1988

Adoption of Newly-Mated Queens: A Mechanism for Proliferation and Perpetuation of Polygynous Red Imported Fire Ants

B. Michael Glancey
USDA

Clifford S. Lofgren
USDA

The Florida Entomologist, Vol. 71, No. 4 (Dec., 1988), pp. 581-587
Published by Florida Entomological Society

ADOPTION OF NEWLY-MATED QUEENS: A MECHANISM FOR PROLIFERATION AND PERPETUATION OF POLYGYNOUS RED IMPORTED FIRE ANTS, *SOLENOPSIS INVICTA* BUREN

B. MICHAEL GLANCEY AND CLIFFORD S. LOFGREN
Insects Affecting Man and Animals Research Laboratory
United States Department of Agriculture
Agricultural Research Service
Gainesville, FL 32604

ABSTRACT

The polygynous form of the red imported fire ant, *Solenopsis invicta* Buren was first reported from Mississippi in 1973; however, the source of the numerous fertile queens in polygynous colonies has remained an enigma. In 1987, 400 queens from a mating flight were marked with a durable paint and released in an area heavily populated with the polygynous form. None were recaptured after one week, but 9 months later, 4 clearly-marked queens were found in a nest 65 meters from their release point. This finding clearly points to adoption. About 5 weeks later, 37 of 107 fertile queens collected from 37 polygynous nests, were found to have partially histolyzed wing muscles and undeveloped ovaries. Mating flights had occurred a few days prior to the queen collections, thus it was apparent that these queens were newly adopted. This observation was verified following a second mating flight one week later. The results of our 3 studies clearly indicate that polygynous *S. invicta* can proliferate and perpetuate their colonies by queen adoption.

RESUMEN

La forma polígama de la hormiga roja importada, *Solenopsis invicta* Buren, fue reportada por primera vez en Mississippi en 1973; sin embargo, la fuente de numerosas reinas fértiles en colonias polígamas ha permanecido un enigma. En 1987, 400 reinas de un vuelo nupcial fueron marcadas con pintura duradera y liberadas en un área altamente poblada con la forma polígama. Ninguna fue recapturada después de una semana, pero 9 meses después, 4 reinas claramente marcadas fueron encontradas en un nido a 65 metros de donde fueron liberadas. Este descubrimiento claramente indica adopción Como 5 semanas después, 37 de 107 reinas fértiles colectadas de 37 nidos polígamos, se encontraron tener histolizados los musculos del ala y ovarios sin desarrollar. Vuelos nupciales habían ocurrido varios dias antes de que se colectaran las reinas, de aquí que es aparente que esas reinas fueron recientemente adoptadas. Esta observación fue verificada en el siguiente vuelo nupcial una semana más tarde. El resultado de nuestros 3 estudios indican claramente que *S. invicta* polígamas pueden proliferarse y perpetuar sus colonias adoptando reinas.

The increasing occurrence of populations of the polygynous form of the red imported fire ant, *Solenopsis invicta* Buren, has become a concern to those faced with controlling populations of this pest ant. Polygynous *S. invicta* tend to have high nest densities (up to 2,000/ha) and reproductive rates which cause greater economic, public health, and environmental problems. Populations of the polygynous form have been reported for all infested states except North and South Carolina and Puerto Rico; however, this probably reflects a lack of surveys for their detection rather than their absence (Glancey et al. 1973, Mirenda & Vinson 1982, Fletcher 1983, Lofgren & Williams 1984, Glancey et al. 1987). The finding of polygynous colonies in Oklahoma in 1987 and in several isolated locations in west Texas (W. A. Banks, USDA, personal communication) suggests also that they may present a greater hazard of spread to uninfested locations.

