Ph.D. Thesis

Forms and background factors of the coexistence between colonies of *Formica fusca* and *Camponotus vagus (*Hymenoptera*,* Formicidae*)* in forest steppe habitats

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Introduction

Various types of interspecific associations exist among ant species. These can be categorized on the basis of the degree of interactions between heterospecific colonies, ranged from simple spatial neighbourhood with loose interaction, to highly specialized social parasitism. The vast majority of studies on interspecific associations in ants have focused on the forms of typical social parasitism, such as temporary parasitism, slavery and inquilinism or associations that belong to "compound nests" representing a higher degree of biological interdependence between heterospecific colonies (i.e., cleptobiosis, lestobiosis, xenobiosis or parabiosis). However, so far, fewer studies have dealt with plesiobiotic associations, and most of these report only observations that might indicate the existence of such associations. Regarding the lack of biotic interdependence and direct contact between the associated colonies, plesiobiosis is considered to be the most rudimentary form of interspecific associations in ants. This relationship denotes the regular nesting of two or more colonies of different species in the direct or close proximity of each other. Direct proximity means that the plesiobiotic colonies occupy the same nesting shelter (e.g., in or under logs, stumps, rocks, etc.). By the classical definition, plesiobiotic partner colonies share the same microhabitat without any further interactions between them. Although plesiobiotic nests are adjacent to each other, they always remain separate as individual units, and the members of heterospecific colonies do not mix. Plesiobionts are potentially hostile to each another, and if the nest galleries accidentally break in, fighting and brood theft may ensue. As a rule, plesiobiotic partner species differ from each other morphologically (e.g., different body size) and/or behaviourally (e.g., different foraging strategies or competitive ability). These differences may promote the coexistence of associated colonies according to the “limiting similarity” hypothesis. Basically, the less similar the species are the more likely they occur together in a plesiobiotic relationship in order to avoid intraspecific competition.

Up to the year 2013, at least 48 different plesiobiotic species pairs have been recorded from various habitat types of the Holarctic region (Kanizsai et al. 2013). New results revealed that up to date the number of plesiobiotic species pairs have been observed in plesiobiotic associations is 55, the number of plesiobiont species is 52 (Gallé et al. 2014).

31 of these belong to the subfamily Formicinae, 17 to Myrmicinae, only 3 to Ponerinae and 1 plesiobiont belong to Dolichoderinae. The four most frequent genera whose members established plesiobiotic relationships were *Formica*, *Camponotus*, *Lasius* and *Myrmica*. Recent studies on plesiobiosis revealed that two species, *Formica fusca* and *Lasius flavus* can be considered as two of the most frequent plesiobionts, on the basis of the total number of their so far known plesiobiotic partner species. The total number of plesiobiotic associations – where the exact number of the observed cases was given – was 69, from which the two most frequent plesiobionts participated in 46 associations, *F. fusca* in 28 cases (60.9 %) and *L. flavus* in 18 cases (39.1 %). New results added further 159 observed plesiobiotic cases, where more than 80 % of these associations were between *Lasius psammophilus* and *Plagiolepis taurica* (Gallé et al. 2014).

Aims and scope

1. Spatial pattern and density of the nests of *F. fusca* and *C. vagus* and background factors influences the coexistence of the heterospecific colonies

1.1. To define the characteristic spatial pattern of nests and the mean nest density of *F. fusca* and *C. vagus*
1.2. To determine a general frequency of plesiobiotic association between *F. fusca* and *C. vagus*
1.3. Which background factors can be considered as the driving forces of the formation of plesiobiotic associations?

1.4. How many plesiobiotic nests can be found within the different forest habitats?

1.5. Determine the preferred type of nesting shelters and the differences in nesting preference between the two species

1.6. Measure the distances between heterospecific nests and calculate the level of aggression

1.7. Observe co-occurrences of *F. fusca* and *C. vagus* workers on baits around plesiobiotic nests

2. The structure of the vegetation and the composition of ant community in different forest habitats

2.1. Determine the composition of the ant community in natural habitats of the two species

2.2. Determine the relative abundance of the two species

2.3. Determine the diversity of the ant community and the structure of vegetation across the three habitat types. Which indicator species characterizing the different habitat types?

