Oecologia (2002) 133:525–533
DOI 10.1007/s00442-002-1060-z

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Variation in nectar robbing over time, space, and species

Received: 25 January 2002 / Accepted: 7 August 2002 / Published online: 21 September 2002

Abstract Spatiotemporal variation in the interactions among plants and animals is widespread; yet our conceptual and empirical understanding of this variation is limited to a few types of visitors, mainly herbivores, pollinators, seed predators, and seed dispersers. Despite the ubiquity of nectar robbing and the strength of its effects on plant fitness, we know relatively little about the magnitude and intensity of spatial and temporal variation in interactions among plants and nectar robbers. The purpose of the present study was to quantify spatial and temporal variation in the interactions between a nectar-robbing bumblebee and its host plants. In the Rocky Mountains of Colorado, USA, over 7 years, and multiple locations, we measured levels of nectar robbing by the bumblebee *Bombus occidentalis* and its interactions with four different host plants, *Delphinium nuttallianum* (Ranunculaceae), *Ipomopsis aggregata* (Polemoniaceae), *Corydalis caseana* (Fumariaceae), and *Linaria vulgaris* (Scrophulariaceae). Significant variation was found in the robbing rates experienced by different species. Within species, there was variation in robbing rates on an annual basis, on a seasonal basis, among different sites, and within sites. This variation may have important consequences with respect to the population dynamics of host plants as well as selection on floral and flowering traits.

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Keywords *Bombus occidentalis* · Plant-animal interactions · Floral larceny · Spatiotemporal variation

Introduction

Variation in the interactions among species is widespread. For example, a growing body of literature has quantified the spatial and temporal variation in interactions among host plants and their herbivores, pollinators, seed predators, and seed dispersers (e.g., Herrera 1982, 1988; Bronstein and Hoffman 1987; Horvitz and Schemske 1990; Root and Cappuccino 1992; Root 1996; Brody 1997). Variation in the direction and magnitude of these species interactions can have profound consequences on the traits that species express (Thompson 1994, 1997) as well as on variation in subsequent community structure and ecosystem function through direct and indirect interactions (e.g., Miller and Travis 1996; Travis 1996; McNaughton et al. 1997). Despite our extensive knowledge of variation in species interactions and the repercussions of such variation, we know relatively little about spatial and temporal variation in the exploitation of mutualisms. Exploiters of mutualisms are organisms that obtain a reward offered by a mutualist without providing a reward in return (reviewed in Bronstein 2001). We focus on the magnitude of spatial and temporal variation in the exploitation of plant-pollinator mutualisms by nectar robbers, in particular the levels of nectar robbing experienced by plants. High levels of spatiotemporal variation in plant-nectar robber interactions may limit the degree to which plants can respond to the selective effects of robbing.

Nectar robbers are birds or insects that remove floral nectar by biting or piercing a hole in the flower, circumventing the floral opening used by legitimate floral visi-

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tors (Inouye 1980). Nectar robbing is widespread, being documented on every continent except Antarctica. To date, we have found reference to 214 plant species in 59 different families for which nectar robbing has been demonstrated, and there are probably many more examples yet to be discovered. In general, it is likely that almost all plants species with tubular flowers or flowers with nectar spurs experience some form of floral larceny.

Floral visits from nectar robbers may have strong positive, negative, or neutral outcomes on the reproductive success of plants (reviewed in Maloof and Inouye 2000; Irwin et al. 2001). These effects may be mediated through direct pathways, i.e., damage to reproductive organs (McDade and Kinsman 1980; Traveset et al. 1998), as well as indirect pathways, by altering the direct relationship between plants and pollinators (Irwin and Brody 1998; Maloof 2001). As in other plant-animal interactions, these direct and indirect effects of nectar robbers on plants are likely to be conditional upon the spatiotemporal context in which they occur, having both ecological and evolutionary repercussions. Our goal here is to quantify the spatial and temporal variation in the interactions between plants and nectar robbers. Understanding variation in these interactions is a starting point to developing hypotheses and predictions concerning the ecological and evolutionary relationships between plants and their exploiters. Moreover, this is a first step towards recognizing the importance of complex, variable relationships between plants and robbers to selection on floral and flowering traits.

In the Rocky Mountains of Colorado, USA, over 7 years, and multiple locations, we measured levels of nectar robbing by the bumblebee, *Bombus occidentalis*, and its interactions with four different host plants, *Delphinium nuttallianum* (Ranunculaceae), *Ipomopsis aggregata* (Polemoniaceae), *Corydalis caseana* (Fumariaceae), and *Linaria vulgaris* (Scrophulariaceae). First, we ask: do robbing rates vary spatially and/or temporally within and among these four species? We then use the hummingbird-pollinated and nectar-robbed montane herb *I. aggregata* as a model system to ask: (1) do robbing levels show within-population heterogeneity?; and (2) are robbing levels correlated with peak flower abundance?

Materials and methods

Study system

Fieldwork was conducted from June through September from 1995 to 2001 in and around the Rocky Mountain Biological Laboratory (RMBL; latitude 38°45′N, longitude 106°59′W, altitude 2,900 m). The RMBL is a high-elevation field station located in the Elk Mountains of Colorado, USA. The RMBL is host to at least five different bumblebee species (Pyke 1982). A short-tongued bumblebee in this region, *Bombus occidentalis*, acts as a nectar robber (mean tongue length=7.1 mm; Pyke 1982) and is the only primary nectar robber in this area (D. W. Inouye, personal communication). The bumblebee uses its toothed mandibles to chew a hole through the corolla of the flower; it then inserts its proboscis into the hole and removes nectar, bypassing the corolla opening used by legitimate pollinators.

