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SPATIAL AND TEMPORAL COMPONENTS OF RESOURCE ASSESSMENT BY FLOWER-FEEDING INSECTS

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SUMMARY

(1) Per-flower insect visitation rates on two plant species within Rocky Mountain subalpine meadows were measured using fluorescent powders and found to be positively correlated with local flower density, suggesting that insects concentrate their foraging in dense patches of flowers.

(2) Visitation rates on both species are also correlated with the presence of other plant species which share the same visitors; these correlations are positive, suggesting cooperative rather than competitive plant-plant relationships, at least insofar as visitation is concerned.

(3) By correlating local visitation rates with flower densities computed over a range of block sizes, the block sizes at which insects assessed flower density differences were estimated to be approximately 1000 m^2 for solitary bees and flies visiting *Potentilla* spp., and 500 m^2 for bumblebees visiting composites.

(4) By correlating local visitation rates with flower censuses from various days before the visitation measurements, the time lags in flower density assessment were estimated to be approximately 1·5 days for the solitary bees and flies, and 0·5 days for the bumblebees.

(5) Implications for plant competition and flowering strategy are discussed.

INTRODUCTION

Animals which are strongly selected for foraging efficiency are expected to tailor their behaviour to their food environment. This presumes that they know what that environment is. They should be able to detect those variations in space and changes through time which have important energetic or nutritional consequences. Specialized flower feeding animals seem to comprise a group in which ‘optimal foraging’ is displayed comparatively clearly (see, for example, Pyke (1974, 1978a, b); Hartling (1979); Hartling & Plowright (1979); Heinrich, Mudge & Deringis (1977); and Heinrich (1979) on bumblebees. Kodric-Brown & Brown (1978) on hummingbirds). In certain situations, these animals encounter a rapidly changing floral environment, and their ability to track changing resources, and the general question of how they perceive and respond to such resources, become subjects of interest. The interest is doubled because, in feeding themselves, many of these animals pollinate flowers.

How animals see flower distributions is then also of evolutionary importance to the plants, but this topic has hardly been explored. (For a recent exception, see Pyke (1978b).) Even the basic information needed to pose simple hypotheses is hard to come by. Even more importantly, restricting the study to the animal ignores the coevolutionary structure

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of the circular system in which the animals' 'optimal foraging' takes place. If plant characteristics modify pollinator behaviour, and pollinator behaviour determines plant success, it follows easily that selection may act on plant characteristics to increase success. Thus, some aspects of animal foraging, optimal or not, may effectively be orchestrated by the plants (Heinrich & Raven 1972). The process has two components: the plants' presentation of various characteristics to the pollinators and the plants' subsequent receipt of reproductive potential from the foraging pollinators. Between these two phases, however, intervenes the complicated filter of the pollinators' perceptions. The effects it introduces may include time lags, mistaken species identities, and various distortions of scale. Of course, the mechanics of selection will ensure that the response of the plant takes these distortions into account. The human observer may misinterpret a plant's adaptive characters by not experiencing the plant as its pollinators do. For example, two plant species which bloom simultaneously and share pollinators, may be assumed to be competing. If pollinators do not distinguish between them, however, the interaction will be different from that expected if they do recognize the difference and forage with flower constancy. If a third plant species is involved, the first two may benefit each other (Bobisud & Neuhaus 1975; Thomson 1975, 1978b). It is not an exaggeration to say that the pollinators' perceptions determine whether such a situation is competitive or not.

This study attempts to identify some of the characteristics of pollinator responses to spatial and temporal variations in flowering. The original aim was to investigate responses of flower visitors to variations in flower density, and to measure time lags in those responses. The experimental design also allowed a rough assessment of the spatial scale at which the animals detected differences in density. In the cases detailed here, the fortuitous co-occurrence of potentially competing plant species permitted some analysis of their interaction.

In considering the interplay of flower densities and visitation rates, several questions may be posed.

(1) Is there a density response such that visitation increases in patches of greater flower density?

(2) Is visitation reduced by the local presence of a potential competitor?

(Questions 3 and 4 assume an affirmative answer to question 1.)

(3) Are there time lags in density responses of visitors? It is unlikely that visitors could detect changes in flower density immediately, and the time between resource change and visitor response may be large enough to have ecological importance.

