Interspecific variation in competitor avoidance and foraging success in sap-attracted insects

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Abstract. Many insect species attracted to fermenting sap often fight for access to this resource, which results in the establishment of interspecific dominance hierarchies. In one such system, the hornet *Vespa mandarinia* (Hymenoptera: Vespidae) behaviourally dominates during the daytime and several subordinate species avoid aggressive interactions in various ways. In order to elucidate the interspecific variation in competitor-avoidance behaviour and its subsequent effect on foraging success, the behaviour of species of hornets, beetles and butterflies at patches (exudation spots) in Japan was recorded. The percentage of individuals that succeeded in visiting a patch following departure from one, or an attempted visit, or after waiting near a patch for ≥ 10 s, did not differ greatly among species, despite the distinctive differences in dominance between *V. mandarinia* and the other species. These results suggest that subordinate species may be equally effective at foraging for sap as the dominant species. The competitor-avoidance behaviour differed among the species. *Vespa crabro* and satyrine butterflies mainly avoided competition by actively moving away from competitors. The beetle *Rhomborrhina japonica* (Coleoptera: Scarabaeidae) often remained close to an occupied patch and waited for the occupant to leave, whereas *V. ducalis* and nymphaline butterflies used both tactics. The different costs associated with fighting or flight may have determined the differences in the foraging tactics of the species studied and behavioural switching in those species utilising both tactics.

INTRODUCTION

Many insect species, such as beetles, wasps, flies and butterflies, visit sap that exudes from various broad-leaved trees; for example, more than 100 species are attracted to sap on the oak *Quercus acutissima* in Japan (Yoshimoto et al., 2005; Yoshimoto & Nishida, 2008). Tree sap communities exhibit many unique characteristics; for example, the community is composed of primarily adult stages, most of whose larvae feed on food other than sap. In addition, antagonistic interactions often occur among some of the species attracted to sap (e.g., hornets and beetles). Thus, tree sap communities are interesting systems for ecological and entomological research, although quantitative studies of these systems are rare.

In a recent study, Yoshimoto & Nishida (2009) documented interspecific dominance hierarchies established through interference competition in tree sap communities. The giant hornet *Vespa mandarinia* Smith (Hymenoptera: Vespidae) was by far the most dominant insect during the day. Among the subordinate species, individuals avoided aggression in various ways: hornet and butterfly species frequently left patches of sap exuded by trees on the approach of competitors or after being threatened by occupants (Yoshimoto & Nishida, 2009), whereas the beetle *Rhomborrhina japonica* Hope (Coleoptera: Scarabaeidae) often remained close to occupied patches until the occupants left (J. Yoshimoto, pers. obs.). Such waiting behaviour and its effect on foraging success is documented for several hornet species (Matsuura, 1969). However, neither the frequency of such waiting behaviour nor the consequences of such competitor-avoidance behaviour for foraging success in other species have been documented. Such research would provide an insight into the mechanisms resulting in variations in behaviour of insects that are attracted to sap and of species coexistence at patches.

In the present study, the patch-visiting behaviour of large diurnal species (hornets, beetles and butterflies) was examined to elucidate the interspecific variation in competitor-avoidance behaviour and subsequent foraging success. First, in order to determine whether species that adopt a competitor-avoiding strategy succeed in feeding at patches, behavioural sequences were recorded. Second, the foraging areas and inter-patch movement of individually marked individuals of several species of hornets and butterflies were quantified in order to detect both intra- and interspecific differences in patch-visiting behaviour. Here, the foraging tactics of each species are described and factors determining the respective tactics discussed.

MATERIAL AND METHODS

Study site

This study was conducted in a temperate secondary forest along the Iwakura River, Kyoto, Japan (35°05′N, 135°47′E, ca. 120 m in elevation). The site is dominated by oak, *Q. acutissima* (Fagaceae), with an admixture of many other deciduous broad-

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leaved trees such as *Styrax japonica* (Styracaceae) and *Mallotus japonicus* (Euphorbiaceae). This type of mixed forest, called Satoyama forest, is typical of Japan and harbours a great diversity of insects (Kato, 2001).