B. occidentalis, like many bumblebees in temperate regions, has an annual life cycle. Overwintering, fertilized, queen bees build nests in the spring and lay eggs and provide food (nectar and pollen) for themselves and their developing larvae. When the non-reproductive workers hatch, and are adequately providing for the nest, the queen will only forage infrequently, if at all. Typically, the colony grows in size throughout the summer. Toward the end of the summer, drones (non-worker male bees) and new queens ("reproductives") are produced. These bees will look for mates, and as cold weather arrives, all bees in the colony will die except the newly fertilized queens, which may or may not successfully overwinter (Prys-Jones and Corbet 1991).

Because *B. occidentalis* requires both pollen and nectar for larval provisioning, the bees will visit some small-flowered plants, such as those in the Asteraceae, for pollen as well as nectar, thus acting as legitimate pollinators. However, on other plant species with concealed nectaries, *B. occidentalis* acts only as a nectar robber. Around the RMBL, *B. occidentalis* robs, to our knowledge, at least eight different plant species, four of which we have studied here. The effects of nectar robbing on plant reproduction are not consistent across these plant species; these inconsistencies may be due, in part, to differences in pollinators and life-history characters (Maloof and Inouye 2000; Irwin et al. 2001). We describe each of the species in phenological order.

The earliest-blooming species, *Delphinium nuttallianum* (Ranunculaceae), flowers from late May to early June. *D. nuttallianum* is a small, self-incompatible, herbaceous perennial pollinated primarily by bumblebees (*Bombus appositus* and *B. flavifrons*) and hummingbirds (*Selasphorus platycercus*) (Waser 1978). Its purple flowers have a nectar spur that is robbed by *B. occidentalis*. The effects of robbing on *D. nuttallianum* are unknown.

The self-incompatible, monocarpic *Ipomopsis aggregata* (Polemoniaceae) has the longest blooming season of the species we studied (early-June to mid-September). The red, tubular flowers of *I. aggregata* are pollinated primarily by hummingbirds (*S. platycercus* and *S. rufus*) (Waser 1978) and are nectar robbed by *B. occidentalis*. In this species, high levels of nectar robbing reduce both male and female reproductive success by 50%, mediated through hummingbird-pollinator avoidance of robbed plants and flowers (Irwin and Brody 1998, 1999, 2000).

Corydalis caseana subsp. *brandegii* (Fumariaceae), a self-compatible, perennial species, blooms from mid-June to September. *C. caseana* has pinkish-white flowers with nectar spurs that are pollinated by bumblebees (primarily *B. appositus*) and nectar robbed by *B. occidentalis*. Although the robbers do not pollinate *C. caseana,* robbing has no negative effect on its reproductive success (Maloof 2001).

Finally, *Linaria vulgaris* (Scrophulariaceae), a late-blooming species (August–October), is a self-incompatible perennial that also reproduces vegetatively. *L. vulgaris* is bumblebee-pollinated and has yellow flowers with nectar spurs that experience robbing by *B. occidentalis*. High levels of robbing in *L. vulgaris* have no effect on female reproductive success (Stout et al. 2000; R. E. Irwin, unpublished data), likely because the plants are not pollen limited (R. E. Irwin, unpublished data; but see Arnold 1982).

In summary, each of these four species are robbed by *B. occidentalis*: in *D. nuttallianum*, the effects of robbers are unknown; in *I. aggregata*, robbers have strong detrimental effects on male and female plant reproduction; and in *C. caseana* and *L. vulgaris*, robbing has a neutral effect on female plant reproduction.

Field methods

Quantification of robbing levels

For each species, we measured robbing by counting the number of holes made in the corollas of flowers as an estimate of robber visitation. We then quantified robbing level per plant or inflorescence as: no. of robber holes/no. flowers open. Although one could argue that measuring robbing in this manner may underestimate robber visitation if robbers use the same robber holes to re-visit flowers, often robbers make new holes rather than using pre-existing holes in this system (R. E. Irwin, personal observation). Therefore, we feel our estimates of robbing based on counting holes in flowers adequately measure natural levels of robber visitation. We should note that for the plant species studied here, to our knowledge, the effect of one versus multiple robber holes in the same flower on plant reproduction or on selection on floral or flowering traits is unknown.

For the earliest blooming plant, *D. nuttallianum*, we measured robbing levels in 1998 and 1999. In 1998, we measured robbing levels once on 24 June at peak flowering at two sites separated by approximately 500 m (both sites were located in the RMBL town site). The sites contained approximately 150 flowering *D. nuttallianum*; we measured robbing on 100 plants/site. In 1999, we measured robbing levels once per week throughout the *D. nuttallianum* flowering season on 30 randomly chosen plants at site 1 and 20 plants at site 2 (the same two sites as used in 1998). At this early point in the season, it is unlikely that worker *B. occidentalis* had emerged; therefore, robbing was likely the result of queen *B. occidentalis* only (R. E. Irwin, personal observation). We calculated the mean robbing level per site in 1998 and mean robbing level per week per site in 1999.

