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Facultative and obligate slave making in *Formica* ants

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Abstract Here we show for the first time that the presumed facultative slave-making ant *Formica subintegra* does not activate outside its nest until July and August, when it raids slaves. A comparative behavioral study of seasonal and daily activities, retrieval of prey, and nest maintenance of *F. subintegra*, the obligate slavemaker *Polyergus breviceps*, and the facultative *Formica subnuda*, shows that the behavioral repertory of *F. subintegra* closely resembles that of *P. breviceps* and clearly differs from the repertory of *F. subnuda*. Unlike *P. breviceps*, *F. subintegra* has retained some nest-building activity which, owing to lack of competence, does not contribute to nest maintenance. We suggested earlier that *F. subintegra* is probably an obligate slavemaker, because it always has in its colonies a large proportion of slaves of the total workforce, whereas *F. subnuda* fares well even without slaves. This, coupled with no foraging in early summer and a raiding period later on, strongly suggests that *F. subintegra* is an obligate slave-making ant.

Introduction

Slave-making ants raid nests of other ant species, capture the developing offspring, and rear them to be slave workers. Facultative slavemakers are able to nest like free-living species, and colonies without slaves are often found. Obligate slavemakers, presumably owing to behavioral and morphological specializations to raiding, depend on slaves for their colony tasks and, thus, usually have in their colonies a large proportion of slaves of the total workforce (Wilson 1971).

The *Formica sanguinea* group consists of 12 slave-makers, ten in North America (Smith 1979; Snelling and Buren 1985), and two in Eurasia (Dlusskij 1967). Because they do not have external morphological modifications for raiding, and some species often live without slaves, they have all been regarded as facultative slave-makers (Creighton 1950; Hölldobler and Wilson 1990). *Formica subintegra*, however, has been observed to have plenty of slaves in its colonies (Talbot and Kennedy 1940), and it has a hypertrophied Dufour's gland in the gaster, which is a derived feature in *Formica*, implying specialized slavemaking (Regnier and Wilson 1971; Wilson and Regnier 1971).

We have previously compared the slavemaking of two members of the *sanguinea* group with that of the obligate slavemaker *Polyergus breviceps* (Savolainen and Deslippe 1996). We found that all colonies of *F. subintegra* had a large proportion of slaves, which nearly equaled the proportion of slaves in colonies of *P. breviceps*. In contrast, only one third of the *Formica subnuda* colonies had slaves and, when present, their proportion ranged between 1% and 30%. Because of these similarities in slave making between *F. subintegra* and *P. breviceps*, and differences between *F. subintegra* and *F. subnuda*, we suggested that *F. subintegra* is probably an obligate slavemaker.

Here we study the behavior of these slavemakers and their slaves in some of the most fundamental colony tasks: seasonal and daily activities, foraging for insect prey, and nest maintenance. Comparison of the behavior of *F. subintegra* in these tasks to those of a facultative and obligate slavemaker is likely to demonstrate whether *F. subintegra* truly is an obligate slavemaker.

Materials and methods

We conducted the field work in Elk Island National Park (53°37'N, 112°58'W) in western Canada between May and September 1992 (for details of the habitat and species, see Savolainen and Deslippe 1996). We selected five mature colonies of *F. subintegra*, *F. subnuda* and *P. breviceps*, which contained *Formica*

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podzolica slaves, and five free-living colonies of *F. podzolica*. We counted the proportion of slaves according to Savolainen and Deslippe (1996).

To observe the activity of ants leaving the nest, we divided the area around each mound at 50 cm from the mound into eight sectors and marked them. We observed each of the eight sectors in turn for 1 min each and noted all individuals leaving the sector, thus obtaining the total activity of the mound in 1 min. During each 1-min observation bout we measured the ambient temperature on the ground surface near each mound. We observed all five replicate nests of each species once a month from May to July on days without rain every second hour between 0800 and 2200 hours. Owing to rain we managed to observe about three nests of each species in August and September.

