Factors Affecting Behavioral Interactions Among Sap-Attracted Insects

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ABSTRACT Aggressive interactions often occur between individuals of various insect species attracted to fermented tree sap. We explored interspecific behavioral dominance hierarchies and factors responsible for such interactions occurring in sap-exuding patches on trees. We observed fighting behavior, departures from patches, and attempted entries into patches (individual approached and then left a patch without feeding) in four hornet species (Vespidae), four butterfly species (Nymphalidae), and one beetle species (Scarabaeidae). Our examination of these interactions indicated that the hornet species, Vespa mandarinia Smith, was the most dominant and that butterfly species were competitively inferior. Both Vespa ducalis Smith and Rhomborrhina japonica Hope were less dominant than Vespa crabro L. and Vespa analis F. in departures and attempted entries into patches, but neutral when it came to fighting behaviors. For most hornet and butterfly species, approach and threat behaviors were mainly responsible for departures and attempted entries, respectively, indicating that individuals of these species avoid fights by recognizing the behaviors of other individuals. These results suggest that competitor-avoidance behaviors play an important role in foraging success at sap sites, highlighting the importance of examining these behaviors as well as aggressions before determining dominance hierarchies. Competitor-avoidance behaviors of subordinate species might enable them to forage in patches and potentially affect the co-occurrence of sap-attracted insects.

KEY WORDS aggression, coexistence, competitor avoidance, dominance hierarchy, interference competition

In many animal species, individuals exhibit competitive interference for resources such as food or space. Interference refers to any activity limiting a competitor’s access to a resource (Miller 1967) and occurs in various manners with differing levels of aggressiveness. For example, direct, severe interactions such as fighting (Forkman and Haskell 2004, Holway and Suarez 2004) and indirect interactions, such as competitor-avoidance behavior (Cresswell 1997, Durant 2000), have been observed. Intra- and interspecific dominance hierarchies are established through interference and are often determined based on the outcome of aggressions or fights (e.g., Forkman and Haskell 2004). However, such hierarchies may not reflect the actual relationships among individuals that avoid competitions, because interactions other than direct aggression are often overlooked using this method of establishment. Thus, it is desirable to examine competitive behaviors, including competitor-avoidance and then to determine dominance hierarchies based on their outcomes. Moreover, examining such behavioral interactions is important in clarifying the mechanisms of species coexistence, because interspecific interference competition can significantly affect community structure (Schoener 1983).

Many insect species are attracted to fermented tree sap (Yoshimoto et al. 2005), and individuals often fight over this resource. Kikuchi (1962) reported competitive dominance hierarchies among species of hornets, beetles, and butterflies visiting willow sap. Matsuura (1969) also documented that Vespa mandarinia Smith was the most dominant among five hornet species visiting oak (Quercus spp.) sap. In a previous study, we found that departure from a patch (an individual spot exuding sap on a tree) without interference (attacks or physical contact behaviors) was more frequent than interference-mediated departure for most species observed (Yoshimoto et al. 2007). However, these behaviors varied among species and with time of year. Various competitor-avoidance behaviors were often observed, such as avoidance of fights by recognizing the approach of dominants or by avoiding occupied patches. Such avoidance behavior may affect foraging success of subordinate species, thereby potentially contributing to their co-occurrence with dominants.

In this study, intra- and interspecific behavioral interactions in patches on oak trees were investigated for major diurnal sap feeders (hornets, beetles, and butterflies) to explore factors responsible for the inter
teractions and to identify foraging patterns of the insects. First, physical fighting was observed to determine interspecific dominance hierarchies in fights (hereafter referred to as aggression dominance). We then focused on patch departure and entry behaviors, describing the interactions that force an occupant to leave a patch or prevent a visitor from entering a patch. Additionally, we determined interspecific dominance hierarchies by synthesizing the outcomes of these interactions and aggression dominance. We also conducted field surveys to estimate the abundances of focal species, and analyzed behavioral contexts in relation to their abundance to search for density-dependent occurrence of interactions. Finally, we discuss plausible factors contributing to variable occurrence of interactions and their implications for species coexistence at sap sites.