While there has been speculation about the origin of polygyny in *S. invicta* there are no reports documenting the specific biological mechanism responsible for either the origin of these populations or the method by which they perpetuate themselves. Because a portion of our laboratory grounds is now infested with polygynous *S. invicta*, we were able to compare differences between monogyne and polygyne populations. Of particular interest was the possibility that the polygyne populations were being sustained through the adoption of newly-mated queens following mating flights. This adoption theory was proposed because orphaned *S. invicta* workers will accept new queens under certain laboratory conditions (Banks et al. 1981), particularly if the new queen is 10-14 days post-eclosion and producing the queen recognition pheromone (Glancey et al. 1981). Also, we have found that laboratory-reared polygynous colonies will often accept newly-mated queens (unpublished observations).

Methods and Results

To test our theory of adoption, we collected about 800 newly-mated and dealate queens on the ground following a nuptial flight around a shopping area on June 15, 1987 near Ocala, Florida. We examined 200 of the queens for insemination and all contained sperm. We then painted 100 each with orange, white, blue and yellow and banded 100 with wire. The queens were painted by applying a small drop of Markal Ball Point Marker (Markal Co., 250 N. Washtenaw Ave., Chicago, Ill.) to the dorsal surface of their thorax and the gaster while they were anesthetized with CO_2. The banding was accomplished by tying fine copper wire around the petiole of the queen while she was inactivated by chilling (Mirenda & Vinson 979). The queens were allowed to recover completely before they were returned to the field. The five groups of 100 queens were released on June 16, 1987 in pre-selected areas around our laboratory that had well defined populations of polygynous colonies. Seven days later, all mounds within 10 meters of each release site were dug up and placed in 5-gallon buckets. The ants were separated from soil by the drip-flotation method (Banks et al. 1981) and all queens examined for paint spots or bands. No marked queens were found. However, nine months later (March 30, 1988), during the sampling of polygynous nests in a nearby pasture area, we found 44 queens in one nest, 4 of which were marked. The nest was located 65 meters from the nearest release point (Fig 1 & 2). The queens were readily identified by bright orange spots on the dorsal side of their gaster and thorax. The means by which the released queens migrated to the nest in which they were captured, through an area highly populated with other polygyne *S. invicta* nests, is unknown. As far as we are aware, this represents the first time that adoption of queens by polygynous field colonies of *S. invicta* has been verified.

In early May, 1988, we collected queens from polygynous colonies in an adjacent area, about 75 m from the site where the marked queens were collected. A rain had occurred on May 13, and the ants had built up their mounds (15 cm or more) so they were easy to locate. Mating flights were noted on May 14 & 15 also. On May 17 we dug up 37 colonies, collected all the dealated females and dissected them to check for insemination and ovarian development. All of the queens were inseminated; however, it was evident that two types of queens were present: a) those that had well developed ovarioles containing 3-4 or more vitellogenic eggs in every ovariole and no fat body or alary muscles, and b) those that had a few ovarioles with 1 vitellogenic egg, but which had fat body and partially histolyzed alary muscles. It was apparent that these latter queens had mated recently and were in the initial stages of ovarian development and egg production. Queens were retrieved from 21 of the 37 nests. The data on the 107

