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INTERACTIONS AMONG SYRPHID FLIES AND BUMBLEBEES ON FLOWERS[1]

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Abstract. Interactions among bumblebees (*Bombus terricola* and *B. vagans* Smith) and small syrphid flies (*Melanostoma mellinum* L. and *Toxomerus marginatus* [Say]) were studied on pasture rose (*Rosa carolina* L.). Dominance interactions took the form: bumblebees > *Melanostoma* > *Toxomerus*. In the absence of bumblebees, *Melanostoma* foraged 41% longer, but the bees only reduced *Toxomerus*' foraging about 4%. The difference in bumblebee impact on the two syrphids resulted from *Toxomerus* rapidly returning after visits by bumblebees, while *Melanostoma* did not. *Toxomerus* used flowers most frequently when *Melanostoma* were not in them. Bumblebee foraging patterns appeared unaffected by either syrphid fly. *Melanostoma* may have a considerably greater impact than bumblebees on *Toxomerus*; a 14% reduction in foraging by *Toxomerus* was recorded in one test. This was because *Melanostoma* occupied flowers for several minutes at a time, while bumblebee visits lasted only several seconds. By affecting *Melanostoma*'s activity, bumblebees inadvertently favored *Toxomerus*, because the latter returned quickly to flowers after bee visits; *Melanostoma* did not.

Key words: bumblebee; dominance; foraging; interspecific competition; Maine; pollen; rose; syrphid fly.

INTRODUCTION

Rates of resource exploitation often decline as a consequence of interference from other individuals. Among mobile animals these interactions usually are reported from closely related species (Miller 1967, Morse 1974), but there is no reason why such interactions should be restricted to them. In fact, circumstantial evidence frequently suggests that interactions between different orders, classes, and even phyla (e.g., Kikuchi 1965, Packard 1972, Morse 1975, Brown and Davidson 1977) may be of major importance. It is usually not understood how the purported interactions take place, or what their costs are to the participants. Further, the effect of these interactions on other animals (third parties) has seldom been addressed (see Neill 1974). The purpose of this paper is to describe interactions among some common insects differing greatly in size and belonging to different orders, to assess their effects on each others' exploitation patterns, and to estimate the costs entailed in these interactions. Exclusion experiments are used to skirt the problem of measuring resource availability at a level that is relevant to the foragers themselves.

The pollen of pasture rose (*Rosa carolina*) attracts large numbers of insects, principally bumblebees (*Bombus* spp.: Hymenoptera, Apidae) and small syrphid flies (Diptera, Syrphidae). Although the bees and flies feed on this resource during broadly overlapping periods, they differ in size by 10–50 fold and exploit the pollen differently. Bumblebees dislodge pollen from the anthers by vibrating their wings rapidly. This pollen adheres to their hair-like setae, from which it is groomed and deposited in pollen baskets (corbiculae) on their hind legs for transport back to the nest (Free and Butler 1959). Small syrphid flies, on the other hand, consume the pollen within the flower (Holloway 1976). Both the bees and flies secure the vast majority of the pollen directly from the tips of the anthers, and there is no suggestion that they partition these anthers in any way. Pasture rose does not produce nectar.

This paper treats the four commonest insect visitors to pasture rose: two species of small syrphid flies and two species of bumblebees. Since I have discussed the relationships between the two bumblebees (*B. terricola* and *B. vagans*) elsewhere (Morse 1978), I have combined their data in this analysis. *Melanostoma mellinum* (L.) is a slender yellow and brown syrphid fly about 7 mm long and 6–8 mg live mass (D. H. Morse, *personal observation*). *Toxomerus marginatus* (Say) is smaller than *Melanostoma*, averaging 5 mm in length and 3–5 mg live mass (D. H. Morse 1979, *personal observation*). It, too, has yellow and brown dorsal markings, although of a much lighter hue than *Melanostoma*. Both species feed constantly when on the stamens of the rose flowers.

