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QUEENS SURVIVAL DURING PLEOMETROSIS IN MONOGYNOUS AND POLYGYNOUS ANT SPECIES (HYMENOPTERA, FORMICIDAE)

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Queens Survival during Pleometrosis in Monogynous and Polygynous Ant Species (Hymenoptera, Formicidae). Stukalyuk, S. & Stelia, V. — The objective of this study is to examine the survival rates of queens in pleometrotic groups of two ant species: *Lasius paralienus* Seifert, 1992 (a monogynous species) and *Solenopsis fugax* (Latreille, 1798) (a polygynous species). The study was conducted in 2020 and 2021 in Odesa, Ukraine. After the nuptial flight, 45 gynes of *S. fugax* and 64 of *L. paralienus* were captured. *Solenopsis fugax* were seated in groups of 5 (9 experiments in total), *L. paralienus* in groups of 5 (8 experiments) and 3 specimens (8 experiments). For *L. paralienus*, the effect of pleometrotic group size on the queens was tested. Maximum duration of the experiment was 115 days for *S. fugax* and 293 days for *L. paralienus* (until only one queen remains or the number of queens does not change significantly). The number of queens (alive, dead and killed), workers and brood were counted once a week. There were no significant differences in mortality between groups of 3 and 5 queens of *Lasius paralienus* ants ($p = 0.06$). The period of main queen mortality occurs shortly after founding of the pleometrotic group. Mortality continues to rise after the emergence of a group of 10–30 workers until only 1 queen remains in group of *Lasius*. When *L. paralienus* queens died naturally, the average number of workers was 7.5, the average number of larvae was 3.32 and the average number of pupae was 5.16. However, when they died due to fights, the average number of workers was 23.89, the average number of larvae was 8.89 and the average number of pupae was 13.89. In the case of *S. fugax*, when queens died naturally, the average number of workers was 5.43. A comparison of the total queen mortality in the pleometrotic groups of the two ant species showed that most queens survive in the polygynous *S. fugax*, whereas all but one die in the monogynous *Lasius*.

Key words: pleometrosis, haplometrosis, *Lasius paralienus*, *Solenopsis fugax*, queens.

Introduction

Ants (Hymenoptera, Formicidae) have several strategies for founding new colonies. These strategies include haplometrosis (the founding of a new colony by a queen after the nuptial flight), pleometrosis (the founding of a new colony by several queens simultaneously) (Zakharov, 1991; 2015). Pleometrosis is common in ants (Rissing et al., 2000). In *L. niger,* for example, up to 18 % of new colonies are founded by multiple (Sommer & Hölldobler, 1995), while in other species of ants this figure can be as high as 40 % (Trunzer et al., 1998).

Pleometrosis ensures rapid colony growth. Additionally, in species with claustral colony founding, such as *Lasius*, queens do not go outside for foraging, which can reduce the likelihood of predation (Diehl-Fleig & De Araújo, 1996; Kolmer & Heinze, 2000). In addition, brood replenishment can occur through plunder of other ant colonies or colony mergers, which is a behaviour observed in some ant species regardless of whether they exhibit haplometrosis or pleometrosis (Balas & Adams, 1996; Rissing & Pollock, 1991; Nonacs, 1993; Eriksson et al., 2019).

Fights between queens after the hatching of the first generation of workers are characteristic of monogynous species such as *L. niger*. In most cases, the more aggressive queen wins these fights and remains alone (Sommer & Hölldobler, 1995; Masoni et al., 2019).

Questions remain about the possibility that pleometrosis is a prerequisite for obligate polygyny in ants, as well as differences of this process in different ant species. Questions about the time of maximum mortality of the intensity of fighting between them and their possible differences in different ant species also require clarification.