3. Background factors of the coexistence of *F. fusca* and *C. vagus* colonies

3.1. Determine similarities and differences in foraging strategies of *F. fusca* and *C. vagus*

3.2. Observe the foraging strategy of *F. fusca* and *C. vagus* in small-scale

3.3. Observe the competitive behaviour of *F. fusca* and *C. vagus*

4. Trophallaxis between the foragers of *C. vagus*

4.1. Determine the characteristic frequency of trophallaxis between *C. vagus* foragers

4.2. Determine the dynamics of trophallactic interactions

4.3. Determine the duration of trophallaxis and the frequency distribution of the different duration interactions

4.4. How many workers participate in trophallactic interactions?

4.5. Determine the size-class distribution of trophallactic partners

4.6. Determine the effects of colony condition (starved and satiated) on trophallactic interactions

4.7. Define the role of trophallaxis in optimalisation of foraging

Materials and methods

Study species

Formica (*Serviformica*) *fusca* Linnaeus, 1758 is a eurytopic and thermophilic species of various habitats distributed mainly in the forest zone. Colonies of this species construct their nests in the ground, under stones, in decaying tree stumps or among decaying litter. *F. fusca* is a typically opportunistic species representing the lowest level of hierarchy in interspecific competition. It is the most frequent host species for temporary social parasitism of wood ants of the subgenus *Formica* s. str. and also a frequent slave species of *Formica sanguinea* and *Polyergus rufescens*.

Camponotus vagus (Scopoli, 1763) is a dendrophilous species inhabiting mainly light and warm coniferous, deciduous or mixed forests. Nests of *C. vagus* occur first of all in decaying tree trunks and logs. In the three-level competition hierarchy of ants, *C. vagus* placed on higher level than *F. fusca*. Being an aggressive species, it defends both its nests and the located food sources.

Study sites

Field works were carried out in two study sites, which were located between the Rivers Danube and Tisza, in the Kiskunság National Park of Hungary. The first habitat (46^{o}22' N; 20^{o}5' E) (where we tested the average nest density of *F. fusca* without the presence of *C. vagus*) was located in the southern Hungarian part of the Kiskunság National Park. It was a mixed forest consisting of oak trees (*Quercus robur*) and sparsely distributed pine (*Pinus nigra*) and poplar trees (*Populus alba*), and there were a thick leaf-litter layer on the forest ground, but only few decaying logs were presented. There were no *C. vagus* nests in the studied forest patches; therefore it was possible to investigate the nest density and nesting behaviour of *F. fusca* without the presence of *C. vagus*. The second forest habitat (where both *F. fusca* and *C. vagus* were occurred) (46 ^{o}41' N; 19 ^{o}36' E) was located in the central Hungarian part of the Kiskunság National Park. Randomly selected plots were settled in patches of pine (*Pinus nigra*) and poplar forests with a number of decaying logs and tree trunks on the forest floor.

Field works

To investigate the frequency of plesiobiotic associations, we randomly chose patches of pine and poplar forests. Ant nests were mapped in randomly selected 100 m^2 plots in both types of forest patches. Altogether 1000 m^2 areas of forest patches were mapped to measure densities of nests and the frequency of plesiobiosis between *F. fusca* and *C. vagus*.

To determine the preferred nesting material, different parameters of occupied nesting shelters (length and width or diameter of logs and tree trunks) were measured. The decaying condition of logs and trunks was estimated by using three values for indicating the decaying level (1= scarcely, 2= moderately, and 3= strongly decaying logs and trunks).