METHODS

I carried out this study in Bremen, Lincoln County, Maine, USA. Most data were gathered in the summer of 1978, with supplementary observations in 1977 and 1979. I censused insect visitors hourly at rose flowers from their initial opening as long as they were visited by insects. These data provided information on arrival times, abundance, relative abundance, and clumping of the insects and the number of roses in bloom. Al-

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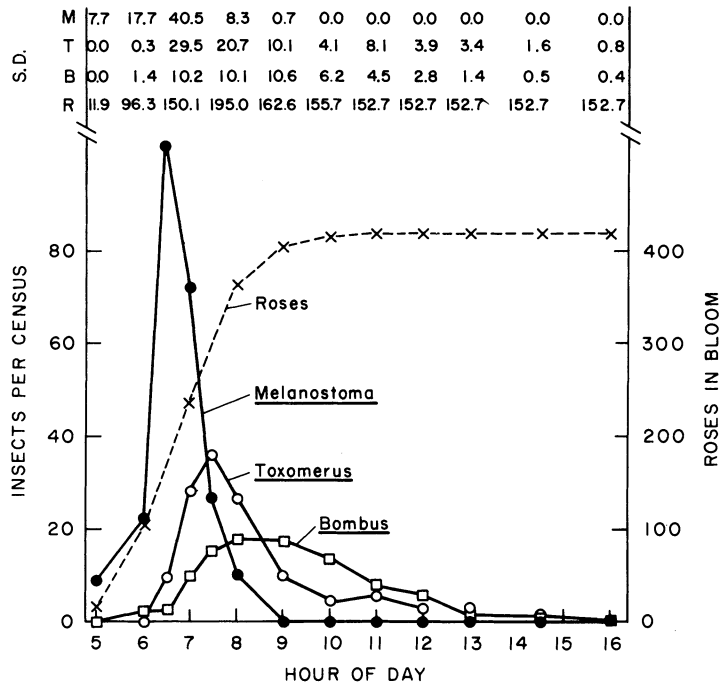

FIG. 1. Numbers of insects per census (solid lines) and number of rose flowers open per census (dashed line) on seven clear days. Closed circles and M = *Melanostoma*; open circles and T = *Toxomerus*; open squares and B = bumblebees; R = roses. One standard deviation is given above the plots for the counts made on the hour and at 1430.

though data were gathered on pasture rose throughout its blooming period, I concentrated this analysis on an 11-d segment (14–24 July) during which numbers of roses were relatively constant on clear days. Numbers were lower on overcast days during this period, and they were analyzed separately. In addition, I ran two sets of experiments. In the first, I chose pairs of flowers, each initially containing two to five *Melanostoma*, prior to the first arrival of bumblebees. I then randomly selected one flower as test and the other as control and counted the number of flies in both flowers each minute until the test flower was visited by a bumblebee. Bumblebees were prevented from approaching the control flower. Subsequent to a bee's first visit to the test flower the number of flies was counted each minute in both flowers until a bee eluded the observer and entered the control flower, or until 30 min had elapsed. I then calculated the number of "fly-minutes" in both flowers during this period and compared them with an equal period of time occurring immediately before the first visit of a bee to the test flower. The periods both before and after the first bee visit ranged from 15–30 min. I ran eight replicates of this experiment.

In the second experiment I enclosed flowers containing *Melanostoma* with cages of coarse window screening and counted the number of flies on them at this time and at each half-hour until they had all left these flowers. The numbers of individuals were compared with the mean number of *Melanostoma* in an adjacent patch of 15–25 flowers. Densities of flies on the caged flowers were probably artificially low, because once an individual flew off a flower it typically contacted the screening, which may have altered its subsequent behavior. I saw no suggestion that a fly returned to a flower after such an experience. Further, the screening prevented the recruitment of additional flies. I ran nine replicates of this experiment. These experiments, and those of the first set, were conducted between 0630 and 0900.

RESULTS

Temporal distribution of insects at roses

Melanostoma was the first insect to visit rose flowers in the morning (Fig. 1), often arriving before sunrise and before the flowers had opened. They arrived significantly earlier than did either bumblebees or *Toxomerus*, their activity peaked earlier than that of the other species, and their numbers declined earlier than in those species ($P < .005$ in one-tailed Wilcoxon signed-ranks tests on the daily times at which 10% of the activity [A_{10}], maximum number of individuals [A_{max}], and 90% of the activity [A_{90}] of a species had occurred). *Melanostoma* typically declined in numbers by 0700, a time that coincided with increasing numbers of bumblebees and *Toxomerus*.