Behavioural observations

The behaviour of four hornet species (*Vespa mandarinia* Smith, *V. crabro* Linnaeus, *V. analis* Fabricius, *V. ducalis* Smith; Hymenoptera: Vespidae: Vespinae), one beetle species (*Rhomborrhina japonica* Hope; Coleoptera: Scarabaeidae: Cetoniinae) and eight butterfly species (*Neope goschkevitschii* Menetries, *Lethe sicelis* Hewitson: Lepidoptera: Nymphalidae: Satyrinae; *Kaniska canace* Linnaeus, *Vanessa indica* Herbst, *Polygonia c-aureum* Linnaeus, *Nymphalis xanthomelas* Esper, *Hestina japonica* Felder, *Limenitis camilla* Linnaeus: Nymphalinae) visiting patches were recorded. The behaviour of individuals was classified into one of seven categories: departure, flew away, visit, attempted visit, waiting, perching and undetermined. The category departure was assigned to those individual that left a patch and remained in sight of an observer until it changed its behaviour. Flew away to those individuals that flew out of sight. Attempted visit to those individuals that approached and then left a patch either without feeding or after remaining at the patch for < 5 s. Visit to those individuals that stayed at the patch for ≥ 5 s. Waiting to those individuals that stayed at a distance of ≤ 10 cm from a patch for ≥ 10 s. When an individual perched on a tree > 10 cm from a patch, it was categorised as perching. A flow diagram indicating all the possible sequences of these behaviours is presented in Fig. 1. Observations began when an individual exhibited any of the following three categories of behaviour: departure, attempted visit, or waiting. Observations stopped when the individual flew away or was lost from sight. All new arrivals on a tree were recorded as different individuals, because newcomers and repeaters were nearly impossible to distinguish without marking. The observations were recorded over a period of 12 days between June and October 2005 and on 6 days between May and June 2006. Supplementary observations on butterfly species were recorded over a period of 12 days between July and October 2006, because few results were recorded as previously these species were uncommon. The behaviour of the insects was recorded daily over a period of 60–180 min between 11:00 and 18:40 h. Both the times and dates on which the insects were observed were arbitrarily determined. Two trees (A and B) were sampled in both years because they harboured more patches (a total of ca. 30 were observed in each year), which attracted more insects than those on other trees in the study area (J. Yoshimoto, unpubl. data). Each tree was observed for 1 or 2 h per day.

A total of 11 individuals of *V. mandarinia*, 14 of *V. crabro* and 40 of *N. goschkevitschii* were individually marked on 25 and 29 May 2006. These species were marked because they were relatively abundant (Yoshimoto & Nishida, 2009). *Vespa mandarinia* and *V. crabro* were anesthetized with ethyl acetate and then marked with a number on the dorsal surface of the thorax using a white paint marker (Mitsubishi Co. Ltd.) and *Neope goschkevitschii* was marked with a number on the ventral surface of both hindwings using a black felt-tip pen. Both marked and un-marked individuals were observed on the same days (on 6 days until 13 June) as when the behavioural sequences were recorded. Behavioural sequences of marked individuals were recorded using the same categories as above. The number of patches visited or for which an attempted visit was observed for each individual in each time slot (1 h) was recorded. In each period, observations were resumed when marked individuals revisited a patch after previously flying away.
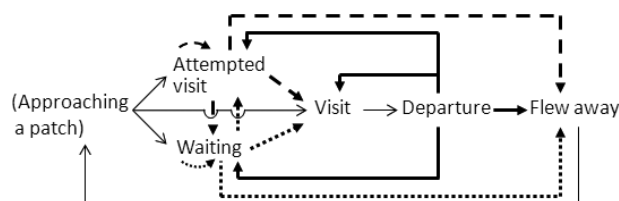
Fig. 1. Schematic diagram of possible behavioural sequences of individual insects visiting patches. The changes in behaviour follow that indicated by the directions of the arrows. Curved and bold arrows indicate repeated occurrence of the same behaviour and behavioural sequences, respectively. The sequences indicated by solid, broken and dotted arrows are those shown in Figs 2, 3 and 4, respectively. "Perching" was omitted from the diagram because it can occur anytime except between visiting and departure (see Material and methods for definitions of each behaviour).