Robbing levels on *I. aggregata* were measured from 1995 to 2001 in a number of different populations. In each population, we chose plants at random as they initiated bolting and then recorded robbing levels on those plants every 4 days throughout the blooming season. Because individual *I. aggregata* flowers only bloom for approximately 3 days, measuring robbing rates every 4 days ensured that we did not record robbing on the same flowers in multiple census periods. The quantification of robbing levels in each year of study started when marked plants initiated flowering and was terminated when plants ceased blooming (approximately 6–12 weeks). In 1995, we recorded robbing rates at five sites, 3 plants/site; in 1996, two sites, 100 plants/site; in 1997, six sites, approximately 90 plants/site; in 1998 and 1999, six sites, 30 plants/site; in 2000, three sites, 30 plants/site; and in 2001, two sites, 30 plants/site. All sites were located in and around the RMBL. All sites harbored at least 150 blooming *I. aggregata*, and sites were separated from each other by at least 600 m. We calculated the weekly robbing levels per site for each year of study for *I. aggregata*.

For *C. caseana* we measured robbing levels once per season near peak flowering (late-July) over 5 years, from 1996–2001 excluding the year 2000, in eight different populations. Seven of the populations were located within 880 m of each other at Kebler Pass; the eighth, and largest, population was located 16 km away at Yule Basin. Each year, at each site, we measured robbing levels on ten inflorescences from different plants. Inflorescences had an average of 25 flowers each. We then calculated the mean robbing level for each population in each year.

Finally, we measured robbing levels on *L. vulgaris* from 1998 through 2001. In 2000, we chose ten different populations of *L. vulgaris* around Gunnison County, Colorado and measured robbing on 30 randomly chosen plants per population near peak flowering on 15 August. All populations contained at least 1000 flowering *L. vulgaris* stalks and were separated from one another by at least 1 km. We calculated the mean robbing level for each site. For all other years, we measured robbing rates in one large population of *L. vulgaris* in the RMBL town site weekly throughout the blooming season. The population contained over 10,000 *L. vulgaris* flowering stalks. In 1998 and 2001, we measured robbing rates on 40 plants, and 1999, on 50 plants. We then calculated the mean robbing level per week.

Do robbing levels vary spatially and/or temporally within and among species?

To examine how robbing levels varied spatially and temporally for *D. nuttallianum*, *I. aggregata*, and *L. vulgaris*, we used a repeated measures ANOVA with site (random effect) and year as main factors and bloom week as the repeated term. Robbing level (arcsine-square root transformed) was used as the response variable here, as well as for all analyses below. Year was not included in the model for *D. nuttallianum* because weekly robbing levels were only measured in one season, and site was not included in the model for *L. vulgaris* because weekly robbing levels were only measured in one site. For *L. vulgaris* robbing data collected in 2000, we measured robbing in multiple sites at one point in the season; in this case we used an ANOVA with site (random effect) as the main factor. Finally, for *C. caseana*, we used an ANOVA to compare levels of nectar robbing among sites (random effect) and years.

To compare how robbing levels varied among species, we calculated the mean peak robbing level for *D. nuttallianum*, *I. aggregata*, and *L. vulgaris* per year. We excluded data collected for *D. nuttallianum* in 1998, *C. caseana* in 1996–2001, and *L. vulgaris* in 2000 because we did not measure robbing levels throughout the plants' blooming seasons and, therefore, are uncertain if we measured peak robbing levels. We used an ANOVA with plant species as the main effect. All statistical analyses were performed with SAS statistical software (SAS Institute, version 5.0.2).

Do *I. aggregata* robbing levels show within-population heterogeneity?

In the above analyses, we examined whether sites differed in robbing levels. But we also hypothesized that if nectar robbers foraged using area-restricted searching or if robbers foraged on specific clumps or groups of plants, as has been shown with pollinating bees (Ackerman et al. 1982), robbing levels could show heterogeneous patterns within populations. Heterogeneity in robbing levels within populations could have important consequences with respect to pollinator visitation and pollen flow and, ultimately, the spatial genetic structuring of plant populations (Zimmerman and Cook 1985).

We examined the spatial heterogeneity of robbing levels within populations of *I. aggregata* only. In 1998 and 1999, we mapped all marked *I. aggregata* in each of the six sites described above in which we recorded robbing levels. Each site was approximately 10 m×10 m in area. All plants were mapped to the nearest 10 cm. We used a geostatistical approach to describe the spatial variation in robbing levels within sites (Isaaks and Srivastava 1989; Rossi et al. 1992). Geostatistical techniques quantify the strength, pattern, and degree of spatial relationships. In our case, we used geostatistics to examine how plants within populations covaried in robbing levels as a function of separation distance. (Supplementary electronic material available at http://dx.doi.org/10.1007/s00442-002-1060-z describes this technique in more detail.)

We used GS+ software (version 3.1.7, Gamma Design Software, Plainwell, Mich.) to calculate isotropic semi-variograms for each *I. aggregata* population separately in 1998 and 1999. Semi-variograms calculate half the average squared difference in robbing levels between pairs of plants against increasing separation distances (the lag interval) (Isaaks and Srivastava 1989). In all cases, mean robbing level per plant in each population was arcsine-square root transformed. We calculated two spatial heterogeneity statistics from the semi-variograms.

1. The nugget-to-sill (N:S) ratio (arcsine-square root transformed) measured the degree of patterning in robbing levels. The lower the N:S ratio, the more spatial patterning the robbing levels exhibit.
2. The range (A_0) measured the distance over which robbing levels were autocorrelated (i.e., patch size).

We then compared these two spatial heterogeneity statistics between years and among sites using a multiple ANOVA (MANOVA).