Before measuring the activity of ants, we counted the number of ants and observed their behavior on each mound surface within a round metal frame (diameter 27 cm, 5.7 dm²). This gives an estimate, albeit of a small area, of the activity of ants maintaining the nest, and opening and closing nest entrances in the mornings and evenings.

Between 27 May and 30 June we collected insect prey from foraging ants returning to their nest. We chose an area off the mound where the number of ants leaving the nest was highest. We collected the booty from the first 50 *F. podzolica* foragers bringing an insect to their nest. At the same time, we collected prey items

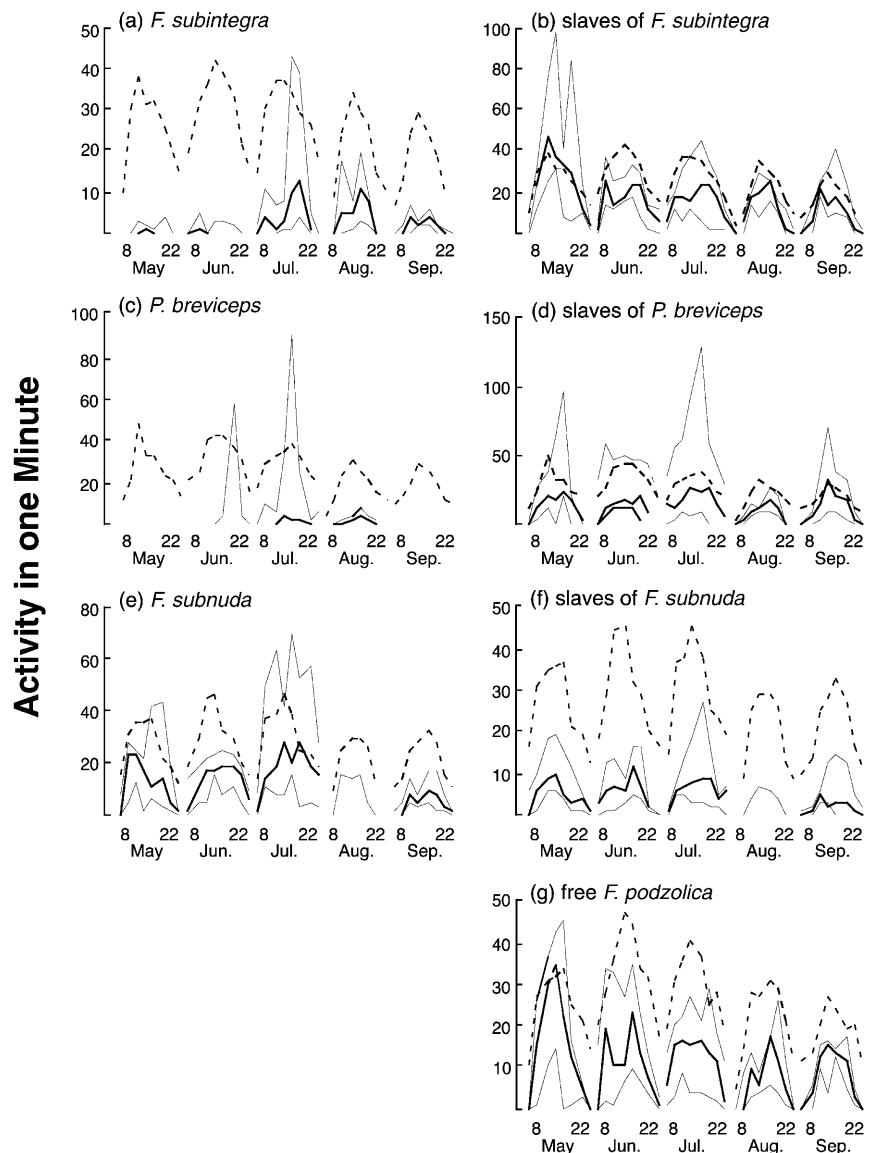
from foraging slavemakers, if any, of each colony. We analyzed the data using Stata 7.0 (Stata Corporation 2001).