Baits were used to investigate the encounters and activity of *F. fusca* and *C. vagus* foragers. One of the studied nests was a plesiobiotic nest, whereas the other studied nest of *F. fusca* was not a plesiobiotically associated one. 16 baits were arranged in a concentric pattern around both nests. Baits were put on the ground at different distances (0.5 m, 1 m, 1.5 m and 2 m) from central nests, and four baits were placed in each distance category. We used a mixture of tuna and honey as baits.

To assess the level of intercolonial aggression, the presence and lack of offensive reactions between workers (1 vs. 1) from neighbouring and distant heterospecific and conspecific colonies of *F. fusca* and *C. vagus* were tested.

To determine the characteristic composition of the ant community, the diversity and relative abundance of epigaeic ant species were sampled with using Barber traps across three habitats including pine and poplar forest patches and the boundary habitat of these forest fragments. During sampling period the vegetation cover was assessed to determine the effect of vegetation structure on ant community composition.

Laboratory experiments

Mature colonies of *C. vagus* and *F. fusca* were reared in laboratory at a temperature of 22 ± 3 ºC with a 12 h photoperiod. The ants were fed with special laboratory food containing the necessary nutrients. The nest of the actual experimental colony was connected to the foraging arena by tube before the start of testing the foraging. Every experiment lasted for one hour and each experimental period started when the first forager entered the arena. Experiments were performed both with starved and with fed colonies. Honey (carbohydrate) or laboratory food (carbohydrate + protein + vitamins) were used as baits. These baits represented the simple and complex food for testing the effects of the type of food on foraging. The time of the arrivals of foragers on baits (including the first discovery of each of the baits), the number of arrivals on each of the baits per experiment, the time interval spent on different food baits by foragers were recorded and the distance of each bait from the entrance of the arena were measured.

In 2012 we reared four queen-right colonies of *C. vagus* in laboratory. The colonies were composed of approximately 200 workers and broods. We tested the trophallactic events in the case of each experimental colony both in starved and satiated conditions. The first set of trials were conducted with starved colonies (i.e., the colony was not fed within 10 days before the experiment), while the second set of trials was conducted with the same but satiated colonies (i.e., the colony was fed one day before the experiment).

During the experiments we recorded the duration (in sec.) of each trophallactic interaction, the number of participants in each trophallaxis, and the size-class (S=small, M=medium and L=large) of the participant initiating the interaction. We measured the total number of trophallactic events/hour both in the starved and satiated colonies. For the analysis of the dynamics of trophallaxis we summarized the number of trophallactic events in intervals of five minutes (12 intervals/hours).

To test the possible effect of the duration of these events, we distinguished two main types of trophallaxis regarding the duration of interactions (i.e., short term and long term trophallaxis). We considered those events that lasted from 1 to 10 sec as “informal trophallaxis” (supposing that they had mostly informal functions), while those lasting 10 to 180 sec as “feeding trophallaxis” (supposing that they had mostly nutrient exchanging functions).

Statistical methods

Statistical analyses were carried out with SPSS package, R and PAST for Windows. If the distribution of data was not normal, I used nonparametric tests. The two-independent-samples tests procedure compares two groups of cases on one variable. From these tests I used the Mann-Whitney U test. The tests for several independent samples procedure compares two or more groups of cases on one variable, from these types of tests I used the Kruskal-Wallis test. To measure how variables or rank orders are related, the bivariate Spearman's rho correlation was used. Linear regression was used for testing the distance dependency of the foraging behaviour of the colonies. Non-linear curve estimation regression was used to test both the dynamics of trophallactic interactions and the frequency-distribution of the different duration trophallactic interactions in both colony conditions. T test procedure was used to determine whether the given R values differ from the values which can be expected in the case of randomness. The paired-samples t test procedure compares the means of two variables for a single group therefore this method was used for comparing the mean number of trophallactic interactions for every five-minute interval of experiments between the different colony conditions. The patterns of nests within the mapped plots were illustrated by using Kernel Density Map function of PAST. To identify whether the colony condition has an influence on the number of partners, the size-class of different partners and the initiator of the interaction, we built a GLMM model with Poisson error term. The same approach was used for testing, whether the number of partners and the colony state has an effect on the duration of Trophallaxis and GLMM was used to test the differences between the three different habitat types (poplar, pine forest patches and edges between these). For characterizing indicator species of different habitat types, the Indicator Species Analysis of Dufrene-Legendre (1997) was used.