Toxomerus and *Bombus* spp. did not differ signifi-

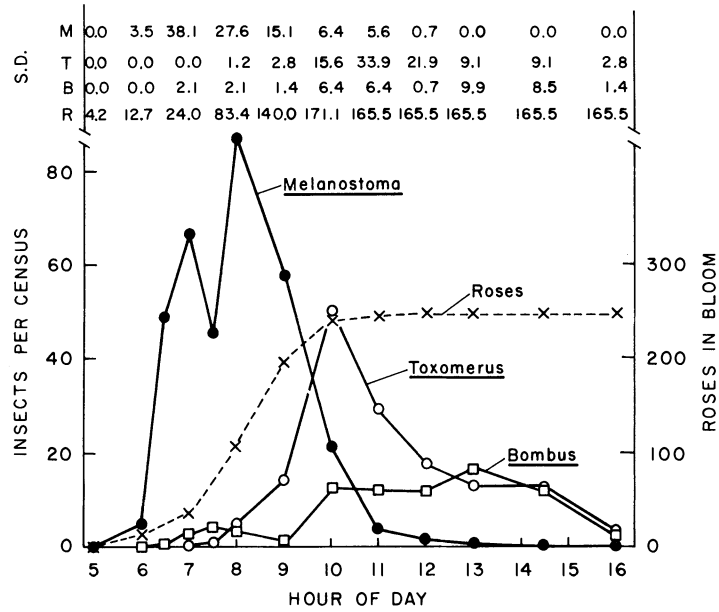

FIG. 2. Numbers of insects per census (solid lines) and number of rose flowers open per census (dashed line) on four foggy days. Closed circles and M = *Melanostoma,* open circles and T = *Toxomerus,* open rectangles and B = bumblebees, R = roses. One standard deviation is given above the plots for the counts made on the hour and at 1430.

cantly in their A_{10} and A_{max} on the roses ($P > .05$ in Wilcoxon signed-ranks tests run as above). Numbers in both genera built up to a peak by 0900, declining rapidly in *Toxomerus* and much more slowly in *Bombus* (Fig. 1). This difference in the rate of decline resulted in significantly different A_{90} between the two genera ($P < .005$).

On overcast days *Melanostoma* arrived later, reached peak numbers later, and remained significantly longer than on clear days (Fig. 2) ($P = .006$ in one-tailed Mann-Whitney U tests, comparing A_{10}, A_{max}, and A_{90} on clear and overcast days). The A_{10} and A_{max} of both *Toxomerus* and *Bombus* also occurred significantly later on overcast days than on clear ones ($P = .006$ in each case), but the A_{90} did not differ significantly for either species ($P > .05$). Although their peak activity occurred later on overcast days, *Melanostoma*'s overall use of rose flowers was significantly greater on these days than on clear days, based on the sums of hourly counts in Fig. 2 ($P = .042$). Numbers of *Toxomerus* and *Bombus* did not differ significantly between overcast and clear days ($P > .05$).

Spatial distribution

Several *Melanostoma* often occurred together on and about the stamens of a single flower (Fig. 3), an area of no more than 1.0–2.3 cm^2, as a consequence often nearly touching each other. No other visitors to these roses regularly attained such a high level of crowding. Rarely as many as 10 *Melanostoma* were seen in one flower, although no more than 6 were seen in one flower during these censuses. At such times *Melanostoma* occasionally displayed to each other by vibrating their wings, a behavior typically resulting in the retreat of an adjacent individual. Seldom, however, did physical contact occur. In each observation where an individual bumped into another one, one individual immediately retreated. These individuals all quickly settled down, however, feeding again within a few seconds ($\bar{x} = 3.5 \pm 2.5$ s, $N = 6$).

Morisita's (1959) index of dispersion indicated that *Melanostoma* were significantly spatially clumped at 0500, 0600, and 0700 in the morning (Table 1) ($P < .001$ in F tests; df 120, ∞). Subsequent to 0700 numbers of individuals (Table 1) were too small, relative to unoccupied roses, to provide a meaningful estimate. Most of the deviation from expectation occurred in a deficit of lone individuals and a surplus of groups of four or five, confirming the impression of clumping.