Table 1 Variation in robbing levels within and among species. For all species except *Corydalis caseana*, robbing levels represent the annual mean peak robbing levels throughout the blooming season (excluding year 1998 for *Delphinium nuttallianum* and year 2000 for *Linaria vulgaris* when we only measured robbing levels once in the flowering season). For *C. caseana*, we measured robbing levels once in the flowering season near peak flowering. We calculated robbing levels as no. of robber holes/no. flowers open. Variation among years represents the maximum variation in robbing levels between the highest and lowest years in the study

Species	Mean robbing level±1 SE (%)	Variation among years (%)	Years in study	Significant variation among years	Significant variation among sites
D. nuttallianum	56.50±8.50	26	2	No	Yes
I. aggregata	66.14±12.14	80	7	Yes	Yes
C. caseana	67.44±3.49	52	5	Yes	Yes
L. vulgaris	79.25±15.34	76	4	Yes	Yes

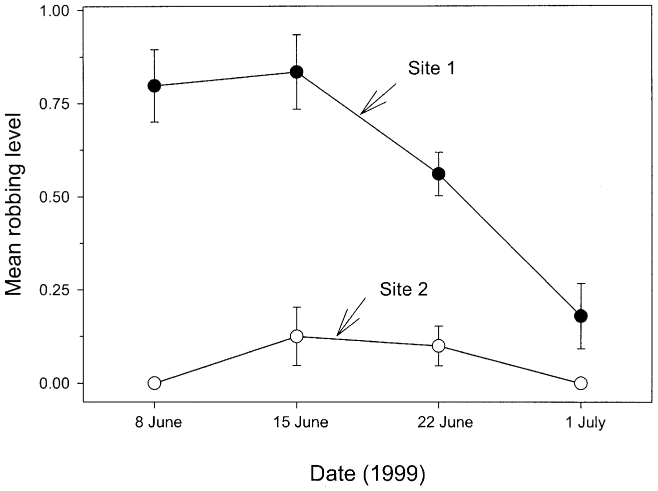


Fig. 1 Seasonal variation in nectar-robbing levels on *Delphinium nuttallianum* in two sites in 1999 (mean per week±1 SE). Robbing levels decreased significantly as the season progressed ($F_{3,164}=5.91$, $P=0.0007$)

Are peak *I. aggregata* robbing levels correlated with peak flower abundance?

From 1998 to 2000, we counted the total number of blooming *I. aggregata* plants and flowers per week in each of the sites described above in which we estimated robbing levels. To examine whether peak robbing levels were correlated with peak flower abundance, we used a Kolmogorov-Smirnov two-sample test (K-S test) to determine whether the robbing and flower abundance distributions differed.

Results

Do robbing levels vary spatially and/or temporally within and among species?

We will first describe the spatial and temporal variation in robbing levels for each individual species followed by a comparison of robbing levels among species. The general trend across species is for substantial spatial and temporal variation in robbing levels.

Delphinium nuttallianum

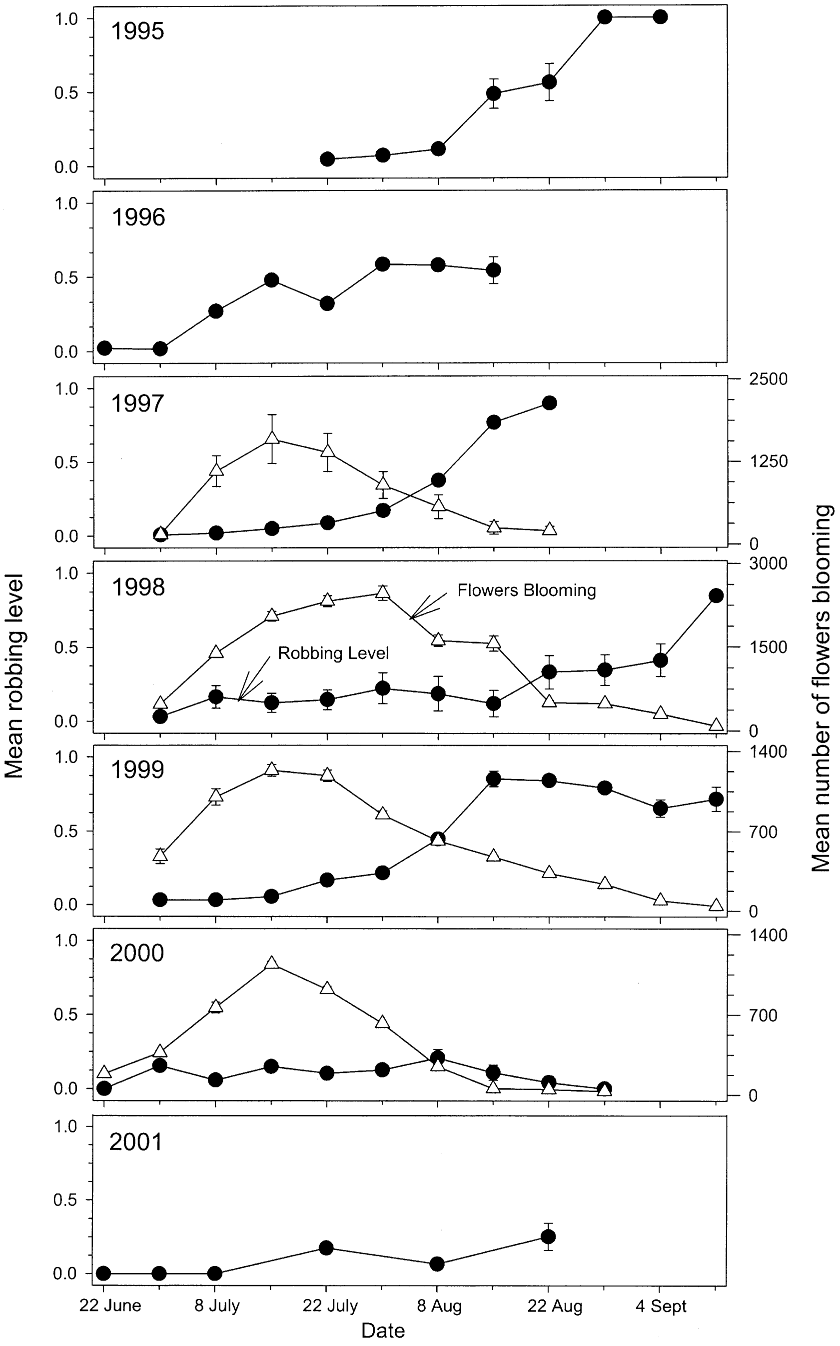
Over 1998 and 1999, robbing levels in the earliest blooming plant, *D. nuttallianum*, ranged from 0% to 200% of available flowers robbed (many flowers had multiple robber holes) with a mean (±1 SE) at peak robbing of 56.50±8.50% (Table 1). *D. nuttallianum* did not differ significantly in robbing levels between the 2 years of study ($F_{1,246}=2.24$, $P=0.14$); however, the sites differed in robbing levels ($F_{1,246}=10.39$, $P=0.0014$). Site 1 received 13% more robbing in 1998 and 87% more robbing in 1999 than site 2. In addition, in 1999 robbing levels varied significantly among bloom weeks ($F_{3,164}=5.91$, $P=0.0007$; Fig. 1). We found a significant reduction in robbing as the season progressed (especially in site 1).