Results

1. *Background factors, spatial pattern and density of nests of F. fusca and C. vagus in different forest habitats*

1.1. Spatial pattern of nests and the mean nest density of *F. fusca* and *C. vagus*

Within the plots without the nest of *C. vagus* the mean nest density of *F. fusca* was 15 nests/100 m^2, whereas within the plots where *C. vagus* occurred also, the mean nest density of *F. fusca* decreased to a lower nest density (7 nests/100 m^2). The nest density of *C. vagus* was 7 nests/100 m^2, too. When the nest density of the two species was the same, the *F. fusca* nested significantly closer to *C. vagus* than to the conspecific colonies. Field observations carried out in the next year revealed a similar mean nest density of *F. fusca* (8/100 m^2), while the mean nest density of *C. vagus* was much lower (1.75/100 m^2) than as it was found in the previous year. The nest density of *F. fusca* was significantly higher than that of *C. vagus* in the patches of both pine and poplar forests. The nest density of *F.*

fusca was similar in both pine and poplar forests, whereas the nest density of *C. vagus* was significantly higher in pine forest patches. The age of forest patches were significantly correlated with nest densities. The measured patches represented a relative early successional stage and the lack of territorial competitor species contributed to higher nest densities of subordinated ant species. The joint spatial arrangement of the two species' nests represented random dispersity, which may cause by the random distribution of the suitable nesting sites. On the basis of the frequency-distribution of the distances measured between the nests of heterospecific colonies, the distance is smaller than 2 m at a 15.28% rate.

1.2. The frequency of plesiobiotic association between *F. fusca* and *C. vagus*

The number of the *C. vagus* nests within plots influenced significantly the number of quasi plesiobiotic nests. The number of true plesiobiotic nests was similar in the different forest habitats; we found altogether 10 true plesiobiotically associated nests/1000 m^2 (Kanizsai et al. 2013). Furthermore we found fertilised gyne of *C. vagus* inside two nests of *F. fusca*.

1.3. Driving forces of the formation of plesiobiotic associations

Two main habitat properties may contribute to the formation of plesiobiotic associations: the scarcity of suitable nesting sites as a forcing factor and the sufficient amount of food sources available, which significantly influence the abundance and reproductivity of ant colonies. When colony density is high, the depletion of food resources by neighbouring colonies may be more intensive, resulting in an increased mortality, especially in the case of incipient colonies. The overlap in diet can enhance intraspecific competition, which may force colonies into the vicinity of heterospecific nests. Therefore, strong intraspecific competition can also contribute to the formation of plesiobiotic associations, especially when colony density is high. However, the role of interspecific competition in the persistence of plesiobiotic association is apparently relevant.

1.4. Number of plesiobiotic nests within the different forest habitats

Nest density of both plesiobiont was higher in managed pine forest plantations and the number of quasi plesiobiotically associated nests was higher within these habitats also.

However, the difference in the number of both the quasi and the true plesiobiotic nests between the two forest types was not significant. The correlation between the number of *F. fusca* nests and the number of quasi plesiobiotic nests was not significant, while the number of *C. vagus* nests significantly influenced the density of quasi plesiobiotically associated nests.

1.5. Preferred type of nesting shelters and the differences in nesting preference between the two species

Colonies of *Camponotus vagus* constructed their nests exclusively in logs and tree trunks, similar to other members of the *Camponotus* genus. On the other hand, *F. fusca,* although preferring trunks and logs, was able to create nests even in the leaf-litter and in the soil. There were significant differences between the nest preference of the two species regarding the width and decaying level of occupied logs.