Materials and Methods

Study Site. This study was conducted in a wooded area in Iwakura, Kyoto, Japan (35°05′N, 135°47′E). The site is a temperate secondary woodland dominated by oak (Quercus acutissima Carruth.), with many other deciduous trees, such as Styrax japonica Sieb. et Zucc. and Mallotus japonicus Muell. Arg.

Aggression Dominance. We observed interspecific fighting behavior between individuals of diurnal insects at sap sites in the daytime on 15 d from May to October 2001. Patches on six Q. acutissima trees (trees A–F) were randomly chosen for observation. We judged a fight to be completed when either of the two combatting individuals retreated or flew away. For practical reasons, observations were restricted to individuals of relatively large species. Other than species, individuals were not distinguished; caste and sex of individual hornets were not determined.

Patch Departure and Entry Behaviors. To identify factors responsible for foraging behaviors and to quantify their frequencies, departure from a patch and attempted entry into a patch were both observed in relation to interactions. Attempted entry was defined as the behavior whereupon an individual approached and then left a patch without feeding. Staying at a patch for <5 s was included as a case of attempted entry on the assumption that feeding rarely occurs in such a short period. Each behavior was recorded based on the presence or absence of interactions and on the species involved. Interactions responsible for patch departures were grouped into four categories (attack, contact, approach, and chase). Attack, contact, and approach behaviors were defined as cases when an individual was forced to leave a patch after being attacked (when it fought or was threatened), incidentally contacted physically (excluding cases when contacted for attack), or approached by another individual, respectively. Chase behavior was defined as the case when an individual left a patch while it continued fighting with another individual or followed it to attack. Chase behavior differed from the other three categories in that the roles of the actor and the receiver of interactions were reversed, and the depictions of the actors (chasing individuals) were recorded. Interactions responsible for attempted entry were recorded in the same categories as described above, except that attack behavior was subdivided into fights and threats. A threat was defined as the case in which an individual was prevented from entering a patch after being threatened by another individual: for example, hornets raise their forelegs or nymphalid butterflies open their wings quickly to threaten others. In satyrine butterflies (e.g., Neope and Lethe spp.), neither attack nor contact behavior was distinguished, because it was almost impossible to separate these behaviors given the agility of these species during encounters and flight. The observations were done on 13 d between June and August 2003, and in October 2003, and on 10 d between May and September 2004. Daily observational time was 60–180 min between 1100 and 1910 hours. Both time and dates that observations were made were arbitrarily determined in both years. Trees A and B were both sampled in both years because they had more patches and more insects. Another four randomly chosen trees also were used (trees G, H, and I in 2003 and tree J in 2004) to increase sample size. All patches below 3 m in height on the trees were observed, although several patches with few individuals were omitted on some days. Patch size greatly varied among the patches and dates; average surface area (mean ± SE) of patches (n = 23) on trees A and B was 376.63 ± 154.20 cm² in 2003 (see Yoshimoto and Nishida 2007 for methods). All interactions were documented by direct observation in the field, except for 3 d in 2003, when we recorded interactions using an 8-mm videotape recorder (CCD-TRV66K, Sony, Tokyo, Japan). These video data were used to obtain additional data on each behavioral context and were analyzed along with the direct observational data.

Species Abundance. Field surveys were conducted to estimate the abundance of each species during the observational period each year (June to August 2003, October 2003, and May to September 2004). Six and eight Q. acutissima trees were monitored in 2003 (trees A–D, J, and K) and 2004 (trees A–D and J–M), respectively. Each tree was observed for 10 min to record the species and number of insects within each patch. The observations were made in the daytime (from 1100 to 1800 hours) for 2 d a month.