Ipomopsis aggregata

Over the 7 years of study (1995–2001) of robbing levels on *I. aggregata*, mean levels of robbing per plant ranged from 0% to 100% of flowers robbed with a mean±1 SE across all years and sites of 66.14±12.14% at peak robbing (multiple robber holes per flower were uncommon; Table 1). In each year of study, we found a significant increase in robbing throughout the season ($F_{11,209}=15.55$, $P<0.0001$; Fig. 2). Robbing levels usually peaked near the end of the blooming season for *I. aggregata*. This pattern varies from that of *D. nuttallianum*, where robbing decreased near the end of *D. nuttallianum*'s flowering season.

To disentangle flower availability from proportion of flowers robbed for *I. aggregata* (i.e., robbing levels may be lower mid-season because more *I. aggregata* flowers are in bloom; Fig. 2), we also examined the number of robber holes (square-root transformed) throughout the season and found a similar trend. Irrespective of the number of flowers open, the number of robber holes (and likely robber activity) increased at the end of *I. aggregata* blooming ($F_{11,189}=4.30$, $P<0.0001$; year 1995 excluded because robbing estimates were recorded as proportions and not numbers of flowers robbed). Interestingly, if *I. aggregata* plants bloomed early in the season, they were able to escape nectar robbing. Averaged across years and sites, 18% of *I. aggregata* avoided robbing by

Fig. 2 Mean seasonal variation in nectar-robbing levels (●) in *Ipomopsis aggregata* populations over 7 years of study, 1995–2001, and mean flower production per week (Δ) from 1997 to 2000 (mean per site per week±1 SE). Robbing levels increased significantly throughout the season ($F_{11,209}$=15.55, P<0.0001) whereas flower production peaked mid-season for *I. aggregata*



finishing their flowering before robbing levels increased markedly.

Levels of robbing on *I. aggregata* not only varied among weeks within years but also among years ($F_{6,209}$=9.92, P<0.0001; Figs. 2, 3). Peak levels of robbing ranged from 100% of flowers robbed in 1995 (1 September) to only 20% in 2000 (8 August) – an 80-fold difference in robbing levels among the highest and lowest years (Fig. 2). Strikingly, robbing levels were very low in both 2000 and 2001 – very few *I. aggregata* flowers experienced robbing. Yet, robbing levels in other species were not particularly low per se in those same years (Fig. 3). Finally, robbing levels also differed significantly among sites ($F_{7,209}$=6.65, P<0.0001). Mean robbing levels (±1 SE) among sites ranged from a low of 2.32±1.94% to a high of 67.20±10.35% within a year.

Corydalis caseana

Robbing levels in *C. caseana* ranged from 0% to 100% robbing with a mean (±1 SE) of 67.44±3.49% (Table 1). Levels of robbing varied both among years ($F_{4,28}$=9.64, P<0.0001) and among sites ($F_{7,28}$=3.25, P=0.012)

