age that are injected with atropine also can be trapped in corners, but the deficits in movement systems are quite different (22). L-DOPA, a dopamine agonist, also can reverse akinesia in 6-OHDA–treated rats (23), but circling and other stereotypies such as gnawing, chewing, and grooming can quickly overwhelm forward locomotion in such animals. In combination with atropine, however, L-DOPA appears to produce a more normal form of walking.

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11. Halfway through the present experiments, six experimental and eight control animals were killed to obtain an estimate of the effectiveness of the 6-OHDA treatment in depleting brain catecholamines. (The remaining animals are still being tested behaviorally.) The animals were killed by decapitation, the brains were quickly removed, and a sample of the caudate-putamen (average weight, 14.4 ± .9 mg) from each brain was assayed according to the method of L. L. Zschaeck and V. D. Ramirez, *J. Neural Transm.* **39**, 291 (1976). With this technique we detected as little as 0.062 ng of transmitter per total tissue sample. Compared with controls, the 6-OHDA–treated rats showed little DA in the caudate-putamen (mean, 0.3 ± .16 ng/mg, which is 5.9 percent of control content; four of these animals showed no detectable DA). Noradrenaline was relatively unchanged (mean, .22 ± .03 ng/mg, which is 89 percent of control content). Dissection was carried out macroscopically following landmarks that closely approximated the extent of the caudate-putamen. Thus, our samples may have included some tissue outside of this neural area.
12. All 16 rats given 6-OHDA also were initially aphagic, adipsic, and showed severe sensory neglect as reported previously (2-4). Subsequently, 14 rats advanced to later stages of recovery typical of rats with lateral hypothalamic lesions. They began to eat palatable foods between 10 and 63 days but were still anorectic and required occasional supplementary intragastric feeding. Eventually, six of these rats began to eat dry food, drank water, and required no further supplementary feeding.
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14. Since the permeability of the rat brain to atropine is not great, large doses are often required to penetrate the blood-brain barrier and produce central effects. [I. Q. Whishaw, T. E. Robinson, T. Schallert, *Pharmacol. Biochem. Behav.* **5**, 275 (1976); S. D. Harrison, Jr., T. R. Bosin, R. P. Maickel, *ibid.* **2**, 843 (1974)]. It remains, of course, to be confirmed that such doses produce their behavioral effects simply by anticholinergic action.
15. Running behavior was never observed. The anticholinergic scopolamine (up to 5 mg/kg) also induced comparable excessive walking in additional akinetic, 6-OHDA–treated rats ($N = 4$).
16. In rats made akinetic and cataleptic by daily injections of reserpine (2 mg/kg), atropine sulfate induced excessive short-step walking beginning at about 8 days after the first reserpine injection.
17. For example, a correlation coefficient of .79 between clinging duration and post-atropine activity in 6-OHDA–treated rats (measures taken at least 30 days after surgery) was significant ($P < .01$).
18. A DA receptor blocking agent (haloperidol, 2 mg/kg intraperitoneally) failed to prevent the increase in locomotion brought about by atropine (50 mg/kg) in 6-OHDA–treated rats ($N = 3$).
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31 May 1977; revised 29 August 1977

Intraspecific Defense: Advantage of Social Cooperation Among Paper Wasp Foundresses

Abstract. *Foundress associations and high frequencies of conspecific nest usurpation are most common where densities of* Polistes metricus *are high. Here nest usurpation occurs primarily in single-foundress colonies resulting in multiple-foundress colonies having significantly greater productivities than single-foundress colonies. This is not true at low densities. Conspecific pressures and not predation or parasitism provide an advantage to cooperating wasp foundresses in* P. metricus.

The ecological factors conducive to the evolution of insect sociality are largely undocumented. Some authors have suggested that various selective pressures have conferred an advantage to a social organization (1), while others argue that two major selective forces, predation (or parasitism) and the benefits of group foraging, are responsible for the evolution of group living (2). I now report that in certain habitats, conspecific pressures provide a pronounced selective advantage to individuals of cooperative foundress associations in the paper wasp, *Polistes metricus*.