(4) At what spatial scale (patch size) is the density response most clearly displayed? If visitors do prefer to work in denser stands of flowers, there must be some size of stand at which they perceive density differences.

STUDY SITES AND METHODS

The major site for this study was a subalpine (2990 m) meadow just southeast of the confluence of Rustler Creek and the East River, about 4 km north of the Rocky Mountain Biological Laboratory at Gothic, Gunnison County, Colorado. A grid of 108 permanent sample points in the form of a 6 × 18 rectangle was laid out. As Fig. 1 shows, a 10 m spacing between centres resulted in a 50 × 170 m grid. At each grid point a 4 m^2 quadrat was located and the open flowers censused through the season.

Measures of visitation rate

The five 100 m^2 areas (marked 1–5 in Fig. 1) were used to give an index of visitation intensity obtained by the following method. A number of 'test' flowers were selected evenly across each block choosing open flowers which had conspecific nearest neighbours. Each was marked with a short red 'twist-tie' located as far down the flower stalk as possible. Around each of these test flowers the nearest conspecific neighbouring flower was located in each of the four compass quadrants. Using a small brush, the stamens were daubed with an aqueous suspension of a finely powdered fluorescent pigment ('Helecon #2267', United States Radium Corp., Morristown, New Jersey) which to human vision is inconspicuous on yellow flowers in white light. The pigment was applied in liquid form, rather than as a dust, to reduce transfer by wind, which had previously been found to be a serious source of error. The water soon evaporated, leaving a slightly caked residue of fine powder. Similar pigments have been used in various studies for marking insects directly or following their flight paths through stands of flowers (e.g. Frankie, Opler, Bawa 1976; Smith 1958) or for monitoring pollen flow from a single source (Stockhouse 1976).

Using multiple sources is intended to ensure that an insect foraging in an experimental area will contact marked flowers often enough that it will always be carrying enough pigment to deposit some on each flower. Positioning of marked flowers around each test flower reinforces this by increasing the probability that the pigment on the insect will be renewed shortly before a visit to a test flower. This depends on a tendency of the pollinators to move between nearest-neighbour plants, which has been documented for some flower visitors (e.g. Levin & Kerster 1968; Free 1970).

After approximately 48 h the test flowers were harvested by picking each with forceps or a hemostat and placing it in a clean glassine envelope. Those which showed traces of fluorescing pigment under ultra-violet light were scored as 'visited'. Because some of these may have been visited more than once, and because an index of animal activity was required, the fraction of flowers visited was converted to the expected number of visits per flower, henceforth, 'visitation rate', using a Poisson assumption, such that

$$\text{visitation rate} = \ln(1 - \text{fraction visited}).$$

The above method can only be considered an exact measure of visitation rate if all visitors pick up pigment immediately upon entering the patch, and if they deposit pigment on every flower they visit. In the absence of a specific test of these assumptions, it is best to regard the resulting index as no more than a measure closely related to visitation. However, in this sense it should be well suited for comparisons between blocks involving similar flowers.

The visitation rates to be discussed in detail here were measured on *Potentilla gracilis* Douglas (Rosaceae), which dominated the entire meadow through midsummer. *Potentilla gracilis* is here visited by both flies and solitary bees; some of the latter are *Potentilla* specialists in this habitat (Susan Anderson, pers. comm.). *Potentilla fruticosa* L. also was present along a (dry) watercourse. Except for the later-blooming *Erigeron speciosus* (Lindley) DC. (Compositae), the two *Potentilla* were by far the most numerous host flowers for the insects which visited them.

Visitation rates were measured on 22 June, 2 July, 7 July, and 27 July. Both flies and bees were observed moving to and foraging at marked flowers without apparent hestitation. For the 22 June measurement sixty test flowers were established in each of the five blocks; for the others, about eighty. Sample sizes vary because of incomplete recovery. The minimum sample was sixty-eight (fifty-eight for 22 June); the maximum, eighty-four.

Correlating visitation with stand parameters

The topographic variation among the five blocks was such that flower densities could be, for instance, declining in a south-facing block while increasing in a north-facing block. The analysis to follow depends on matching the block-to-block ups and downs of visitation rate with ups and downs of resource levels. These variations occur in space as well as time.