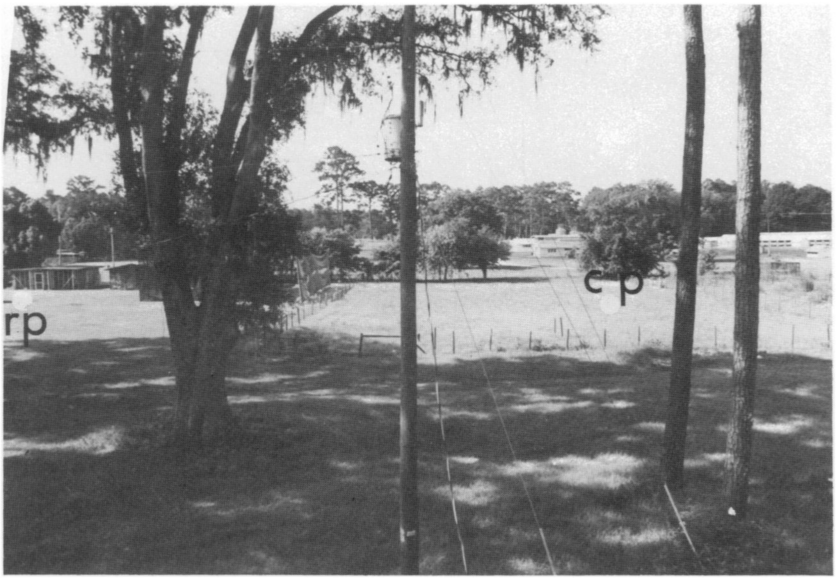

Fig. 1. Photograph of pasture area in which marked queens or banded queens were released (rp = release point, cp = capture point).

queens collected are shown in Table 1. Ten of the 21 nests contained 1 to 8 newly-mated queens; 7 contained only newly-mated queens.

On May 20, another mating flight occurred the day after a rainfall. Six days later, we collected ants from two nests located at the base of oak trees about 100 meters from the location of the previous collection site. The data on queens from this collection also are presented in Table 1. In Nest 1, 52 of 72 (74%) of the queens were adopted, and in Nest 2, 12 of 22 (55%) were adopted. Observations of the wing muscles indicated various stages of histolysis. In neither nest did we find any males, alate females, or sex brood.

Discussion and Conclusions

In light of these observations, it is apparent that a principle method by which polygynous colonies of *S. invicta* prepetuate themselves is via adoption of newly-mated queens following their mating flights. However, we do not know the specific conditions which favor adoption, since it is obvious that not all queens are accepted. The possibility of intranidal mating as an alternative explanation for the 2 queen types does not seem logical since it would require a change in mating behavior of *S. invicta* for which there is no documented evidence. On the other hand, mating flights of males and females from polygynous colonies are documented (W. A. Banks, personal communication) and flights from nests in our test site were observed during May, 1988. The fact that the newly-mated queens were detected within 6 days of mating flights, and no sexual brood and/or alate males or females were present in the nests we excavated, clearly favors adoption of queens from local nuptial flights alighting near these nests rather than intranidal mating. There was no way for us to determine whether the new queens were from polygynous or monogynous colonies.

Another factor favoring adoption is the recent research of Morel et al. (In press) which demonstrates a lack of aggression between workers of polygynous colonies and