The aim of our research is to analyze the impact of pleometrosis on the survival strategies of queens in two ant species: *Lasius paralienus* Seifert, 1992 and *Solenopsis fugax* (Latreille, 1798). In *Lasius paralienus*, despite pleometrosis, all queens die except for one, resulting in a monogynous colony. In *Solenopsis fugax*, on the other hand, many queens survive, leading to a polygynous colony. Thus, our study demonstrates that in obligate monogyny, pleometrosis does not alter this strategy, whereas in polygynous species, pleometrosis promotes the survival of multiple queens. For *L. paralienus*; we considered the group effect (3 and 5) and its influence on queen mortality; for *S. fugax*, we tested how much the number of queens in the pleometrotic group would change in the case of polygyny.

Both species are widespread: *L. paralienus* is predominantly a European species (North — to Sweden, in Ukraine elsewhere), Caucasus and Asia Minor, whereas *S. fugax* is distributed in Southern and Middle Europe, south and central part of Eastern Europe, North-Western Africa, in the Asia Minor, Middle East, Caucasus, Afghanistan, Kazakhstan, Middle Asia, south part of Western Siberia, all over Ukraine (Radchenko, 2016). *Solenopsis fugax* is a kleptobiont species, known for its ability to live in close proximity to nests of larger ant species or within their nests, stealing brood from the host ants. This behaviour is facilitated by the small size of its workers (Radchenko, 2016). *Solenopsis fugax* can form colonies with hundreds of thousands of workers and at least 10 queens, indicating a polygynous structure (Seifert, 2018). The exact mode of founding new colonies in this species is not well-studied, but it is presumed to be haplometrotic (claustral). Radchenko (2016) mentions both monogynous and oligogynous colonies in this species, suggesting that new colonies can be founded by a single queen or by groups of queens. Adoption of fertilised queens after the nuptial flight is also possible. In addition to its kleptobiont behaviour, *Solenopsis fugax* can establish nests independently, where it tends root aphids and feeds on the carcasses of invertebrates and vertebrates.

During the analysis, we formulated the following research questions:

1) What is the effect of a group of 3 or 5 queens in *Lasius paralienus* on queen mortality? Given that the colony ultimately becomes monogynous, it is evident that larger founding groups would experience higher mortality rates.

2) At what number of workers does fighting between queens start and their mortality increase? The expected outcome suggests that the more workers are introduced simultaneously, the quicker these conflicts will arise.

3) Compare total queen mortality of two ant species in pleometrotic groups. We found that there was virtually no queen mortality in polygynous *Solenopsis*. There is mortality in *Lasius paralienus* (probably monogynous according to the literature, Seifert, 2018).

Material and Methods

Experiments

Species were determined using (Radchenko, 2016; Seifert, 2018). *L. paralienus* and *S. fugax* queens were captured in Odesa (Ukraine) on 6 September 2020, immediately after the nuptial flight, which

Fig. 1. General view of the experimental formicarium.

corresponds to the standard time frame for these species in this region (Stukalyuk et al., 2022). The choice of *S. fugax* is due to the fact that this species also has a mass nuptial flight and it is not difficult to collect a large number of queens at the same time. We collected all queens of both species in one day. *S. fugax* queens were placed in groups of 5 (total of 9 experiments, 45 queens). *L. paralienus* queens were also placed in groups of 5 (8 experiments, 40 queens) and 3 (also 8 experiments, 24 queens). Formicaria were used for the experiment, each consisting of plaster (thickness 4 cm, length 0.5 m, width 0.5 m). The top of the formicarium was covered with glass. The formicarium had 5 identical chambers connected by a common passage (fig. 1). We provided this number of cells to test whether all queens would occupy the same cell or one cell each.

Along the edge of the formicarium there was a groove for humidification, which was outside the glass. Humidification was applied according to the hygrometer readings (at 80 % humidity). All queens were kept under the same conditions. At room temperature (20–24 °C), ants were kept in darkness, and temperature was monitored as needed using an electronic thermometer. On 29 December 2020, all ants were put into hibernation (in a refrigerator at +3 °C), from which they were removed on 20 February 2021. Observations were made once every 7 days, at the same time (12 noon). A magnifying glass was used for this purpose (magnification up to 10 times).

