

rate in either direction.' Yet, upon replotted the same data in terms of period, they conclude that, '... the gradient drops off very steeply at the shorter-period end of the scale (to the right) and much more gradually at the longer period end of the scale (to the left)'. Conflicting statements such as these make it apparent that care must be exerted to assure that the replotted data correctly reflect the actual behaviour of the animals.

Several points must be made to better understand how one can arrive at such opposite conclusions. For the purpose of comparing the original rate data with the same data plotted in terms of period (bottom of Gaioni & Evans' Fig. 1), the abscissa had to be expanded greatly without comparable expansion of the ordinate. Expansion of a graph's axis can sometimes lead to misinterpretations of the data (Huff 1954). For comparative purposes, we include the original figure that appeared in Miller (1983b), from which the top of their Fig. 1 had been redrawn. The expanded abscissa on the redrawn Fig. 1 greatly attenuates the increasing gradient at the slow repetition rates and the decreasing gradient at the fast rates. When these data are replotted in terms of period (bottom of their Fig. 1), the decreasing gradient is re-introduced in a highly exaggerated fashion while the increasing gradient is virtually eliminated. The reason for this is that the points composing the decreasing gradient are highly compressed, while those composing the increasing gradient have been greatly expanded. As Gaioni & Evans note, this is due to the unequal intervals introduced by converting rate to period. What is important to remember is that the actual data have not changed; rather, one of the gradients is rendered more dramatic because of the compression of intervals at shorter periods (or faster repetition rates).

If one examines the repetition rates slower than 1.0 and faster than 1.6 notes/s (i.e. the optimal rates affecting behavioural inhibition) rather than the rates above and below the optimal range (i.e. 0.8–2.0 notes/s), it is apparent that gradients formed by these slower and faster rates are about equal in slope. One cannot properly compare all of the rates above the optimal range with those below the range because the number of rates tested by Miller (1983b) are not equivalent. Miller examined five rates above 2.0 notes/s but only three rates below 0.8 notes/s. However, when one examines a comparable number of rates at equal intervals from the optimal rates of 1.0 and 1.6 notes/s, the slopes of the gradients are about the same. (In fact, the ascending gradient is slightly steeper than the descending gradient, which is opposite to Gaioni & Evans' observation.) Since the level of inhibition is decreased in about equal amounts as the rates are decreased and increased from the optimal rates, a graph that exaggerates one gradient over the other, in a sense, misrepresents the actual behaviour of the animals.

While the first author appreciates the attempt by Gaioni & Evans to further strengthen his claim that the reduction of inhibition occurs fairly abruptly above the optimal range, it should be noted that this has already been demonstrated by him in an earlier article (Miller 1983a). We agree with Gaioni & Evans that period is a useful measure of temporally patterned stimuli, especially when it is readily apparent that such stimuli are not separated into discrete bouts. This was noted by Scoville & Gottlieb (1980). Because in some cases, such as ours, stimuli are segregated into discrete bouts and because the presentation of data in terms of period can be misleading, we feel that, at least for our purposes, repetition rate is a better measure.

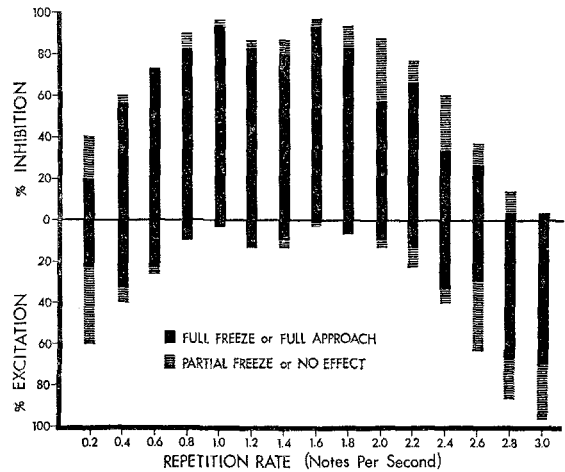


Fig. 1. Percentages of domestic mallard ducklings showing inhibition (Full Freeze and Partial Freeze) and excitation (Full Approach and No Effect) at each of 15 repetition rates of the mallard maternal alarm call ($n=30$ ducklings per repetition rate). Copyright 1983 by John Wiley & Sons, Inc.

