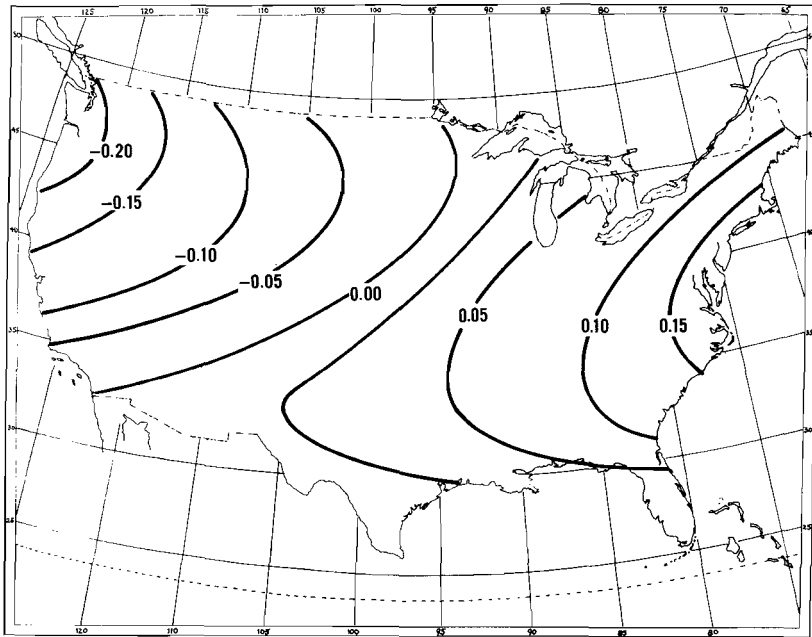


Fig. 2. Trend surface map (5th degree fit) of coordinate two with longitude and latitude.

the east. Specimens from hot arid regions away from the coast had varying amounts of ferruginous on more body areas with ferruginous replacing the black entirely on some segments. Specimens from the eastern part of coordinate two (positive scores) are described under coordinate one.

The contour lines of figure 3 showed a somewhat poorly defined trend in the central United States. The highest negative values occurred from the Canadian border through the Dakotas, Nebraska, Iowa, and Minnesota. Positive values were restricted to the northwest and northeast. The width of the contour lines indicated that changes occurred gradually over wide geographic areas. The dominant colors represented by this trend included yellows and browns through the central states (negative values), extreme melanism with yellows and blacks in the northwest. None of the remaining coordinates produced a significant fit with longitude and latitude.

Trend surface analysis of the three factors extracted in the analysis of the coefficient  $C = 2w/(A + B)$  showed similar results. Factor I (55.7%) was distributed west of the 100th meridian exclusive of the arid southwest; factor II (15.7%) extended throughout the eastern U.S. and Canada west to approximately the 100th meridian; and factor III (8.4%) was found in arid regions of the southwestern U.S.

#### CLIMATE AND COLOR TRENDS

A trend surface analysis produced a highly significant fit of average monthly rainfall (May through September) with longitude and latitude (Figure 4) but not for temperature. In general, contour lines of equal average precipitation ran in a north-south direction decreasing from east to west. Monthly averages ranged from 76.2 mm (3.0 inches) in the southeast to 12.7 mm (0.50 inches) in the extreme southwest. Comparison of Figure 4

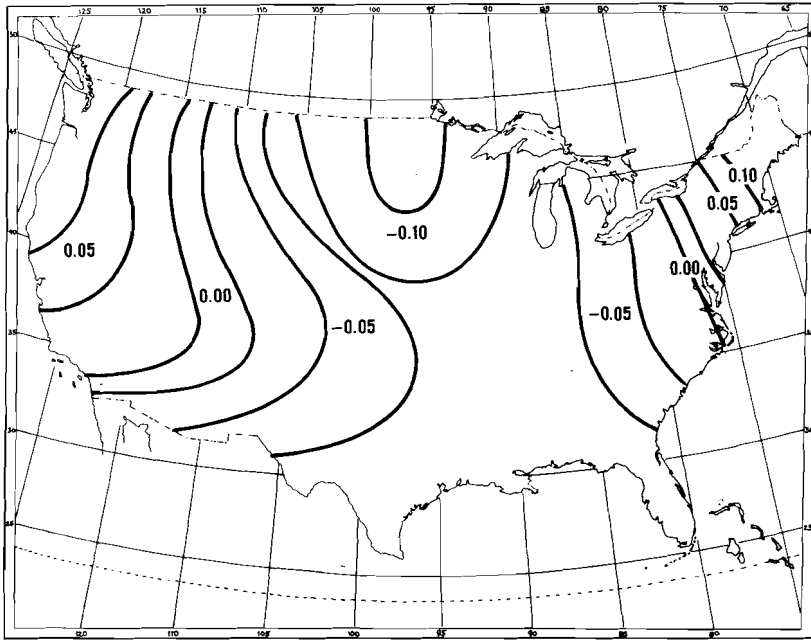


Fig. 3. Trend surface map (5th degree fit) of coordinate three with longitude and latitude.

with Figures 1 and 2 revealed that many of the color trend contour lines approximately paralleled the rainfall contour lines.