Data analyses

Foraging success after leaving a patch (visiting success after departure) was assessed for each species as follows. First, the number of individuals that left a patch and then succeeded in visiting a patch at least once was counted and the results pooled across patches, time and year. Then, the percentage of individuals that exhibited each category of behaviour, except those only exhibiting undetermined behaviour, was compared among those species for which the total number of observations was each > 25. Datasets for marked individuals were excluded from the calculations of visiting success for *V. mandarinia*, *V. crabro* and *N. goschkevitschii* because the method of determining total abundance differed for marked and unmarked individuals. As mentioned above, all newly unmarked individuals were considered to be different individuals. In addition, the total frequency of each behavioural category shown by each species immediately after departing from a patch was obtained and the percentage in each category compared among species. Statistical comparisons using chi-squared tests were only conducted for visiting success. Analyses excluded species whose expected values were < 5. When significant differences were detected, multiple pairwise comparisons were conducted using Bonferroni corrections.

Similarly, visiting success either after an attempted visit or after waiting was compared among species whose total frequencies were > 25 and > 15, respectively. Patterns of behaviour immediately after each of the two target behaviours were also compared among species. Additionally, to examine the post-waiting foraging success at the level of subfamily within the Lepidoptera, visiting success was compared between Satyrinae and Nymphalinae after pooling data from 2006 for each subfamily. All interspecific comparisons were made using the same methods as above.

Interspecific differences in the patterns of visiting patches were examined using datasets for marked individuals of *V. mandarinia*, *V. crabro* and *N. goschkevitschii*. First, the mean number of patches visited per hour (P_e) or for which attempted visits occurred per hour (P_{ae}) was calculated for each re-observed individual, after excluding 0 data (time slots when no visit or attempted visit were recorded) in order to prevent the underestimation of the parameters. Second, Simpson's index of diversity ($1/D$; Simpson, 1949) was used to represent the foraging area of each individual. The index was derived as follows:

$$\frac{1}{D} = \frac{1}{\sum\limits_{i=1}^{S}\left(\frac{n_i}{N}\right)^2} \quad (1)$$

TABLE 1. Percentage of individuals of species of hornet (Vespidae: Vespinae), a species of beetle (Scarabaeidae: Cetoniinae) and species of butterfly (Nymphalidae: Satyrinae and Nymphalinae) that succeeded in visiting a patch (until flying away) after leaving, or after failing to visit or after waiting close to a patch. Species abbreviations are in parentheses.

| Subfamily | Preceding behaviour | | |
Species	Departure	Attempted visit	Waiting
Vespinae			
Vespa mandarinia (Vm)	**45.8**[a]	**58.6**	100.0
Vespa crabro (Vc)	**39.1**[a]	**35.9**	–
Vespa analis (Va)	55.6	55.6	–
Vespa ducalis (Vd)	**38.9**[ab]	20.0	60.0
Cetoniinae			
Rhomborrhina japonica (Rj)	**53.1**[a]	41.7	**80.0**[a']
Satyrinae			
Neope goschkevitschii (Ng)	**15.5**[b]	**31.9**	**31.3**[b']
Lethe sicelis (Ls)	**21.9**[ab]	53.8	25.0
Nymphalinae			
Vanessa indica (Vi)	**29.7**[ab]	46.2	50.0
Kaniska canace (Kc)	**25.0**[ab]	18.2	83.3
Polygonia c-aureum (Pc)	0	100.0	0
Nymphalis xanthomelas (Nx)	10.0	0	100.0
Hestina japonica (Hj)	50.0	66.7	100.0
Limenitis Camilla (Lc)	0	33.3	100.0

