

LETTER TO THE EDITOR

Apparent task specialization among cofounding ant queens

Jürgen Heinze  and Sarah Koller

LS Zoologie/Evolutionsbiologie, Universität Regensburg, Regensburg, Germany

Dear Editor,

The establishment of a new colony is a critical phase in the life of an insect society. Young ant queens may avoid the high risks of solitary founding by starting new colonies together with other young queens (pleometrosis). Foundress associations may produce first workers faster and have a higher survival rate than solitary foundresses (Bernasconi & Strassmann, 1999). Because cofoundresses are typically not related, pleometrosis is rarely associated with a clear division of labor (Jeanson & Fewell, 2008). Instead, queens share tasks and later use to fight for nest ownership (Heinze, 1993; Bernasconi & Strassmann, 1999). Nevertheless, in a few cases cooperative founding is associated with division of labor, and one cofoundress specializes on risky tasks, such as nest excavation (Helms Cahan & Fewell, 2004) or foraging (Rissing *et al.*, 1989; Kolmer & Heinze, 2000).

We investigated the behavior of cofounding queens of the cosmopolitan tramp ant *Cardiocondyla obscurior* (Wheeler, 1929). While most colonies of this ant species are founded by budding of mature colonies (Stuart, 1990; Schrempf & Heinze, 2007), the finding of nests with grouped queens (Heinze & Delabie, 2005) suggests the occasional occurrence of pleometrosis. We set up 58 foundress associations in two seasonally distinct observation periods (31 in February, 27 in July 2019). Cofounding queens came from the same stock colonies originally collected in Ilhéus, Brazil in 2009. Cofoundresses were thus related, which reflects the structure of the invasive populations of *C. obscurior*, in which all individuals are genetically very similar (e.g., Heinze *et al.*, 2006). Three queen pupae, one wingless ergatoid male, five workers, and five larvae all from the same colony were

placed into 10 cm Ø Petri dishes with a regularly moistened plaster floor and a 1 cm Ø cavity serving as nest. Colonies were kept in incubators at 12 h 28 °C : 12 h 23 °C day–night cycles and provided with diluted honey, *Drosophila*, and chopped cockroaches at least twice per week. After queens had mated and shed their wings, we removed the male and the workers, marked queens with Edding® paint markers and recorded their location (in the nest, outside of the nest) by scan sampling (scan duration approximately 10 s, scan interval ≥ 15 min). In period 1 the position of queens was recorded on 2–30 days (median 11 days) spread over 2–41 days (median 14 days; 27–447 scans per nest, median 164). In period 2, colonies were scanned until two of the three queens had died (57–356 scans per nest, median 117 scans, during 5–35 days, median 13 days, spread over 35–85 days, median 52 days). Queens found dead were dissected under a Leica EZ4 binocular microscope to determine their reproductive status. Alitrunk length was measured using a Wild M10 microscope at 125×. Ovarian development and alitrunk length were evaluated blindly without knowing the foraging status of queens. To determine whether foraging influences life span, we compared the longevity of queens that contributed to <20% of the observations outside with those of queens that contributed to >50%. Statistical analyses were conducted using Statistica 6.0 (StatSoft, Tulsa, OK).

Queens were observed in the foraging arena during approximately 1/10 of the scans (period 1: median 14.8%; period 2: 9.4%) and differed significantly in their contributions to the outside observations: one queen spent almost no time outside, another contributed to most of the outside observations, and the third queen showed intermediate values (Fig. 1). The shares of queens in outside observations differed significantly from an equal contribution in 18 of 31 colonies from period 1 and 12 of 27 colonies from period 2 (χ^2 -tests, $P < 0.05$ corrected for multiple comparisons following Benjamini & Hochberg, 1995). In the remaining colonies, similar differences in location were observed, but the total number of outside

Correspondence: Jürgen Heinze, LS Zoologie / Evolutionsbiologie, Universität Regensburg, 93040 Regensburg, Germany. Tel: +49 941 943 2475; fax: +49 941 943 3304; email: juergen.heinze@ur.de