The 0700 data for *Toxomerus* (Table 1) were analyzed similarly and indicated that this species was also more clumped than predicted by chance ($P < .001$). Too few individuals appeared at 0500 and 0600 to provide an adequate data base for testing, and subsequent to 0700 there were, as in the case of *Melanostoma,* so few individuals, relative to the number of unoccupied roses, that statistical tests are open to question. However, there was a modest deficit of lone individuals and a correspondingly greater number of groups of two or three than predicted.

During the censuses bumblebees inevitably foraged one to a flower ($N = 758$ observations), thus maintaining the maximum possible dispersion. If one en-

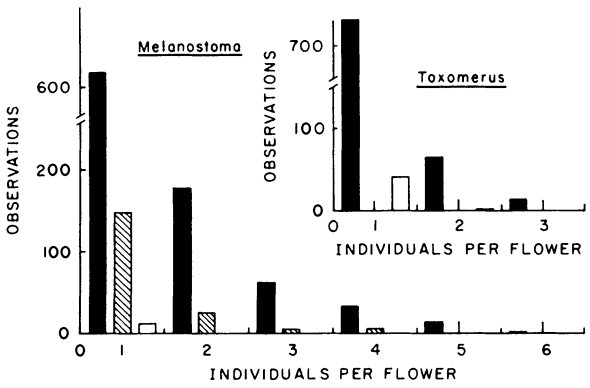

FIG. 3. Number of observations of 1–6 *Melanostoma* and *Toxomerus* (inset) per rose flower during censuses. Solid histogram = new flowers; cross-hatched = buds; open = yesterday's flowers.

tered a flower occupied by another, almost instantly one or both of them left.

Interactions between bumblebees and syrphid flies

Bumblebees gathered pollen by rapidly vibrating their wings and grovelling about in the base of the cup of the flower, in some ways analogous to a bulldozer. They almost always caused small syrphid flies to vacate a flower when they arrived (Table 2). There was no evidence that bumblebees avoided these syrphid flies. During experiments reported in the next section, bumblebees foraged in 18 out of 19 flowers they approached that contained *Melanostoma*.

Few *Melanostoma* returned subsequent to being routed from a flower by a bumblebee. However, most *Toxomerus* remained in the vicinity of the flower (Table 2), a highly significant difference ($P < .001$ in a χ^2 test), usually returning almost immediately after the bee left. Most frequently *Toxomerus* hovered from 2 to 5 cm above the flower while the bee fed; at other times, they only retreated to the back or to the distal edge of a petal.

TABLE 2. Responses of syrphid flies displaced at rose flowers by bumblebees.

Species	Left vicinity of flower	Remained in vicinity of flower: Moved just outside flower	Hovered over flower	Moved to edge of flower
Melanostoma mellinum	32	0	0	4
Toxomerus marginatus	5	6	21	2

Experiments with Melanostoma *and bumblebees*

Bumblebees prevented from visiting flowers by the observer: *Melanostoma*'s activity declined strikingly more rapidly (over 2.5 times) on test flowers after a bumblebee's visit than on paired control flowers ($P = .005$ in a one-tailed Wilcoxon signed-ranks test) (Table 3). Most flies did not return once they were displaced from a flower by a bee: in four of the eight replicates none returned. In one of the eight replicates the test flower was only touched by the bee, thus not depleted; however, the same pattern held.

Caging experiments: The caging experiments produced similar results, with the number of flies on flowers outside of the cages declining nearly 2.5 times faster over the 1st h than on the flowers inside the cages ($P = .25$ in a one-tailed Wilcoxon signed-ranks test) (Table 4).

Interactions between Toxomerus *and* Melanostoma

In nine observations in which *Toxomerus* and *Melanostoma* came into bodily contact, *Melanostoma* prevailed in each case (significantly different from a 50-50 distribution: $P = .028$ in a Fisher's exact test). Therefore, the differences in visitation patterns of

TABLE 1. Combined censuses of syrphid flies on roses during clear days, 14–24 July.

