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Animal behaviour

Juveniles and the elderly defend, the middle-aged escape: division of labour in a social aphid

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In colonies of social insects, non-random spatial positioning within the colonies may reflect division of labour and improve colony efficiency. Here, we describe a novel defence system in the colony of a gall-forming social aphid, Quadrartus yoshinomiyai (Nipponaphidini), where young and old defensive aphids move towards the dangerous area typically associated with a higher risk of predation, whereas the middle-aged reproductive individuals move away. Younger nymphs and post-reproductive adults of Q. yoshinomiyai concurrently defend against predators that intrude after their galls open. In natural open galls, both types of defenders were preferentially located around the open area vulnerable to invasion by predators, whereas reproductive individuals remained in the safer areas. In addition, when a hole was artificially made in closed galls, these morphs located themselves in similar spatial positions to the natural open galls within 12 hours. The defensive system led by oldest and youngest individuals may reflect the possibility of future reproduction for these insects, thereby optimizing colony efficiency in a seasonally changing environment, according to the reproductive values of colony members.

1. Introduction

Division of labour is a prominent feature in the colonies of social insects, where specialized individuals constitute castes to perform their various tasks. Such specialization is considered to improve the efficiency of colony function [1]. In many social invertebrates, specialized castes show non-random spatial distribution patterns that are correlated with their functional roles, suggesting optimization of colony efficiency [2–5]. However, within-group conflict also generates non-random spatial arrangement of individuals of a group. For example, in non-clonal social organisms such as eusocial Hymenoptera, dominance interactions between workers resulting from kin-selected reproductive conflict promotes the selfish movement of individual workers, thus generating a non-random spatial distribution pattern [6,7]. Thus it is difficult to distinguish whether cooperative or competitive interaction generates a spatial distribution pattern found in a colony of social organisms that reproduce sexually.

Gall-forming aphids provide useful material to study optimal spatial organization because of clonal reproduction [8]. They live in a closed space and reproduce parthenogenetically: they are thus expected to have no kin-selected conflict within a colony if there is no migration between galls (but see [9–11]). They have evolved different levels of sociality many times independently, where some colony members perform altruistic tasks at the expense of reproduction [12,13]. A previous study showed a task-related spatial distribution pattern in the gall-forming social aphid Pemphigus spyrothecae [14]. In open galls of P. spyrothecae, morphologically specialized defenders are preferentially located in the area vulnerable to predation, whereas reproductive morphs are located in safer areas. However, it has remained unclear how these different morphs change their spatial positioning to generate the task-related spatial pattern during opening of galls.
The aphid *Quadrartus yoshinomiyai* has a unique social system that consists of two distinct types of defensive individuals—
young and old. This species forms a completely closed gall on
its primary host. When matured, the gall opens to let winged
adults migrate to its secondary host, and then two morphs
protect their colony against intruding predators. Younger
nymphs, which are mainly first-instar nymphs and can poten-
tially develop into winged adults, attack predators with their
styles [15]. In addition, wingless adults, most of which are the
mothers and some are the grandmothers of the winged adults
(K. Uematsu 2011, unpublished data) and stopped producing
the nymphs around the time of gall opening, defend the
colony by sticking themselves to predators with waxy secretion
[16]. Thus, gall opening is the cue to promote the temporal divi-
sion of labour over reproduction. Previous studies, however,
have not investigated how colonies of *Q. yoshinomiyai*, which
include these two types of defenders, organize each member’s
behaviour after galls open to optimize their colony function.

Here, we investigate spatial distribution pattern and its
development in *Q. yoshinomiyai* colonies, in order to deter-
mine whether spatial positioning is specialized to improve
efficiency of colony function. We tested the hypothesis
that the colony members change their spatial positioning in
tune with their shift to defensive or reproductive tasks.
From this hypothesis, we made the following predictions:
(i) both wingless adults and younger nymphs will aggregate
around the gall entrance at which predation risk is highest;
(ii) their spatial distribution pattern will change after the
gall opens. We confirmed these predictions by observations
of the spatial distribution in natural open galls and the move-
ment of colony members when a hole is made in the closed
galls, i.e. artificially opened galls.

2. Material and methods

*Quadrartus yoshinomiyai* forms conspicuous galls on its primary
host plant *Distylium racemosum*. A gall founder forms a closed
gall, where it produces viviparous offspring that develop into
wingless adults [16]. The gall lasts for about fourteen months
(from April to June of the next year), and inside a gall, the second
and most of the third generations grow to wingless adults, and
some of the third generation and almost all of the fourth gener-
ations born from the wingless adults grow to winged adults
(K. Uematsu 2011, unpublished data). The closed gall matures
and forms an exit hole in early to mid-April of the second year,
then the winged adults escape from the open gall via the exit
hole and migrate to the secondary host plant. The wingless
adults and their younger offspring defend their colonies in the
open galls. The galls dry up before mid-June. The mature galls
were observed and collected at Shinkiba and Wakasu, Tokyo,
Japan, and some were brought to the laboratory for further analysis.

