Mass Recruitment by Army Ants

Abstract. *A single army ant (Ecitoninae) can attract and direct scores of workers to prey by means of a chemical trail and momentary contact between the recruiter and workers on a raid column. Recruited workers, in turn, attract more ants, resulting in a continuous stream of recruits. While the recruitment mechanism is basically similar, the speed and the number of ants recruited are greater for army ants than for other ants.*

Recruitment to food or nest sites occurs in all major eusocial insect groups: termites, bees, wasps, and ants (*1, 2*). Among ants, recruitment by various chemical and mechanical means has been reported for members of four major subfamilies (Ponerinae, Myrmicinae, Dolichoderinae, and Formicinae) (*1, 3–11*). The discovery of recruitment in the army ants *Eciton hamatum, E. rapax*, and *E. burchelli* adds a fifth subfamily, the Ecitoninae.

Army ants are noted for their highly organized foraging behavior. They hunt in continuous exploratory columns extending sometimes more than 100 m in several directions from their bivouac. We recently found by close observation of marked individuals at the tips of raid columns that there was rapid communication concerning the location of prey.

Army ants are not easily kept, nor do they behave normally under laboratory conditions; hence all experiments were conducted in the field. Under field conditions, however, recruitment is difficult to observe because one must locate prey in advance of the army ants, and workers must be individually marked. In order to observe recruitment closely and standardize the observations we used the following procedure. Potential recruiters were obtained by lowering a wasp nest into a raid column and allowing several ants to attack the nest. Polistine wasp colonies were used because army ants of the genus *Eciton* are highly excited by such prey. Furthermore, many polistines construct nests on leaves or branches that can be detached and carried for some distance. In this way a compact prey source can be brought close to an army ant column for testing.

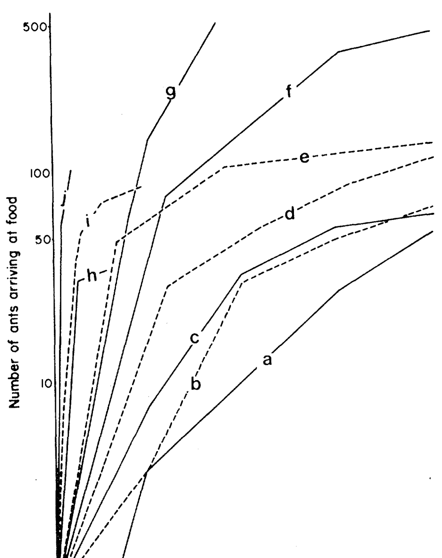

Fig. 1. Comparison of recruitment responses of eight species of ants: (a) *Camponotus sericeus* (*6*), (b) *Crematogaster ashmeadi* (*7*), (c) *Camponotus socius* (*8*), (d) *Pogonomyrmex badius* (*9*), (e) *Formica fusca* (*10*), (f) *Myrmica americana* (*11*), (g) *Solenopsis invicta* (*5*), (h to j) *Eciton hamatum* (present study). *Camponotus sericeus* is a tandem runner; *C. socius* is a group recruiter; all others are mass recruiters.

The nest with the attacking ants was removed from the raid column, placed in a plastic bag, and a test ant was marked with a spot of paint and transferred via a leaf from the wasp nest to vegetation 20 to 30 cm from a raid column. Usually the ant was placed on a vine or branch propped up and directed toward the raid column to serve as a "runway" for the ant and to minimize wandering from the release point. This procedure was extremely effective in inducing recruitment. Of 89 trials, 76 percent were successful.

The recruiter intermittently dragged her gaster as she moved from the release point. A chemical trail was deposited, as was indicated by the subsequent behavior of the ants. Unlike recruiters of most other ant species, when the recruiter reached the raid column, she made no attempt to return to the nest but ran 5 to 10 cm in each direction in the raid column, contacting workers briefly with her antennae and body. Repeatedly, she ran along the path between the raid column and the release point, continually contacting new workers and apparently reinforcing the chemical trail. Within 30 seconds after the recruiter reached the raid column, ants were diverted from the column and followed the recruitment trail. Normally, 50 to 100 ants or more were recruited in the first minute.