Species	Number of individuals per flower	Time: 0500	0600	0700	0800	0900	1000	1100	1200	1300	1430	1600
Melanostoma mellinum	0	107	512	1803	3854	4319	4522	4549	4558	4558	4558	4558
	1	29	140	238	120	55	25	9	...	...	...	...
	2	11	42	72	31	17	3	...	...	...	...	...
	3	6	19	26	6	11	...	...	...	...	...	...
	4	6	8	5	6	8	...	...	...	...	...	...
	5	1	8	2	3	...	...	...	...	...	...	...
	6	...	1	1	...	...	...	...	...	...	...	...
Toxomerus marginatus	0	160	729	1903	3778	4259	4453	4470	4501	4526	4540	4553
	1	...	1	119	197	138	89	78	56	32	17	5
	2	...	...	25	17	12	5	7	1	...	1	...
	3	...	...	4	3	1	3	3	...	...	...	...

TABLE 3. Mean numbers (±1 SD) of *Melanostoma mellinum* on rose flowers during eight periods of 15–30 min before and after first visit of bumblebee to available flower. An available flower is one from which the observer is not excluding bumblebees.

Category	Number before first visit of bumblebee to available flower	Number after first visit of bumblebee to available flower	Percentage of *Melanostoma* remaining at flowers
Available flower	1.5 ± 0.3	0.3 ± 0.2	20.0
Unavailable flower	2.0 ± 0.7	1.1 ± 0.2	55.0

Toxomerus and *Melanostoma* are unlikely to result from *Toxomerus* replacing *Melanostoma*. *Toxomerus* retreated by flying directly out of the flowers ($N = 5$), moving to the edge of a petal ($N = 2$) or moving to a nearby leaf ($N = 2$). Over the census period, 5.2% of *Toxomerus* sightings and 3.6% of *Melanostoma* sightings were made in flowers containing individuals of both species. *Toxomerus* usually merely perched on the petals, while *Melanostoma* fed in the middle of the flowers. It is unlikely that *Toxomerus* depleted the pollen sufficiently to exclude *Melanostoma,* as pollen dehisced continuously during the time that the two species overlapped.

Intraspecific interactions between syrphid flies and interactions between bumblebees

Intraspecific interactions between *Melanostoma* were infrequent and of short duration. Only six displacements were noted in 894 fly-minutes of observations (experiment reported in Table 3), and foraging was disrupted for only an average of 3.5 ± 2.5 s, or 0.04% of total foraging time. No aggressive interactions were observed between *Toxomerus* individuals.

Interactions between bumblebees took place about every 3rd min on pasture rose. The contacts and the consequent cessation of feeding occupied a minimum of 6.5% of *terricola*'s time on the roses, and 6.8% of *vagans*' time (data in Morse 1978).

Impact of the interactions on the participants

Calculations in this section are based on the assumption that visitors gathered pollen constantly while in the flowers. Both *Melanostoma* and the bumblebees met this criterion, as did *Toxomerus* except for a few exceptions (mating, displacement to the edge of a flower by another species).

TABLE 4. Mean numbers (±1 SD) of *Melanostoma mellinum* on rose flowers before and after screening of nine control flowers.

Category	Number at time of screening	Number 1 h after screening	Percentage remaining after 1 h
Unscreened area	1.4 ± 0.2	0.5 ± 0.1	35.7
Screened area	2.7 ± 0.4	2.2 ± 0.4	81.5

TABLE 5. Arrival and departure times of insects and opening times of flowers on six mornings in mid-July, ±1 SD

Time of flower opening (*Melanostoma* arrive before flowers open)	0602 ± 44.9 min
Arrival time of bumblebees	0644 ± 32.6 min
Time between opening of flowers and first appearance of bees	42.0 ± 23.8 min
Time last *Melanostoma* seen	0835 ± 76.9 min
Time from first bumblebee arrival to last observation of *Melanostoma*	111 ± 100.3 min