Only values in bold letters were included in the analyses. Different letters attached to values in a column indicate significant differences (no superscript indicates a non-significant result).

where S is the total number of visited patches, N is the total frequency of visits and n_i is the frequency of visits to patch i for each marked individual. Larger values of the index indicate more extensive foraging because the value is higher when an individual visits more patches more evenly. The index was calculated separately for visits and attempted visits, abbreviated as $1/D_e$ and $1/D_{ae}$, respectively. P_e, $1/D_e$, and P_{ae} were each compared among the three species using Kruskal-Wallis tests. Multiple pairwise comparisons were made using Bonferroni corrections. $1/D_{ae}$ was only compared between *V. mandarinia* and *V. crabro* because the sample size for *N. goschkevitschii* was too small ($n = 3$). Two neighbouring patches on tree B became one large patch on the final day (13 June) due to an increase in sap flow; consequently, for observations prior to 13 June, these two patches were also treated as a single patch in the analyses.

RESULTS

Behavioural sequences

The visiting success after departure significantly differed among the eight species (Pearson $\chi^2 = 36.815$, $df = 7$, $P < 0.001$; Table 1). There was no significant difference among *V. mandarinia*, *V. crabro* and *R. japonica*, and all these species re-visited patches significantly more frequently than did *N. goschkevitschi*. Both *V. mandarinia* and *V. crabro* behaved similarly after leaving a patch (Fig. 2). *Vespa ducalis*, *R. japonica* and *K. canace* all tended to wait close by to occupied patches more frequently than the other species. The behaviour of the two satyrine species was also similar, as both of these species frequently flew away.

The visiting success after an attempted visit did not significantly differ among the three species (Pearson $\chi^2 = 5.743$, $df = 2$, $P = 0.057$; Table 1). *Vespa mandarinia*, *V. crabro* and *N. goschkevitschii* all tended to visit a patch or

fly away after frequent attempts (Fig. 3). Moreover, *V. crabro* and *V. analis* often attempted to repeatedly visit a patch.

The number of successful visits following waiting was significantly higher in *R. japonica* than in *N. goschkevitschii* (Pearson $\chi^2 = 10.644$, $df = 1$, $P < 0.01$; Table 1). Individuals of *N. goschkevitschii* tended to fly away more often than did those of *R. japonica* and *K. canace* (Fig. 4). At the subfamily level, the percentage of successful visits following waiting was significantly higher in Nymphalinae (76.9%) than in Satyrinae (30.0%; Pearson $\chi^2 = 6.945$, $df = 1$, $P < 0.01$).

Individual foraging patterns

The frequency of re-observation was much higher in both *V. mandarinia* (81.8%) and *V. crabro* (71.4%) than in *N. goschkevitschii* (27.5%), although the difference
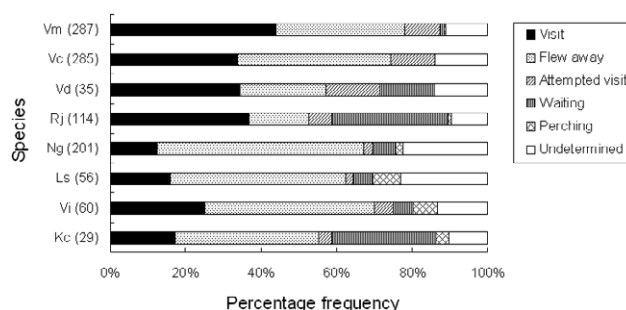

