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Ecological comparisons of robber fly species (Diptera: Asilidae) coexisting in a neotropical forest

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Summary. Data regarding seasonal abundance, microhabitat preference, and diet were collected over 3 field seasons for adults of 15 robber fly species on Barro Colorado Island, Panama. The species comprised 2 distinct "thermal guilds"; light-seeking (hereafter LS) species foraged in sunlit areas, while shade-seeking (SS) species foraged only in deep shade. All species were rare during the dry season. During the rainy months, most SS species had flight periods of 2–3 months, and no temporal segregation was apparent. In contrast, most LS species had flight periods of only 4–6 weeks, and a distinct sequence of occurrence was evident during 2 years of censusing. Most SS and LS species displayed a pronounced specificity for perches of a particular substrate type. However, the ranges of perching heights utilized varied considerably among species. Dietary comparisons revealed that mean and maximum prey sizes increased with increasing robber fly size, while minimum prey sizes were constant. Robber fly species <20 mg fed primarily upon nematocerous Diptera, whereas larger species generally fed upon a wide variety of prey types. For each thermal guild, the actual mean overlap for a particular niche dimension was compared to mean overlaps generated by randomly assigning species to thermal guilds. No significant differences from the random null hypothesis were found for the SS guild. However, niche complementarity between dietary and spatial overlaps and dietary overlap was apparent among the 5 large LS species.

Few studies of predatory arthropods have compared large numbers of coexisting species along temporal, spatial, and trophic niche "dimensions." Crowley and Johnson (1982) and Pearson and Mury (1979), for example, made ecological comparisons within large assemblages of predatory insects but used only spatial/temporal and spatial/trophic data, respectively [see also Istock (1966)]. Similarly, Gertsch and Riechert (1976), Post and Riechert (1977), Uetz (1977) described ecological interactions among coexisting spiders using only spatial and spatial/temporal data, respectively. At the other extreme, several studies (Townsend and Hildrew 1979; Lenski 1982, 1984) provided data for all 3 principle niche dimensions but dealt only with pairs of interacting species. Still other studies (Enders 1974; Van Zant et al. 1978; Brown 1981; Giller and McNeill 1981; Spence 1981, 1983; Spence and Scudder 1980) are intermediate in this regard, i.e., they consider only 1 or 2 niche dimensions while comparing only a few coexisting species. I am aware of only 2 studies (Turner and Polis 1979; Riechert and Cody 1983) that compare a relatively large number of predatory arthropod species along temporal, spatial, and trophic dimensions. [See Spiller (1984) and references therein for experimental studies of interspecific competition among spiders.]

Among predatory insects, adult robber flies present an excellent opportunity for ecological study. Adults of most species are visual, sit-and-wait predators that perch in conspicuous sites and attempt aerial capture of flying insect prey. Following a successful capture, the robber fly returns to its perch and sucks the contents of its prey with a well-developed hypopharynx. Capture of a feeding asilid with an aerial net thus yields an intact prey item and an unharmed predator, which can be identified and then released. Conspicuousness in the environment and method of feeding thus allow quantitative descriptions of seasonal occurrence, microhabitat preference, and diet for any particular species.

The present study provides such descriptions for 15 robber fly species in a lowland Neotropical forest. These data in turn were used in 2 different sets of analyses. First, in order to detect any community-wide patterns in habitat and food utilization, interspecific comparisons were made separately for temporal, spatial, and trophic dimensions. Then, indices of species similarity (overlaps) were computed for each niche dimension considered, and the actual mean overlap for a particular dimension was compared to a distribution of means generated by a specific randomization procedure. These tests were performed to investigate the possibility that observed ecological differences among the asilid species studied are the result (in part at least) of interspecific competition for a limiting resource.

This study is a companion to an earlier investigation (Shelly 1984a) in which the foraging behaviors of many of these same robber fly species were compared. The major results of this previous paper were i. species could be clearly distinguished as light-seeking (hereafter LS) or shade-seeking (SS), ii. LS species foraged in sunlit areas (ranging from small sun flecks to large tree fall gaps) and maintained body temperatures 8–10° C above ambient, while SS species foraged in deep shade and had body temperatures approximately equal to ambient, iii. large (>100 mg) LS species foraged and relocated more frequently than SS species of similar size, and iv. distances of attack and relocation flights

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were dependent only on body mass and were independent of preferred light level. Additionally, Morgan et al. (1985) found a pronounced difference between LS and SS species in their ability to physiologically control thoracic temperature. The LS species tested were able to reduce thoracic heat stress by increasing the flow of haemolymph to the abdomen (where heat was lost), while SS species were apparently unable to do so.

In light of these behavioral and physiological differences, I consider the groups of LS and SS species to represent distinct guilds. As defined by Root (1967), a guild is a group of species that use the same resource in a similar way. Since robber flies as a group are sallying insectivores, the term guild here refers, not to foraging tactics per se, but to habitat use (i.e., shaded vs. sunlit perch sites) and the accompanying effects upon foraging behavior, thermoregulatory physiology, and prey availability (noted in Discussion). These differences in the "adaptive syndrome" (Eckhardt 1979) between SS and LS species suggest that, for any species, ecological interactions with other guild members are more likely to have selective importance than are interactions with species belonging to a different guild. Consequently, statistical tests comparing actual and randomly generated mean overlaps were performed separately for the SS and LS guilds.

Materials and methods

Study site

Field work was conducted on Barro Colorado Island (BCI), Panama, during February–August 1979, April–August 1980, and April–July 1981. The island (~1,500 ha) is covered by a lowland tropical moist forest (Holdridge et al. 1971) with different sections varying between 60–130 years in age (Knight 1975). Mean monthly air temperatures vary only slightly throughout the year (Croat 1978), but rainfall is highly seasonal. The wet season typically extends from April to mid-December, and the average total rainfall during these months is approximately 250 cm (Croat 1978). During the dry season average total rainfall is only 20 cm (Croat 1978).

Body size measurements

Wet weight and body length measurements were obtained for 5 males and 5 females of each robber fly species studied. Wet weight measurements were made to the nearest 0.001 g using a Mettler analytical balance. Individuals were weighed within 3–4 h of capture. Body length measurements were made to the nearest 0.1 mm using a dissecting microscope equipped with a disc micrometer.

Relative abundance estimates

Relative abundances of robber fly species were monitored in 1979 and 1980 using a census method. Each month was divided into two 15 day sampling periods; this interval was chosen to permit reliable censusing within a relatively large portion of the forest. During each period, I patrolled areas adjacent to the same set of trails and identified and counted every robber fly encountered. Thus, while BCI is covered by a network of narrow foot trails, censusing was not confined to the trails. Instead, trails were used as reference lines for exploration of adjacent forest sections (generally within 40–60 m of a trail). The areas of the island sampled purposely included forest sections of varying age and topography. Censuses were conducted between 0930–1530 h, since all species studied were active at ground level during these hours. Sky conditions, of course, varied during censuses, but no censusing was conducted during periods of heavy rain.

Actual censusing was conducted in the same manner each day. I walked slowly through the forest and attempted to check all potential perch sites within a "visual transect" approximately 6–8 m wide and 2–3 m high. As described in Results, the species studied perched primarily on the upper surfaces or tips of leaves and branches. Preferred perch sites were thus relatively conspicuous and easily monitored. While censusing, I did not move about in a completely random manner but instead walked rather haphazardly from 1 light patch to another. Owing to gaps in the canopy, light patches of varying sizes (from small sun flecks to large tree-fall gaps) irregularly and abruptly interrupted the deep shade of the forest. Routes were thus chosen to insure censusing of both shaded and sunlit areas.