Data Analyses. Using the data obtained in 2001, dominance hierarchies were examined among the following species that interacted against at least three species or at least 16 times; subjects included four species of hornet (Vespa mandarinia Smith, Vespa crabro L., Vespa analis F., and Vespa ducalis Smith; Hymenoptera: Vespidae; Vespiinae), one species of beetle (Rhomborrhina japonica Hope; Coleoptera: Scarabaeidae: Cetoniinae), and two species of butterfly (Neope goschkevitschii Menetries and Lethe sicelis Hewitson; Lepidoptera: Nymphalidae: Satyrinae). The species names were abbreviated in the table as follows: Vm (V. mandarinia), Vc (V. crabro), Va (V. analis), Vd (V. ducalis), Rj (R. japonica), Ng (N. goschkevitschii), and Ls (L. sicelis). The data were pooled.
across months because a preliminary analysis detected no distinct seasonal pattern in the outcome of fights. Two dominance matrices were constructed using total scores and daily scores. Total scores were defined as the total frequency of wins and losses, whereas daily scores were defined as the number of winning and losing days (as determined by the relative frequencies of wins and losses in a day, e.g., a winning day had more wins than losses). These two types of scores were analyzed together because total scores alone could potentially be outweighed by data obtained on days with an unusually high occurrence of fighting. The proportion of fights won was calculated as the ratio of win frequency to fight frequency for the total scores and as the ratio of total winning days to total fighting days for the daily scores.

The data for patch departures were pooled across patches and time for each focal species for each behavioral category in 2003 and 2004. The following analyses excluded departures that were probably the result of artificial circumstances, such as proximity of a human observer. The proportions of these categories were compared among the following nine species whose total observation frequency was >25 in each year: V. mandarinia, V. crabro, V. analis, V. ducalis, R. japonica, N. goschkevitschii, L. sicelis, Kaniska canace L., and Vanessa indica Herbst (both Lepidoptera: Nymphalidae: Nymphalinae). Two hornets (V. analis and V. ducalis) in 2003 and three butterflies (L. sicelis, K. canace, and V. indica) in 2004 were excluded from the comparison because of small sample sizes (≤25). The species names were abbreviated in the tables and figures as above, with the addition of K. canace (Kc) and V. indica (Vi). The proportion of departures mediated by interactions (attack, contact, approach, chase, and unidentified interactions) was compared among these species in each year using a chi-square test. The same analyses tested for a difference in the proportions of the received interactions (attack, contact, and approach) among these species, after excluding the data sets of both chase and unidentified interactions. Post hoc multiple pairwise comparisons were made with the Bonferroni corrections when significant differences were detected. In addition, the proportions of departure with or without interactions were compared for each species in each year using a two-tailed binomial test. The same analyses tested for a difference in the proportions of departure mediated by intra- and interspecific interactions (whether an individual left a patch after it interacted with a conspecific or heterospecific individual) for each species in each year.

The data for attempted entry were analyzed similarly. Contexts of attempted entry by behavioral category or by intra- and interspecific interactions were compared among the following seven species whose total observation frequency was >25 in each year: V. mandarinia, V. crabro, V. analis, V. ducalis, R. japonica, N. goschkevitschii, and V. indica. Vespa ducalis in 2003; R. japonica in 2004; and V. indica in 2004 were excluded from the comparison because of small sample sizes (≤25). V. analis in 2003 also was excluded despite a total observation frequency >25, because the frequency of attempted entries deterred by identified interactions was too low (n = 3). The proportions of attempted entry with interactions or with the received interactions (fight, threat, contact, and approach) were each compared among species in each year using a chi-square test. Post hoc multiple pairwise comparisons were made with the Bonferroni corrections when significant differences were detected. The proportions of attempted entry with or without interactions and of attempted entry deterred by intra- or interspecific interactions were each compared using a two-tailed binomial test. Dominance relationships were estimated from proportions both of interaction-mediated or received interaction-mediated departures and of attempted entries. Species with the lowest proportions were considered to be the most dominant. These results were then compared with aggression dominance to check for discrepancies. Interspecific behavioral dominance hierarchies were determined based on the results of the comparison.

Intra- and interspecific interactions were investigated in relation to abundance as follows. The total number of individuals (abundance) for the nine species was obtained from the field survey data. Then, the correlation was calculated between their abundance and the total frequency of departures mediated by intraspecific interactions in each year. The percent frequency of these departures also was examined in relation to the abundance in each year. Similarly, the correlation was examined between the abundance and the total or percent frequency of attempted entries deterred by intraspecific interactions in each year. All relationships were analyzed using Kendall’s rank correlation. These analyses were conducted using STATISTICA 1999 edition (StatSoft, Tulsa, OK).