Results

F. subintegra did not activate until July (Fig. 1a). It was less often present in May–June (62 absent vs 13 present) than in July–September (37 absent vs 51 present) ($G=29.46$, $df=1$, $P<0.001$). *P. breviceps* raided in June and July (Fig. 1c). The activity of *F. subnuda* did not change between May–June (7 absent vs 69 present) and July–September (13 absent vs 67 present) ($G=1.75$, $df=1$, $P=0.19$; see Fig. 1e). The slaves (Fig. 1b, d, f) and free-living *F. podzolica* (Fig. 1g) were active all summer. The median proportions of slaves of the total workforce were 87, 83 and 10% in the five colonies of *P. breviceps*, *F. subintegra* and *F. subnuda*, respectively.

The activities of *F. subintegra* and *P. breviceps* resulted from seven and three slave raids, respectively. In the

Fig. 1 Seasonal (May–September) and daily (between 0800 and 2200 hours) activities of **a** *Formica subintegra*, **b** slaves of *F. subintegra*, **c** *Polyergus breviceps*, **d** slaves of *P. breviceps*, **e** *Formica subnuda*, **f** slaves of *F. subnuda* and **g** free-living *Formica podzolica*; dark solid line gives median activity of individuals per minute of five nest replicates, fine solid lines minimum and maximum activities, and the dashed line is mean ambient temperature. Only one of five *F. subnuda* nests was studied in August. Note the different scales of the figures



biggest raid of *F. subintegra* (27 July) the number of individuals increased from three to 43 per minute between 1400 and 1600 hours (temperature 30 and 26°C, respectively), and then declined to nine individuals per minute till 1800 hours (21°C). Three raids of *F. subintegra* targeted previously raided colonies of *F. podzolica*. In the biggest raid of *P. breviceps* (25 July) the numbers of individuals were five, 93 and 94 individuals per minute at 1200, 1400 and 1600 hours, respectively (temperatures at those times were 33, 35, and 33°C), and then declined to 13 individuals per minute till 1800 hours (26°C).

We saw four raids of *F. subnuda*, the first of which took place in May. In two raids, some of the *F. subnuda* workers tended aphids in nearby trees, the others raided a nest. In these raids, serious fighting between the slave-makers and the workers of the raided colonies took place. Once (on 27 July) *F. subnuda* attacked two *F. podzolica* colonies simultaneously both at 10 m from their mound, and at least 100 *F. podzolica* workers defended their colony against the raiders, injuring a large number of *F. subnuda* workers. The *F. subnuda* ants usually managed to bring only a few offspring, if available, to their nest.

F. subintegra and *P. breviceps* did not bring any insect prey to their nests when items were collected; but later we saw two *F. subintegra* workers carrying an insect to the mound. While *F. podzolica* carried 50 items to each of the five colonies (250 items), *F. subnuda* brought 17, 21, 27, 67, and 68 items (200 items) during the same time period (Wilcoxon signed-rank test, $n=5$, $P=0.22$). When the item numbers were weighted by the activities of the species, *F. podzolica* brought significantly more items to the nest than *F. subnuda* (Wilcoxon signed-rank test, $n=5$, $P=0.043$). The activities were, however, measured either two weeks before or after we collected the items.

F. subintegra workers were less often present on the mound surface in May–June (69 absent vs 6 present) than in July–September (44 absent vs 44 present) ($G=37.16$, $df=1$, $P<0.001$). The numbers on the mound surface correlated positively with the activity ($r_s=0.51$, $n=163$, $P<0.001$). The largest numbers of *F. subintegra* within the frame were 17 and 19 individuals at 1800 hours in July and August, respectively. The *F. subintegra* workers were moving soil particles in their mandibles along with their slaves to open and close nest entrances. A closer look showed that *F. subintegra* moved soil from one spot to another, regardless of the nest entrances, which did not contribute to the maintenance of the nests.