Census efforts were timed to check for constancy among sampling periods. In 1979 censuses were conducted from 1 February–21 August. I generally censused 3–5 h/day for 11–13 days during each sampling period. With 2 exceptions, the sampling periods included 38–42 h of censusing. The exceptions were: 16 May–30 May when I walked approximately 3/4 (31 h) of the census routes and (2) 16 August–21 when I walked approximately 1/2 (17 h) of the census routes. In 1980 censuses were conducted from 15 April–26 August. In this year I generally censused 1–3 h/day for 11–13 days during each sampling period. All sampling periods in 1980 included 19–22 h of censusing. To allow valid inter-period comparisons both within and between years, all census estimates were converted to individuals seen per 10 h of searching effort.

The seasonal abundance data are obviously incomplete, since the censuses were not conducted through the entire wet season. Several factors suggest, however, that adult robber flies are relatively rare during the latter part of the wet season. First, on a collecting trip during the late wet season and early dry season, Curran (1930) found only a small number of forest-dwelling asilids. Second, light trap data for a 3 year period indicate that insect abundance on BCI decreases dramatically during the late wet season (Wolda 1978a). As prey level declines, it appears likely that asilid abundance would display a concurrent decrease. Third, as will be shown in Results, most asilid species were most abundant in the early wet season months (April–June) and became increasingly rare through July and August.

Description of perch sites

In addition to the SS-LS distinction (Shelly 1984a), perch sites were also described in terms of height above ground and substrate utilized. Heights were measured to the nearest 1 cm using a tape measure. Preliminary observations prompted the use of the following substrate type categories: leaf surface, woody stem or branch (where tip and non-tip sites were distinguished), herbaceous stem or branch (where tip and non-tip were distinguished), the ground, log surface, and tree trunk (including tree buttresses). No attempt was made to identify plant species used as perching surfaces. In addition, within a category living and dead substrates were not distinguished.

Robber fly diets

Dietary comparisons were based on prey taken from feeding robber flies. Upon encountering a feeding individual, I captured both predator and prey with an aerial net, identified and released the robber fly, and then transferred the prey item to an appropriately labelled vial. Prey items were later measured to the nearest 0.1 mm (total body length excluding wings) using a dissecting microscope equipped with a disc micrometer. Weight measurements were not made for prey, since the degree of weight loss due to the asilid's feeding was not known. With the exception of Diptera and Hymenoptera, insect prey were identified to order (spiders were identified only as Arachnida). In recognition of large, intra-ordinal variation in flight speed, dipteran prey were placed into nematocerous, brachycerous-calypterate, and acalypterate-phorid subdivisions, and hymenopteran prey were categorized as ants, bees-wasps or parasitoids-sawflies.

Measurement of ecological similarity and breadth

Ecologists have used a variety of indices to quantify ecological similarity or overlap among coexisting species (Hurlbert 1978). The statistical properties of these indices are largely unknown, but several recent studies (Hurlbert 1978; Ricklefs and Lau 1980; Linton et al. 1981; Smith and Zaret 1982) have compared the biases of selected indices using analytic or simulation techniques. Based on the results of Linton et al. (1981), I chose Schoener's (1968) index for use in this study:

$$\text{Overlap} = 1 - \tfrac{1}{2} \sum_{i=1}^{n} |p_{ij} - p_{ik}|$$

where p_{ij} and p_{ik} are the proportions of the ith resource state used by the jth and kth species, respectively, and n is the number of the resource states for a particular niche axis. Among the indices compared, Linton et al. (1981) found that only Schoener's (1968) measure provided accurate estimates of overlap over most of the potential range of overlap values. Note that overlap values are used here only as indices of similarity and not as estimates of the competition coefficients in the Lotka-Volterra equations. For a particular dimension, niche breadth of species k was calculated as $B_k = \sum (p_{ij})^{-1}$, where p_{ij} and n are defined as above (Levins 1968). Overlap and breadth values were both calculated using the intervals or categories given in the appropriate table or figure. The field data presented for each species included measurements from both sexes, since field determination of sex was difficult and therefore unreliable for most species.

Statistical analyses of overlap values

Much discussion (e.g., Colwell and Futuyma 1971; Vandermeer 1972; Sale 1974; Schoener 1982, 1983) has focused on the utility of ecological overlap values as measures of interspecific competition. As is often noted, the major problem arises from the fact that high overlap could indicate either intense competition if the critical resource(s) is limiting or weak (or no) competition if this resource is superabundant. Since resource availability is often extremely difficult to measure, interpretation of overlaps along a single niche dimension becomes problematic. As a result of this difficulty, some workers (most notably Connell 1980, 1983) content that experimental studies are necessary to identify the processes responsible for patterns observed in biological communities. This position would appear extreme, however, given the consistent finding among nearly 30 studies (listed by Schoener 1982) that in temporally varying environments overlap between species decreases during periods of low resource availability. This latter result presumably reflects the tendency during "lean" times of species to "specialize" upon a particular set of resources to which it alone is best adapted (Schoener 1982). These latter studies are particularly important, since they show "overdispersion of niches" among ecologically similar species when competition is potentially most intense.

Since the appropriate experiments (e.g., removal or addition of species, manipulations of species densities, etc.) were not feasible for the system under study, I tested for specific patterns in the observed overlaps and (based on the presence or absence of these patterns) made inferences regarding the importance of interspecific competition. Owing to the interdependence of overlaps, testing of null hypotheses can not be conducted using statistical tests requiring normally and independently distributed variables. Also, because of this interdependence, a predicted frequency distribution of overlaps can not simply be obtained from some existing theoretical model. Rather, an expected distribution can be obtained using computer-generated simulations which randomly combine elements of the actual data [see Pimm (1983) for discussion].

In this paper such simulations are used to test the null hypothesis that the actual mean overlap within a thermal guild for a particular niche dimension is greater than or less than the mean overlap expected if species were randomly assigned to that guild [procedure derived from Pimm (1983)]. Specifically, for each simulation 9 of the 15 species were randomly assigned to 1 set (corresponding in size to the SS guild) and the remaining 6 assigned to a second set (corresponding in size to the LS guild). For each set, overlaps were calculated for all pairs of species, and a mean overlap was computed. This procedure of random assignment was repeated 200 times, generating 200 means for each set. The actual mean overlap was then compared to the corresponding distribution of randomly generated means. If, for a 1 tailed test, 10 (5%) or less of the simulated means were greater than the actual mean, I concluded that the actual overlaps were significantly greater than expected by chance. If 10 or less of the simulated means were less than the actual mean, I concluded that the actual overlaps were significantly less than expected by chance.

Results and discussion

LS and SS species groups

The LS and SS groups included 6 and 9 species, respectively (Table 1). With the exception of *Cerotainia feminea*, the LS species were all relatively large and ranged from approximately 150–350 mg. In contrast, the SS species had a more even distribution of body sizes; 5 SS species were 10 mg, 2 were between 15–50 mg, and 3 were 120 mg. Regarding taxonomic composition, 3 LS species were in the subfamily Apocleinae, and 2 belonged to the Laphriinae. Within the SS group, 4 of species were in the Laphriinae, and the remaining 5 species represented 4 additional subfamilies.