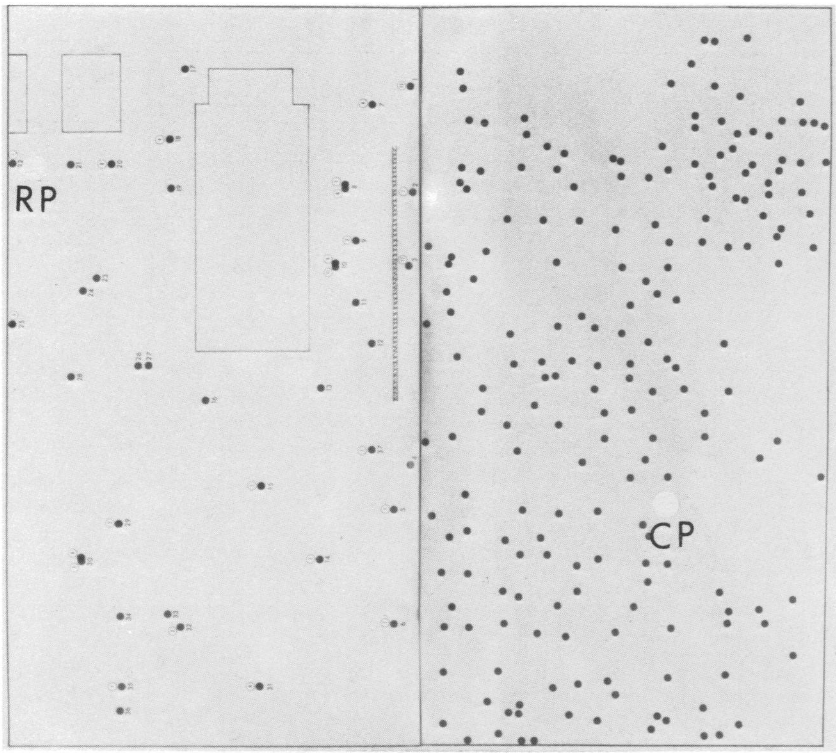

Fig. 2. Schematic map of pasture area showing location of multiple queen mounds and the release (rp) and capture (cp) locations (distance = 65m).

toward workers of monogynous colonies. The lowered aggression levels in polygynous populations are attributed to a greater variability in the polygyne template caused by highly variant discriminators derived from multiple matrilines, as well as exposure to a greater variety of environmental cues. From this evidence we infer that polygynous workers might be less hostile to newly-mated queens, thus allowing their adoption.

We conclude that polygynous *S. invicta* colonies are able to proliferate and perpetuate by adoption of newly-mated queens. While our observations indicate adoption immediately following the nuptial flight, we cannot rule out later adoption of claustral founding queens. Adoption of queens directly after a mating flight has been reported for *Formica ulkei* (Scherba 1958) and *Formica opaciventris* (Scherba 1961); however, in these instances the queens returned to the same cluster of nests from which they took flight.

Numerous other questions remain to be answered, particularly how individual polygynous populations originate. Ross & Fletcher (1985) speculate that they arise through kin selection and/or mutualism. It seems reasonable to us that both factors are involved. Tschinkel & Nierenberg (1983) discuss the importance of relatedness on the social biology of *S. invicta* in the United States. Because the original introduction of *S. invicta* into the Mobile, Alabama area between 1933 and 1940 involved only a small number of females, they suggested that relatedness could be associated with the development of polygyny. However, *S. invicta* queens were shipped from Mobile in nursery

TABLE 1. OVARIAN STAGE[a] OF INSEMINNATED QUEENS COLLECTED FROM *S. INVICTA* POLYGNOUS FIELD COLONIES.

Mound No.	No. Queens	Ovarian Stage 1	Ovarian Stage 2	Mound No.	No. Queens	Ovarian Stage 1	Ovarian Stage 2
Observation Area No. 1 (May 17, 1988)							
1	13	0	3	12	4	4	0
2	1	0	1	13	8	8	0
3	17	0	17	14	1	0	1
4	1	0	1	15	3	3	0
5	7	0	7	16	2	2	0
6	4	0	4	17	7	4	3
7	7	1	6	18	4	4	0
8	2	0	2	19	2	0	2
9	20	9	11	20	1	0	1
10	1	1	0	21	1	0	1
11	1	1	0	Totals	107	37	70
Observation Area No. 2 (May 26, 1988)							
1	72	52	20				
2	22	12	10				
Totals	94	64	30				

[a]Stage 1 = some ovarioles with one vitellogenic egg, fat body present, wing muscles partially histolyzed.
2 = all ovarioles with 3-4 vitellogenic eggs, no fat body or wing muscles.

stock to hundreds of other locations in the southern United States in the 1940's and 1950's (Culpepper 1953, Lofgren 1986). Most of the shipments probably involved only one or, at most, a few colonies. Tschinkel & Nierenberg (1983) state that these "outlier populations" could result in even higher degrees of relatedness associated with "second founder effects and higher inbreeding". Thus, it is easy to conceive of polygynous populations arising at various locations due to high genetic similarity in combination with pleometrotic colony founding. Once a polygynous founder colony becomes established, lowered worker aggression levels (Morel et al., In press), queen adoption and colony budding or fission (Vargo & Porter, in press) take over as the mechanisms by which polygynous colonies are populated and enlarged.