The following parameters were considered:

a) the number of living queens;

b) the number of dead queens was determined by their lack of movement, often found at the far end of the formicarium, exhibiting a characteristic posture of being hunched with immobile legs, and sometimes positioned with their legs up. In cases where no damage was present, such queens were considered to have died from natural causes (such as exhaustion of reserves, infections, parasites, etc.);

c) queens found with signs of damage — severed limbs, head, dismembered thorax — were considered dead, indicative of mortality due to fights;

d) the number of egg sacs. At the beginning of colony development, queens lay eggs in separate sacs (each in its own sac), then they are combined into one sac, usually after the appearance of the first larvae. The number of eggs could not be accurately counted, so we chose the number of egg sacs as a parameter:

e) the number of larvae — larvae of all ages counted;

f) queen grouping was considered separately — either they were all together in one group, or individually.

For each queen group, the experiment was considered complete when only one queen remained. For queen groups with more than one queen, the experiment was continued. After the first generation of workers emerged from pupae, the young ant colonies were fed with sugar syrup and insects (*Drosophila* sp.), which had been previously killed by freezing after each count.

The maximum duration of the experiment was 115 days for *S. fugax* and 293 days for *L. paralienus*.

Statistical analysis

The computations were done with Past 4.13 software. The Kruskal-Wallis test was used to compare parameters (average number of deaths due to natural causes and as a result of queen fights, number of workers in pleometrotic groups). A Kaplan-Meier plot was also used, a graphical representation used in survival analysis (in our case of queens) that gives an estimate of survival probability over a given period of time. It is a curve that shows how the probability of survival changes as a function of time or length of observation. This curve can be constructed from survival data from observational or research studies. The Kaplan-Meier plot is particularly useful for analysing the time to an event, such as death or occurrence of a particular health condition.

Results

Effect of groups of 3 and 5 queens in *Lasius paralienus* on their mortality. We found no significant differences in mortality between the groups (chi-square = 3.5, p = 0.06, fig. 2).

However, it can be assumed that there is a trend, and further experiments may be needed to clarify this. No worker ants eclosed until the end of winter. In all cases the queens occupied one chamber, i. e., the effect of pleometrosis appeared. Another interesting observation is that when there were 5 or 3 queens in a group, there was one common egg pouch, but when there were 2 or 3 queens left, 2 egg were formed in about a quarter of the cases (3 out of 16).

The period of prime queen mortality most often occurs shortly after formation of the pleometrotic group.

For *S. fugax*, no clear pattern was observed; queens died both with no workers but with a large brood and with 12–19 workers, but their number per pleometrotic group remained almost unchanged (table 1). In this species, queens also occupied one chamber in all cases, and in all but one case a common egg was observed.

In *L. paralienus*, the number of workers varied widely from 12 to 39, but the most violent fights between queens occurred in the group of workers of 21 to 39, and 2 to 3 queens could be killed at a time (table 1).

The average number of queens that died of natural causes and as a result of fights did not differ in *L. paralienus* (Kruskal-Wallis test, $Chi^2 = 1.171$, p = 0.1695). The number of workers in the group when the queen died or was killed differed by a factor of 3: there were more in the latter case ($Chi^2 = 8.953$, p = 0.002). There were also 2.5 times more larvae ($Chi^2 = 3.872$, p = 0.037) and almost 3 times more pupae ($Chi^2 = 5.345$, p = 0.017) when queens died.