Table 1. Body lengths and wet weights of shade- and light-seeking species of robber flies. Values represent means based on measurements from 10 individuals (5♀/5♂). Standard deviation is given in parentheses. The letter following each species name represents the subfamily to which the species belongs, where La – Laphriinae, O – Ommatiinae, D – Dasypogoninae, A – Apocleinae, and Le – Leptogastrinae

	Length (mm)	Wet weight (mg)
Shade-seeking		
Senobasis corsair (D)	18.7(1.5)	143.6(30.1)
Senobasis clavigera (D)	15.4(1.8)	46.1 (7.4)
Eumecosoma tarsalis (La)	5.3(0.6)	4.0 (1.5)
Hybozelodes sp. (La)	5.0(0.4)	4.9 (1.6)
Glaphyropyga dryas (A)	11.0(0.9)	16.3 (3.6)
Ommatius sp. (O)	18.6(2.2)	121.4(15.5)
Smeryngolaphria numitor (La)	28.2(4.8)	233.0(42.7)
Oidardis sp. (La)	4.8(0.3)	4.2 (1.5)
Psilonyx sp. (Le)	9.2(1.6)	5.0 (1.7)
Light-seeking		
Mallophora fairchildi (A)	17.7(0.9)	145.0(17.3)
Efferia sp. (A)	30.4(3.1)	346.6(80.9)
Promachus sp. 1 (A)	26.3(2.7)	193.4(38.8)
Promachus sp. 2 (A)	24.3(1.8)	181.1(30.7)
Lampria mexicana (La)	19.2(1.9)	195.0(43.6)
Cerotainia feminea (La)	5.4(0.6)	4.6 (1.8)

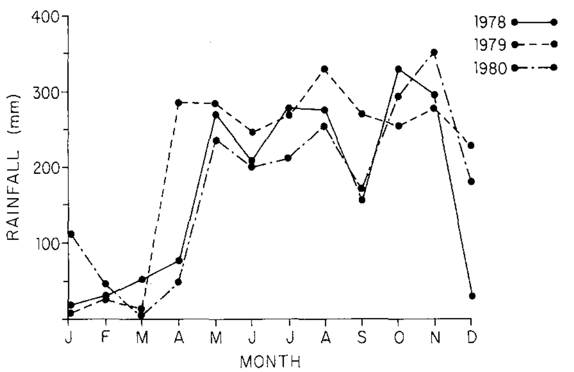

Fig. 1. Monthly rainfall totals (mm) for 1978–1980, Barro Colorado Island, Panama

It should be noted that the 15 species studied represent only a subset of the approximately 65 asilid species found on BCI (E.M. Fisher, personal communication). Among those species not included, approximately 45 were infrequently encountered, understory inhabitants too rare for study, and 3 were found perching only along the banks of small streams. Observations on the foraging and/or reproductive behavior of some of these other species are presented elsewhere (Shelly and Weinberger 1981; Shelly 1984b, 1985).

Seasonal abundance

Relation to rainfall. Adults of SS and LS species were not active during the dry season. (Rainfall data for 1978–1980 are presented in Fig. 1). During the dry seasons months of February and March, 1979, only 12 adults of all SS species and 4 adults of all LS species were seen in 161 h of censusing. As rainfall increased in April, 1979, several SS species (*Ommatius sp.*, *Smeryngolaphria numitor*, and *Senobasis corsair*) and LS species (*Mallophora fairchildi* and *Efferia* sp.) were more frequently encountered, and by late May most species were relatively common. Given these results in 1979, censuses in 1980 were not conducted during

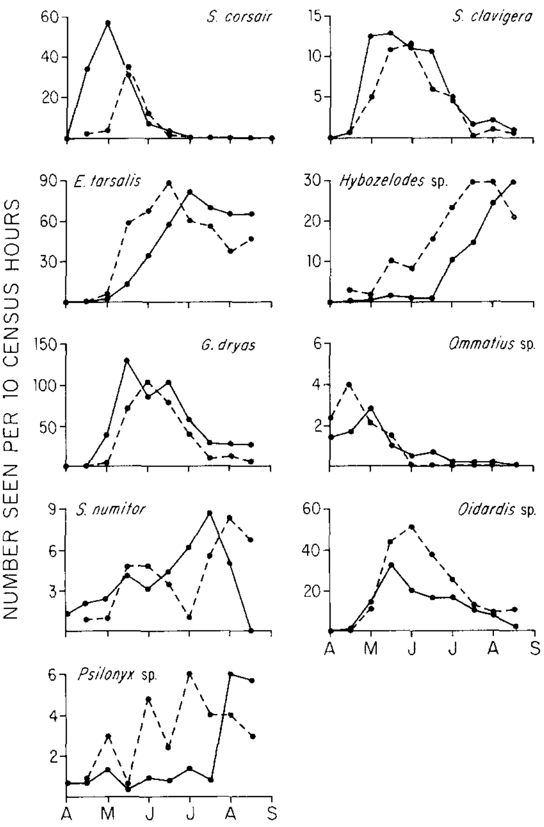

Fig. 2. Relative abundance of shade-seeking species in 1979 (●——●) and 1980 (●---●). Each value represents the number of individuals seen per 10 h of census effort during a particular 2 week sampling period

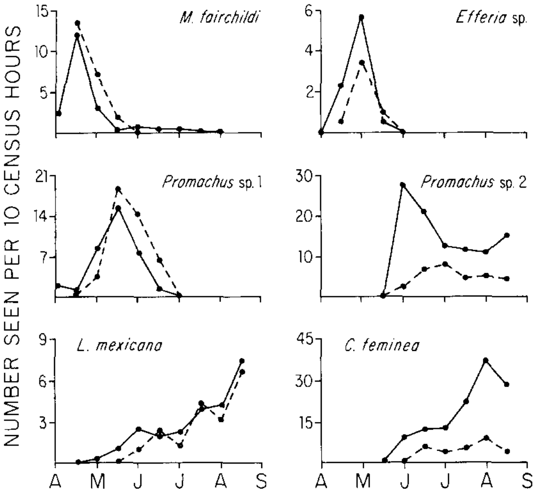

Fig. 3. Relative abundances of the light-seeking species in 1979 (●——●) and 1980 (●---●). Each value represents the number of individuals seen per 10 h of census effort during a particular 2 week sampling period

Table 2. Perching substrates for shade- and light-seeking robber fly species. Each value represents the proportion of all observations for a species in a particular substrate category. Sample size is given in parentheses for each species

	Leaf	Woody branch Tip/not tip	Herbaceous stem Tip/not tip	Log	Tree trunk	Ground
Shade-seeking						
S. corsair (249)	19.7	0/74.3	0/6.0			
S. clavigera (204)	9.3	0/84.7	0/5.9			
E. tarsalis (235)	100.0					
Hybozelodes sp. (188)	100.0					
G. dryas (259)		96.1/0	3.8/0			
Ommatius sp. (97)		0/86.6	0/13.3			
S. numitor (133)	64.6			14.3	15.8	5.3
Oidardis sp. (290)	6.9	83.5/0	9.7/0			
Psilonyx sp. (97)		69.0/0	31.0/0			
Light-seeking						
M. fairchildi (249)	92.9	0/7.1				
Efferia sp. (43)		0/67.4	0/16.3	7.0	9.3	
Promachus sp. 1 (230)	50.9	0/40.4	0/3.9	3.0	0.9	0.9
Promachus sp. 1 (241)	50.6	0/44.4	0/5.0			
L. mexicana (106)	87.7	0/10.4		1.9		
C. feminea (198)	8.6	80.8/0	10.6/0			

the dry season but were started at the onset of the wet season (mid-April).