Adoption can have definite advantages for newly-mated queens by providing them with instant care. An example is provided by Ross & Fletcher (1986) who found that diploid male-producing queens could not establish colonies by themselves but did survive in polygynous colonies. This example can be extended to predict an overall increase in survival potential for queens. For example, in March 1988 we estimated through excavations and subsampling that the nests in the polygyne field populations at our laboratory harbored about 4,000 queens per acre. Glancey (1975) reported collection of over 4,000 queens in one year from 36 mounds along a ditch bank 45 m long by 1 m wide. If

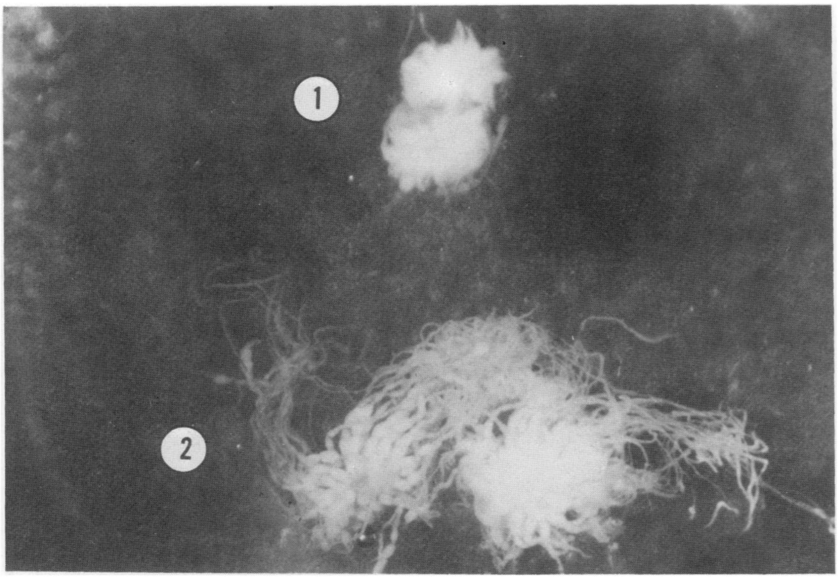

Fig. 3. Two types of ovaries found in queens from polygynous colonies. Class 1 queens had fat bodies, alary muscles, were inseminated and had only a few ovarioles with a single egg. Class 2 queens were inseminated also, but lacked fat body and alary muscles. Every ovariole possessed 3-4 vitellogenic eggs.

we assume the same number of newly-mated queens from nuptial flights alight in monogyne and polygyne populations, it follows that their chances for execution by the foraging monogyne workers will be much greater than by polygyne workers.

Disadvantages must also be associated with adoption. Lowered production of sexuals (Vargo & Fletcher 1987) indicates a decreased genetic input for each queen into future generations. The increased production of brood and workers causes an extreme foraging load and potential lack of food. This undoubtedly is reflected in the production of extremely small workers (Greenberg et al. 1985) and our personal observation that large numbers of dead worker "bone piles" are associated with polygynous populations.

In the long term, it may be that negative aspects of polygyny will work against polygynous *S. invicta* populations. However, in the meantime, they pose a greater hazard to agriculture, public health and the environment (Lofgren 1986), especially to other ant species (Vargo & Porter, in press). Without a doubt, polygyny has added a new dimension to the fire ant problem.

References Cited

BANKS, W. A., C. S. LOFGREN, D. P. JOUVENAZ, C. E. STRINGER, P. M. BISHOP, D. F. WILLIAMS, D. P. WOJCIK, AND B. M. GLANCEY. 1981. Techniques for collecting, rearing, and handling imported fire ants. USDA/SEA publication AAT-S-21, April.

CULPEPPER, G. H. 1953. Status of the imported fire ant in the southern states in July 1953. U.S. Dept. Agric., Agric. Res. Admin., Bur. Entomol. Pl. Quar. E-867. 8 pp.