Many species of *Polistes* are facultatively social before the emergence of the first workers, with varying percentages of the foundresses (gynes) being joined by other overwintered foundresses that, for some reason, have not started nests of their own. Such joining foundresses are commonly dominated by the queen (dominant foundress) and essentially behave as workers. These subordinate foundresses are thought to contribute relatively little to the production of colony reproductives (3). After the emergence of the first workers, colonies are eusocial, with a reproductive division of labor between the queen and her workers, who assist the queen in the production of other workers, males, and potential foundresses (3). Comparative studies of conspecific multiple- and single-foundress colonies in the same habitat should provide evidence of the advantages, if any, accruing to members of a social organization relative to a solitary existence.

Field studies were conducted from 7 April to 1 September 1977 on 74 naturally nesting *P. metricus* colonies located in five sites near Lawrence, Kansas. Site 1 contained 40 wooden boxes (10 by 20 by 30 cm, the open side covered with "chicken wire" mesh) fastened to 1.5-m high poles arranged uniformly in a 5- by 8-m grid. Site 2 contained 20 similar-sized metal boxes dispersed over a 50- by 80-m trailer park. Fourteen of the wooden boxes and eight of the metal boxes were occupied by nesting *P. metricus*, which indicates that nest sites were not limiting factors. The remaining sites (3, 4, and 5) were two sheds and a barn, respectively.

The five sites were divided into two groups and ranked by density within each group. Group 1 consisted of sites 1 and 2, in which wasps nested in boxes; site 1, with boxes 1 m apart, was ranked higher in density than site 2 with boxes 15 m apart. Group 2 consisted of sites 3, 4, and 5, in which wasps nested in buildings; the sites were ranked by the number of nesting wasps per volume (cubic meters) in each building.

Foundresses were multiply marked for individual recognition with Pactra enamel as soon as they began nest construction or joined a nest. Normally colonies were censused at sunrise every other day (73 censuses). At each census, the number of adults, pupae, and larvae at the nest and any evidence of parasitism or predation were recorded.

In addition, behavioral observations were made on 55 separate days (105 hours) with emphasis on colonies at site 3 prior to the emergence of the first workers. Observations were sufficiently detailed to determine dominance ranks of foundresses in multiple-foundress associations.

Single-foundress nests were consistently left unattended more often than multiple-foundress nests in the same habitats ($P < .005$, paired-difference t-test). In 1203 minutes of observation, single- and multiple-foundress colonies were unattended 46.2 and 12.8 percent of the time, respectively. In a comparison of multiple- and single-foundress colonies of the same age (719 minutes of observation), one-, two-, and three-foundress colonies were unattended 29.0, 9.8, and 0.7 percent of the time, respectively. Thus, triple-foundress colonies were almost always attended by at least one foundress, usually the queen.

Although no predation was recorded at the five sites (*4*), all nests with the exception of five at site 4 were parasitized by a pyralid moth (*Chalcoela iphitalis*) or a sarcophagid fly (*Sarcophaga polistensis*). Therefore, almost all nests were parasitized to some extent, and the presence of additional foundresses did not reduce the incidence or apparent severity of parasitism.

Site density rankings within groups paralleled the frequency rankings of multiple-foundress nests at the time of the first worker emergence (Table 1). Thus, high wasp densities were associated with high frequencies of multiple-foundress colonies. In fact, in one densely populated habitat, site 1, all colonies were multiple-foundress nests by the time of emergence of the first workers (Table 1), a frequency much higher than previously reported for this species (*5*).

Multiple-foundress queens survived longer on their nests than either subordinates or single foundresses at all sites (Table 1) [$P < .05$, Student-Newman-Keuls' test (*6*)]. Consideration of colonies not destroyed by human activities showed that, at low wasp densities (site 5), mean nest tenure of single foundresses was not significantly different from that of subordinates of multiple-gyne nests (Table 1). However, at high wasp densities (sites 1 and 3), subordinates had significantly greater average nest tenure than lone foundresses. Multiple-foundress colonies also tended to survive longer (lower mortality of multiple-foundress colonies) than single-foundress colonies at all five sites, as reflected in the increasing proportion of multiple-foundress colonies at the time of emergence of the first workers (Table 1).

The period of the colony cycle prior to the emergence of the first workers was characterized by frequent aggressive encounters between foundresses. Preemergence aggression has also been noted for

Table 1. Habitat comparisons of *P. metricus* colonies.