A similar correspondence between adult abundance and seasonal variation in rainfall has been observed for asilids inhabiting a tropical forest in Kenya. Although individual species were not distinguished, Denlinger (1980) trapped large numbers of adult asilids during the biannual wet seasons but very few during the intervening dry months. The restriction of adult activity to the rainy months may reflect a decrease in prey availability during the dry season. Both in central Panama (Galindo et al. 1956; Robinson and Robinson 1970; Chaniotis et al. 1971; Wolda 1977, 1978a, 1979, 1980; Wolda and Fisk 1981; Ackerman 1983) and in other tropical habitats with seasonal rains (Bates 1945; Davis 1945; Dobzhansky and Pavan 1950; Janzen and Schoener 1968; Gibbs and Leston 1970; Janzen 1973; Buskirk and Buskirk 1976; Leston 1977) the species diversity and abundance of most insect taxa studied are lowest in the dry season and peak during either during the dry-wet transition or during the wet seasons. [Notable exceptions include adults of some moths (Ricklefs 1975; Greenfield 1983), butterflies (Owen and Chanter 1972; Ehrlich and Gilbert 1973), horse flies (Fairchild 1942; Goodier 1966; Clarke 1968), and solitary bees (Heithaus 1979)]. The fact that the peak abundances of other predatory (Gibbs and Leston 1970; Wolda 1978a) and parasitic insects (Owen and Chanter 1970) and web-building spiders (Robinson and Robinson 1970; Lubin 1978) also occur in rainy seasons suggests that temporal variation in prey abundance is an important determinant of the life history patterns of many arthropod predators in tropical habitats characterized by seasonal rains.

Unfortunately, the biology of the immature stages is completely or largely unknown for any of the robber fly species on BCI (see below). As a result, it is not known whether the timing of adult activity additionally reflects certain developmental requirements of the larval and/or pupal stages. That prey abundance alone does not determine the timing of adult activity is suggested by the finding that certain species on BCI fed exclusively or primarily upon bees and wasps, i.e., insects that might be more common during the dry season peak of tree and shrub flowering [as reported by Heithaus (1979) for a Costa Rican forest].

The robber fly species on BCI presumably spend the dry season in the larval stage of the life cycle. Although few data exist for asilids (see Knutson 1972), the egg and pupal stages are relatively short among the species studied, lasting approximately 4–10 days (Davis 1919; Reinhard 1938; Musso 1981) and 15–40 days (Davis 1919; Osterberger 1930; Clements and Bennett 1969; Musso 1981), respectively. The larval stage makes up the great majority of the life cycle and for most species studied lasts approximately 1 year (Felt 1915; Davis 1919; Copello 1927, 1942; Osterberger 1930; Kinoschita 1940; Clements and Bennett 1969; Musso 1981). Larval periods <1 year have never been reported for robber flies, and several species are believed to have larval stages lasting 2–3 years (Davis 1919; Kinoschita 1940; Yesipenko 1967).

Despite the large population sizes of most of the common species (see below), oviposition was observed for only 3 species on BCI. Females of *S. numitor* and *Lampria mexicana* were seen ovipositing in crevices on the surfaces of decaying logs, and a female of *Promachus* sp. 1 was seen ovipositing in the end of a dead branch. Since the larval habitats are unknown for most species, the potential role of larval interactions in promoting ecological differences among the adults can not be directly assessed. However, since low temporal overlap among adults of the LS species constituted a major finding (see next section), the potential role of larval interactions in determining the sequential occurrence of different LS species will be considered later.

Duration and timing of flight periods. The duration and timing of flight periods were similar in 1979 and 1980 for most SS and LS species (Figs. 2 and 3, respectively). For most SS species, abundances were greatest in May and June and then declined throughout July and August. With the exception of *S. corsair*, however, pronounced peaks of abundance

Table 3. Taxonomic composition of the diets of shade-seeking and light-seeking robber fly species. Each value represents the proportion of all prey (*n*) collected for a species within a particular taxonomic category

	n	Para	Ants	Acul	Odon	Col	Nem	Brach/ Cal	Acal	Hom	Hem	Lep	Other[a]
Shade-seeking													
S. corsair	178	5.0	11.8	2.2		74.1					6.1		
S. clavigera	91	13.2	20.9	4.4		27.5	6.6	6.6	2.2	14.3			4.4
E. tarsalis	244	4.1	4.9			0.8	68.0		22.1				
Hybozelodes sp.	198	9.6	5.0			21.2	47.5		11.6	2.0			3.0
G. dryas	295	1.3	19.7			27.1	25.4		5.7	11.2	0.7	4.1	4.7
Ommatius sp.	40		10.0			17.5	20.0	7.5	10.0	22.5		2.5	10.0
S. numitor	62	6.4			1.6		11.3	38.7	1.6	4.8	1.6	24.2	9.6
Oidardis sp.	232	6.0	11.2			17.2	54.3		3.4	2.6		0.9	4.4
Light-seeking													
M. fairchildi	48		10.4	89.6									
Efferia sp.	31		3.2	9.7	25.8	22.6		29.0		3.2	6.4		
Promachus sp. 1	137	2.9	7.3	39.6	3.6	31.4		8.7	0.7	0.7	3.6	0.7	0.7
Promachus sp. 2	120	2.5	12.5	38.3	10.0	10.0	2.5	9.2		3.3	2.5	6.7	2.5
L. mexicana	35		8.6	2.8		42.8				17.1	17.1		11.4
C. feminea	136	5.9	10.3			11.8	58.8		5.9	2.2			3.6

Prey taxa abbreviations (l to r): Parasitoid, Ants, Aculeate, Odonata, Coleoptera, Nematocera, Brachycera/Calypterate, Acalypterate, Homoptera, Hemiptera, Lepidoptera

[a] Other includes: Orthoptera, Strepsiptera, Psocoptera, Isoptera, Mecoptera, Dermaptera, Thysanoptera, Arachnida, Trichoptera

were not observed. Instead, shade-seeking species were relatively common over a 2–3 month interval. For *S. corsair*, peak abundances accounted for 43% and 65% of the total number of individuals seen in 1979 and 1980, respectively. In contrast, among all remaining SS species, peak abundances accounted for 21%–40% of the totals during both years.

In contrast to most SS species, several LS species had short flight periods with distinct peaks of abundance. *Mallophora fairchildi*, *Efferia* sp. and *Promachus* sp. 1 displayed pronounced abundance peaks and were common only over 4–6 weeks intervals. In addition, unlike the SS species a distinct temporal sequence of peak abundances existed among the LS species. In both years this sequence was: *M. fairchildi* (late April), *Efferia* sp. (early May), *Promachus* sp. 1 (late May), *Promachus* sp. 2 (June–July), *C. feminea* (August), and *L. mexicana* (August).

Annual variation. Species differed greatly in the extent to which their relative abundances varied between 1979 and 1980. For each species the standardized values (i.e., individuals seen/10 h) were summed over all census periods for each year. The 1980 totals differed by as much as 79% (for *C. feminea*) to as little as 1% (for *S. numitor*) of the 1979 totals. Despite the large range of between-year differences in abundance, 1980 totals differed by <30% of the 1979 totals for 8 of the 15 species studied. In fact, compared to various homopteran families censused on BCI (Wolda 1977), the 15 asilid species collectively displayed a lower annual variation in abundance. Using Wolda's (1978b) index of annual variability (AV = variance of log R where $R = N_i/N_{i-1}$ and where N represents a species abundance in years i and $i-1$, respectively), I obtained an AV value of 0.061 for the robber fly assemblage. In comparison, only 1 of 11 homopteran families studied had an AV value <0.07 (Wolda 1977). In a comprehensive survey, Wolda (1978b) also calculated AV values for a great diversity of insect taxa occurring in a wide variety of habitats. Among the 138 studies included, only 18 reported lower AV values than that found for the robber fly assemblage on BCI. Although Denlinger (1980) did not quantify the degree of annual variation, he did report that annual abundance of asilids (species were not distinguished) was relatively constant over a 5 year study period. While more data certainly need to be collected for asilids, data presented here and by Denlinger (1980) suggest that asilid populations show little annual variation compared to most other insect taxa.