Thus, queens engage into fights at a certain size of worker groups and also at approximately the same amount of brood. For *S. fugax*, there was always one queen death per observation. The number of workers in this case was approximately the same as in the same situation in *L. paralienus*, and the number of larvae or pupae did not differ (Chi^2 = 1.18,

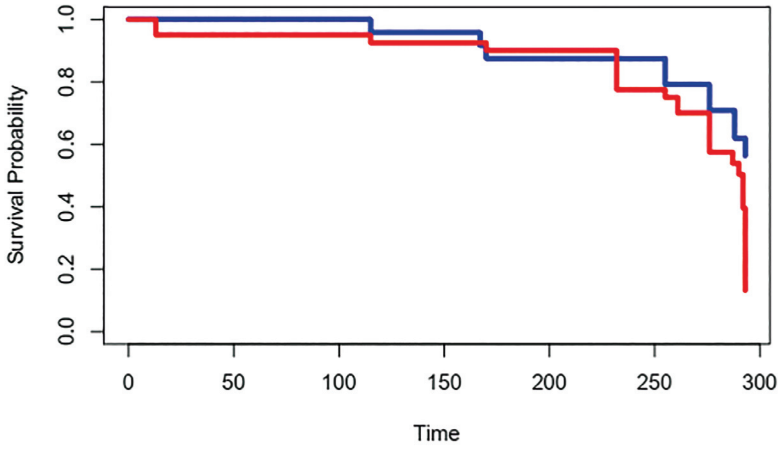

Fig. 2. Survival of queens in *Lasius paralienus* in groups of 3 and 5 queens. Red line is for 5-queen pleometrotic group, blue line is for 3-queen pleometrotic group.

Table 1. Average number of queen deaths by natural causes and in fights in *Lasius paralienus*, *Solenopsis fugax* and the average number of workers and brood with them

Species	N	Min	Max	Sum	Mean	Std. Error
L. paralienus #dead queens	19	1	2	23	1.210526	0.096092
L. paralienus # killed queens	14	1	3	14	1.555556	0.242161
L. paralienus # of workers with dead queens	14	0	35	105	7.5	3.062984
L. paralienus # of workers with killed queens	9	14	39	215	23.88889	2.855037
S .fugax # dead queens	7	1	1	7	1	0
S. fugax # of workers with dead queens	7	0	19	38	5.428571	2.87731
L. paralienus # of larvae with dead queens	19	0	20	63	3.315789	1.27974
L. paralienus # of larvae with killed queens	9	0	32	80	8.888889	3.509687
L. paralienus # of puppaes with dead queens	19	0	20	98	5.157895	1.588083
L. paralienus # of puppaes with killed queens	9	0	34	125	13.88889	3.084209
S. fugax # of larvae with dead queens	7	0	26	69	9.857143	4.682432
S. fugax # of puppaes with dead queens	7	0	6	6	0.8571429	0.8571429

p = 0.1737), as it varied greatly. In *L. paralienus*, workers had not yet hatched in 8 out of 19 cases when the queen died naturally, and in *S. fugax* in 4 out of 7 cases. In all cases, workers were present when *L. paralienus* queens died. Thus, for both species, in almost half of the cases, the natural death of the queen occurs when there are no workers present, and death due to fights (for *L. paralienus*) occurs when the workers have hatched.

In *L. paralienus*, there were no larvae or pupae in 12 and 10 cases of dead queens, respectively, and only 1 case of dead queens. In *S. fugax*, dead queens produced no pupae in 6 cases and no larvae in 4 cases. Thus, in this species, queen deaths from natural causes occur in the absence of brood in most cases.

Comparison of total queen mortality in two ant species in pleometrotic groups.

A comparison between the monogynous *L. paralienus* and the polygynous *S. fugax* showed that in the latter the number of queens at the end of the observation period practically did not change, whereas in *L. paralienus* only 1 queen remained in 13 cases (Chi^2 = 12.92, p = 0.0002, fig. 3, table 2).