Since the intensity of melanism was probably determined by the effect of temperature on the rate of development, hythergraphs (Figure 5) were constructed for three different areas based on meteorological records of temperature and rainfall. These hythergraphs were composites based on extremes of all included stations. The areas were chosen from the results of the trend surface analysis: (1) eastern United States (high positive factor scores of coordinates one and two); (2) western United States (high negative factor scores of coordinate one); and (3) southwestern United States (high negative factor scores of coordinate one).

The range of average temperatures for areas 1 and 2 was remarkably alike for the April-October nesting season (Fig. 5). The major differences between these two areas were the amount and distribution of rainfall. The difference in temperature-rainfall conditions within the range of areas 1 and 3 were dissimilar. Temperatures were higher and rainfall lower for area 3. Also, the two wettest months (July and August) for area 3 were the two driest months for area 1. The hythergraph constructed from ranges of temperature and rainfall rather than monthly averages resulted in considerable overlap between areas 1 and 2 and less between areas 2 and 3. However, during the period from May to September when most of the specimens were collected, virtually no overlap occurred. There was almost no overlap between the hythergraphs of areas 1 and 3 and conditions during the developmental season were quite dissimilar (area 1 is warm and wet, area 3, hot and dry).

The line of demarcation (zero contour lines of trends one and two) between eastern, western, and southwestern color patterns vacillated across the 100th meridian. In general,



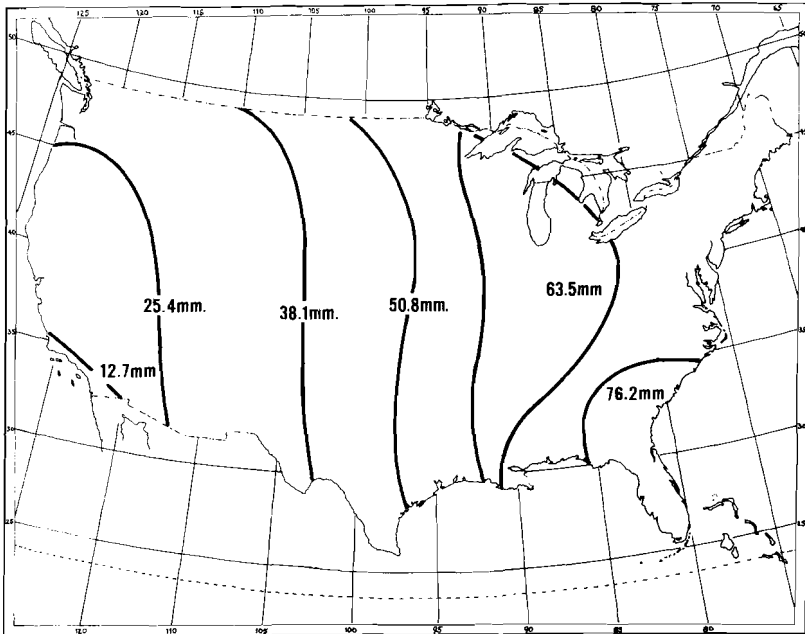


Fig. 4. Trend surface map (4th degree fit) of average monthly rainfall for May, June, July, and August with longitude and latitude.

this line was associated with an east-west annual rainfall of 50-60 cm. The superposition of temperature conditions (occurring latitudinally) in the eastern United States accounted well for the ranges of infraspecific forms recognized within *fuscatus*.

The range limits of the two western forms were most closely associated with rainfall amounts and distribution (late summer vs. winter). Additionally, the average temperatures were much cooler within the range of area 1.

#### EXPERIMENTAL REARINGS

Specimens kept at 33 percent humidity for four to five days showed little notable differences from the nest specimens. Some body parts were lighter in color (yellow in place of ferruginous, ferruginous in place of black) while others appeared darker (black or ferruginous in place of yellow, black in place of ferruginous). After six to eight days, at least 75 percent of the body parts were lighter than the nest adults and if nine or more days were required for emergence, 100 percent of the body parts were lighter in color than those of the nest adults.

There were no apparent differences between experimental specimens kept at 54 percent humidity and nest adults. Specimens kept in the desiccator up to 11 days before emergence were both lighter and darker than nest adults and no trend could be discerned.