Among the species on BCI, there were no detectable patterns in the amount of annual variation. Relative differences in abundance between 1979 and 1980 (regardless of the direction fo change) were not significantly different between LS and SS species, small (<20 mg) and large species, or dietary "specialists" (breadth values <3.50 for taxonomic composition of diet, see below) and "generalists" ($P > 0.05$ for all comparisons; 2-tailed Mann-Whitney U-test). Similarly, in comparing these same groups, I found no significant differences in the directions of changes in abundance between years ($P > 0.05$ for all comparisons; 2-tailed Fisher exact probability test).

Perch sites

Perching substrate. Next to the LS-SS dichotomy, the most striking result regarding preferred perching sites was the pronounced specificity displayed by most species for perches of a particular substrate type (Table 2). Among both SS and LS species, 6 species perched exclusively and 7 species perched primarily (>69% of the observations) on 1 substrate type. Substrate preferences fell into 3 distinct groups: horizontal leaf surfaces (5 species), woody branch tips (4 species), and woody branches but not at the tip

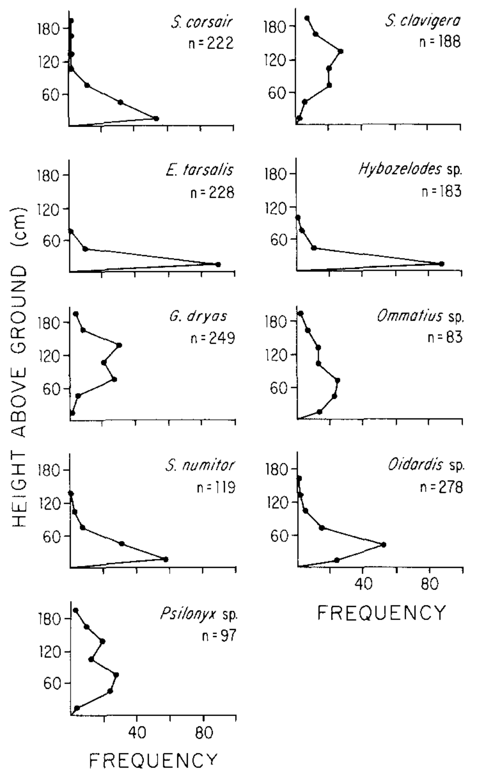

Fig. 4. Perching heights of the shade-seeking species. Each value represents the proportion of all measurements (n) for a particular species within a particular 30 cm interval

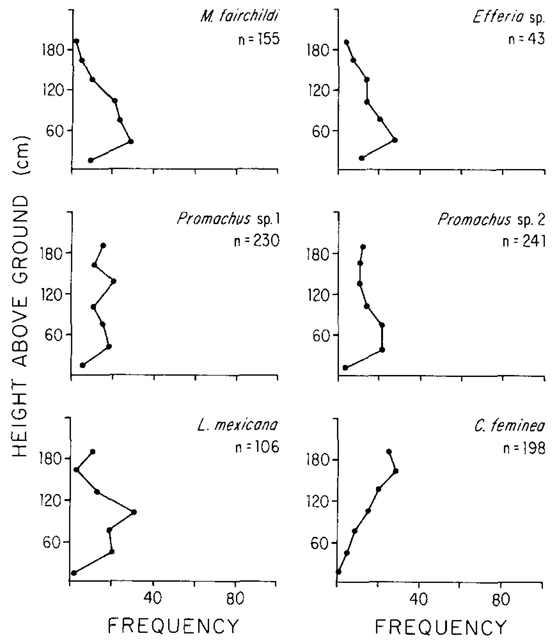

Fig. 5. Perching heights of light-seeking species. Each value represents the proportion of all measurements (n) for a particular species within a particular 30 cm interval

(hereafter referred to as branch stems; 4 species). The 2 *Promachus* spp. were the only species not displaying marked substrate specificity; each of these species perched on leaf surfaces and woody branches in nearly equal frequencies.

The factor(s) promoting substrate specificity is unknown. If particular types of prey are more likely to be found in the immediate vicinity of particular perching substrates, then a species may select that substrate which would maximize its encounter rate with preferred prey. This explanation seems unlikely, however, since most species usually attacked prey that were >15 cm from the perch (Shelly 1984a). That is, potential prey were probably just flying by a perch and were not approaching the perch for a particular "reason." In addition, similarly sized species using different perching substrates consumed similar types of prey (compare *Oidardis* sp. and *Hybozelodes* sp. in Tables 2 and 3). Alternatively, individuals of species may perch on that substrate type in which females of the species oviposit. Although few ovipositions were seen, these observations did not reveal a direct correspondence between perching and oviposition substrates. Females of both *L. mexicana* and *S. numitor* were seen to oviposit in rotting logs, but individuals of these species were only rarely (2% and 14%, respectively) observed perching on logs. Similarly, a female of *Promachus* sp. 1 oviposited in a dead branch, but individuals of this species perched, not only on branches, but on leaf surfaces as well. A similar lack of correspondence between perching and oviposition substrates has been reported for other asilid species as well (Lavigne and Holland 1969; Dennis and Lavigne 1975; Lavigne 1984). Finally, by perching on a particular type of substrate individuals of a species may increase the probability of successfully locating a potential mate. That is, substrate specificity may effectively reduce the spatial complexity of the forest understory by restricting mate searching behavior to a single type of substrate. Although some species that use the same substrate also have broad temporal overlap (e.g., *Eumecosoma tarsalis* and *Hybozelodes* sp.), substrate specificity would greatly reduce the chances of engaging in heterospecific courtship or mating attempts. Note, however, that such "mistakes" do occur between species using the same substrate; attempted matings between *E. tarsalis* and *Hybozelodes* sp. were observed on 4 different occasions.

Species using leaf surfaces did not differ significantly in body size from those using branches (regardless of position on the branch; $P>0.05$, 2-tailed Mann-Whitney U-test). However, among the species using branches, those that perched at the tip were small (<20 mg), whereas those that perched along the stem were large (>100 mg). This finding may have reflected 2 separate factors. First, large species simply may be unable to position all their legs to rest on a small point directly beneath their body. Second, and biologically more interesting, small species may gain an advantage by perching on branch tips, since by doing so individuals were able to "swivel" and thus increase the relative volume of habitat searched from any 1 perch site. In contrast, large species were unable to turn on their perches (nor were they ever observed to walk), and these species remained stationary while perching, making only slight movements of the head.

Perching height. Whereas most species used only 1 type of substrate, species varied considerably in the ranges of perching heights utilized (Figs. 4 and 5). On one hand, several SS species almost always perched within 60 cm of the ground. In contrast, other SS species and the LS species frequently perched between 30–150 cm above ground. Preferred perching height was apparently unrelated to body size as no significant correlation was found between the

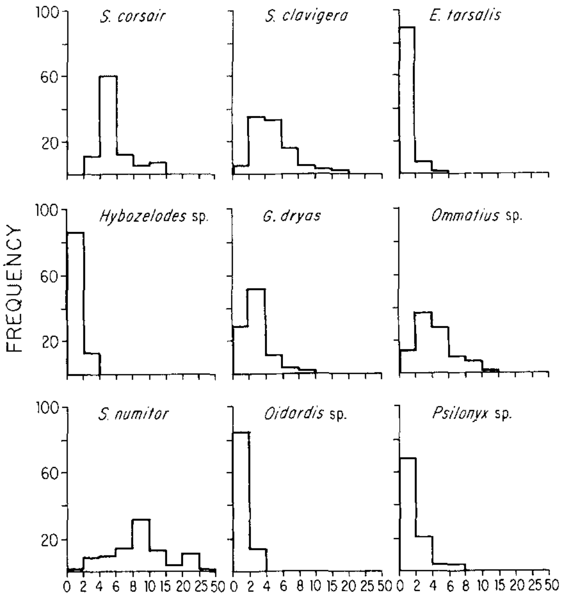

Fig. 6. Prey size frequency distributions for shade-seeking species. Number of prey taken for each species equals that given in Table 3