FLETCHER, D. J. C. 1983. Three newly-discovered polygynous populations of the fire ant, *Solenopsis invicta* and their significance. J. Georgia Entomol. Soc. 18: 538-543.

GLANCEY, B. M., C. H. CRAIG, C. E. STRINGER, AND P. M. BISHOP. 1973. Multiple fertile queens in colonies of the imported fire ant, *Solenopsis invicta*. J. Georgia Entomol. Soc. 8: 237-238.

GLANCEY, B. M., A. GLOVER, AND C. S. LOFGREN. 1981. Pheromone production by virgin queens of *Solenopsis invicta* Buren. Sociobiology 6: 119-121.

→ GLANCEY, B. M., J. C. E. NICKERSON, D. P. WOJCIK, J. TRAGER, W. A. BANKS, AND C. T. ADAMS. 1987. The increasing incidence of the polygynous form of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), in Florida. Florida Entomol. 70: 400-402.

GLANCEY, B. M., C. E. STRINGER, C. H. CRAIG, AND P. M. BISHOP. 1975. An extraodinary case of polygyny in the red imported fire ant. Ann. Entomol. Soc. Amer. 68: 922.

GREENBERG, L., D. J. C. FLETCHER, AND S. B. VINSON. 1985. Differences in worker size and mound distribution in monogynous and polygynous colonies of the fire ant, *Solenopsis invicta* Buren. J. Kansas Entomol. Soc. 58: 9-18.

LOFGREN, C. S. 1986. The economic importance and control of imported fire ants in the United States. pp. 227-256. *in* Economic impact and control of social insects. S. B. Vinson (ed.), Praegor Press, N.Y., N.Y. 421 pp.

LOFGREN, C. S. 1986. History of the imported fire ants in the United States. pp. 36-49. *in* C. S. Lofgren and R. K. Vander Meer (eds.), Fire ants and leaf-cutting ants: Biology and management, Westview Press, Boulder, Colo. 435 pp.

→ LOFGREN, C. S., AND D. F. WILLIAMS. 1984. Polygynous colonies of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae) in Florida. Florida Entomol. 67: 484-486.

→ MIRENDA, J. T., AND S. B. VINSON. 1979. A marking technique for adults of the red imported fire ant. Florida Entomol. 62: 279-281.

MIRENDA, J. T., AND S. B. VINSON. 1982. Single and multiple queen colonies of imported fire ants in Texas. Southwest Entomol. 7: 135-141.

MOREL, L., R. K. VANDER MEER, AND C. S. LOFGREN. In press. Comparison of nestmate recognition between monogynous and polygynous populations of the fire ant, *Solenopsis invicta* Buren. Ann. Entomol. Soc. Am.

ROSS, K. G., AND D. J. C. FLETCHER. 1985. Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. 17: 349-356.

ROSS, K. G., AND D. J. C. FLETCHER. 1986. Dipolid male production—a significant mortality factor in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. 19: 283-291.

SCHERBA, G. 1958. Reproduction, nest orientation and population strucure of an aggregation of mound nests of *Formica ulkei* Emery ("Formicidae"). Insectes Soc. 5: 201-213.

SCHERBA, G. 1961. Nest structure and reproduction in the mound-building ant *Formica opaciventris* Emery in Wyoming. J. New York Entomol. Soc. 69: 71-87.

TSCHINKEL, W. R., AND N. C. E. NIERENBERG. 1983. Possible importance of relatedness in the fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae) in the United States. Ann. Entomol. Soc. Am. 76: 989-991.

VARGO, E. L., AND D. J. C. FLETCHER. 1987. Effect of queen number on the production of sexuals in natural populations of the fire ant, *Solenopsis invicta*. Physiol. Entomol. 12: 109-116.

VARGO, E. L., AND S. D. PORTER. In press. Colony reproduction by budding in the polygyne form of the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am.