Site	Group	Colonies (N)			Nesting wasps/m^3 (N)	Multiple-foundress colonies (proportion)		Mean nest tenure (days)					
								Multiple-foundress colonies				Single-foundress colonies	
								Queen		Subordinate			
		Total	Multiple-foundress	Single-foundress		Initial	At worker emergence	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
1*	1	14	7	7		.5	1.0	68.5	14.85	31.38†	18.89	8.93	7.67
2‡	1	8	6	2		.75	.8	62.33	7.03	33.56	21.67	38.0	31.48
3	2	19	9	10	1.0	.5	.6	96.50	9.50	56.30†	32.95	34.31	27.08
4§	2	10	2	8	0.17	.2	.2	76.0	14.14	53.0	18.38	45.33	32.07
5	2	23	2	21	0.03	.1	.1	89.0	0	39.0	0	42.0	25.14

*Nest boxes spaced 1 m apart. †$P < .05$, Student-Newman-Keuls' test, subordinate versus single foundress. ‡Nest boxes spaced 15 to 20 m apart; nests destroyed by human activities on 19 June. §Nests destroyed by human activities on 8 July.

Table 2. Nest usurpation and productivity comparisons between multiple- and single-foundress colonies. Unless otherwise stated, productivities are computed from the mean number of males and females on the nest from 22 to 29 August, a period when nests no longer contained brood. At site 1 only two multiple-foundress colonies were consistently attended by more than one foundress, and only two single-foundress colonies survived to the approximate time of first worker emergence.

Site	Group	Multiple-foundress colonies (N)	Single-foundress colonies (N)	Mean nest usurpations per colony		Productivity			
						Multiple-foundress		Single-foundress	
				Multiple-foundress	Single-foundress	$\bar{X}$	S.D.	$\bar{X}$	S.D.
1*	1	7	7	2.5	7.0	12.57†	12.54	0.86	2.27
2‡	1	6	2	0.16	0.50	14.50	12.80	7.50	10.6
3	2	9	10	0.14	0.75	14.50§	14.16	4.00	4.50
4‡	2	2	8	0.0	0.13	19.50	4.95	18.25	16.81
5	2	2	21	0.0	0.11	8.50	3.54	6.71	9.24

*Mean nest usurpation based on two multiple- and two single-foundress colonies. †$P < .025$, one-tailed t-test. ‡Productivity estimated from last record of total number of workers, pupae, and larvae. §$P < .05$, one-tailed t-test.

closely related species (3). Eighteen falling fights (grappling foundresses fell to the ground) between marked foundresses and potential joiners or usurpers were recorded at nests in sites 1 and 3; on two other occasions a single foundress was observed being killed by a usurper, which then replaced the dead wasp on the nest. Another single foundress remained on a nest as a subordinate after she was aggressively attacked by a wasp which then became the queen. Foundresses from three nests that had lost their broods to parasites were observed making repeated, unsuccessful attempts to either join or usurp remaining multiple-foundress colonies. In addition to the 18 falling fights of marked foundresses, nearly daily records of falling fights between unidentified gynes were noted at site 1, a habitat of high wasp density. Two foundresses were found dead in their nest boxes at site 1, and three injured foundresses were recorded at site 3.

Nest usurpation, in which a marked foundress was replaced by either a marked or unmarked foundress, was more common at single- than at multiple-foundress nests (Table 2, $P < .05$, paired-differences t-test and χ^2 contingency table). This conclusion is strengthened by the fact that the majority of usurpations of nests classified as multiple-foundress (36 of 60) occurred either before subordinates had joined the nest or after they had been lost. When usurpation occurred at a colony containing multiple foundresses, the usurper replaced a subordinate foundress. Nest usurpation was extremely frequent at site 1 and common at site 3, both habitats of high wasp density (Table 2). In fact, at site 1, only two triple-foundress nests displayed sufficient stability to allow ranking of foundresses in dominance. Minimal nest usurpation was recorded at site 5, the habitat of lowest wasp density. At site 5, wasps marked upon initiation of nests normally remained with their nests throughout the season.