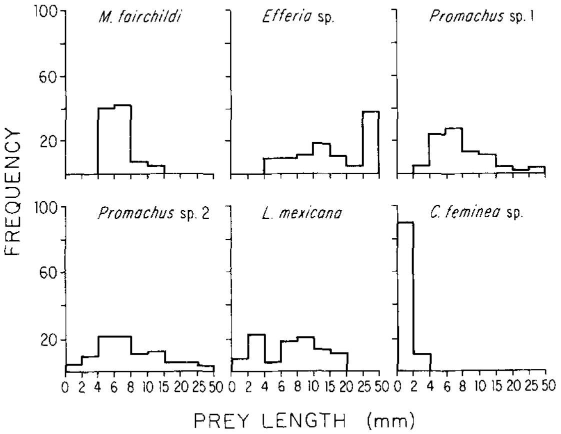

Fig. 7. Prey size frequency distributions for light-seeking species. Number of prey taken for each species equals that given in Table 3

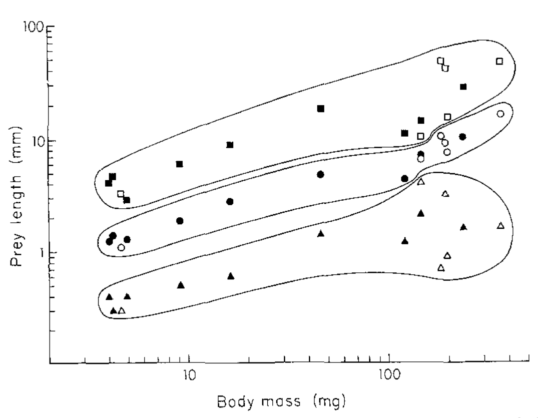

Fig. 8. Mean (*circles*), maximum (*squares*), and minimum (*triangles*) prey sizes for shade-seeking (*closed symbols*) and light-seeking (*open symbols*) robber fly species

median perching height of a species and its body mass ($P > 0.05$; Spearman rank correlation).

Although quantitative data are lacking, all LS species appeared to undergo daily vertical migrations through the canopy. LS species were most frequently encountered between 0900–1530 h (the interval during which perching heights were measured) and were relatively scarce in the early morning or late afternoon. This daily pattern suggests that LS species spend the night and early morning in the canopy, descend in mid-morning by following shafts of light to the forest floor, and then move upward to the canopy in the late afternoon. Although the sampling intervals were short, observations from a canopy tower (40 m above ground) were consistent with this interpretation. Over 3 consecutive days, I saw 7 individuals of LS species between 0630–0800 h and none between 1100–1300 h. Assuming vertical migration occurs, I propose that the descent to the forest floor was unrelated to thermoregulation (since during midday individuals could bask either in the canopy or near the forest floor) and more likely reflected a greater availability of prey nearer the ground. However, the ascent would appear to have a thermoregulatory purpose, since by moving upward as the sun sets individuals could continue basking long after the sunlight ceased to strike the forest floor. In contrast to the LS species, SS species were found near the ground at all times, including immediately after sunrise and just prior to sunset. Moreover, while SS species were encountered during sunny and cloudy conditions, LS species were rarely seen when skies were overcast. LS species presumably perched in the canopy during cloudiness to gain exposure to the greatest light level available.

Independence of perching height and substrate. The preferred perching height of a species was unrelated to the type of substrate utilized. No significant differences were found in the median perch heights of species using leaf surfaces, branch tips, or branch stems, respectively ($P > 0.05$ for all comparisons; 2-tailed Mann-Whitney U-test). Median heights of <40 cm and >105 cm were noted for species in each of these substrate categories.

Diet

Prey size. Consumption of prey of different sizes has long been considered an important factor permitting coexistence among potentially competing species (Hutchinson 1959). Perhaps because of this, theoretical studies of limiting similarity between species often (e.g., May and MacArthur 1972; May 1974; McMurtrie 1976) cite prey size as an example of a resource dimension included in their models. One assumption of these models (MacArthur and Levins 1967; May and MacArthur 1972) is that the resource utilization curves are identical in shape among species (Gaussian distributions are often assumed, but see May 1974; Roughgarden 1974; McMurtrie 1976 for consideration of other distributions). With respect to prey size, this assumption appears valid for various avian predators. Hespenheide (1971) reported that prey size distributions closely approximated normal curves (using log transformed data) for the insectivorous, piscivorous, and molluscivorous species considered. To my knowledge, however, similar tests have not been performed for any group of predatory insects.

Distributions of prey size were strongly skewed to the right for most SS and LS species (Figs. 6 and 7, respectively). Consequently, I tested for normality (following Zar 1974: 97) using log transformed data for each species. Following transformation, these distributions did not differ significantly from normal for any species <100 mg ($P>0.05$ in all cases). However, significant departures ($P<0.05$) from normality were noted for 3 of the 7 larger species. Although this finding may simply reflect an inadequate sample for *L. mexicana*, this possibility seems unlikely for either *S. corsair* or *M. fairchildi*. Although data from more species are needed, these results suggest that, although reasonable for predatory birds (Hespenheide 1971), the normality assumption may be inappropriate for other groups of predatory species (see also Roughgarden 1974 and Schoener and Gorman 1968).

Again using data for all 15 robber fly species, I investigated several other trends relating to prey size. First, I determined the minimum, (arithmetic) mean, and maximum prey lengths for each species and plotted these values against the species' body mass using log transformed axes (Fig. 8). Slopes for mean and maximum prey sizes differed significantly from zero (following Zar 1974: 208) while that for minimum prey sizes did not ($P=0.05$ for all tests). Robber fly body mass explained 96% and 78% of the total variation in mean and maximum prey sizes, respectively, but only 42% of that in minimum prey sizes. The relative constancy of minimum prey sizes is illustrated by the observation that the minimum prey sizes of the largest and smallest asilid species (347 mg vs 4 mg) were similar, 1.6 mm and 0.4 mm, respectively. In contrast, the maximum prey sizes of these same species differed greatly, 45.5 mm vs. 4.1 mm, respectively. These results are consistent with data for a wide variety of predatory taxa. Increases in mean and maximum prey sizes with increasing predator size have been reported for predatory fish (Jackson 1961; Werner 1974), opistobranchs (Paine 1965), lizards (Schoener and Gorman 1968; Sexton et al. 1972), birds (Hespenheide 1971), and snails (Leviten 1976). Similarly, minimum prey size is generally constant relative to predator size (Turner 1959; Jackson 1961; Paine 1965; Menge 1972; Wilson 1973, 1974 but see Menge and Menge 1974, Hespenheide 1975, and Leviten 1976 for exceptions).

As these data suggest, both the ranges and breadth values of prey sizes consumed increase with increasing asilid size ($P<0.001$ for both tests; Spearman rank correlation). That larger species feed upon a greater diversity of prey sizes probably reflects several factors. First, larger asilids are capable of capturing and subduing larger prey. Second, larger robber flies may capture small prey if this requires minimal time and energy. Indeed, the capture by *Efferia* sp. (the largest species studied) of a 1.6 mm homopteran (the smallest prey recorded for that species) occurred when the prey flew within centimeters of the perching asilid. Finally, since large insects are much less abundant than small insects (Schoener and Janzen 1968; Janzen and Schoener 1968; Beaver and Baldwin 1975; Hespenheide 1975), large asilids may attack small prey if larger, more preferred prey are not encountered within a cetain period of time.