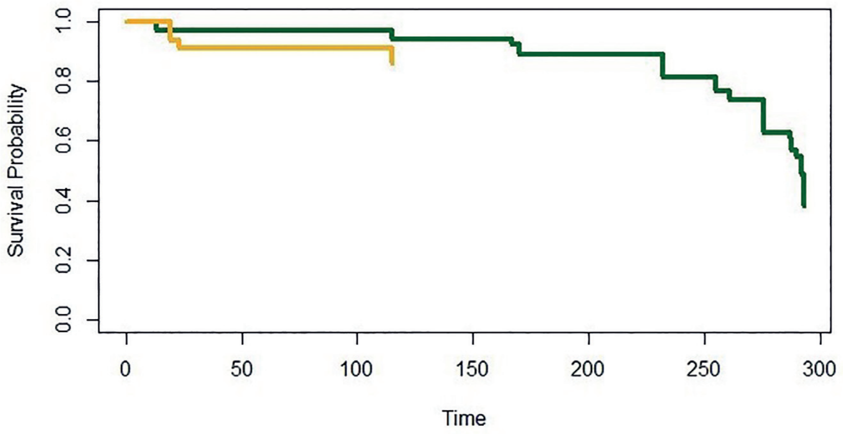

Fig. 3. Survival curve for two ant species. Orange line is for *S. fugax*, green line is for *L. paralienus*.

Table 2. Results of comparison of the number of surviving queens for ant species

Species	N	Observed	Expected	(O-E)^2/E	(O-E)^2/V
Lasius paralienus	64	34	45.71	2.999	14.138
Solenopsis fugax	45	6	9.96	1.572	2.189

Note. (O–E)^2/E is the contribution of the squared residuals to the chi-squared according to expectations, (O–E)^2/V is the contribution of the squared residuals to the chi-squared according to variables.

For *L. paralienus*, in isolated cases where more than 1 queen remained at the end of the experiment, the number of workers did not exceed 11 for the group of 5 queens and 7 pupae; from 2 to 27 workers and 15 pupae for a group of 3 queens. It appears that the group effect may have an impact on the onset of fighting between queens, but more research is needed to confirm this. Thus, in polygynous ant species in pleometrotic groups, most queens survive, whereas in monogynous ants all but one die.

Discussion

The results of our study provide valuable insights into the dynamics of pleometrotic groups in ant species, focusing primarily on *Lasius paralienus* and *Solenopsis fugax*. We observed that queen mortality in pleometrotic groups peaked shortly after their formation, highlighting the intense competition and aggression among queens, particularly in related groups. This early mortality pattern suggests that initial group dynamics play a crucial role in determining colony success and queen survival.

Interestingly, we found no significant differences in mortality between groups of 3 and 5 queens in *L. paralienus*, although there was a trend suggesting potential effects that warrant further investigation. Our results also showed that the presence of workers and the stage of brood development significantly influenced queen mortality. In both species, queens were more susceptible to mortality when workers were present, highlighting the complex interplay between group size, worker activity and queen survival.

In terms of colony dynamics, our observations suggest that pleometrotic groups of intermediate size may be more stable and productive than very large groups or single queens. This is consistent with previous studies suggesting that optimal group sizes can increase colony fitness without leading to excessive competition among queens. However, we did not observe a clear division of labour among queens in our experimental conditions, in contrast to findings in other ant species.

Overall, our study contributes to the understanding of how pleometrotic groups influence colony establishment and stability in ants. The findings highlight the importance of considering both internal group dynamics and external environmental factors in shaping the social structure and reproductive strategies of ant colonies. Further research is needed to explore the mechanisms underlying queen-queen interactions, the adaptive significance of pleometrosis, and its implications for ant colony ecology and evolution.

In nature, groups of 2–4 queens are most common, but sometimes their number can reach 9 per group (Bartz & Hölldobler, 1982). In *Oecophylla smaragdina* (Fabricius, 1775), increasing the number of queens in a group does not increase the fecundity of each queen, but may increase future colony size (Offenberg et al., 2012). In the leafcutter ant *Acromyrmex versicolour* (Pergande, 1893), mycelial proliferation is an important factor, with no difference in colony growth rates between haplometrosis and pleometrosis (Cahan & Julian, 1999).

