

RANGE EXTENSION AND SOLITARY NEST FOUNDING
IN *POLISTES EXCLAMANS*
(HYMENOPTERA: VESPIDAE)*

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It is generally difficult to document temporal changes in the geographic distribution of insect species because of the sporadic nature of collections made primarily for taxonomic study and specimen identification. Therefore some new distribution data providing an unusual amount of evidence for range extension in the social wasp *Polistes exclamans* Viereck seem of interest. Several states have been added to the known range of *P. exclamans* in the last twenty years; and *P. exclamans* is now abundant in east-central Missouri, where it was almost certainly absent two decades ago. Solitary nest founding by *P. exclamans* queens may enhance the ability of this species to colonize new areas.

Porter (1963) first suggested that *P. exclamans* may be extending its range. He reported new records from Maryland and New Jersey, noting that these states are considerably north of the northernmost previous records for *P. exclamans* in the Atlantic Coast states.

A collecting trip to St. Louis and Jefferson Counties, Missouri, in July, 1967, provided the first evidence of range extension by *Polistes exclamans* in the midwestern United States. The purpose of the trip was to collect specimens of *Polistes* species observed by the Missouri naturalist Phil Rau prior to his death in 1948. Rau repeatedly mentioned (e.g., in Rau 1929, 1942a, 1942b) that only four species of *Polistes* existed in Missouri: *P. pallipes* (= *metricus*), *P. rubiginosus*, *P. annularis*, and *P. variatus* (= *fuscatus*) (Rau's determinations by J. Bequaert). However, I found *P. exclamans* nests common in barns and abandoned buildings in southern St. Louis County, and collected specimens of *P. exclamans* in six of the eight localities where *Polistes* wasps were found (other species collected were *P. metricus*, *P. fuscatus*, and *P. rubiginosus*). Three of the 1967 *P. exclamans* localities were frequented by Rau during his studies of *Polistes*: "Meramac Highlands", an area near the Meramac River about eight miles southwest of St. Louis (first mentioned in Rau and Rau, 1918); Kirkwood, Rau's home town for 24 years (first mentioned as a study locality in Rau, 1941); and a farm near

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the present Beaumont Reservation, 18 miles southwest of St. Louis, the former site of some "woodcutters' cabins" often visited by Rau during the years 1945-1947 (Rau, unpublished manuscript).¹

There is little doubt that Rau would have noticed and reported *P. exclamans* in the St. Louis region if the species had been present there during his lifetime. He published 39 papers and one book chapter (Rau and Rau, 1918) on the *Polistes* of 43 named localities in that area during the years 1918-1946, and devoted his last years to writing a book dealing exclusively with the bionomics of *Polistes* (Rau, unpublished manuscript). Furthermore, Rau would have been unlikely to confuse *exclamans* with any of the Missouri species he recognized, since it has a distinctive appearance and nest form appreciated and described by Rau when he collected it in Texas (Rau, 1943). Therefore it seems reasonable to conclude that the present abundance of *Polistes exclamans* in southern St. Louis County, Missouri, is due to colonization in that area during the last twenty years.

Examination of museum collections (see Acknowledgments) has revealed specimens of *P. exclamans* from nine states not considered part of the species range in 1951 (Bohart, 1951) (Table 1). Eight of the new state records are in the northeastern quarter of the species range, suggesting a generally northward expansion in the eastern half of the United States. Since climate-related range fluctuations are quite common in animals, and there are numerous examples of northward expansion in North America during the present century (see Mayr, 1963), climatic change and/or adaptation to more northern habitats must be considered as possible contributing factors in the expansion of *P. exclamans*. However, there are pre-1950 records of *P. exclamans* from northern Kansas, Nebraska, and Iowa — north of all the new records (Table 1) — suggesting that the expansion may not bear a simple relationship to climate.

A possible behavioral basis for range expansion in *P. exclamans* was suggested by field observations of newly founded *Polistes* colonies on and near the University of Oklahoma Biological Station (Marshall County, Oklahoma). Nests of *P. annularis*, *P. apachus*, *P. fuscatus*, *P. metricus* and *P. rubiginosus* observed between 20 April and 11 May, 1966, were commonly attended by more than one female (foundress). However, each except one of more than 100 *P. exclamans* colonies was attended by a single female; the one exception had only two foundresses. Solitary nest founding² predominated even

¹Phil Rau's son, Mr. David Rau, kindly helped in locating these sites.

²I prefer this term to the older "haplometrosis" or "monogyny", and the term "social nest founding" to "pleometrosis" or "polygyny", for reasons given in West, 1967b.

Table 1
New state records of *Polistes exclamans* Viereck.