Temporal variation was accounted for by calculating three flower density measures: the density on the day of marking the flowers (day 0); the density the day before (day −1); and the day before that (day −2). To qualify spatial variation, the grid pattern of census points was used to compute the average density in each of three differentially sized blocks, centred on the block where the visitation was measured (Fig. 1). The block sizes are 100, 900, and 2500 m^2, and the density at each block size is computed as the simple mean of the densities of the quadrats contained in the block. For density measures, there are thus nine combinations of block size and census day. Both visitation rates and densities were standardized by dividing each value for a particular experiment by the total of the five values for that day; this ensured comparability between data for different days, despite fluctuations in the overall density of visitors.

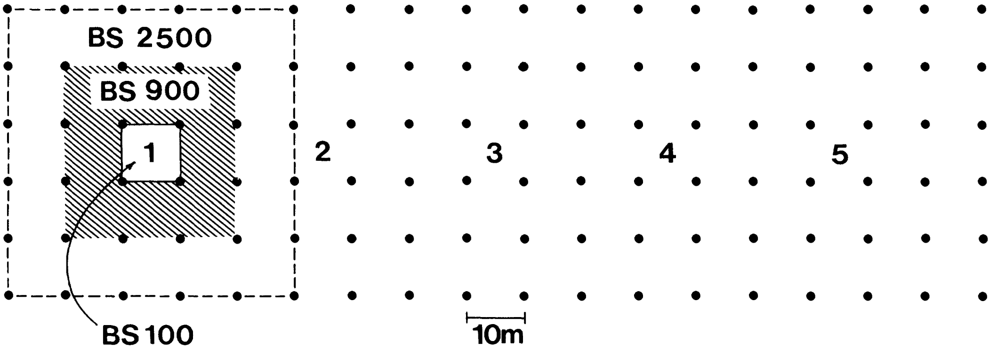

FIG. 1. The sampling grid, showing Blocks 1–5 where visitation rates were measured, and the three spatial Block Sizes BS 100, 900, and BS 2500.

Minor site: measures on Senecio crassulus

One set of five measures of visitation, with accompanying census data, was obtained for a population of *Senecio crassulus* Gray (Compositae) from a different meadow in the same valley (site IB in Thomson 1978a; 3280 m altitude). *Senecio crassulus* is primarily visited by short- and medium-tongued bumblebees, e.g. *Bombus sylvicola* Kirby, *B. frigidus* F. Smith, *B. bifarius* Cresson, *B. occidentalis* Greene, and *B. flavifrons* Cresson. The sampling grid was laid out and the data were gathered and treated in the manner described for *Potentilla*, although heads, not flowers, were censused.

RESULTS

Tables 1 and 2 give summaries of visitation-density correlations for the *Potentilla* and *Senecio* data respectively. The raw data are tabulated in the Appendix. The correlations suggest answers to the questions just posed.

TABLE 1. Analysis of *Potentilla* visitation

block size (m²)	census day	Correlation of visitation rates on *gracilis* with: 1. density of *gracilis*			2. density of *gracilis* − *fruticosa*			3. density of *gracilis* + *fruticosa*			partial correlation of *gracilis* visitation with *fruticosa* density, *gracilis* density held constant	
		r	P	rank	r	P	rank	r	P	rank		
100	0	0·2578	0·136	9	0·1922	0·208	9	0·2936	0·105	9	0·1655	0·249
100	−1	0·3343	0·075	8	0·2597	0·134	8	0·3527	0·064	8	0·1203	0·312
100	−2	0·3818	0·048	7	0·3029	0·097	5	0·3840	0·047	7	0·0913	0·355
900	0	0·4698	0·018	6	0·2882	0·109	7	0·4387	0·027	6	0·1167	0·317
900	−1	0·5430	0·007	2	0·3597	0·060	2	0·4907	0·014	2	0·0961	0·348
900	−2	0·5470	0·006	1	0·4019	0·039	1	0·5047	0·012	1	0·0809	0·371
2500	0	0·4750	0·017	5	0·2988	0·100	6	0·4633	0·020	4	0·1284	0·300
2500	−1	0·4985	0·013	3	0·3382	0·072	4	0·4743	0·017	3	0·1062	0·333
2500	−2	0·4780	0·017	4	0·3570	0·061	3	0·4561	0·022	5	0·0858	0·363

