Abstract*

The role of individual differences in food utilization and interference competition: case studies on five ant species (Hymenoptera: Formicidae)

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The importance of individual differences in spatio-temporal population processes is a relatively young recognition in ecology (Hassel and May 1985, Łomnicki 1988, Grimm and Railsback 2005). In social insect biology, however, the study of individual differences has much longer history and mainly connected with the division of labor and the cast systems. These sociobiological aspects have been avoided by the interest of theoretical ecologists, although e.g. E. O. Wilson (1987) clearly stated its significance in the ecological success of ants. The within-community success (i.e. the amount of energy effectively allocated to maintenance and reproduction) of a population depends on its position (rank) in the competition hierarchy; the amount of maximal consumable energy; the energy loss due to the lower rank; the cost of the maintenance of the rank (i.e. competition) and the additional disadvantages of being subordinated (e.g. being injured or killed in the combats). In terms of time spent on different subtasks (partly sensu Ratnieks and Anderson 1999, Anderson and McShea 2001) at substantial food sources, this means that the competitor's best strategy is to allocate more time to utilize resources instead of guarding, protection or escaping. A neutral model assumes that the different tasks are randomly or regularly dispersed among the individuals present at the food source only if the transitions between the tasks are equal and prompt. Otherwise there is a loss of time when switching from one task to another, increasing the span of periods without activity and decreasing the length of eating and handling times. In this latter case, specialized individuals are more effective, which leads to aggregated distribution of behavioural units among individuals.

In this paper we analyze the time allocation between different subtasks within the main task of foraging at permanent and substantial food sources on five ant species. We studied the following subtopics as follows: (1) the temporal distribution of subtask in the studied ant species, (2) transitional frequencies between different subtasks and (3) the distribution of the information content in the individuals' subtask repertoire.

The studied species were: *Camponotus vagus*, *Cataglyphis aenescens*, *Formica pratensis*, *Formica rufa* and *Liometopum microcephalum.* We investigated the bahaviour of the ants' workers in field conditions at baits with and without competitors belonging to different species. The studies were made in different parts of Hungary, majority of them at Bugac, in the Kiskunság National Park. Green plastic discs of 10 cm diameter were placed onto the surface of soil and fixed with pins. Small pieces of a mixture of tinned liver past or tuna and honey were used as bait and put in the centre of the discs. The behaviour of ants was filmed by video cameras and the records were analyzed in the laboratory. One set of observations spanned about for 60 minutes. When analyzed the behaviour of the individual ants, we distinguished eleven different subtasks: (1) eating; (2) aggressive (erected, threatening pose, poison spraying, attacking alien species workers); (3) staying at the bait without function; (4) grooming (usually self-grooming); (5) aggressively guarding; (6) excited (running around the bait, drumming on the plastic disc and sometimes slipping because of the fast movement); (7) feeding nestmates by trophallaxis; (8) carrying object (usually dry leaf, small stems, rarely very small food particles); (9) being aggressive to conspecific workers; (10) carrying alien workers from the disc (in most cases without killing or injuring it) and (11) escaping.

Subtask frequencies were more or less similar in all species. The differences are partly brought about by the habitat properties and the presence or absence of competitors (e.g. *Myrmica sabuleti, Formica fusca*, *Tetramorium caespitum*) and in the case of *L. microcephalum* a Sphecoid predator (*Tracheliodes curvitarsus*). The transition probabilities between the subtasks are not equal and prompt. Most transitions are going through an inactive phase. The distribution of subtasks is uneven among individuals (variance/mean > 6; c^2 >482, p<<0.0001 in all subtasks and all species). This indicates individual differences in the performed activities.

On the basis of NMDS ordination of the studied worker ants, the individual differences are the strongest in the case of *Formica rufa*, where the individuals form two groups and the task histogram is bimodal along

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* Extended abstract of the presentation held at the 4th Central European Workhsop of Myrmecology, 15-18.09.2011, Cluj-Napoca, Romania

the first ordination axis. Imperfect segregations or smooth transitions were observed in the other species. The axes of NMDS ordination were well correlated with subtask frequencies. The eating and aggressive functions are negatively correlated, as a rule, the frequencies of these two task forms and the absence of function are responsible for the segregation of individuals along the first axis. In the case of *C. aenescens*, the first axis selects the „lazy" and „diligent" workers.

In conclusion, we found subtask-level individual differences within the foraging function in all studied species. These differences promote the foraging success. The most complete individual subtask specialization was observed in *Formica rufa*, whereas at most imperfect specialization was found in the other species.

Acknowledgments

This presentation is supported by the European Union and co-funded by the European Social Fund. Project number: TÁMOP-4.2.2/B-10/1-2010-0012

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