If we placed prey at the end of the recruitment path, workers contacting it returned to the raid column and enlisted others. Thus, a continuous stream of ants to the prey was established almost immediately. Surprisingly, if no prey was placed at the end of the recruitment trail, the initial response was the same. That was due, as we learned from observing marked individuals, to an effect we call "secondary recruitment." Brief contact with a recruiter or the trail of a recruiter was sufficient to induce some workers to recruit. Secondary recruitment was not sustained because in the absence of prey recruitment began to decline after about 4 minutes. Also, recruits began to stray from the path and to search the vegetation in the vicinity. Generally, after about 10 minutes all recruits abandoned a recruitment path that did not lead to prey. The initial recruiter, however, sometimes continued her recruitment activity 20 minutes or more although there was little worker response. It should be emphasized that only a single prey contact without subsequent attack or feeding was necessary to initiate such persistent recruitment. Control ants removed from a raid column and released without prey contact did not recruit.

Army ants deposit hindgut material to make foraging trails which guide workers into new raiding territories (*12*). The responses of ants indicate that the trail put down by a recruiter after discovering prey is qualitatively different. Near the distal ends of raid trails, ants usually move ahead a few centimeters and then turn back, but when a recruitment trail is encountered, ants move along the path without stopping. Also, workers on heavily reinforced foraging trails were diverted to the recruitment trail of a single worker. These properties suggest that the recruitment trail is either an entirely different substance from the foraging trail or perhaps a combination of the hindgut material and some other substance such as a mandibular or abdominal-gland secretion.

The function of the recruitment trail and the recruiter's activity were separated by the following bioassays. To test the response of the ants to the recruitment trail alone, we removed the recruiter with a straight-tube aspirator immediately after she reached the raid column but before contact with workers (*13*). Of seven such trials, three resulted in low recruitment (Table 1). The best response was eight recruits, all of which followed the path to the recruiter's release point.

Table 1. Recruiter removal tests. Results are given as numbers recruited.

Recruiter removed	Recruiter replaced*
8	
0	
5	25
3	30
0	9
0	4
0	0

*Replaced after 5 minutes elapsed with no recruitment.

After each of the above trials, the recruiter in the aspirator was returned to the raid column. The effect of replacing her was dramatic; in one trial where only three workers had been recruited without the recruiter, 15 workers were recruited within 15 seconds, and by the end of the trial 30 workers had been recruited. Two tests that were unsuccessful without the recruiter were successful when she was replaced (Table 1).

These experiments show that the recruitment trail contains the essential information necessary for recruitment, but the response is lower than when combined with recruiter activity.

Response of workers to recruiter contact in the absence of a recruitment trail was determined by allowing potential recruiters to drop off a wasp nest to vegetation a few centimeters from a raid column. Ants on the column became visibly excited within seconds, and in a few minutes had ascended vegetation and were randomly searching upward in the vicinity of the wasp nest. The ants searched for almost a half hour, and several workers came within a few centimeters of the nest. Most likely, the ants would have located and attacked the nest except for the intervention of a hard rain. Similar searching has been observed prior to raids on other wasp nests. Thus, even without a recruitment trail, a recruiter releases searching behavior which may lead to prey capture.

Ant recruitment is based primarily on chemical and tactile signals. The expression and information content of those signals vary among ant species and result in diverse recruitment systems. Compared to other recruitment systems, that of army ants is among the most efficient in terms of gathering large numbers of workers quickly. In the relatively primitive system, called "tandem running," constant recruiter contact is necessary for orientation, and only one worker is recruited at a time (*14*). More advanced recruitment systems rely increasingly on chemical trails for orientation. In the system we term "group recruitment," orientation by the recruiter is still essential, but a chemical trail allows a large group of ants to follow a single leader. If the leader is removed, the group disbands (*3*). Group recruitment grades into "mass recruitment" in which the chemical trail is the primary orientator. Here the greatest efficiency is achieved. Less dependency on a single recruiter for orientation results in more continuous recruitment. The recruiter, however, still retains an important role. For example, in *Monomorium venustum* contact with the recruiter mobilizes the ants to search for an odor trail put down by the recruiter outside the nest. The ants do not follow the trail unless previously activated by the recruiter (*4*). In *Solenopsis invicta* the recruiter "alerts" workers to a chemical trail by vibratory antennal contact; the trail itself attracts and orients the recruits (*5*). Similarly, in army ants the recruiter enhances the response of workers to the recruitment trail.

In addition to an efficient recruitment mechanism, the most important feature of army ant foraging is the continuous raid columns that reduce delay between prey encounter and recruitment even 100 m or more from the bivouac. A comparison of initial recruitment rates for army ants and other ants indicates that army-ant recruitment is the highest (Fig. 1) (*4–10*). The comparison is made with some reservation since no standard procedure for measuring recruitment was used in the various studies. The results, however, agree well with expectation; the tandem-running ant, *Camponotus sericeus*, is slowest; the group-recruiter, *C. socius*, is intermediate; and the mass-recruiting *Solenopsis invicta* and *Eciton hamatum* are the fastest.