Results

Interspecific Dominance Hierarchies. V. mandarinia almost always defeated all other species (Table 1), indicating that V. mandarinia was the most dominant in fighting. The results also showed that butterfly species are competitively inferior. The pattern of aggression dominance among hornet species other than V. mandarinia was obscure. The fighting success of V. crabro was about the same as that of V. ducalis, which did not defeat V. analis. Aggression dominance between these hornet species and R. japonica was also unclear; both V. ducalis and V. crabro were slightly more dominant than R. japonica, and fights between V. analis and R. japonica were infrequent.

The proportion of interaction-mediated departures significantly differed among focal species in both 2003 (Pearson $\chi^2 = 323.1, P < 0.001$) and 2004 (Pearson $\chi^2 = 91.4, P < 0.001$; Table 2). A significant difference also was detected in the proportion of departures mediated by the received interactions (attack, contact, and approach) in both years (2003, Pearson $\chi^2 = 394.6, P < 0.001$; 2004, Pearson $\chi^2 = 97.8, P < 0.001$). The proportions were lowest for V. mandarinia in 2003, whereas they were significantly much higher for
Vespa mandarinia (Vm) — 11 (5) 6 (3) 21 (3) 7 (1) 11 (3) 1 (1) 57 (16) 0.95 (1.00)
Vespa ducalis (Vd) 0 (0) — 6 (2) 0 (0) 29 (2) 0 (0) 0 (0) 35 (4) 0.61 (0.31)
Vespa crabro (Vc) 0 (0) 5 (2) — 0 (0) 4 (2) 8 (3) 1 (1) 18 (8) 0.56 (0.57)
Vespa analis (Va) 0 (0) 5 (2) 0 (0) — 0 (0) 0 (0) 2 (2) 7 (4) 0.24 (0.50)
Rhomborrhina japonica (Rj) 0 (0) 1 (0) 2 (1) 1 (1) — 0 (0) 0 (0) 4 (2) 0.00 (0.29)
Neope goschkevitschii (Ng) 1 (0) 0 (0) 0 (0) 0 (0) 0 (0) — 0 (0) 1 (0) 0.05 (0.00)
Lethe sicelis (Ls) 0 (0) 22 (9) 14 (6) 22 (4) 40 (5) 19 (6) 4 (4) 122 (34)
Total 1 (0) 22 (9) 14 (6) 22 (4) 40 (5) 19 (6) 4 (4) 122 (34)

Rows show the frequency of wins, whereas columns show the frequency of losses (total scores). The numbers of winning and losing days are shown in parentheses (daily scores). The proportion of wins by a species is calculated from each of the two scores (the proportions derived from daily scores are shown in parentheses).

Table 1. The outcomes of fights among four species of hornet (Vespa), one species of beetle (Rhomborrhina), and two species of butterfly (Neope and Lethe) in 2001 (species abbreviations are also shown)

Table 2. The frequency of patch departure with or without interactions, compared using a two-tailed binomial test (**P < 0.001), for nine species in 2003 and 2004 (abbreviations of species names are as in Fig. 1)

The frequency of departure with the received interactions (attack, contact, and approach; see Materials and Methods for the definitions of these categories) are shown in parentheses. The percent frequencies of interaction-mediated departure were each compared among species using a chi-square test in each year (different letters indicate significant differences). The percent frequencies of departure mediated by the received interactions are also shown in parentheses, analyzed as for interaction-mediated departure.

Contexts of Patch Departure. Among interaction-mediated departures of these species, chasing behavior was most important in both V. mandarinia and V. crabro in 2003, and approach was most important in both V. crabro (in 2004) and V. analis (Fig. 1). For V. ducalis, attack and approach were the two most important factors. Intraspecific interactions resulted in significantly more departures than interspecific interactions for both V. mandarinia and V. crabro in 2003; however, the opposite pattern was detected for other hornet species (Fig. 2). Above all, both V. analis and V. ducalis caused the departure of one another most frequently.