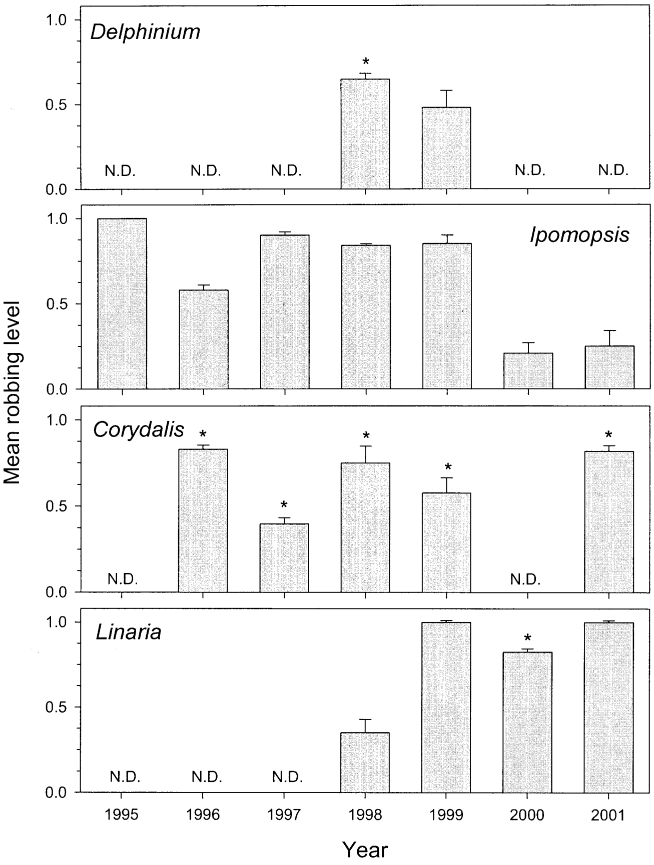


Fig. 3 Peak robbing levels averaged over sites (mean±1 SE) for the four plant species studied from 1995 to 2001. *N.D.* No data were collected in that year, * robbing was only measured once during the flowering season

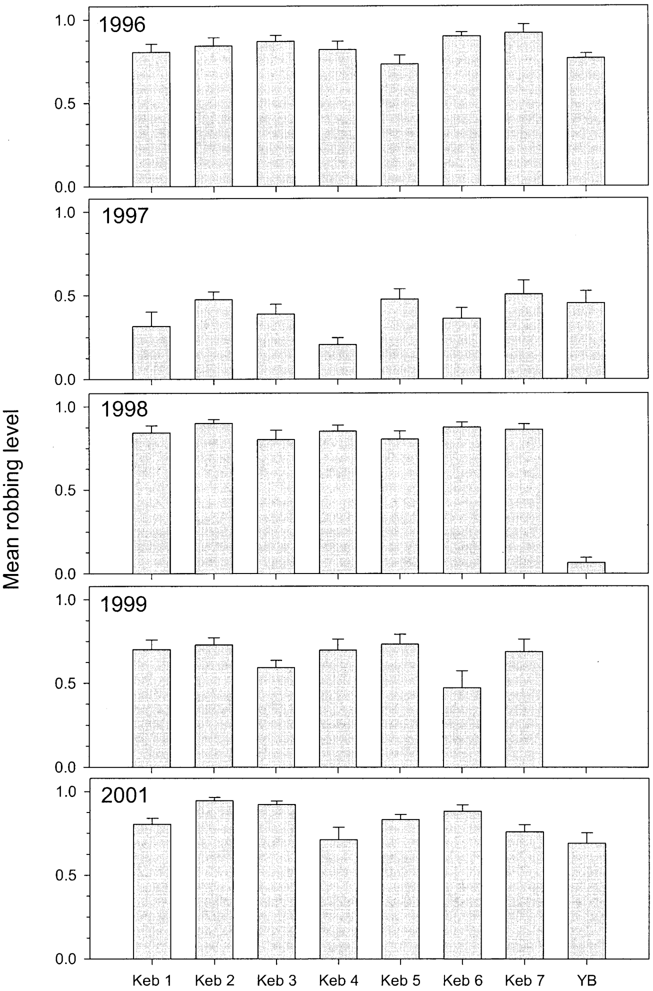


Fig. 4 Mean proportion of flowers robbed (±1 SE) in eight *Corydalis caseana* populations over 5 years of study. Robbing levels varied significantly among populations ($F_{7,28}$=3.25, P=0.012) and among years ($F_{4,28}$=9.64, P<0.0001). The first seven sites (*Keb 1–7*) were located within 880 m of one another at Kebler Pass; the last site (*YB*) was located 16 km away at Yule Basin

(Fig. 4). Looking at robbing levels on an annual basis, over a number of years, a very interesting pattern emerges. We see that robbing levels varied radically from year-to-year – robbing levels varied by 52% between the highest and lowest robbing years (Fig. 4). In addition, individual sites varied from year-to-year in robbing levels. For example, at the Yule Basin site where the majority of flowers had been robbed in 1996, suddenly robbing dropped to zero from 1997 through 1999, but rebounded again in 2001. Meanwhile, the Kebler Pass sites experienced more consistent patterns of robbing throughout all years with a slight decrease in robbing levels in 1997 (Fig. 4).

Linaria vulgaris

Robbing levels in the late-blooming *L. vulgaris* ranged from 0% to 100% of available flowers robbed with a mean (±1 SE) at peak robbing of 79.25±15.34% (Table 1). Robbing levels varied significantly among years (year 2000 excluded because robbing levels were only measured once during the season; $F_{2,423}$=399.27, P<0.0001; Fig. 3). Average robbing levels were very low in 1998 (mean±1 SE: 23.22±2.45%); while in 1999 and 2001, robbing levels averaged >85%. Robbing levels also varied among weeks within years ($F_{6,423}$=9.19, P<0.0001); however, there was no seasonal trend, per se, in this variation. In addition, in 2000, robbing levels showed among-site variation ($F_{9,290}$=77.60, P<0.0001). Mean robbing levels per site ranged from a low of 2.72% to a high of 100% of flowers robbed.

