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INDIVIDUAL ANTS SPECIALIZE ON PARTICULAR APHID HERDS (HYMENOPTERA: FORMICIDAE; HOMOPTERA: APHIDIDAE)

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Abstract.—Three ant-aphid associations were each observed for ten consecutive days. Eighty-one percent of 103 individually-marked ant foragers visited only one of many conspecific aphid groups on a particular plant. Specialization on particular herds may help ants maximize their net energy gain from aphid honeydew.

Ant species have coevolved to different degrees with trophobionts, homopterans and lepidopterans from which they acquire food (Wilson, 1971). For example, ant tending and obtaining "honeydew" from aphids is commonly seen in many habitats and has been studied numerous times (see Auclair, 1963, and Way, 1963, for authoritative reviews of this symbiosis). Because there appear to be no reports of individual ant foragers specializing on particular herds of honeydew-producing aphids, we relate our discoveries regarding this specialization and speculate on its adaptive significance.

Three associations of ants and aphids were observed from 29 June to 4 August 1978 on the property of the University of Michigan Biological Station, Cheboygan County, Michigan. Association 1 was the ant *Formica subnuda* Emery tending the aphids *Pterocomma* sp. on branches and *Chaitophorus nigrae* Oestlund on leaves of *Salix interior* Rowlee. Association 2 was *Formica subsericea* Say tending *C. nigrae* on leaves of *S. interior*. Association 3 was *Camponotus noveboracensis* (Fitch) tending *Chaitophorus* sp. on petioles of *Populus tremuloides* Michx. Each association was examined for ten consecutive days from 0215 to 2300 hours and from one to four times ($\bar{x} = 2$) per day. Ants were removed from aphid herds and marked for individual recognition on their thoraces and gasters with fast-drying enamel paints and replaced on herds within 3 min.

A total of 158 ants was marked in the three associations; 65% of them (103) were seen again on at least one of the ten days during which associations were observed. Eighty-one percent of the 103 ants were seen at only one of all conspecific herds on particular plants. Ten percent changed herds once; 6%, twice; and 3%, thrice. The ants showed a mean herd constancy

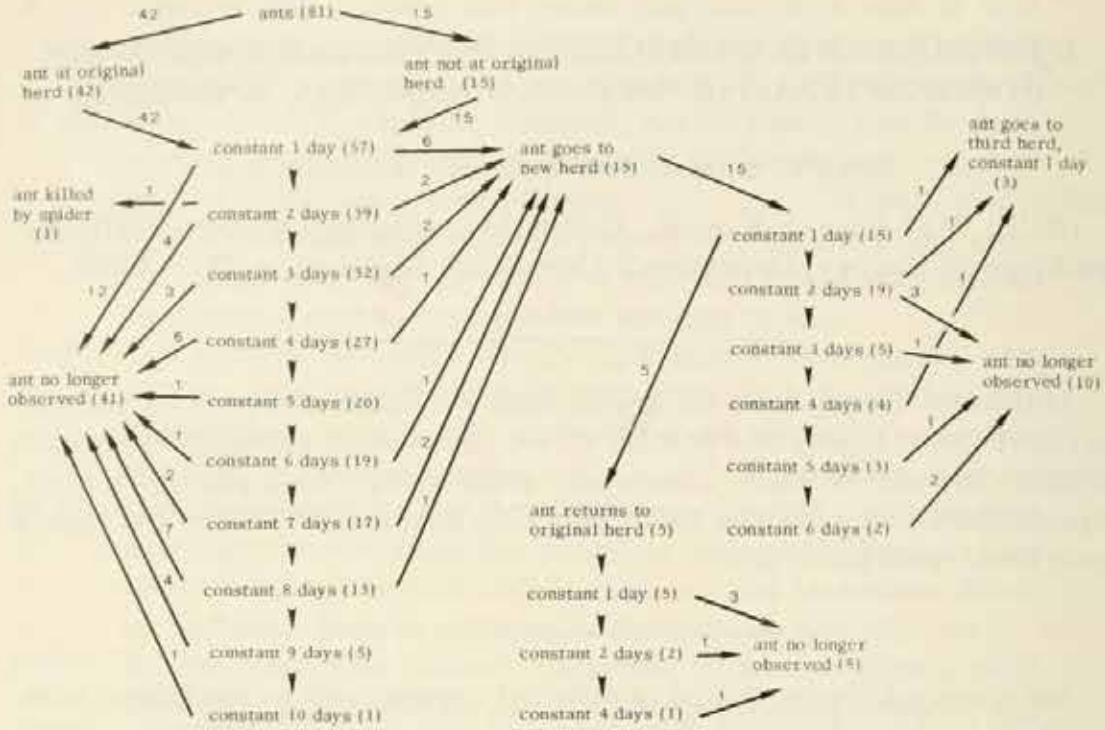

Fig. 1. Movements of individually-marked *Formica subnuda* foragers among herds of *Pterocomma* aphids all on a 6 m^3 bush of *Salix interior*, approximating the bush as a cylinder. Eighty-one ants were marked. After marking, 24 ants disappeared, 42 ants returned to their original herds, and 15 moved to a second herd. Five of the 15 ants returned to their original herds, and 3 moved to a third herd. Observations were made for ten consecutive days.

of four days; such a short constancy may be due to mortality or task changing. Movements of *Pterocomma*-tending ants of association 1, which had the greatest number of marked ants, are shown in Fig. 1. Ants of associations 2 and 3 behaved similarly. Ants in an association did not appear to interact aggressively with one another, suggesting that they were from the same colony. In addition, a short study at the Biological Station showed that individually-marked ants of *Formica subsericea* also specialized on particular groups of honeydew-producing *Kermes kingi* Cockerell (Kermesidae) of *Quercus rubra* L.

Ants that changed herds usually went to the nearest adjacent herd, based on the distances that they would have to travel along stems. In association 1, 14 of 15 ants changed to the nearest adjacent herd. This is significantly different from a hypothetical case in which all ants moved to a herd which was not the nearest one to their original herd ($P = 0.0005$, Fisher's exact probability test). In association 2, 5 of 6 ants changed to the nearest herd ($P = 0.0076$), and in association 3, 5 of 8 ants changed to the nearest herd

($P > 0.05$). Association 3 ants may have moved to closest herds based on distances over leaves rather than stems.

An experiment was attempted to examine the possibility that ants return to their original herds after being artificially removed from them and placed at new herds. However, the ants were extremely wary and jumped off plants when they were approached within 3 cm, or else they jumped off after they were placed on new herds. Their wariness may have resulted from their previous experiences with an investigator during marking.

In conclusion, this study reveals that individual ants of the same colony tend to visit only one or few of many herds of conspecific aphids on a particular plant for up to ten days and perhaps longer. This specialization on particular herds may be an integral part of such ants maximizing their net energy gains from aphids. By being constant to particular herds, these ants could move directly between such herds and their nests and avoid wasting time and energy in searching for untended aphids or competing with other aphid-tending ants. Further study is needed to elucidate the adaptive significance of this ant specialization; whether the ants recognize particular aphid herds or are constant to certain locations on aphid-harboring plants; why ants "decide" to tend one aphid herd rather than another; why ants change herds; and related subjects. The phenomenon of *Ortsreu*, patrolling only certain portions of a colonial feeding territory by a particular ant forager (Oster and Wilson, 1978), is likely to be related to aphid herd specialization. Finally, our investigation indicates that studies of ergonomic optimalization in honeydew-collecting insects should take into consideration that foragers may specialize on particular groups of honeydew-producing insects.

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