The impact of the bees on *Melanostoma* was the interspecific interaction of greatest magnitude. *Melanostoma* had an average of only 42 min of foraging to themselves in the early morning before being interrupted by bumblebees (Table 5). They then foraged over an average period of another 111 min after the bees arrived. Therefore, almost three-fourths of *Melanostoma*'s foraging period occurred after bumblebees began to visit (111 of 153 min = 73%: Table 5). Foraging activity of *Melanostoma* at unprotected flowers was only 43% of that at screened flowers 1 h after the screens were added (35.7% of original foraging, vs. 81.5%, Table 4), so that they foraged an average of 48 min after the time bumblebees arrived. Thus 53% (48 of 90 min) of foraging on screened flowers took place subsequent to the arrival time of bumblebees, and it required more than twice as long (111 min) to accomplish the same fraction on unprotected flowers. Therefore, foraging in roses by *Melanostoma* consisted of roughly equal amounts of high- and low-efficiency foraging (with and without bumblebees). If they were able to forage for the entire 111 min (rather than 48 min) after the bees' arrival, *Melanostoma* could spend an average of 41% more total activity (periods before and after arrival of bees, combined) at the roses. This estimate assumes that *Melanostoma* would cease activity at the same time of day if bees were absent. Considerable day-to-day variance actually occurred in the length of "bee-free" periods enjoyed by *Melanostoma* (Table 5). Using the mean foraging gain of 41%, one SD in the "bee-free" period encompassed differences in overall foraging gain of 23% to 59%.

In contrast, the impact of bumblebees on the foraging of *Toxomerus* was light, averaging between 2% and 5% during the peak of the day (Fig. 4). The results in Fig. 4 were determined as follows: first, the mean number of visits of a bumblebee per hour ($V_{\bar{x}}$) was calculated. These bees required an average time (t_1) of 12.2 s (combined mean for *vagans* and *terricola,*

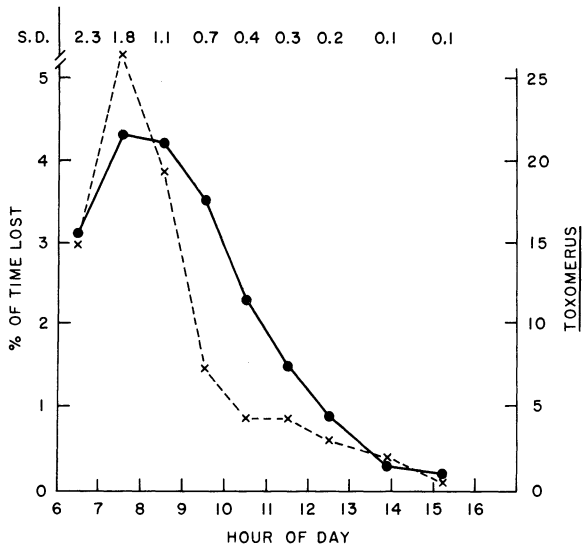

FIG. 4. Percentage of foraging time lost by *Toxomerus* as a consequence of bumblebee visits to roses (solid line), with one standard deviation given above the plot; number of *Toxomerus* on roses (dashed line).

weighted for their differences in abundance) to forage in a rose and to reach the next flower (Morse 1978).

$$V_{\bar{x}} = 3600 \text{ s}/t_1.$$

Thus, an average of 295.1 flowers would be visited per bee per hour. Multiplying $V_{\bar{x}}$ by the number of bees (N) recorded at the hourly censuses (Fig. 1), one obtains the total number of visits by bumblebees to flowers per hour (V_T).

$$V_T = V_{\bar{x}} \cdot N.$$

Knowing the number of flowers in bloom (F) at a given hour (Fig. 1), one can calculate the average number of visits per hour by a bumblebee to a flower (V_F).

$$V_F = V_T/F.$$

Bumblebees foraged in a flower an average time (t_2) of 9.0 s (combined weighted mean for *vagans* and *terricola*) (Morse 1978), and in eight timed observations it took *Toxomerus* 2.4 (±0.7) s to return (R) after a bumblebee left. Each visit of a bumblebee thus cost a *Toxomerus* an average of 11.4 s of foraging time. By multiplying the time that a visit of a bumblebee kept *Toxomerus* from a flower ($t_2 + R$) by the number of bumblebee visits to a flower (V_F) one can calculate the mean amount of time (T) that bumblebees prevent *Toxomerus* from foraging each hour.

$$T = V_F(t_2 + R).$$

In Fig. 4 I have converted this figure into the percentage of time that *Toxomerus* were prevented from foraging each hour.

The numbers of bees and flowers at a given time were both subject to considerable day-to-day variation (Fig. 1). This resulted in SD's of time lost by *Toxomerus* that ranged from 18.7% to 74.8% of the mean, depending on the time of day. Early morning variation was by far the highest. *Toxomerus*' foraging peak overlapped broadly with that of the bumblebees (Fig. 1); however, even at these times they were interrupted only slightly over 4% of the time (Fig. 4). The similarity of these two peaks suggests that bumblebees were not causing *Toxomerus* to change their foraging patterns.