(a) Spatial distribution pattern of aphids within natural
open galls

Twenty galls of *Q. yoshinomiyai* each with an exit hole were collected
on 10 April 2007 and 10 April 2009 (two galls from each of six trees
in 2007 and four trees in 2009). Each gall was immediately removed
from the tree and cut into three sections: (i) the section around the
exit hole, located within 5 mm of this opening; (ii) the bottom half of
the gall except around the exit hole; and (iii) the upper half of the
gall. Each section was immediately preserved in 70 per cent ethanol
and brought to the laboratory. The content of each section was
examined under a dissecting microscope, and the numbers of the
following morphs were recorded: (i) wingless adults, (ii) winged
adults, (iii) third or fourth-instar nymphs with wing buds (WB
nymphs), (iv) second or third-instar nymphs without wing buds
(NB nymphs), and (v) first-instar nymphs.

(b) Spatial distribution pattern of aphids within
artificially opened galls

Thirty-one closed galls of *Q. yoshinomiyai* were collected from six
trees at the sites and brought to the laboratory on 10 April 2009
and 7 April 2010. In the laboratory, two protuberances of the
galls were marked for each gall by a polyvinyl chloride tape, a
hole of 2 mm in diameter was bored on one of the protuberances,
and another protuberance was used as a control. The galls were
maintained at 20°C under a dark condition in an incubator.
Twelve hours later, each gall was cut into two sections: (i) the sec-
tion around the artificial hole, located within 5 mm of the bored
hole of protuberance; and (ii) the section without an artificial hole
(control), located within 5 mm of the tip of the protuberance.
Each gall section was preserved and examined as described above.

(c) Data analysis

The gall sections collected from the artificially opened galls
contained very few winged adults, thus the winged adults
were excluded from the following analysis. All other data were
checked for normal distribution by a visual inspection and the
one-sample Kolmogorov–Smirnov test. Since all of them
deviated from normal distribution, they were analysed with
non-parametric statistics. All statistical analyses were conducted
using the software R v. 2.9.2.

3. Results

(a) Spatial distribution pattern of aphids within natural
open galls

In the gall section around the exit hole, the proportions of
wingless adults and first-instar nymphs were significantly
higher than those in either the bottom half section or the
upper half section (Steel–Dwass test, for wingless adults:
\( p < 0.001 \) in both cases; for first-instar nymphs: \( p = 0.024 \)
versus the bottom half and \( p < 0.001 \) versus the upper half).
By contrast, the proportions of winged adults, WB
nymphs and NB nymphs were all significantly lower in the
gall section involving the exit hole than in the other gall sec-
tions (Steel–Dwass test, for winged adults: \( p < 0.001 \) in both
cases; for WB nymphs: \( p < 0.001 \) in both cases; for NB
nymphs: \( p = 0.004 \) versus the bottom half and \( p = 0.003 \)
versus the upper half; figure 1). No significant difference in the
proportions of all morphs was found between the bottom half section and the upper half section (\( p > 0.1 \)).

(b) Formation process of spatial distribution pattern
during gall opening

In the gall section around the artificial hole, the numbers of
wingless adults and first-instar nymphs were significantly
higher than those in the control section without an artificial
hole (Wilcoxon signed-rank test, \( p < 0.001 \) in both cases, figure 2a,b). By contrast, the number of WB nymphs and
NB nymphs were significantly higher in the control section
(Wilcoxon signed-rank test, \( p < 0.001 \) for WB nymphs and
\( p = 0.029 \) for NB nymphs, figure 2c,d). When comparing a
section around natural exit hole and the control section of the
galls collected in the field within 1 or 2 days of opening,
the numbers of these morphs showed a similar pattern (see
the electronic supplementary material).

4. Discussion

We demonstrated that the morphs of the social aphid
Q. yoshinomiyai exhibit non-random spatial distribution
patterns within the open galls in the field. As predicted,
defensive first-instar nymphs and wingless adults showed a
tendency to be placed around the exit hole, whereas reproduc-
tive older nymphs and winged adults showed a tendency to
be placed in a deeper area of the galls, consistent with the
previous study in other social aphids [14]. In addition, our field
observation and laboratory experiments revealed that defensive
morphs move towards the artificial as well as the natural
hole, whereas reproductive morphs move away from the
holes. These results are consistent with our predictions and
support the hypothesis that the spatial distribution patterns
of the aphids reflect their task-related division of labour.
After galls open, Q. yoshinomiyai colonies are likely to respond
to the threat of predation, and optimize their defensive and
reproductive strategy through spatial reorganization.

In the artificially opened galls, dynamic migration of the
colony members occurred within 12 h in darkness, suggesting
the presence of some recruitment mechanisms. Future studies
should clarify the mechanism of the information transmission
between colony members and which cues—for example,
chemical or tactile ones—elicit responses of the aphids after
gall opening.

This study reveals an adaptive spatial arrangement of a
previously unknown type of temporal division of labour, in
which the youngest and the oldest individuals move towards
the dangerous areas to respond to the threat of predation and
middle-aged reproductive individuals reproduce at the end
of the galling season. The evolution of this social system in
a clonal group can be understood as the result of adaptation
at the group level as well as at the individual level [8]. After
galls open, the residual reproductive value of the first-instar
nymphs is much lower than other older aphids because the
galls will be exposed to predation risk and nutritional decline
owing to desiccation [15]. Thus, Q. yoshinomiyai colonies may
optimize their group phenotype by minimizing the cost of
altruistic defence at the group level, according to the repro-
ductive values of colony members under seasonally
changing environments. In addition, because they defend
their colonies in quite different ways, it is of interest to inves-
tigate whether the combination of the young defenders
attacking with stylets and old defenders sticking with waxy
secretion has synergistic benefits for the colony fitness,
which can also explain why these different types of defenders
are evolutionarily maintained.

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