Variation in robbing levels among species

D. nuttallianum, *I. aggregata*, and *L. vulgaris* varied significantly in robbing levels ($F_{2,33}$=4.82, P=0.0146). *L. vulgaris* experienced significantly more robbing than all other species examined (Table 1, Fig. 3). Further, we also found variation among species in seasonal levels of nectar robbing. In *D. nuttallianum*, robbing levels decreased throughout its blooming season (Fig. 1). Conversely, robbing levels increased throughout the blooming season of *I. aggregata* (Fig. 2), and in *L. vulgaris*, robbing levels stayed high throughout the season with minor week-to-week variation with no trend in robbing per se.

Do *I. aggregata* robbing levels show within-population heterogeneity?

Overall, the geostatistical results indicate that the robbing levels were heterogeneous within *I. aggregata* populations, but this heterogeneity did not vary among populations or years. We found no difference in N:S ratios or robbing patch sizes between years (MANOVA: $F_{2,8}$=0.34, P=0.72) or among sites (MANOVA: $F_{8,8}$=0.79, P=0.63). The average N:S ratio was low (mean±1 SE: 0.09±0.03), indicating relatively high spatial patterning in robbing levels within populations. The average patch size of robbing (±1 SE) was 1.59±0.40 m. (See supplementary electronic material at http://dx.doi.org/10.1007/s00442-002-1060-z for more detail.)

Are *I. aggregata* robbing levels correlated with peak flower abundance?

Peak *I. aggregata* flower abundance did not correlate with peak robbing levels (K-S test: P<0.0001 in all cases). Robbing levels increased to peak levels approximately 2–5 weeks after peak flower abundance (Fig. 2).

Discussion

Studies of nectar robbers, and their interactions with plants, have generally been restricted to only a few locations, only a few years, or only one or two species of plants (e.g., Roubik 1982; Arizmendi et al. 1996; Goulson et al. 1998; Traveset et al. 1998; Navarro 2000; Lara and Ornelas 2001; Arizmendi 2001; Utelli and Roy 2001). Given these restricted data sets, it has been difficult to understand the magnitude of geographic and temporal variation in nectar robbing. In this study, we examined nectar robbing in four species, in multiple sites, over 2–7 years. We found an amazing level of complexity in plant-robber interactions. The interactions between host plants and their nectar robber, *Bombus occidentalis*, varied through time, and throughout the landscape, at every hierarchical scale examined.

When plant species were examined individually, we found that mean robbing levels varied from year to year in all species except *D. nuttallianum* (Table 1). But robbing rates were only measured for 2 years in *D. nuttallianum* and, given the levels of variation we found in the other species that were examined for longer time periods, we expect annual variation in robbing levels would eventually be apparent for *D. nuttallianum* as well. Annual variation in robbing levels was also found by Navarro (2000) in northwest Spain. From 1993 to 1996, robbing of *Anthyllis vulneraria* by two *Bombus* spp. ranged from 66% to 76%, but in 1997, robbing levels dropped to 0%. Conversely, in studies of only a single year, the reported robbing levels are very high [98%, Higashi et al. (1988); 99%, Guitián et al. (1993); 84%, Olesen (1996); 96%, Stout et al. (2000)]. Although this may be an artifact of negative data not being reported, we would caution researchers to refrain from assuming that the values from a single year are typical.

Interestingly, although the majority of species showed annual variation in robbing rates, there was no pattern of similarities among species. In 1997, for instance, robbing rates were low for *C. caseana* and high for *I. aggregata*; and in 2001, robbing rates were low for *I. aggregata* and high for *C. caseana* and *L. vulgaris* (Fig. 3). We have no explanation for this, but it seems unlikely that large-scale weather patterns were responsible for the variation, as has been proposed in another study on plant-robber interactions (Navarro 2000). A more likely scenario may be the effect of various predators and parasites on individual bumblebee nests. Small mammals may invade and destroy nests, and a number of different insect parasites may also do the same, including cuckoo bees, wax moths, conopid flies, mites and nematodes (Prys-Jones and Corbet 1991). Some plant species may occupy more suitable nesting or foraging sites for *B. occidentalis*, so that the local density of robbers may be variable across populations. Conversely, variation in the rates of nectar removal by legitimate pollinators may explain variation in robbing levels among sites of the same species and/or among species, especially if nectar is a limiting reward in the environment (Soberón and Martinez del Rio 1985; Arizmendi 2001). Furthermore, spatial or temporal variation in the intensity of flowering by other species that *B. occidentalis* visits may play a role in variation in the magnitude of robbing of another focal species. Now that we have quantified the magnitude of variation in interactions between nectar robbers and their host plants, the challenge is to understand why this variation occurs and what it means in an ecological and evolutionary context.

Ideally, studies of plant-robber interactions should record robbing levels throughout the season instead of at only a single point in the season. Data collected throughout the season are useful in illustrating the match (or mismatch) between the phenology of the flowers and that of the robbers. When robbing data were collected throughout the season for *D. nuttallianum* and *I. aggregata*, we found that robbing levels peaked for the two species in different parts of the season. For example, robbing levels were highest on early blooming *D. nuttallianum* in mid-June (Fig. 1), but robbing levels were highest on *I. aggregata* in late August and early September (Fig. 2). These divergences in peak robbing dates may result from the life cycle of *B. occidentalis* colonies. When *D. nuttallianum* begins blooming, the queen bees are foraging and robbing rates are likely high. Robbing then declines as queens start to set up nests and incubate eggs. For *I. aggregata*, robbing started out low (likely during queen incubation) and then increased throughout blooming season, likely because of hatching workers. Robbing was high in almost all weeks for *L. vulgaris*, probably because it bloomed latest, at the peak of *B. occidentalis* robber worker activity. The sequential blooming of these three plant species may facilitate robber activity, akin to sequential pollinator facilitation (sensu Waser and Real 1979). Early blooming *D. nuttallianum* may support robbers that then visit later blooming species, such as *I. aggregata* and *L. vulgaris*. This hypothesis remains to be tested.