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References

- Gaioni, S. J. & Evans, C. S. 1984. The use of rate or period to describe temporally patterned stimuli. *Anim. Behav.*, **32**, 940–241.
- Huff, D. 1954. *How to Lie with Statistics*. New York: Norton.
- Miller, D. B. 1983a. Alarm call responsivity of mallard ducklings: I. The acoustical boundary between behavioral inhibition and excitation. *Dev. Psychobiol.*, **16**, 185–194.
- Miller, D. B. 1983b. Alarm call responsivity of mallard ducklings: II. Perceptual specificity along an acoustical dimension affecting behavioral inhibition. *Dev. Psychobiol.*, **16**, 195–205.
- Scoville, R. & Gottlieb, G. 1980. Development of vocal behaviour in Peking ducklings. *Anim. Behav.*, **28**, 1095–1109.

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Brood-colony Recognition in *Cataglyphis cursor* Worker Ants (Hymenoptera: Formicidae)

In insect sociobiology, one of the central questions is the mechanism of kin recognition (Wilson 1975; Hölldobler & Michener 1980). Recognition of nest-mates has been demonstrated only in the primitively social sweat bee *Lastoglossum zephyrum* where individuals recognize the

degree of relatedness of relatives (Greenberg 1979). Some recent papers on bees and wasps also indicate discrimination between related individuals (Breed 1981; Getz & Smith 1983; Pfenning et al. 1983).

In the ants, colony recognition is frequent, at least in territorial species. This seems to be good evidence for worker/worker kin recognition as demonstrated in *Pseudomyrmex* by Mintzer (1982). So worker/kin recognition may be general in social insects, but we do not have any idea about worker/brood recognition. I studied this problem in a highly social insect, the ant *Cataglyphis cursor*. This species, always monogynous (Cagniant 1976), is very interesting because it is possible to observe numerous worker and brood exchanges between adjacent colonies in the field (De Haro 1981; Pondicq, personal communication). This gives colony recognition biological significance.

Experiments were conducted with two colonies, collected in the same area, each consisting of a queen, about 150 workers, and numerous larvae. Newborn ants were marked on the day of their eclosion with a label applied to the abdomen. Each colony received two groups of young ants: one control group reintroduced to their native colony (total 18 ants) and one experimental group of ants introduced to a foreign colony (total 26 ants). Each worker was followed during 3 weeks, with several daily observation periods of 5 min each, during which all activities were recorded and timed. Behaviour was classified into five groups: Inactivity (isolated, in group of workers, or in groups of workers with brood); Walking in

the Nest; Adult Interactions (interactions between adopted workers were rare and were excluded); Individual Grooming; and Brood Nursing. Data are given as percentages. For each group the median was calculated and the Mann-Whitney *U*-test was used for analysis.

Results are given in Table I. It can be seen that young ants up to 5 days old are Inactive most of the time ($62.3 + 14.2 = 75.5$ for controls). Major differences appear during the first 5 days in their relations with the brood: the control ants remain Inactive on the brood, attending them some of the time, but the adopted workers do not do this (median percentage time Inactive on brood = 14.2 for controls and 0 for adopted ants). This is confirmed by the fact that 15/18 (83%) control ants exhibit this behaviour (Inactive on brood) in comparison with 9/26 (35%) adopted ants. Adopted workers spend less time caring for the brood of their host colony. Later there are also differences between the two groups, especially during the 10–14 day period, for Inactivity in group of workers and Walking in the Nest. Behavioural patterns are sometimes reversed in ants of various ages: for example Inactivity in group is more important at 10–14 days for adopted ants (51.3% versus 27%) but less important at 15–21 days (42% versus 67%).

The following conclusions can be made. Firstly, newly-emerged workers integrate into a foreign colony without difficulty, as described previously by early authors working on other species (Forel 1874; Fielde 1903); secondly, the ontogeny of this process is not the same as in the controls; and thirdly, adopted workers are less

Table I. Change in Time Budget for the Principal Activities of Ants in Relation to their Age

| Behaviour | | Age (days) | | | |
|------------------------|----|------------|-------|-------|-------|
| | | 2–5 | 6–9 | 10–14 | 15–21 |
| Inactivity In group | Ad | 64.2 | 55.25 | 51.3 | 42 |
| | C | 62.3 | 51.6 | 27 | 67 |
| On brood | Ad | 0 | 18.9 | 1.4 | 0 |
| | C | 14.2 | 12.1 | 0 | 6 |
| Walking in the Nest | Ad | 8.3 | 6.7 | 7.8 | 12.9 |
| | C | 5.0 | 8.1 | 20 | 10.5 |
| Adult Interaction | Ad | 3.3 | 2.2 | 0.4 | 2.85 |
| | C | 1.7 | 1.05 | 1 | 0.85 |
| Brood Nursing | Ad | 0 | 1.25 | 0.95 | 0.4 |
| | C | 1.11 | 2.01 | 1.80 | 0.7 |
| Individual Grooming | Ad | 2.77 | 3.33 | 3.05 | 4.4 |
| | C | 2.33 | 2.36 | 3.87 | 2.7 |

Figures given in the table are median % of time.