P. breviceps was infrequent on the mound surface: 69 absent vs 6 present in May–June, 67 absent vs 13 present in July–September ($G=2.51$, $df=1$, $P=0.11$). We never saw *P. breviceps* workers move soil in their mandibles on the mound surface. *F. subnuda* was active on the mound surface all summer: 34 absent vs 42 present in May–June, and 39 absent vs 41 present in July–September ($G=0.25$, $df=1$, $P=0.62$); the maximum number was nine individuals at 1600 hours in May.

Discussion

How does behavior affect the course of an organism's evolution? According to Mayr (1963) a shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behavior; the other adaptations to the new niche, particularly the structural ones, are acquired secondarily. Numerous examples suggest that behavioral change often precedes external morphological evolution (Wcislo 1989). Thus, behavior has probably been a key factor in the evolution of animal diversity (Futuyma 1998).

Like most other Hymenopteran facultative social parasites (Wcislo 1989), *F. subnuda* does not have any morphological modifications to slave making, and colonies without slaves are often found (Savolainen and Deslippe 1996). Lack of specialization is seen in its raiding behavior which resembles the predatory behavior and territorial exclusion of the territorial *Formica* species (Mabelis 1979; Savolainen and Vepsäläinen 1989) more than specialized slave raiding. The raids of *F. subnuda* last for several hours, intensive fighting takes place, and in the end dead ants of both species abound around the nest (this study). Similar observations have been made on the North American *Formica wheeleri* (Topoff and Zimmerli 1991) and the European *Formica sanguinea* (Grasso et al. 1992; Mori et al. 2000). Also, *F. subnuda* may raid *F. podzolica* colonies in May when only eggs are available in the nests (this study). *F. subintegra* and *P. breviceps* do not experience such raiding costs.

The behaviors of *F. subnuda* and *F. subintegra* are dramatically different. *F. subintegra* has a large proportion of slaves in its colonies (Talbot and Kennedy 1940; Savolainen and Deslippe 1996), and an obvious raiding season can be distinguished (Talbot and Kennedy 1940; this study). Presumably owing to the enlarged Dufour's gland and its potent chemicals (Regnier and Wilson 1971) *F. subintegra* is able to maintain a large proportion of slaves in its colonies (Savolainen and Deslippe 1996), a condition typical to obligate slavemakers of the genus *Polyergus* (Talbot 1967; Hölldobler and Wilson 1990; Savolainen and Deslippe 1996).

To be an obligate slavemaker implies, by definition, the inability to carry out successfully the basic colony tasks (Wilson 1971). In slavemakers some behaviors are greatly reduced or completely absent when the functions are filled with slaves (Wilson 1975; Mori and Le Moli 1988). But can these behaviors be induced when the slaves are removed? Wilson (1975) removed the slaves from the obligate slave-making ant *Leptothorax duloticus*. After the removal, the behavioral repertoire of the slavemakers expanded dramatically: the *L. duloticus* workers still never carried or handled any insect prey, but they took part in brood rearing and nest building. In nest building the workers carried pieces of nest material around in their mandibles but did not succeed in placing them together to form a plug at the nest entrance. Thus, the behavioral modifications of *L. duloticus* no longer allowed survival without the slaves.

We did not take slaves away from the *F. subintegra* colonies, but our behavioral observations on *F. subintegra* correspond to the behavior of slaveless *L. duloticus* workers. Like *L. duloticus*, *F. subintegra* almost never carried any insect prey. It tried to maintain its nest along with the slaves, but lack of competence characterized the behavior. Thus, it is possible that *F. subintegra* would not survive without the slaves either. A preliminary molecular phylogeny shows that *F. subintegra* shares a common ancestor with the rest of the North American members of the *sanguinea* group (R. Savolainen, unpublished). Thus, the separate evolutionary history of *F. subintegra* in North America, and the ecological and behavioral observations on its slavemaking (Savolainen and Deslippe 1996; this study) strongly indicate that *F. subintegra* is an obligate slave-making ant.

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