At 65 percent humidity, (reared) wasps tended to be darker after seven days than those from nests, but the results were not conclusive. Darker individuals predominated at 76 percent humidity. After five days the wasps tended to be darker than those of the nest adults. No related color differences could be shown between temperatures of 22.2° or 26.6° C and too few wasps survived at 35° C to draw any conclusion regarding effects of this temperature.

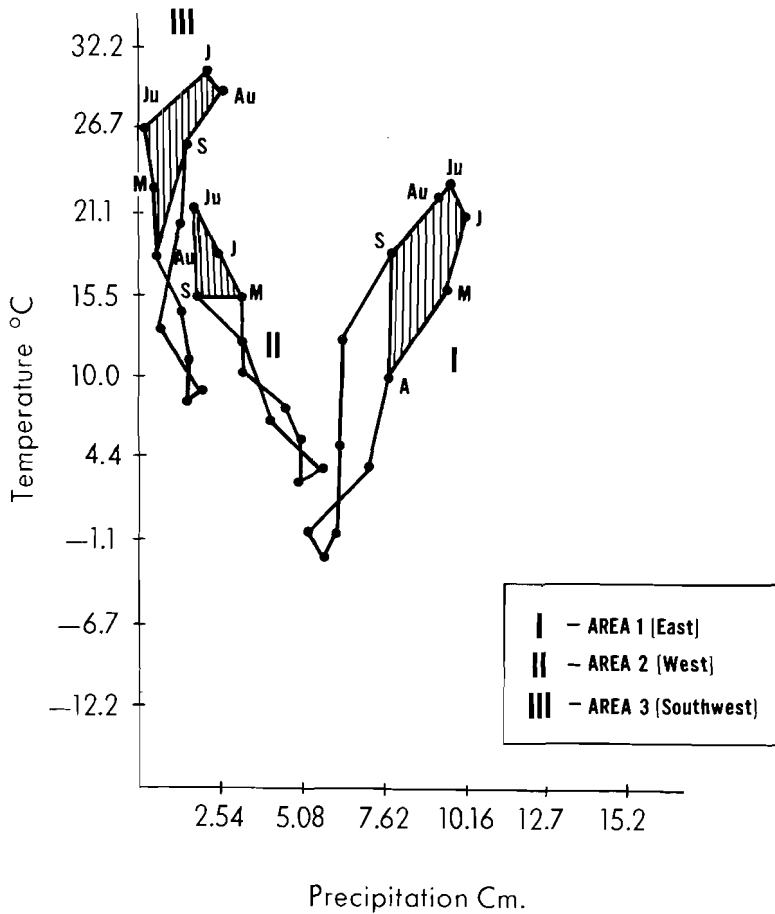


Fig. 5. Hythergraphs representing average temperature and rainfall conditions for: I the east, II the west, and III the southwest. Shaded areas represent active developmental season for *Polistes* spp.

#### DISCUSSION

It became quite apparent at the time of examining and recording the many color variations from museum specimens that the current subspecies recognitions within *Polistes fuscatus* were untenable. Some of the more obvious evidences for this conclusion were: (1) several "subspecies" were sympatric, synchronic, and syntopic; (2) two or more "subspecies" were taken from the same nest; (3) many "subspecies" determinations were apparently based on locality rather than on color expression; (4) the recognition of *P. f. pallipes* involved misidentification and confusion with *P. metricus* Say which, in many instances, made up the bulk of the material identified as *P. f. pallipes*; and, (5) in the relatively restricted areas of sympatry, the colors and/or color patterns were not ones of intergradation, but objectively discrete termina of respective clines. While these appeared

subjectively to satisfy subspecific criteria, in reality they represented parallel or convergent expressions as would be expected under identical (or nearly so) climatic conditions to which both populations were subjected. Though constituting certain problems of specific determination, the color/color pattern of one species was not reproduced in another, even in the areas of sympatry, being wholly continuous within one, and wholly discontinuous within the other.

Principal coordinates analysis subsequently confirmed that color and color patterns were to some extent clinal under broad climatic conditions. Laboratory rearings provided evidences that changes in color were affected by temperature-moisture combinations.

Basic coloration in *Polistes* is at least a dual expression of cuticular pigments (brown: cinnamon-brown to black) and of epidermal pigments (yellow) (Enteman, 1904). This condition is somewhat analagous to coloration in some species of *Bombus* (Friese and Wagner, 1904), *Bembicinus* (Krombein and Willink, 1950) and Sphecidae in Madagascar (Arnold, 1944).

While the phenetics of these situations can be described and interpreted, the genetic aspect is poorly understood, and Bequaert's (1940) plea for genetic studies remains valid. Interpretation of field and experimental data indicated the following hypotheses concerning coloration in *Polistes*.