Size relationships between predator and prey are further illustrated by comparisons, for each species pair, of overlap in prey size with relative size differences (larger: smaller ratios of the body masses of the asilid species compared). If all 15 species are compared, 105 pairwise comparisons result with overlaps and body mass ratios ranging from 0–0.98 and 1–87, respectively. For the sake of clarity, I have not presented the individual points but instead give mean overlaps for particular intervals of the body mass ratios (Fig. 9). As expected from the above analyses, mean overlaps decreased as relative size differences increased. Additionally, I calculated, for species pairs within the 1–2 interval, separate mean overlaps for pairs in which both species were <10 mg and for pairs in which both species were >100 mg (all species pairs in the 1–2 interval fell into 1 of these categories). The mean overlap among species <10 mg was 0.90 while that among species >100 mg was only 0.58. The lower overlap among larger species is presumably the direct consequence of the fact that these species consumed prey from a larger range of sizes than did the smaller species.

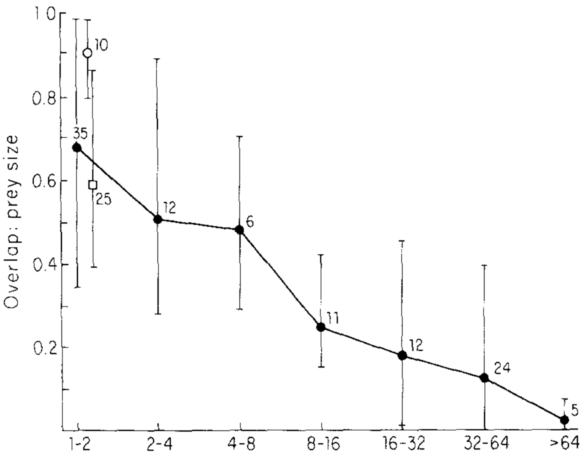

Fig. 9. Overlap in prey size plotted against relative size differences of species compared. Solid circles represent mean overlaps for all species pairs within the designated intervals. Within the 1–2 interval, mean overlaps for species pairs in which both species are <10 mg (o) and both are >100 mg (□) are presented. Numbers represent sample sizes; bars represent 1 SD

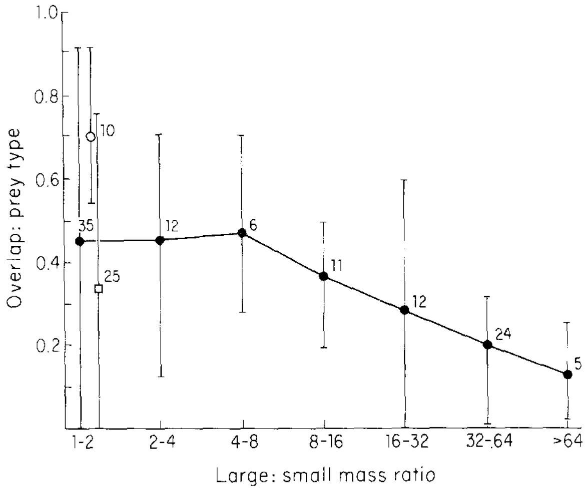

Fig. 10. Overlap in prey type plotted against relative size differences of species composed. See Fig. 9 for explanation of symbols

Prey type. The diversity of prey types actually available to an asilid species is partially determined by the range of prey sizes utilized. Since maximum prey size increased while the minimum size did not (Fig. 10), larger species captured, not only prey types of generally small size, but also prey types of relatively large size, which were essentially unavailable to the small species (Table 3). Odonates, aculeate Hymenoptera, and brachycerous/calypterate Diptera, for example, were for the most part simply too large for the small species to capture and subdue. The most obvious trend was the decrease in the dietary importance of nematocerous Diptera with increasing asilid body mass ($P<0.001$; Spearman rank correlation). Among species <10 mg, nematocerans comprised 39%–68% of the diet. However, among species >100 mg consumed nematocerans infrequently (0%–20% of the diet), and 5 were never found feeding upon this prey type. Large species generally fed upon a diversity of prey types and did not collectively display a tendency to feed primarily upon a single prey type.

Despite these findings, breadth values for prey type were not significantly correlated with body mass. The lowest breadth values for prey type were obtained for 2 of the largest species, namely *S. corsair* and *M. fairchildi* which fed primarily upon beetles and aculeate Hymenoptera, respectively. Because of the "specialization" of these 2 species, breadth values for prey type were not significantly correlated with body mass ($P>0.05$; Spearman rank correlation). If *S. corsair* and *M. fairchildi* are omitted from analysis, the weak positive correlation becomes significant ($P<0.01$; Spearman rank correlation).

Size-related trends in the taxonomic composition of diets are further illustrated by plotting overlap in prey type against the relative size difference of the species compared (Fig. 10; as in the corresponding plot for prey size, only mean values are presented for the respective intervals of mass ratios). These overlaps tended to decrease as relative size differences increased, although the mean for the 1–2 interval was less than those for the 2–4 and 4–8 intervals. As with prey size, I calculated, for species pairs within the 1–2 interval, separate mean overlaps for pairs in which both species were <10 mg and for pairs in which both species were >100 mg. Reflecting the shared importance of nematocerous Diptera, the mean overlap among species <10 mg was 0.70, and the variance was relatively low (coefficient of variation = 0.18). In contrast, the mean overlap among species >100 mg was only 0.34, and the variance was large (coefficient of variation = 0.56). Among these large species, the lower overlap in prey type compared to that for prey size (0.34 vs. 0.58) reveals that dietary differences among species >100 mg were primarily the result of differences in the types, and not the sizes, of prey consumed.

While this low overlap in prey type was in part a simple consequence of the increased diversity of prey types available to larger species, it also resulted from differences betwen LS and SS species. Most importantly, several of the large LS species frequently consumed aculeate Hymenoptera, whereas none of the large SS species did so. Approximately 40% of the prey taken from the 2 *Promachus* spp. were aculeate Hymenoptera, and the corresponding value for *M. fairchildi* was nearly 90%. In contrast, *Ommatius* sp. and *S. numitor* were never found eating this prey type, and aculeate Hymenoptera comprised only 2% of the diet of *S. corsair*.

Large LS and SS species also differed in the amount of conspecific and confamilial predation observed. Cannibalism was not recorded for any SS species but was noted for *M. fairchildi* (once), *Promachus* sp. 1 (twice), and *Promachus* sp. 2 (thrice). Similarly, only 4 instances of confamilial predation were observed among the SS species. These included (predator-prey): 1 *Ommatius* sp./*Psilonyx* sp., 2 *S. clavigera*/*G. dryas*, and 1 *S. clavigera*/*S. corsair*. In comparison, LS species were seen feeding upon other LS species on 15 occasions. Other asilids were actually an important dietary constituent for *Efferia* sp., and approximately 25% (7/31) of its diet consisted of *M. fairchildi* and *Promachus* sp. 1. *Promachus* sp. 1 was observed feeding on *Promachus* sp. 2 in 6 instances, this representing 4 of its diet. Conversely, *Promachus* sp. 2 was seen consuming *Promachus* sp. 1 on 3 ocassions, this representing 3% of its diet. The potential role of intra-asilid predation in promoting low temporal overlap among the large LS species will be considered in a later section.