The departure context varied yearly for R. japonica. Interaction-mediated departures were significantly more frequent than departures without interactions in 2003, but the proportions of the former and the latter were about the same in 2004 (Fig. 1). Departures after attack were most often observed in both years. Moreover, intraspecific interactions resulted in significantly more departures than interspecific interactions in both years (Fig. 2).

All butterfly species were often forced to leave a patch after being approached by other individuals (Fig. 1). In addition, departures upon attack or contact also occurred frequently in nymphaline species (K. canace and V. indica) and satyrine species (N. goschkevitschii and L. sicelis), respectively. Interspecific in-

V. ducalis, R. japonica, and the four butterfly species in both years. No significant difference was detected among these subordinate species except between the proportion of interaction-mediated departures of R. japonica and that of N. goschkevitschii in 2003. Moreover, interaction-mediated departures occurred significantly less frequently than departures without interactions for three of the hornet species (V. mandarinia, V. crabro, and V. analis), whereas the opposite was true for three of the butterfly species (N. goschkevitschii, L. sicelis, and V. indica).

The proportion of attempted entries deterred by interactions also differed significantly among focal species in both 2003 (Pearson $\chi^2 = 71.9, P < 0.001$) and 2004 (Pearson $\chi^2 = 17.4, P < 0.01$; Table 3). Similar results were obtained in the attempted entries deterred by the received interactions (fight, threat, contact, and approach) in both years (2003, Pearson $\chi^2 = 64.7, P < 0.001$; 2004, Pearson $\chi^2 = 17.1, P < 0.01$). The proportions also tended to be lower for the three hornet species than for others, although no significant difference was detected among V. mandarinia, V. crabro, V. ducalis, and N. goschkevitschii. Attempted entries without interactions occurred significantly more frequently than those with interactions for V. mandarinia (in 2003) and V. analis; however, the opposite pattern was detected for V. ducalis, R. japonica, N. goschkevitschii (in 2004), and V. indica.
Interactions resulted in significantly more departures than intraspecific interactions did for all species except *N. goschkevitschii*, in which the proportions of departures mediated by intra- and interspecific interactions were similar in both years (Fig. 2). All species were often forced by *V. mandarinia* and *V. crabro* to leave a patch, and *L. sicelis* suffered from frequent interactions with *N. goschkevitschii*.

**Contexts of Attempted Patch Entry.** Threatening behavior often deterred the entry of all hornet species (Fig. 3). Contact also frequently prevented the entry of *V. mandarinia* and *V. crabro*, whereas fighting was the major factor affecting *V. ducalis*. Conspecifics deterred entries significantly more frequently than heterospecics did for *V. mandarinia* in 2003, whereas the opposite was true for *V. crabro* (in 2004), *V. analis*, and *V. ducalis* (Fig. 4). *V. mandarinia* often deterred entries of all other hornet species mainly through threat. In addition, *V. analis* and *V. ducalis* often prevented the entry of one another; a similar negative interaction was observed in their departure behavior.

For *R. japonica*, the proportion of attempted entries caused by fighting was highest among all species (Fig. 3). The proportion of attempted entries deterred by conspecifics was also highest (Fig. 4); this also was attributed to frequent intraspecific fighting.

Among butterflies, contact deterred entries most often for *N. goschkevitschii*, whereas both fight and threat behaviors often impeded entry of *V. indica* (Fig. 3). Intra- and interspecific interactions deterred entries in similar proportions for *N. goschkevitschii* in 2004, whereas heterospecics (only *V. mandarinia*) prevented entries significantly more frequently than conspecifics for *V. indica* (Fig. 4).

**Effects of Abundance on Interactions.** In 2003, *R. japonica* was the most abundant (36.1%), followed by *V. crabro* (31.7%) and *V. mandarinia* (17.1%; Fig. 5). In 2004, *R. japonica* was again the most abundant (47.5%), followed by *V. mandarinia* (28.5%).

The frequency of attempted entry with the received interactions (fight, threat, contact, and approach; see Materials and Methods for the definitions of these categories) are shown in parenthesis. The percent frequencies of attempted entry deterred by interactions were compared among species using a chi-square test in each year (different letters indicate significant differences). The percent frequencies of attempted entry deterred by the received interactions are also shown in parentheses, analyzed as for attempted entry deterred by interactions.