Of 15 observations of conspecific nest intrusions into multiple-foundress colonies, the queen and her subordinates cooperated in defense five times. In the remaining ten observations, only one foundress was present on the nest during the intrusion. Here intruders were repelled by queens (six observations) or subordinates (four observations). In a series of experiments conducted before the emergence of the first workers, a live, tethered *P. metricus* gyne was presented to five different multiple-foundress colonies. In each presentation the tethered gyne was jointly attacked by the queen and her subordinates.

At low densities, single-foundress nests were nearly as productive as multiple-foundress colonies (Table 2). These findings are consistent with previous research at site 2 on *P. metricus* with similar wasp densities (7). In addition, a laboratory comparison of productivity in multiple- and single-foundress colonies of *P. fuscatus*, in which nest usurpation was prevented by experimental design, failed to detect significant productivity differences between multiple- and single-foundress colonies (8).

It is always to the queen's advantage, in terms of her longevity and the survival of the colony, to accept joiners. Queens of multiple-foundress colonies undoubtedly enjoy greater longevity than solitary foundresses because they spend more time on the nest and less time foraging (9). However, when wasp densities are low and nest usurpation infrequent, it is not advantageous for most foundresses, in terms of longevity and colony productivity, to join a more dominant foundress. Under these conditions, selection favors foundresses that initiate their own nests rather than join established colonies. If one makes the assumption that joiners are frequently sisters of the queen, it may be that the inclusive fitnesses of both queens and potential joiners are maximized by solitary nest founding at low frequencies of nest usurpation.

Under conditions of high wasp density and concomitant frequent nest usurpation it is in the best interest of less-dominant foundresses, in terms of longevity and colony productivity, to join an established queen rather than attempt to construct a nest. At high densities, single-foundress colonies have little chance of success, and foundresses frequently join established nests or attempt to usurp other colonies. It may be that other selective factors besides conspecific pressures provide an advantage to foundress cooperation in different habitats or for other species.

At high densities, single-foundress colonies, because of frequent nest inattendance or inability to defend against conspecifics, are especially vulnerable to usurpation. Several single-foundress colonies had a series of as many as eight different foundresses (queens) before the emergence of the first workers. When nests are usurped, foundresses use the future workers (brood) of presumably nonrelated gynes to rear their own reproductives. It is not surprising, in view of the aggressiveness of workers, that nest usurpation ceased at the appearance of the first workers.

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References and Notes

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2. R. D. Alexander, *Annu. Rev. Ecol. Syst.* **4**, 325 (1974).
3. The life cycle and behavior of *Polistes* wasps are discussed in detail by M. J. West Eberhard [*Misc. Publ. Mus. Zool. Univ. Mich.* **140**, 1 (1969)]. Subordinate *P. metricus* foundresses are normally driven from the nest by the queen about the time of first worker emergence (G. J. Gamboa, unpublished data).
4. Birds are common nest predators of *P. fuscatus* in Ontario, Canada (D. L. Gibo, personal communication).
5. P. Rau [*Ann. Entomol. Soc. Am.* **33**, 617 (1940)] reported that *P. pallipes* (=*P. metricus*) rarely built nests cooperatively, and M. K. Bohm [thesis, University of Kansas (1972)] recorded 8 of 91 *P. metricus* colonies as having multiple foundresses.
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10. I thank H. Dew for the use of the nest boxes she constructed at site 1; C. A. Callahan, J. Dropkin, B. Heacock, B. Sabel, and S. Wiltjer for their assistance in data collection; and C. D. Michener for his assistance and critical review of the manuscript. Partially supported by NSF grant BMS-75-07654; W. J. Bell and C. D. Michener, principal investigators.

7 October 1977; revised 13 December 1977

Handedness in Duckweed: Double Flowering Fronds Produce Right- and Left-Handed Lineages

Abstract. *Frond lineages of* Lemna perpusilla *Torr. (strain 6746) show handedness with respect to frond emergence sequence and flowering that is related to the pocket of origin on a double flowering mother frond. Flower position is a fundamental manifestation of frond asymmetry.*

The duckweed, *Lemna perpusilla* Torr. (strain 6746) (1) reproduces vegetatively through the production of daughter fronds at two meristematic areas (pockets) within the proximal end of a mother frond (Fig. 1a) (2, 3). Fronds of this clone are said to be left-handed because the first daughter frond emerges

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