- 1) There are two sequences of color expression which are independent in expression and appear to be antagonistic (i.e., tend to replace one another);
- 2) Phenotypic expression differs with sex, yellow being more prominent in haploid males than in diploid females;
- 3) Phenotypic expression is broadly correlated with macroclimatic factors but is really an expression of temperature-humidity conditions at the nest site (microclimate);
- 4) Each regional population exhibits a range of color variation which could be manipulated experimentally under controlled conditions to produce many (most) of the variations to be found in that region, but which could not be manipulated experimentally to produce the forms unique or predominant in other regions;
- 5) Color and color patterns change in response to seasonal climatic conditions and similar forms appear as a result of similar climatic conditions not wholly related to seasonal time;
- 6) In the periphery of the range of each set of color patterns there is a tendency to approach the color patterns of the adjacent sets. However, numerical analysis shows these to be areas of overlapping color patterns, not intergrading.

Applying the results of this study to the populations of *fuscatus* the most logical interpretation of the color pattern trends is that there are three species involved. The distributions of these species are shown in Figure 6. These would be catalogued (with infraspecific categories listed in parenthesis without status designation):

*Polistes aurifer* Saussure 1853

(*anaheimensis* Provancher 1888; *montanus* Bequaert 1940; *centralis* Hayward 1933; *utahensis* Hayward 1933)

*Polistes fuscatus* (Fabricius) 1793

(*nestor* Fabricius 1793; *laurentianus* Bequaert 1942; *pallipes* Lepeletier 1836; *exilis* Saussure 1853; *variatus* Cresson 1972)

*Polistes* sp. (undescribed species—"yellow form")

Variation within a geographic area is clinal with the percentage of ferruginous increasing over black with higher temperature and lower humidity. Typical *fuscatus* can be manipulated experimentally to exhibit the entire color range of *fuscatus* (including "*pallipes*" and "*variatus*"); however, specimens resembling *aurifer* or the yellow form could not be produced.

The range of *aurifer* (negative factor scores of coordinate two, Fig. 2) and *P. fuscatus* (positive factor scores of coordinates one and two, Figs. 1 and 2) are to a large extent abutting and, where sympatry does occur, the color forms are objectively discrete. There

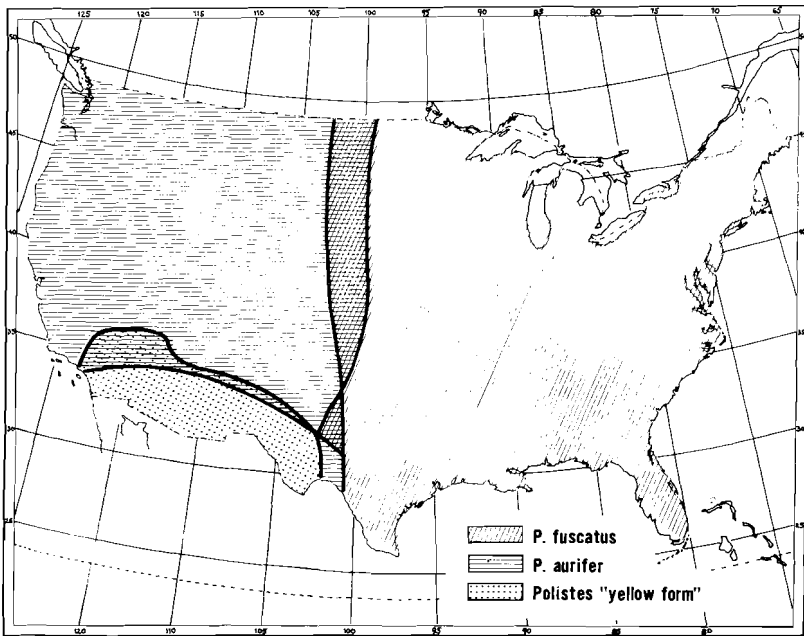


Fig. 6. Distribution map of *Polistes fuscatus*, *Polistes aurifer*, and *Polistes* "yellow form".

is no apparent intergradation or production of intermediate populations. The range of the undescribed "yellow form" (negative factor scores of coordinate one, Fig. 1) barely overlaps with that of *aurifer*, but the color expressions are separable, though convergent.

Vegetational units (a phytosociological indication of climate) correlate well with the range limits of the wasp species. Hythergraphs of average temperature-humidity conditions are also non-overlapping for the ranges of the wasp species. Considerable overlap occurs among the hythergraphs based on ranges of conditions which is certainly responsible for parallel color expression among the species.

The contiguous distribution of "*Polistes fuscatus* auct.," with taxonomically identifiable and geographically located populations, appears to satisfy the criteria of subspecific recognition. However, the absence of intergrading forms in regions of sympatry, or the disjunction of variation; the discreteness of intrapopulation clines though with environmentally-induced convergence of expression; and the virtual lack of sympatry, is best interpreted by the recognition of three species.

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