**Table 3.** The frequency of attempted patch entry with or without interactions, compared using a two-tailed binomial test (*P* < 0.05, ***P* < 0.001), for seven species in 2003 and 2004 (abbreviations of species names are as in Fig. 1)

| Species | 2003 | 2004 |
|---------|------|------|
|         | Interaction | No interaction | % Interaction | Interaction | No interaction | % Interaction |
| Vm      | 19 (19) | 39 | * | 32.8* (32.8*) | 13 (12) | 16 | ns | 44.5ab (42.9ab) |
| Vc      | 80 (76) | 90 | ns | 47.1* (45.8*) | 27 (22) | 30 | ns | 47.4ab (42.3ab) |
| Va      | 58 (49) | 3 | *** | 95.1b (94.2b) | 17 (17) | 32 | * | 34.7* (34.7*) |
| Vd      | 5 (5) | 11 | ns | 31.3* (31.3*) | 20 (19) | 7 | * | 74.1b (73.1b) |
| Rj      | 24 (23) | 3 | *** | 88.9b (88.5b) | 28 (26) | 12 | * | 70.0b (68.4b) |
| Ng      | 24 (23) | 3 | *** | 88.9b (88.5b) | 28 (26) | 12 | * | 70.0b (68.4b) |
| Vi      | 24 (23) | 3 | *** | 88.9b (88.5b) | 28 (26) | 12 | * | 70.0b (68.4b) |

The frequency of attempted entry with the received interactions (fight, threat, contact, and approach; see Materials and Methods for the definitions of these categories) are shown in parenthesis. The percent frequencies of attempted entry deterred by interactions were compared among species using a chi-square test in each year (different letters indicate significant differences). The percent frequencies of attempted entry deterred by the received interactions are also shown in parentheses, analyzed as for attempted entry deterred by interactions.
abundance of *V. crabro* was much lower in 2004 than in 2003, whereas the opposite was true for *V. ducalis*. All butterfly species except *N. goschkevitschii* had low abundances in both years.

The frequency of intraspecific interaction-mediated departures was significantly and positively correlated with abundance in both 2003 (Kendall $\tau = 0.667, n = 9, P < 0.05$) and 2004 (Kendall $\tau = 0.765, n = 9, P < 0.01$). Percent frequency of intraspecific interaction-mediated departures was also significantly and positively correlated with abundance in both years (2003: Kendall $\tau = 0.551, n = 7, P < 0.05$; 2004: Kendall $\tau = 0.741, n = 8, P < 0.05$).

![Fig. 2](https://academic.oup.com/aesa/article-abstract/102/2/201/8564)

Fig. 2. Context of patch departures by intra- and interspecific interactions for nine species in 2003 and 2004 (abbreviations of both species names and years are as in Fig. 1). Opponent species responsible for departure are shown for each focal species. Species contributing $<5\%$ to the total frequency (given in parentheses) were pooled as "others (O)." The proportions of departures mediated by intra- and interspecific interactions were compared using a two-tailed binomial test ($*P < 0.05$, $**P < 0.01$, and $***P < 0.001$).

![Fig. 3](https://academic.oup.com/aesa/article-abstract/102/2/201/8564)

Fig. 3. Context of attempted patch entry for seven species in 2003 and in 2004. The proportion of attempted entries is shown by the same factor categorized in Fig. 1, except for $F$ (fight) and $T$ (threat). The total observation frequency for each species is given in parentheses.
Discussion

Interspecific Dominance Hierarchies. The results of interspecific fights, patch departures, and attempted patch entries all suggest that *V. mandarinia* is by far the most dominant species, whereas the butterfly species are much less dominant. *V. mandarinia* is the world’s largest hornet and shows high levels of aggressiveness and potent venom (Ono et al. 2003). These properties confer an overwhelming competitive advantage to this species. By contrast, butterflies are submissive species with few competitive characters (Takeuchi 2006), which would deter them from violently fighting for food resources.