In fact, the long periods that *Melanostoma* occupied flowers in the absence of bumblebees might have precluded *Toxomerus* from using these flowers even more than did the bumblebees. If so, the negative effect of bumblebees on *Toxomerus*' foraging would be more than balanced by the secondary positive effect of driving away *Melanostoma,* thus making the overall relationship between *Toxomerus* and bumblebees a positive one. Some evidence exists to support this suggestion. The attendance of *Toxomerus* was recorded during the second half of the experiment in which bumblebees were prevented from visiting certain selected flowers (Table 3). In the eight replicates run, five *Toxomerus* entered a flower, one each in five of the replicates. Every flower was one from which bees had displaced *Melanostoma*. The time of occupation was 27.5 min out of a total of 198 min of observation during this part of the tests (5.5 ± 4.3 min/individual). This constituted visitation during 14% of the time at bumblebee-visited flowers, vs. 0% at those not visited by bees and still occupied by *Melanostoma*. It must be reemphasized, however, that *Toxomerus* and *Melanostoma* sometimes occurred together in the same flowers. Further, the faster decline of *Melanostoma* than *Toxomerus* when bumblebees did not interfere suggests that *Melanostoma* may not have presented this potent a deterrent to *Toxomerus* over the entire time during which pollen was available.

The estimates in this section do not include the energy expended by syrphids flying out of a flower when they are displaced. I assume that this factor is small relative to the energy loss resulting from being denied access to a flower. I also assume that the impact of the syrphid flies on bumblebees is negligible. Certainly the syrphid flies do consume small amounts of pollen that might otherwise be gathered by the bees. However, no evidence exists to suggest that their presence modifies the visitation patterns of the bees.

The importance of pasture rose and other flowers

This is not a closed system; however, pasture rose is the major protein source for all of the species when it is available. During July many bumblebees concentrated their activities on roses from first arrival until pollen was exhausted at midday, only then switching to other flowers. Pollen supplies often become depleted in bumblebee nests at this time of year, a conse-

quence of the heavy protein demands made on them by peak brood production (reviewed in Morse, *in press*). Alternate rapidly gathered sources of pollen were extremely limited, although meadowsweet (*Spiraea latifolia*), another favored pollen source of bumblebees, commenced to bloom before the end of the roses' flowering period. *Melanostoma* were recorded on the fewest food sources: roses and sporadically on timothy grass (*Phleum pratense*). *Toxomerus* also fed sporadically on timothy, and later in the year regularly visited goldenrods (*Solidago* spp.), which commenced to bloom after the roses passed their peak flowering period. They were also seen occasionally on other flowers, especially meadowsweet. However, the numbers of *Toxomerus* on roses far exceeded those on other flowers simultaneously in bloom (D. H. Morse, *personal observation*).

Discussion

Temporal distribution

The temporal distribution of *Melanostoma* was primarily influenced by the bumblebees' foraging patterns, which in turn were limited by weather conditions (Heinrich 1972) and the availability of pollen (Morse 1978). Since the bumblebees depended largely on honey stored in their nests for fuel to exploit the rose pollen, high energy demands resulting from low temperatures or low resource availability may have made foraging unprofitable for them.

It is unclear why *Melanostoma* did not re-enter flowers immediately after a bumblebee departed, as did *Toxomerus*. However, the change in activity patterns by *Melanostoma* that accompanied exclusion of bumblebees resembled the results of Kikuchi (1965), who screened daisies with netting of a mesh size that excluded large visitors only. Smaller insects then changed from an early morning–late afternoon foraging regime to one in which regular midday foraging took place as well. The eventual decline in numbers of *Melanostoma* having the exclusive use of rose flowers (caging experiments) may have resulted from these flies satiating themselves with pollen. This decline resembled the one seen under natural conditions on foggy days (Fig. 2), when bees were scarce and temperature and humidity changes were minimal.