Table 4. Mean overlaps for the SS and LS (both including and excluding *C. feminea*) guilds. Values in parentheses represent the number of simulated means that are greater than/less than the actual mean for 200 trials

	SS guild	LS guild (incl C. fem)	LS guild (excl C. fem)
Seasonal occurrence			
1979	0.49 (21/179)	0.28 (190/10)	0.25 (198/2)
1980	0.54 (19/181)	0.25 (195/5)	0.21 (200/0)
Perch site			
Height	0.47 (144/56)	0.71 (21/179)	0.78 (3/197)
Substrate	0.23 (181/19)	0.39 (21/179)	0.55 (4/196)
Diet			
Prey type	0.43 (24/176)	0.34 (25/175)	0.49 (19/181)
Prey size	0.44 (23/177)	0.41 (43/157)	0.59 (3/197)

Statistical analyses of overlap values

Results. Within the SS guild, the actual mean overlap for each niche dimension considered did not differ significantly from that expected by chance assignment of species into thermal guilds (Table 4). Two tests were marginally significant, ($P<0.10$); the actual mean overlaps for seasonal occurrence in 1980 and perching substrate were greater than and less than, respectively, the mean overlaps expected by random assignment of species. Within the LS guild, (*C. feminea* included), actual mean overlaps for seasonal occurrence in both 1979 and 1980 were significantly less than expected by random arrangement, while for the remaining dimensions actual means did not differ significantly from random (Table 4). Since *C. feminea* (5 mg) is so much smaller than the other 5 LS species (145–350 mg), I also performed the random arrangement procedure with this species excluded. The actual mean overlap among the 5 large LS species was significantly less than that expected by chance arrangement for seasonal occurrence in both 1979 and 1980 but was significantly greater for perching height, perching substrate, and prey size. Moreover, the null hypothesis that overlap in prey type was greater than expected by chance was marginally significant ($P<0.10$).

Interpretation. The analyses performed revealed no evidence that overlaps within the SS guild differed significantly from the random null hypothesis. Although significantly low temporal overlap was noted for the LS guild (*C. feminea* included), interpretation of this result is difficult since no significant trends were found for any of the other dimensions. However, the findings for the 5 large LS species (*C. feminea* excluded) clearly suggest a coupling of high dietary and spatial overlaps with low temporal overlap. I propose that this temporal segregation may minimize competition for limited food resources among species that use similar perching sites. In particular, the low temporal overlaps among species feeding primarily upon aculeate Hymenoptera (*M. fairchildi* and both *Promachus* spp.) suggest that this prey type may be limiting. The niche complementarity observed is analogous to that reported for some vertebrate taxa (Cody 1974; Schoener 1974; Pianka and Pianka 1976; Werner 1977; Pianka and Huey 1978).

It should be noted that while conclusive data are lacking, visual estimates indicate that large LS and SS species encounter different spectra of available prey. Morgan and Shelly (unpub. data) attempted to identify all insects $\gtrsim 5$ mm flying through an equal volume ($5\ \text{m} \times 5\ \text{m} \times 5\ \text{m}$) of light gap and shaded area during a 1 h period. Aculeate Hymenoptera, Lepidoptera, and Coleoptera were the most frequently sited prey in the light gap, comprising 47%, 37%, and 7%, respectively, of the total sample ($n = 94$). In contrast, aculeate Hymenoptera and Lepidoptera represented only 17% and 5%, respectively, of the total sample ($n = 57$) at the shaded site. At this site, Coleoptera, Odonata (all Zygoptera), and non-nematocerous Diptera (mostly Tipuliidae and Stratiomyiidae) were the most common prey, comprising 30%, 23%, and 23%, respectively, of the total sample.

The large number of aculeate Hymenoptera seen in the light gap (44 in 1 h) does not invalidate the suggestion that such prey may be in short supply. First, the count was confined to 1 light gap which, if near an active bee or wasp nest, might have had an unusually large number of hymenopteran visitors. Also, the volume of habitat sampled was approximately 60 times greater than the "searching volume" of an individual of any large LS species (Shelly 1984a). Third, capture efficiencies (% of attacks that were successful) of the large LS species were very low, ranging from only 3%–6%. Finally, the high body temperatures of the large LS species presumably resulted in high mass-specific metabolic rates and the subsequent demand for high rates of food intake (Morgan et al. 1985).

In addition to reducing potential competition for food, low temporal overlap may also minimize the risk of predation by other asilids. *Efferia* sp. appears to play a particularly important role in this regard. Temporally "sandwiched" between *M. fairchildi* and *Promachus* sp. 1, *Efferia* sp. displayed only moderate dietary overlap with these species but frequently preyed upon them. The size advantage enjoyed by *Efferia* sp. appears critical in these interactions, since it allowed this species to successfully capture and subdue *M. fairchildi* and *Promachus* sp. 1 while simultaneously protecting it from falling prey itself to either of these species.

It should be noted that, aside from attacks by other asilids, predation did not appear to be an improtant cause of adult mortality for either the LS or SS species. In addition to asilids, known invertebrate predators of robber flies include mantids, scorpionflies, wasps, true bugs, and most importantly, spiders (review in Lavigne et al. 1978). During this study, however, I never saw an attempted capture of an asilid by any of these predators. While censusing, I examined 769 webs of 3 of the most common understory araneids (*Nephila clavipes, Araneus tuonabo*, and *M. schreibersi)* and did not find 1 captured asilid. One *S. clavigera* was seen to strike a web, but it escaped almost immediately. Similarly, diurnally active hunting spiders appeared to have negligible impact upon asilid populations. Regarding vertebrate predators, birds (Reid 1955; Colyer and Hammond 1951) and lizards (Milstead and Tinkle 1969) occasionally eat asilids. Their impact upon asilid populations is probably very slight, however, and I never saw an attempted capture of any asilid by any vertebrate. Asilids are also known to host parasitic fungi and mites (Colyer and Hammond 1951), but no obviously parasitized individuals were seen in the entire study.

Finally, the sequential occurrence of the large LS species could have conceivably evolved to stagger oviposition periods and consequently reduce competition, not among adults, but among larvae. However, this explanation appears unlikely for the following reasons. First, as noted earlier, limited observations indicate that LS species do not all oviposit in the same type of substrate. Since asilid larvae and their prey (primarily immature stages of other insects; Knutson 1972) are not very mobile, spatial isolation would seem to more effectively reduce larval competition than would sequential oviposition periods. Second, as noted above, for all species studied thus far, the larval stage lasts at least 1 year and may extend to 3 years. The long duration of the larval stage suggests that 2–4 weeks intervals between oviposition periods would only slightly reduce temporal overlap among the larvae of different species. Third, a larva may require only 1 or several prey in the entire course of its development (Osterberger 1930; Daniels 1966; Clements and Bennett 1969). In contrast, large LS adults probably consume >10 prey items/day (Shelly 1984a). Thus, the adult appears to be the primary feeding stage in the life cycle [see also Oldroyd (1964)], and it is therefore during this stage that intense competition for food would be most likely to occur.

Concluding remarks

The present findings prompt 2 general remarks regarding the ecological "organization" of terrestrial insect communities. First, studies of insect thermoregulation typically view microhabitat selection as a short-term response to varying thermal conditions [see May (1979) and Casey (1981) for reviews]. That is, most researchers examine microhabitat selection as a behavioral mechanism by which ectothermic insects can regulate their body temperature (e.g., escaping high ground temperatures by moving onto vegetation). In contrast to this emphasis upon short-term behavior, few studies have rigorously investigated species-specific selection of thermally different microhabitats. This oversight is particularly unfortunate, since it ignores a potentially important means by which species can be distinguished ecologically, behaviorally, and physiologically. Indeed, it appears that an LS-SS dichotomy may characterize other insect taxa. Heinrich (1972) studied the thermal biology of several species of butterflies in New Guinea and classified them as sun-loving or shade-loving. Similarly, Shelly (1982) documented distinct SS and LS behaviors in adult damselflies and found pronounced differences in the foraging and relocation rates of LS and SS species. In light of such results, it appears essential that studies of insect communities include, as do those of lizard communities (e.g., Lister 1976; Roughgarden et al. 1981), descriptions of the preferred body temperatures [(the "thermal niche" sensu Lister (1976)] for all species.

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