Aggression dominance, based on the outcomes of fights in 2001, was not evident among other species (three hornet species and *R. japonica*), whereas the results of departures and attempted entries suggested that both *V. ducalis* and *R. japonica* were less dominant than the other two species. The results of *V. ducalis* differ partly because we did not record cases when individuals retreated before being attacked (or after being approached) in 2001. Matsuura (1984) reported that *V. ducalis* was the mildest and the least dominant of five hornet species including *Vespa similima* Smith. Accordingly, the results of departures and attempted entries are more likely to reflect the actual dominance of *V. ducalis* at sap sites. Another reason for the higher proportion of interaction-mediated behaviors in *V. ducalis* and in *R. japonica* may be that both of these species often persist around occupied patches (J.Y., unpublished data). These individuals usually approach the patches again for feeding opportunities after waiting for a while, which would result in being attacked or threatened by the occupants. Thus, such behavior of *V. ducalis* and *R. japonica* might be responsible for their higher susceptibility to interactions in patches. The proportion of interaction-mediated behaviors was similar among *V. mandarinia*, *V. crabro*, and *V. analis*, although *V. mandarinia* was much more dominant in fighting. This may be partly due to their frequent avoidance of competition and of encounters with dominant species, as described later in more...
Interaction Contexts and Foraging Strategy. Density-dependent occurrence of interactions was detected in both departures and attempted entries; the frequencies of intraspecific interaction-mediated behaviors were both positively correlated with abundance, and similar relationships were detected between percent frequency of each behavior and abundance. This is simply because the rate of encounters with conspecifics in patches is likely to increase with increased density of the species.

The contexts of departures and attempted entries also varied among species and years for several of the species. For most species of hornet and butterfly, however, approach and threat behaviors were mainly responsible for departures and attempted entries, respectively. These results suggest that individuals of these species avoid fights by recognizing the behaviors of other individuals, again indicating the importance of competitor-avoidance behaviors in foraging at sap sites. In addition, departures caused by chasing behavior also often occurred for V. mandarinia and V. crabro. This is attributed to their active aggression against conspecifics and heterospecifics; individuals of both V. mandarinia and V. crabro often chased and attacked other individuals, which could increase the probability of incidental departures as a result of chasing individuals.

For R. japonica, both departures and attempted entries mediated by attacks or fights occurred frequently. When individuals of R. japonica were attacked by dominants, they usually retreated and waited around a patch until the dominants flew away, instead of avoiding attacks beforehand. They actively fought with conspecific individuals, but they rarely attacked heterospecifics. Thus, its fighting pattern and high abundance are responsible for the greater influence of intraspecific interactions on both departures and attempted entries in R. japonica.

Direct interference (attack and contact) contributed more to attempted entries than to departures for almost all species, suggesting that these interactions play a more significant role before entry into a patch than after entry. Hornets often refrained from visiting occupied patches even when the occupants showed no aggressive behavior (J.Y., unpublished data). Individuals of the yellowjacket Vespula maculifrons Buysson avoid resource patches with pinned wasps or hand-painted drawing pins (Parrish and Fowler 1983). This implies that visual cues alone may elicit competitor-avoidance behavior in hornet (Vespa) species, although further examination of their cognition mechanisms is needed to clarify this behavior. At the very least, for hornets and butterflies it is clear that aggressive behavior of occupants facilitates attempted entry or competitor-avoidance behavior of visitors at foraging sites.

Competitor-avoidance behavioral types differed between hornets and R. japonica; the former tended to avoid attacks and actively moved between patches, whereas the latter often waited nearby after being attacked, as mentioned above. In most cases, the individuals that left or waited nearby eventually had a chance to forage, presumably because occupants usually left a patch within a few minutes and unoccupied patches were common (Yoshimoto et al. 2007). These behaviors of subordinate species might enable them to forage in patches, potentially affecting the co-occurrence of sap-attracted insects. However, intraspecific dominance hierarchies can lead to different foraging tactics among individuals of the same species (Nakano and Furukawa-Tanaka 1994). Moreover, size or abundance of food resources can alter the frequency or outcome of interference (Parrish 1984, LeBrun 2005) and influence foraging tactics (Nakano et al. 1999). Examining the patterns and processes of interactions of sap-feeding insects in relation to these factors is the next step toward elucidating the mechanisms of species coexistence.

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