The adaptive value of rapid mass recruitment is shown by test raids of army ants on wasp nests. Small numbers of ants were readily thrown off nests by wasps, whereas large numbers caused wasps to abandon the nest, leaving their brood behind. The most common prey of army ants are colonies of insects and arthropods often larger than the ants themselves. Such prey can only be subdued by a massive and swift attack requiring efficient communication. The combination of continuous foraging columns, a recruitment trail that attracts and orients workers, secondary recruitment, and persistent recruiters results in the efficient gathering of the large attack force essential for army-ant raiding.

RUTH CHADAB
CARL W. RETTENMEYER
Biological Sciences Group, University of Connecticut, Storrs 06268

References and Notes

1. E. O. Wilson, *The Insect Societies* (Belknap, Cambridge, Mass., 1971), pp. 247–262.
2. M. G. Naumann, in preparation.
3. A. Collart, *Rev. Zool. Afr.* **15**, 249 (1927); C. Baroni Urbani, *Proceedings of the Seventh Congress of the International Union for the Study of Social Insects, London. 1973*, p. 12
4. R. Szlep and T. Jacobi, *Ins. Soc.* **14**, 25 (1967).
5. E. O. Wilson, *Anim. Behav.* **10**, 139 (1962).
6. B. Hölldobler, M. Möglich, U. Maschwitz, *J. Comp. Physiol.* **90**, 108 (1974), figure 2b.
7. R. H. Leuthold, *Psyche* **75**, 343 (1968).
8. B. Hölldobler, *Z. Vergl. Physiol.* **75**, 133 (1971).
9. ——— and E. O. Wilson, *Psyche* **77**, 393 (1970), figure 6a.
10. D. I. Wallis, *Behaviour* **23**, 167 (1964).
11. G. L. Ayre, *Can. Entomol.* **101**, 120 (1969).
12. M. S. Blum and C. A. Portocarrero, *Ann. Entomol. Soc. Am.* **57**, 793 (1964); J. F. Watkins II, *J. Kans. Entomol. Soc.* **37**, 22 (1964).
13. The aspirator consisted of a glass tube attached to a rubber tube with a piece of fine netting inserted between the tubes to stop insects.
14. E. O. Wilson, *Psyche* **66**, 29 (1959).
15. We thank L. Morales and M. E. Rettenmeyer for assistance during fieldwork, the Summer Institute of Linguistics for providing facilities at Limoncocha, Ecuador, and C. W. Schaefer and J. A. Slater for comments on the manuscript. Supported by NSF grant GB-31716 and the University of Connecticut Research Foundation.

31 January 1975; revised 11 March 1975

Heritability of IQ: Methodological Questions

The major thesis of Layzer's article "Heritability analyses of IQ scores: Science or numerology?" may be educed from his conclusion (*1*, p. 1265) that "published analyses of IQ data provide no support whatever for [the] thesis that inequalities in cognitive performance are due largely to genetic differences." From this two corollaries follow, one being that therefore no valid inferences can be drawn in respect to genetic differences in IQ between races, the other being that it is therefore pointless to speculate about the possible emergence of hereditary meritocracies. I will not deal with these corollaries but will attempt to examine the basic argument on which they rest.

This argument reduces to three main criticisms: (i) that the heritability concept is confused and the estimation of heritability (h^2) is feasible only if a number of unrealistic simplifying assumptions are made; (ii) that IQ tests have neither validity nor reliability; (iii) that, apart from the intrinsic defects of IQ tests, most of the data purporting to demonstrate that they measure differences which have some genetic basis are seriously flawed.

It is certainly true that the concept of heritability is complex and estimating it difficult. It seems to me, however, that Layzer compounds and exaggerates this complexity and difficulty. His figure 1, for example, shows the phenotypic responses of three genotypes, x_1, x_2, x_3, to a changing environment, y (in the caption to the figure the x and y are erroneously transposed). Now I find nothing particularly damaging to the heritability concept emerging from the hypothesized relationships depicted. Thus whether h^2 at y_1 should be greater or smaller than at y_2, where the development of the trait is maximal, constitutes an interesting and potentially soluble problem and not some basic and intractable mystery about heritability. Such problems are of great importance in behavior genetics and have, in fact, been considered by a