Variation in robbing *within* a season may have important consequences with respect to selection on flowering phenology. For example, late-blooming *D. nuttallianum* experienced lower levels of robbing than those that bloomed early (Fig. 1). If robbing reduces plant fitness components, selection would favor later blooming in this species. However, the opposite may be the case for *I. aggregata*. Late-blooming *I. aggregata* experienced higher levels of nectar robbing than those that bloomed early (Fig. 2), and high levels of robbing in this species reduce both male and female fitness components by 50% (Irwin and Brody 2000). Selection exerted by nectar robbers may favor early blooming in this species. However, late-blooming *D. nuttallianum* and early blooming *I. aggregata* overlap in flowering and compete for the services of hummingbird pollinators (Waser 1978). Therefore, selection exerted by robbers and selection exerted by pollinators may occur in opposing directions in these two species. Here, the importance of nectar robbers as agents of selection on flowering phenology is likely interpretable only in light of the spatiotemporal variation in plant-pollinator interactions as well. In complete contrast, in species that may benefit from robber interactions, such as *C. caseana* (Maloof 2001), we might expect the distributions of robber activity and peak flower abundance to converge.

The spatial variation in nectar robbing was just as pronounced as the temporal variation. Robbing levels in all plants we studied varied significantly among sites (Table 1). Sometimes this variation was quite dramatic, as in the case of *D. nuttallianum*, where during the same year, one site experienced 87% more robbing than another site (Fig. 1); or in the case of *C. caseana*, where one population (YB) experienced close to zero robbing while the other populations experienced 49–75% robbing (Fig. 4). Similarly, Helen Young (personal communication) found that populations of *Impatiens capensis* in Vermont, USA separated by <10 m, as well as those hundreds of kilometers apart, varied widely in robbing levels. Further, this pattern of among-site variation in robbing levels appears to be common in other study systems as well (Guitián et al. 1994; Morris 1996). Variation in levels of robbing among sites may have profound implications, either positive or negative, on plant population dynamics in these sites, depending on the fitness outcome of the plant-robber interaction (Irwin et al. 2001). In addition, these hot and cold spots of robber activity may influence population-level differences in selection on floral and flowering traits, resulting in inconsistent selection pressures across the landscape (Thompson 1994, 1997).

Here we have seen that there is variation in robbing on different species in the same year, and that there is variation in robbing on the same species among different sites. However, it is difficult to separate the species variation from the spatial variation because, although these studies were conducted in the same region, the study sites of the various species were not identical, even though many of the species can grow sympatrically. Variation in robbing levels fueled by community-level interactions among host plants that share a common nectar robber is not well understand and deserves further attention (Irwin et al. 2001).

Finally, we also found heterogeneity in robbing levels within a single site. This within-site heterogeneity in robbing levels may influence pollinator flight patterns (reviewed in Maloof and Inouye 2000). For example, many foraging pollinators exhibit predictable movement patterns based on area-restricted searching in response to varying nectar levels (Pyke 1978; Zimmerman and Cook 1985). After visiting an unrewarding, nectar-robbed plant, a pollinator may be more likely to fly a further distance before visiting another plant, a foraging mechanism that might move the pollinator out of an unrewarding patch of robbed plants (Zimmerman and Cook 1985; Maloof 2001). Changes in pollinator flight behavior after visiting robbed plants may influence pollen flow and plant outcrossing distances within and among populations as well as the spatial genetic structure of plant populations, assuming there are direct links between pollinator visitation, pollen donation, and siring success.

Research on the interactions between plants and nectar robbers is undoubtedly growing both conceptually as well as empirically. We provide evidence here, gathered over 7 years of study, that robbing levels vary over space and over time at multiple hierarchical levels. This variation may have implications for the population dynamics of host plants as well as for selection on floral and flowering traits. Clearly more studies are needed to understand the magnitude and importance of spatiotemporal variation in the exploitation of plant-pollinator mutualisms by nectar robbers. By linking variation in interactions with subsequent fitness outcomes, these studies will call attention to the importance of spatiotemporal changes in species interactions to plant population dynamics and to the evolution of floral and flowering traits.

Acknowledgements The authors would like to thank the following field assistants who helped with data collection over the last 7 years: D. Cariveau, P. Flanagan, S. Keller, H. Prendeville, A. Toth, J. Vineis, and David Inouye's Rocky Mountain Wildflower Earthwatch teams of 1996, 1997 and 1998. In addition, D. Inouye, W. Morris, J. Shykoff, H. Young, and one anonymous reviewer provided valuable comments on the manuscript. During this work, J. E. M. was supported by grants from Earthwatch and its research corps, Salisbury University Foundation, Sigma-Xi, and a National

Science Foundation Research Training Grant in the Biology of Small Populations (DBI-9602266); R. E. I. was supported by grants from the National Science Foundation (DEB-9806501 and DEB-0089643).

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