Toxomerus' activities were in part a consequence of the interactions between bumblebees and *Melanostoma*. Although routed from flowers by the bees, *Toxomerus*' tendency to return immediately permitted them more foraging time in a flower than if it were occupied by *Melanostoma*. Kikuchi (1965) did not consider such second-order interactions in his studies. One may question the significance of *Melanostoma* excluding *Toxomerus* from rose flowers, given the abundance of flowers appearing later in the day that *Toxomerus* could visit. However, if *Toxomerus* required considerable time to obtain a complete meal of pollen, interference by *Melanostoma* early in the morning may have prevented them from completing this meal before bumblebees consumed the day's supply of pollen. Although pollen frequently fell beneath the stamens during bumblebee visits, continued visits by these bees after dehiscence was complete resulted in this pollen either being collected or knocked out of the flowers. Taken together these results are adequate to establish the existence of interference competition in this system.

Spatial distribution

The clumping of *Melanostoma* may have been the consequence of a shortage of opened flowers at the time that individuals initially searched for them. Since the pollen in these flowers probably considerably exceeded the ability of the flies to eat it before the bumblebees arrived, aggressive behavior would serve little function and might occupy much of the limited uninterrupted time available. Even though more flowers opened as the morning progressed, *Melanostoma*'s long visitation periods may have contributed to their continued clumping. Further, as numbers of bumblebees increased, they may have displaced *Melanostoma* to less exposed flowers already containing conspecifics.

Clumping in *Toxomerus* was not as extreme as in *Melanostoma*. In *Toxomerus*, the excess of twosomes over the number predicted may have been related to reproductive activities. Although only four copulating pairs were seen during these censuses, many copulating pairs were observed at pasture roses on 25–28 July, immediately after the census period. No mating activity of *Melanostoma* was noted at the flowers.

The limit of one bumblebee per flower was, on the other hand, an apparent consequence of their large size and the vigorous activity of their pollen gathering. Typically, if a bumblebee entered a flower already containing another bumblebee, one or both would instantly leave, probably a consequence of the resulting vibrations or the collision between individuals that would otherwise quickly occur.

The frequency and significance of short-term temporal partitioning

Most recorded examples of interspecific aggressive displacement involve alternate feeding sites, habitats, or nest sites (Morse 1974). Temporal partitioning, where reported, usually occurs on a seasonal basis, and where differences in activity patterns take place during a day, there is usually no convincing evidence that the same food items are contested (see Schoener 1974). The relationships described in this paper and among certain other flower-visiting insects do not easily fit any of these patterns.

Segregation is spatial rather than temporal in several other flower-based systems (e.g., Johnson and Hubbell 1974, 1975, Morse 1977, Inouye 1978). It is the

apparent consequence of aggressive interference in some stingless bees (Johnson and Hubbell 1974), avoidance in some bumblebees (Morse 1977), and exploitation in other bumblebees (Inouye 1978). Both Holmes (1974) and Benest (1976) have, however, reported temporal segregation between bumblebees and honeybees (*Apis mellifera*), which may be a consequence of the honeybees' effective exploitative capabilities. More generally, Kikuchi's (1965) data suggest that short-term temporal displacements of flower- and sap-visiting insects are widespread. Kikuchi noted several examples of temporal displacement that disappeared when the smaller, subordinate insects were given preferential access to flowers. Other reported cases of temporal differences between large and small insect visitors to flowers (e.g., Rahman 1940, Schlising 1970) could have a similar basis, even though they are typically attributed to differences in preferred foraging times.

Of the studies discussed here, only in Kikuchi's are the potential competitors as different in size or methods of exploitation as the bumblebees and syrphid flies of the present study. Even so, these differences apparently do not constitute the basis for resource partitioning on a spatial basis. Another major distinction may be made between the bumblebee–syrphid fly interactions and those among various bee species discussed here: there is no evidence that the bumblebees in this study respond in any way to the syrphid flies. Their mere physical presence apparently suffices to make the rose flowers unsatisfactory to one of the species of syrphid flies.

The present observations are noteworthy in demonstrating, (1) the mechanism by which the temporal partitioning takes place, (2) that interactions between pairs of species (here, *Bombus* spp. and *Melanostoma*) may affect the opportunities open to a third species (*Toxomerus*), and that (3) these interactions may occur between taxonomically distant species of greatly differing size and other attributes.

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