Ad=adopted; C=controls.

When not indicated, differences are not significant; Mann-Whitney *U*-test.

attracted by host larvae during the first days. We can hypothesize that adopted workers recognize these larvae as non-sisters. Brood species recognition has been suggested in *Myrmica*: Elmes & Wardlaw (1983) exchanged brood amongst different species and found that 'larvae tend to survive best when reared by their own workers, and in some cases were not adopted by foreign workers', yet surviving larvae had normal growth rates.

One alternative explanation is the possible effects of alien workers on brood care: if young alien workers are being recognized it might inhibit brood rearing behaviour; the inhibition must be of short duration, and disappear after 6 days (see Table I: after 6 days the introduced workers behave like the controls). Experiments where broods are exchanged could be useful in testing this possibility.

In spite of these reservations, our data are the first in support of brood kin recognition in ants. It will be interesting to compare the results of exchanges between colonies collected from distant regions as greater conflict may be induced between more distant nests of ants. We plan to use enzymatic electrophoresis as an indication of genetic distance to estimate the relatedness between colonies from the same area and from distant areas. In order to explain the mechanisms of this discrimination we may have to invoke both endogenous and exogenous factors (Jutsum et al. 1979). Learning during the first days of adult life is also possible (Jaisson 1975, 1980; Buckle & Greenberg 1981) and the phenomenon of larval conditioning also needs to be investigated in the future.

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References

- Breed, M. D. 1981. Individual recognition and learning of queen odours by worker honeybees. *Proc. nat. Acad. Sci.*, **78**, 2635–2637.
- Buckle, G. R. & Greenberg, L. 1981. Nest mate recognition in sweat bees (*Lasioglossum zephyrum*). Does an individual recognize its own odour or only odours of its nestmates? *Anim. Behav.*, **29**, 807–809.
- Cagniant, H. 1976. Distribution, écologie et nid de la fourmi *Cataglyphis cursor*. *Vie Milieu*, **26**, (C), 265–276.
- De Haro, A. 1981. Valeur adaptative de la monogynie chez les sociétés de *Cataglyphis iberica* Emery 1906 (Hym. Formicidae). In: *Compte rendu Union Internationale Etude des Insectes Sociaux*. Toulouse: Presses Université Paul Sabatier.
- Elmes, G. W. & Wardlaw, J. C. 1983. A comparison of the effect of a queen upon the development of large hibernated larvae of six species of the genus *Myrmica* (Hym. Formicidae). *Insectes soc.*, **30**, 134–148.
- Fielde, A. 1903. Artificial mixed nests of ants. *Biol. Bull. mar. Biol. Lab.*, **5**, 320–325.
- Forel, A. 1874. *Les Fourmis de la Suisse*. Basel, Switzerland: H. Georg.
- Getz, W. M. & Smith, K. 1983. Genetic kin recognition: honey bees discriminate between full and half sisters. *Nature, Lond.*, **302**, 147–148.
- Greenberg, L. 1979. Genetic component of bee odor in kin recognition. *Science, N.Y.*, **206**, 1095–1097.
- Hölldobler, B. & Michener, C. D. 1980. Mechanisms of identification and discrimination in social Hymenoptera. In: *Evolution of Social Behavior*, (Ed. by H. Markl), pp. 35–58. Weinheim, West Germany: Verlag Chemie GmbH.
- Jaisson, P. 1975. L'imprégnation dans l'ontogénèse des comportements de soins aux cocons chez la jeune fourmi rousse (*Formica polyctena*). *Behaviour*, **52**, 1–37.
- Jaisson, P. 1980. Environmental preference induced experimentally in ants (Hym. Formicidae). *Nature, Lond.*, **286**, 388–389.
- Jutsum, A. R., Saunders, T. S. & Cherrett, J. M. 1979. Intraspecific aggression in the leaf-cutting ant *Acromyrmex octospinosus*. *Anim. Behav.*, **27**, 839–844.
- Mintzer, A. 1982. Nestmate recognition and incompatibility between colonies of the acacia-ant *Pseudomyrmex ferruginea*. *Behav. Ecol. Sociobiol.*, **10**, 165–168.
- Pfenning, D. W., Reeve, H. K. & Shellman, J. S. 1983. A learned component of nest-mate discrimination in workers of a social wasp, *Polistes* (Hym. Vespidae). *Anim. Behav.*, **31**, 412–416.
- Wilson, E. O. 1975. *Sociobiology: the New Synthesis*. Cambridge, Mass.: Harvard University Press.

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