Fig. 2. Percentage frequency of behavioural categories recorded immediately after leaving a patch (see Material and methods for definitions of each behavioural category) for eight species (see Table 1 for abbreviations of species names). The total number of observations on each species is given in parentheses.
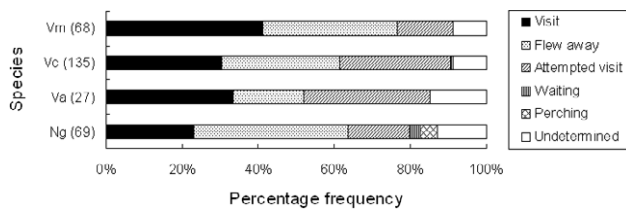
Fig. 3. Percentage frequency of behavioural categories for four species recorded immediately after an attempted visit to a patch (see Table 1 for abbreviations of species names). The total number of observations on each species as in Fig. 2.
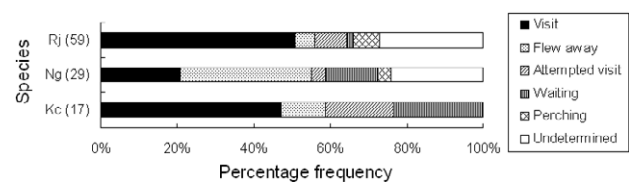

Fig. 4. Percentage frequency of behavioural categories for three species recorded immediately after waiting by a patch (see Table 1 for abbreviations of species names). The total number of observations on each species as in Fig. 2.

was only marginally significant (Pearson χ^2 = 5.163, df = 2, P = 0.076; Table 2). All parameters of foraging behaviour also tended to be higher in the hornets than in *N. goschkevitschii*; the difference was significant for attempted visits (P_{ae}: H = 8.243, df = 2, P < 0.05) and marginally significant for visits (P_e: H = 5.630, df = 2, P = 0.060; $1/D_e$: H = 4.764, df = 2, P = 0.092). These results indicate that per unit time hornets visit more patches more frequently and more extensively than the butterflies. For *N. goschkevitschii*, ten out of 11 re-observed individuals visited only one patch per hour. Inter-tree movement (visiting patches on different trees) was observed for one individual.

Among the hornet species, all mean values of foraging parameters were very similar for *V. mandarinia* and *V. crabro*, and $1/D_{ae}$ did not significantly differ between the two species (H = 0.003, df = 1, P = 0.957; Table 2). More individuals of *V. crabro* (n = 5) exhibited inter-tree movement compared to *V. mandarinia* (n = 1), although only one individual of each species visited both trees repeatedly.

DISCUSSION

There were few differences in the foraging success of the hornet, beetle and butterfly species measured in terms of the incidence of departures, attempted visits and waiting, despite the distinctive differences in dominance between *V. mandarinia* and the other species (Yoshimoto & Nishida, 2009). These results suggest that subordinate species are as successful at foraging as dominant species,

even though they may have to wait to visit a patch. The number of successful visits may have been underestimated, because those individuals that flew away and whose subsequent behaviour was not tracked, may have eventually succeeded in visiting other patches. Patches were rarely monopolised by hornets, mainly due to the brevity of their visit, and thus unoccupied patches were common at the study site (Yoshimoto et al., 2007). Consequently, species with low visiting success (e.g., *N. goschkevitschii*) may have more foraging opportunities if measured over a longer time span than used in this study.

Competitor-avoidance behaviour varied greatly among the species studied. The most striking was the frequent occurrence with which waiting was recorded in *R. japonica*: individuals remained close to patches after departure or an attempted visit much more often than did other species. This is associated with the fighting tactics of this species, in which individuals usually retreat and remain close to a patch after being attacked by dominants (Yoshimoto & Nishida, 2009).

The behaviour of the three hornet species also differed: *V. ducalis* exhibited waiting behaviour more frequently than did *V. crabro* and *V. analis*. This difference may have occurred in part because *V. ducalis* is the least dominant of the five hornet species, including *V. simillima xanthoptera* Cameron (Matsuura, 1984). Accordingly, when individuals of *V. ducalis* tried to visit other patches, they less frequently displaced an occupant compared to the other hornet species and thus more frequently stayed in the area and waited for the occupant to leave. In contrast, the results suggest that, after failing in its attempt to

TABLE 2. Patterns in the behaviour exhibited by two species of hornet and one species of butterfly when visiting patches in 2006. Both visits and attempted visits to patches were also recorded for those marked individuals that were observed more than once. The mean number of patches visited and or attempted to visit per hour (P_e and P_{ae}, respectively) and the foraging area indices ($1/D_e$ and $1/D_{ae}$; see text for method of calculation) are shown. All values are means ± SE.