TABLE 2. Analysis of *Senecio crassulus* visitation

block size (m²)	census day	Correlation of visitation rates on *S. crassulus* with: 1. density of *S. crassulus*			2. density of *S. crassulus* + *Helianthella quinquenervis* + *Helenium hoopesii*			3. density of *S. crassulus* + *H. quinquenervis* + *H. hoopesii* + *Agoseris glauca*		
		r	P	rank	r	P	rank	r	P	rank
100	0	0·9074	0·033	1	0·9665	0·007	4	0·7034	0·185	4
100	−1	0·8971	0·037	2	0·9789	0·003	1	0·4835	0·409	8
100	−2	0·8809	0·048	3	0·9674	0·007	3	0·2623	0·677	9
900	0	0·7933	0·109	4	0·9690	0·006	2	0·8620	0·060	1
900	−1	0·7630	0·133	5	0·9487	0·014	5	0·7364	0·1558	2
900	−2	0·7358	0·156	6	0·9317	0·021	6	0·4905	0·401	7
2500	0	0·0699	0·911	9	0·8221	0·088	7	0·7389	0·154	3
2500	−1	0·0783	0·900	8	0·8148	0·092	8	0·6905	0·197	5
2500	−2	0·0840	0·893	7	0·8076	0·098	9	0·6005	0·284	6

Density response

There is a positive relationship between density of *Potentilla gracilis* and its visitation rate at every spatio-temporal census combination: the correlations are quite ($P < 0{\cdot}01$) significant for the best combination. For *Senecio crassulus*, significant ($P < 0{\cdot}05$) correlations are found at three of the nine combinations. A positive, reasonably linear response to flower density seems to characterize the foraging of both bumblebees and the 'solitary-bee and fly' visitors of *P. gracilis:* foragers prefer 'hot spots' of dense floral resource.

Interspecific competition

If *P. fruticosa* competes with *P. gracilis* for visits, the visitation rate on *gracilis* should be lower in those blocks where *fruticosa* is present. Expressed differently, visitation on *gracilis* should correlate better with the density of *gracilis* minus the density of *fruticosa* than with the density of *gracilis* alone. This is not the case; the opposite is true. In fact, the *gracilis* visitation rate is approximately as well correlated with the combined density of *gracilis* and *fruticosa* as it is with *gracilis* alone.

This can also be seen in the partial correlation of *gracilis* visitation with *fruticosa* density with *gracilis* density held constant (Table 1). While the significance levels are not high, all the correlation coefficients are positive, indicating a slight tendency for the presence of *fruticosa* to enhance the visitation rate on *gracilis* rather than reduce it competitively. The visitors may, in effect, sum these densities when choosing their foraging site. I have found similar effects in other systems (Thomson 1975, 1978a, b); the explanations I proposed depended on the visitors responding to local concentrations of resource. These explanations receive some support from the demonstration that *Potentilla* visitors do show a hot spot response.

Time lags and spatial scale

With the density response confirmed, its nature can be probed. Table 1 ranks the nine census combinations from the best (1) to the worst (9) predictor of visitation. It is possible to separate the effect of census day and block size by observing, for instance, the ranking of the three census days within each block size. Thus for block size 100, the ranks are: first, day −2; second, day −1; third, day 0. For block size 900 the same ranking obtains. For block size 2500, the ranks are: first, day −1; second, day 0; third, day −2. Summing the ranks of each day for the three block sizes gives an *overall* ranking of census days; days −1 and −2 tie with a summed rank of 5, while day 0 trails with a rank of 8. Using the same procedure to order block sizes, one finds that 900 gives the best overall correlation (rank sum = 4), then 2500 (sum = 5), and finally, block size 100 gives the worst correlation (sum = 9).

While this allows overall ranking, it should be interpreted cautiously, for the procedure assumes an independence of block size and census day components which has not been shown and which may not even be expected. One might suppose, for example, that the most detailed information about resource abundance in space (the block size 100 data) would be the hardest to keep up to date. This suggests that, except for the purpose of rough comparisons, the census day-block size combinations should be treated *as* combinations and not be further broken down.