State	Locality	Date	Collection
Illinois ¹	Williamson Co.	1958	Southern Illinois Univ. ²
Indiana	Posey Co.	1958	Purdue Univ.
	Perry Co.	1960	" "
	Floyd Co.	1965	" "
Kentucky	Nelson Co.	1957	Purdue Univ.
	Bardstown	1958	" "
Maryland	Prince George Co.	1958	Univ. of Maryland
	" " "	1959	Los Angeles County Mus.
	Public Landing	1959	Cornell Univ.
	Plummers Island	1961	" "
	Salisbury	1960	see Porter, 1963
	Cambridge	1960	" " "
Missouri ¹	Columbia	1966	Univ. of Calif. Davis
	Boone Co.	1966-7	Univ. of Missouri
	St. Louis Co., Jackson Co.	1967	Mus. of Compar. Zool.
New Jersey	Penn State Forest	1955	see Porter, 1963
	Lebanon State Forest	1955	" " "
	Metuchen	1960	" " "
New Mexico	Eddy Co.	1956	Cornell Univ.
	Roswell	1956	Purdue Univ.
Tennessee	Benton Co.	1953	Los Angeles County Mus.
Virginia	Gloucester	1959	Univ. of Maryland
	Eagle Rock	1961	Los Angeles County Mus.
	York Co.	1962	" " " "

at "popular" nesting sites: eighteen single-foundress *exclamans* colonies located in close proximity beneath the porch roof of a small abandoned cottage were dispersed, rather than clustered, beneath the shelter. Furthermore, *P. exclamans* was the only *Polistes* species among the six common in the area to occupy artificial nesting places erected at the Biological Station on 1 April—the species was exceptional in colonizing these newly available sites. Eickwort (in

¹The collection of the Illinois Natural History Survey contains 15 specimens of *P. exclamans* from Macoupin Co. Illinois for the years 1890-1910, and the University of Missouri collection contains one specimen recorded from Boone Co., Missouri, 1940. However, these states are listed as "new records" here because they were not included in Bohart, 1951, and because of the paucity of *P. exclamans* in early collections from these areas.

²collection examined by R. M. Bohart.

press) reports that solitary nest founding also predominates in Kansas populations of *P. exclamans*.

These associated tendencies of *P. exclamans* foundresses to disperse and to move into newly available nesting sites would promote range expansion. In contrast, social foundresses tend to remain and reproduce near their place of origin. In *Polistes fuscatus* and *P. canadensis*, foundress associations are composed of siblings which begin new colonies near the parental nest site (West, 1967a), and there is indirect evidence that this occurs in other species having social nest founding (see Hamilton, 1964; West, 1967a).

The mode of nest founding of *P. exclamans* within the newly occupied portions of its range is unknown. While most foundresses were solitary in the populations of *P. exclamans* observed in Oklahoma and Kansas (above), the same species commonly exhibits social nest founding in Texas (Rau, 1943; Caskey, 1955). Similarly, Rau (1942b) found only solitary foundresses in *P. fuscatus* (= "*variatu*s") in Missouri, whereas in Michigan social nest founding was most common in that species (West, 1967a, b). Geographic variation in mode of nest founding has also been noted in the European wasp *P. gallicus* (see Hamilton, 1964). Thus, while it has been traditional in the literature on social wasps (e.g., Wheeler, 1922) to regard mode of nest founding as a constant feature of a species, it is probably better to consider most *Polistes* "polyethic" in this respect, with mean size of foundress group differing from locality to locality and from year to year. Various factors, including parasitization (Eickwort, in press), nest site availability, number of overwintering siblings, and dominance relations among foundresses, may affect the frequency of solitary nest founding and the size of foundress groups (see West, 1967a). As the observations of this study suggest, solitary nest founding might be expected to increase in frequency in areas where there is opportunity for (and advantage in) expansion; and the ability of some *Polistes* species to colonize new sites might be limited or delayed by selection for social nest founding.

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Natural History Survey (W. E. LaBerge); University of Arkansas (E. P. Rouse); University of Missouri (W. R. Enns); and Los Angeles County Museum of Natural History (E. M. Fisher). R. M. Bohart kindly sent data from other collections examined by him, and H. E. Evans examined specimens of *P. exclamans* at the American Museum of Natural History. I have personally obtained data from collections at Cornell University and the Museum of Comparative Zoology.

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THE MATING BEHAVIOR OF
GROMPHADORHINA PORTENTOSA (SCHAUM)
(BLATTARIA, BLABEROIDEA, BLABERIDAE,
OXYHALOINAE): AN ANOMALOUS PATTERN
FOR A COCKROACH¹

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This communication is the fourth in a series of largely descriptive papers dealing with the mating behavior of cockroaches. (see Barth, 1961; Barth, 1964; Roth and Barth, 1967; and Barth, ms in preparation). The aim of this series is twofold: first to provide background information for experimental studies, and second to provide the detailed comparative information necessary for a study of the evolution of mating behavior within the Blattaria. A more general introduction to the series may be found in Barth (1964). The anomalous mating behavior of the Madagascar cockroach, *Gromphadorhina portentosa*, (Schaum) forms the subject of this communication.

MATERIALS AND METHODS

Stock cultures of *G. portentosa* were maintained as described by Barth (1964) for *Byrsotria fumigata*. The observations on mating behavior were made in the evening (the normal active period for these animals) under red illumination in specially designed observation chambers (for details, see Barth, 1964). The ethological terms employed in the description of the behavior patterns have been previously defined by Barth (1964).

RESULTS AND CONCLUSIONS

Gromphadorhina portentosa is a large, heavy-bodied wingless species found under debris on forest floors in Madagascar (see Plate 6

¹No. 4 in a series of papers entitled "The Mating Behavior of Cockroaches".

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