1.6. Distances between heterospecific nests and the level of aggression

There was no distance-dependent regularity regarding the aggression between *F. fusca* and *C. vagus* workers, we observed 12 aggressive interactions only from the 40 tests between the workers of the two species. No aggressive interactions were observed between conspecific workers of *F. fusca* either from neighbouring or from distant nests, while the distance between the *C. vagus* nests significantly influenced the aggression between conspecific workers, aggressive interactions were observed between workers from distant nests.

1.7. The rate of the workers of *F. fusca* and *C. vagus* co-occurrence on baits around plesiobiotic nests

A lower co-occurrence rate of the workers of *F. fusca* and *C. vagus* was observed around a nest of *F. fusca* surrounded by three neighbouring nests of *C. vagus* (quasi plesiobiotic nest). On the other hand, a higher co-occurrence was observed around a nest of *F. fusca* that was in a truly plesiobiotic relationship with only one nest of *C. vagus*. According to the baiting experiments around this plesiobiotic nest, the highest co-occurrence at community level was between *F. fusca* and *C. vagus*.

2. *The structure of the an community within the measured habitats*

2.1. Composition of the ant community in natural habitats of the two species

The diversity and abundance of epigaeic ant species were determined across three habitats including pine and poplar forest patches and the edges that separate these forest fragments. 18 species of ants were identified, which belonged to three different subfamilies and 8 genera. Among the collected species, the submissive *F. fusca* was the most abundant in each habitat type. Beside *F. fusca*, *Lasius platythorax* was the most abundant species in the managed pine plantations, while *Myrmica sabuleti* and *Lasius niger* were abundant species in poplar forest patches. In edges, *Myrmica sabuleti* and *Tapinoma subboreale* were the most abundant species after *F. fusca*.

2.2. Relative abundance of the two species

Pitfall traps collected altogether 4771 ant individuals. Barber-trap catches of ants were similar in each habitat type. Among the collected species, *F. fusca* was the most abundant in each habitat type. The number of the collected workers of *F. fusca* was more than 53 % (2569 individuals) of the whole pitfall-trap catches of ants, whereas the number of collected *C. vagus* workers was about 2 % (99 individuals) of the collected ants.

2.4.The diversity of the ant community and the structure of vegetation across the three habitat types

On the basis of the assessed vegetation cover, the vegetation structure of edges differed significantly from the habitat structure of pine plantations and poplar forest patches. According to this, the community composition of ants significantly differed in edges than in forest patches. We measured the highest diversity in edges, all species which were collected with the traps occurred in boundary habitats (Gallé et al. 2014b).

3. *Background factors of the coexistence of F. fusca and C. vagus colonies*

3.1. Foraging strategies of *F. fusca* and *C. vagus*, similarities and differences

The success in discovery of food baits was not influenced by the quality of food or the starving condition of the colonies, neither in *C. vagus*, nor in *F. fusca*. There was no significant difference between the two species regarding the time of the first discovery of baits.

The attendance of baits by *F. fusca* workers was not influenced by the complexity of food; they visited both type of food at a similar rate. Although preliminary experiments demonstrated that the complexity of food influences the attendance of baits by *C. vagus*, the new results represents that it had no significant effect.

F. fusca workers spent a similar time interval on different types of food, whereas *C. vagus* workers spent significantly longer time on complex food baits in 2011, and spent longer time on simply food in 2012. Generally *C. vagus* foragers spent significantly shorter time interval on food baits than *F. fusca* foragers.

There was no significant difference between starved and fed *F. fusca* colonies in connection with the hourly attendance of baits by foragers. The foragers of starved and fed *F. fusca* colonies visited the baits in similar proportion. In contrast, *C. vagus* foragers of starved colonies visited the baits more frequently than foragers of fed colonies. There was significant difference between fed *C. vagus* and fed *F. fusca* colonies. The foragers of fed *F. fusca* colonies visited the baits more frequently than fed *C. vagus* foragers. In contrast, the starved *F. fusca* and *C. vagus* foragers visited the baits in a similar proportion.