Parameters	*Vespa mandarinia*	*Vespa crabro*	*Neope goschkevitschii*
No. marked individuals	11	14	40
No. re-observed individuals	9	10	11
Visits			
P_e	1.315 ± 0.143	1.348 ± 0.140	1.030 ± 0.030
$1/D_e$	2.226 ± 0.429	2.248 ± 0.345	1.388 ± 0.142
Attempted visits			
P_{ae}	1.315 ± 0.322[a]	1.302 ± 0.183[a]	0.409 ± 0.241[b]
$1/D_{ae}$	2.385 ± 0.504	2.265 ± 0.345	(1.593 ± 0.593)

Different letters attached to values in a row represent significant differences (no superscript indicates a non-significant result). The value in parentheses was not included in the analyses.

visit a patch, *V. crabro* primarily moves elsewhere in search of unoccupied patches. The frequency of successive attempts by *V. analis* implies that this species also avoids competition by employing a similar moving-away tactic. Both *V. crabro* and *V. analis* are smaller than *V. ducalis* (Matsuura, 1984), which may also favour their agile inter-patch flight abilities.

Matsuura (1969) reports that hornets often failed to forage at patches occupied by many dominant individuals, which is inconsistent with the results presented here. This discrepancy may be due to a difference in resource abundance; the observations of Matsuura (1969) were made in April, when there are likely to be fewer patches (the author did not record the abundance of this resource). Although such foraging failures might be exceptional, it is necessary to determine the behavioural interactions in relation to the availabilty of sap throughout the exudation period in order to clarify the seasonal variation in foraging success, as resource abundance can alter the outcome of interference (e.g., Parrish, 1984) and affect foraging tactics (e.g., Nakano et al., 1999).

Observations of individually marked insects revealed that the butterfly and hornet species had different foraging patterns. *Neope goschkevitschii* visited fewer patches less often per unit time than either *V. mandarinia* or *V. crabro*, suggesting that butterflies forage for sap over a longer interval than hornets. Furthermore, the frequency of post-waiting foraging success was much higher in Nymphalinae than Satyrinae. Nymphaline species sometimes threatened patch occupants by quickly opening their wings, which even caused hornets to retreat (J. Yoshimoto, pers. obs.). Thus, nymphalines actively tried to increase foraging opportunities by a combined strategy of inter-patch movement, waiting, and threatening. The lower frequency of post-waiting foraging success in satyrines may have been due primarily to the higher incidence of active chasing flights recorded for these species, presumably associated with courtship behaviour. This behaviour was often observed in *N. goschkevitschii* during early summer and autumn, and it typically reduced subsequent foraging success. Another possibility is that *N. goschkevitschii* perched near to patches solely to rest; such tree-perching behaviour is reported for *L. sicelis* (Ide, 2001).

Although the nymphalid butterflies and *R. japonica* feed on other fermenting materials, such as rotten fruit, tree sap appears to be a necessary resource, because fruit is not always abundant in and around the study site. Tree sap is also important for omnivorous hornets, because it is an important source of carbohydrates (Matsuura, 1984). Accordingly, foraging success at patches may be important for the survival of these species.

To summarise, this study of foraging behaviour indicates that hornets and butterflies tended to avoid interference competition by moving away from competitors, and after being attacked or displaced, the beetle *R. japonica* remained near patches waiting for an opportunity to forage. Additionally, the waiting tactics of *V. ducalis* and nymphaline species depend on the circumstances. By avoiding competitors, even subordinate species may be able to forage successfully for sap. It is likely there are different costs associated with fight or flight in the different species and in behavioural switching in species utilising both tactics; such issues remain to be studied.

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