In *Lasius niger* (Linnaeus, 1758) groups of 2 queens, the more fertile one often survives (Sommer & Hölldobler, 1992, 1995; Aron et al., 2009), and the group effect promotes faster worker development compared with the haplometrosis (Teggers et al., 2021). Larval development is faster in a group of 2 queens, but pupation is slower than in individual queens (Kipyatkov, 1979). There is also a decrease in overall fecundity in the group, but an increase in the percentage of food eggs laid, which increases the survival rate of *L. niger* queens (Kipyatkov, 1979).

Interestingly, pleometrotic groups of intermediate size appear to be more productive than large groups of 9 queens or single queens (Shaffer et al., 2022), with *Solenopsis invicta* Buren, 1972 having the most fecund pleometrotic group of 5 queens (Tschinkel & Howard, 1983). Increasing the group size to 6 queens may lead to a division of labour between them, with some digging and others caring for the brood (Jeanson & Fewell, 2008). However, under our conditions, no such division was found in any of the species.

The period of prime queen mortality. It is interesting to note that fights between queens are more frequent when they are related (Nonacs, 1990). This could be a reason for the frequent fights between queens in *L. paralienus*. In our experiment, most of the deaths in both ant species occurred shortly after the formation of pleometrotic groups. Stress (unfavourable environmental conditions, Sanmartín-Villar, 2023) is often the cause of death of queens at the initial stage. According to other data, under experimental conditions fights between haplometrotic queens were more frequent than between pleometrotic queens (Cahan & Julian, 1999). For *L. niger*, 60 % queen mortality from pleometrotic groups has been reported under experimental conditions (Madsen & Offenberg, 2017), meaning that competition between queens can be quite intense. The second peak in queen mortality, but as a result of fights, occurred in our experiments after the emergence of workers, confirming previously reported data (Sommer & Hölldobler, 1995).

In some cases, possibility of founding new colonies by pleometrosis and the transition of mature colonies to polygyny has been noted (Alloway et al., 1982; Trunzer et al., 1998). It seems that this is also true for *S. fugax*. Zakharov (2011) admits that the consequence of pleometrosis may be primary polygyny in some cases. It is also interesting to note that a reverse transition from polygyny to monogyny is also possible (Schrempf & Heinze, 2007).

Early queen mortality may be related to soil pathogens, such as fungal infections, and queens in pleometrotic groups may have greater survival compared with haplometrotic queens (Pull et al., 2013).

According to the literature, early mortality (before the appearance of the first generation of workers) is associated with reproductive competition between queens in the group, and mortality is higher than for haplometric queens. In any case, the formation of pleometrotic groups was largely facilitated by a transition from aggression to tolerance between queens (Overson et al., 2014). Apparently, in addition to presence of a group of workers of a certain size, presence of sufficient brood (larvae and pupae) from which workers can soon emerge is not the only reason for fighting between queens.

Conclusions

A study of the effect of pleometrotic groups consisting of 3 and 5 queens in *Lasius paralienus* ants revealed no statistically significant differences in mortality between these groups ($\text{Chi}^2 = 3.5$, $p = 0.06$). However, the trend observed suggests a possible effect that needs to be confirmed by further studies.

In general, deat of queens in both ant species occurred shortly after formation of the pleometrotic group, which is typical for this species.

It was found that the most severe fights between queens in *L. paralienus* were observed in presence of a large number of workers, indicating influence of the worker group size on occurrence of conflicts between the queens.

A comparison of the total queen mortality in pleometrotic groups in different ant species confirmed that in polygynous species, such as *S. fugax*, most queens survive, whereas in monogynous species, including *L. paralienus*, all but one queen die. The comparison between *L. paralienus* and *S. fugax* showed a statistically significant difference in queen survival ($\text{Chi}^2 = 12.92$, $p = 0.0002$).

In *L. paralienus*, there was a statistically significant association between the number of workers and cases of natural death versus deaths due to fighting ($\text{Chi}^2 = 8.953$, $p = 0.002$).

We experimentally confirmed that *S. fugax* can establish new colonies independently and through pleometrosis.

Author contributions

S. Stukalyuk — statistical data processing and article writing, V. Stelia — conducting experiments.

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