3.2. Foraging of *F. fusca* and *C. vagus* in small-scale

The arrival rate on food baits by *C. vagus* workers was not influenced by the tested small-scale distance of baits in the foraging arena neither in starved nor in fed condition. In contrast, the arrival rate on baits by *F. fusca* workers was altered even by the tested small-scale distance of baits, the number of arriving *F. fusca* workers decreased significantly with the increasing distance of baits both in starved and fed condition (Kanizsai et al. 2011; Kanizsai 2012).

3.3. The competitive behaviour of *F. fusca* and *C. vagus*

The former exclusive exploitation of food by *F. fusca* promoted that the number of its workers increased on baits. After the appearance of *C. vagus* workers, the number of *F. fusca* workers decreased significantly in the foraging arena, a competitive exclusion was observed on baits. During the observation the co-occurrence of the heterospecific workers on baits was only 13 occasion from 132.

4. Trophallaxis between the foragers of C. vagus

4.1. The frequency of trophallaxis between foragers

The hourly attendance of baits by foragers and the number of trophallaxis between them were similar both in starved and fed colonies. The mean number of trofallaxis between starved workers (≈158) was significantly higher than that of fed workers (≈68) per experiment.

4.2. The dynamics of trophallactic interactions

The dynamics of trophallactic events was similar under starving and satiated conditions; both tendencies showed significant quadratic curve fit with a maximum point of the curve. There were significant differences between the starved and satiated colonies with regard to the mean number of trophallactic interactions within the 5 minutes intervals of the experiments, more interactions were between starved foragers (Kanizsai et al. 2014).

4.3. The duration of trophallaxis and the frequency distribution of the different duration interactions

The duration of trophallactic events lasted from 1 to 181 mp with a mean of 16.68 mp. The frequency-distribution of the different duration trophallactic interactions showed an exponential trend, where the short interval trophallactic events were more frequent than the longer ones, both in starved and satiated colonies. The duration of interactions was significantly influenced by the colony condition, the number of partners and the size-class distribution of partners.

Short term "informal" trophallaxis was more frequent in fed colonies, whereas the prolonged "regurgitational" type was more frequent in satiated colonies (Kanizsai et al. 2014).

4.4. The number of trophallactic partners

In the case of starved colonies, 2-5 workers participated in each trophallactic event, but more than 88 % of the analyzed cases took place between 2 workers. In the case of satiated colonies, 2-3 workers participated in each trophallactic event, and more than 98 % of the analysed cases were between 2 workers. The starvation level of colonies significantly influenced the number of participants in trophallactic interactions.

4.5. Size-class distribution of trophallactic partners

Most of the trophallactic interactions involving two partners occurred between the medium size-class workers in both the starved and satiated colonies. Trophallaxes were initiated mostly by the small size-class workers when their partner belonged to the medium size-class, while the initiators of interactions were mostly the large workers when their partner was a small or medium size-class worker.

4.6. The effects of colony condition on trophallactic interactions

The mean number of trofallaxis between starved workers (≈158) was significantly higher than that of fed workers (≈68) per experiment. There were significant differences between the starved and satiated colonies with regard to the mean number of trophallactic interactions within the 5 minutes intervals of the experiments. The duration of interactions was significantly influenced by the colony condition, whereas there were no significant differences between the starved and satiated colonies regarding the size-class distribution of trophallactic partners.

4.7. The role of trophallaxis in information-flow among foragers

We observed a higher number of prolonged interactions between foragers from starved colonies than from satiated ones, although short-term interactions were more frequent in both colony conditions. Different rates of the short term and prolonged interactions may provide information about the current nutritional requirements of the colony, enhancing the speed and efficiency of colony responses to feeding stress. Frequent short term trophallaxis may not only contribute to a high level of cooperation during retrieval of food among foragers, but also maintain the integration of colony members even outside their nest (Kanizsai et al. 2014).

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