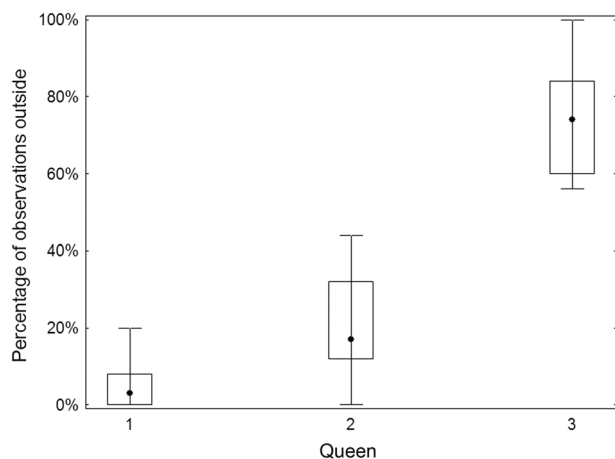


Fig. 1 Apparent task specialization of foundress associations of the ant *Cardiocondyla obscurior*. Within each of 58 three-queen associations, individual queens were ranked according to their share in all observations of queens from this founding association being outside of the nest. Shown are medians, quartiles, and ranges of the percentages.

observations was too low to reach statistical significance: the P -values of individual χ^2 -tests were negatively correlated with the number of outside observations (Spearman's rank correlation, $n = 58$, $r_s = -0.661$, $P < 0.00001$). Queens in the foraging arena were occasionally seen feeding or carrying food items. No aggression among queens could be observed.

Queens laid eggs in all experimental colonies. Dissections revealed sperm in the spermathecae of 49 of 80 queens, three spermathecae were empty. The remaining 28 queens had already decayed. The ovaries of 26 of the 49 mated queens contained maturing oocytes, in other queens the ovarioles were elongated but without oocytes. Queens with and without oocytes did not differ in the percentage of outside observations (median, quartiles, 17 queens with eggs: 25%, 8%, 46%; 21 queens without eggs: 38%, 13%, 59%; Mann–Whitney U -test, $U = 155$, $P = 0.499$). Similarly, 11 queens responsible for most of the observations outside the nest did not differ in alitrunk length from 15 queens, which spent most time inside ($U = 147.5$, $P = 0.959$). Across all colonies, the frequency of staying outside did not have an influence on queen life span ($n = 21$ colonies, six colonies, in which all queens contributed to more than 20% of the outside observations, excluded. Life span of queens contributing to <20% of outside observations vs. life span of queens contributing to >50% of the outside observations: log-rank test with censored data, $WW = 1.309$, $P = 0.659$; Fig. 2).

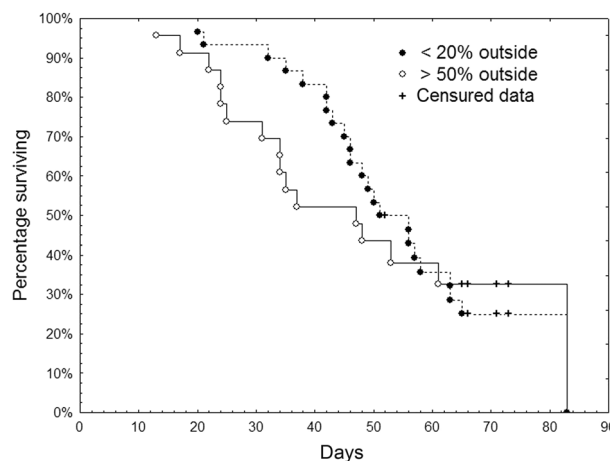


Fig. 2 Survival rate of queens in 13 founding associations of *Cardiocondyla obscurior* with significant task specialization. Shown are survival rates of queens contributing to <20% or >50% of the observations during which one of the queens was observed outside of the nest.

Our study suggests task specialization of particular *C. obscurior* foundresses similar to that in two other ant species, in which founding queens forage. Like in *Acromyrmex versicolor* (Rissing *et al.*, 1989), but in contrast to *Neoponera inversa* (Kolmer & Heinze, 2000), we could not observe aggressive interactions that might have forced individuals to take over foraging. Queens engaging in more than 50% of the outside activities differed neither in body size nor in reproductive status from queens that stayed mostly inside. It therefore remains unclear how queens allocate tasks. Individual queens might vary in their propensity to forage, and the differences among queens might have emerged without social feedback (e.g., Bonabeau *et al.*, 1998). Alternatively, task specialization might be driven by inconspicuous antagonism and social feedback, which we failed to observe. Foraging-specialists and nest queens did not differ in survival rate. This might be different under natural conditions, where queens would have to forage over longer distances than in our artificial nests and would be exposed to predators and pathogens. Given that most mature colonies of *C. obscurior* contain multiple queens (Heinze & Delabie, 2005) it is likely that surviving cofoundresses continue to live together after successfully starting a new colony. Task specialization and division of labor might explain the higher success of foundress associations of *C. obscurior* compared to that of solitary queens: 10 of 20 groups of four queens, but only two of 40 solitary queens managed to rear brood to the pupal stage (Stuart, 1990; see also Schrempf & Heinze, 2007).

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Disclosure

The authors declare that they have no conflicts of interest.

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