The conclusion is that the flies and bees responsible for moving the dye among *Potentilla* flowers are, as a group, concentrating on areas of high flower density, more or less regardless of plant species; that they are assessing variation in abundance of flowers at the fairly coarse spatial scale of perhaps 1000 m^2 patches; and that they respond rather slowly to temporal changes in resource level, lagging between 1 and 2 days behind.

It now becomes an interesting question whether other kinds of visitors show the same patterns. The bumblebee-pollinated *Senecio crassulus* has a quite different ranking of census day-block size combinations (Table 2). I suspect that the extraordinarily high correlation coefficients are largely fortuitous, in that the analysis is based on only five measures of visitation. The rankings may still be informative, however. Visitation is correlated with local density of *S. crassulus*, but better correlation is obtained by including the densities of *Helianthella quinquenervis* (Hooker) Gray and *Helenium hoopesii* Gray, which are also yellow bumblebee-visited composites. If a fourth yellow bumblebee composite, *Agoseris glauca* (Pursh) D. Dietrich, is included, the correlation drops. *Agoseris* may be a true competitor for visitors to *Senecio*, but this may also be an artefact related to diel bloom time; *Agoseris* heads are open only in the morning (see Discussion).

Using the *Senecio-Helianthella-Helenium* data set to compare the effect of census day and block size, the census days rank (best to worst): first, day 0 (rank sum = 4); second, day −1 (sum = 5); third, day −2 (sum = 9). The block sizes rank: first and second (tie), 100, 900 (both sums = 5); third, 2500 (sum = 8). Compared to a mixture of solitary bees and flies, bumblebees have a more precise spatial fix on patchy resources and also seem to be more up to date.

DISCUSSION

Density response and competition

The positive relationship between local flower density and per-flower visitation does not seem particularly surprising; one would hardly expect a *negative* correlation. However, one might expect visitation to be constant throughout the meadow. At least, this is a tacit assumption of several visitation models in the literature (e.g. Levin & Anderson 1970; Straw 1972; Thomson 1975; Waser 1977, 1978a). This might happen if the amount of reward received at each flower were the dominant determinant of visitor behaviour. As it is, visitors are concentrating on particular flowers rather than spreading their effort evenly, so their reward at each flower is presumably lower than it could be. If they are foraging optimally, one would expect that the loss in reward might be offset by the reduced cost of between-flower travel, and therefore that search costs, which some modellers have ignored (e.g. Oster & Heinrich 1976), may be rather important in this case. Whether these suppositions are correct or not, it is clear that visitors recognize and respond to ‘hot spots’ of greater flower density. It is also noteworthy that, if evidence of this relationship had been sought only at the one most obvious density combination (block size 100 and day 0) a significant correlation would not have been found.

A simple response to increased density need not require true knowledge of overall flower distribution. A behavioural mechanism as uncomplicated as increasing the turning rate as the distance flown between flowers decreases (cf. Pyke 1974, 1978a) would be sufficient to concentrate foragers in denser flower patches. However, the existence of a time lag argues for at least a memory of the previous day’s foraging spot. Although this would seem to ensure that the choice of locale would always be imperfect (if resources are changing), it is very likely a more efficient programme than finding a new area each day.

This density response could be important in determining the outcome of competition by plant species for visits. To abstract the process somewhat, consider a pollinator equally capable of extracting rewards from both flower species A and B. Assume the animal responds positively to bloom density. Two ways of 'calculating' density can be distinguished: on the one hand, visitors could respond to one species only, essentially counting A and ignoring B; alternatively, they could count A plus B. In the former instance, one would expect flower-constant foraging. The latter tactic would usually, though not necessarily, be associated with inconstant foraging, and would be most likely to occur when species A and B had rather similar flowers. The latter tactic could be shown theoretically to be more efficient for certain distributions of flowers; it is also a better approximation to the observed results for both sets of measures.

Thus it seems that *Potentilla fruticosa* may augment *P. gracilis* visitation, *Helenium* and *Helianthella* may help *Senecio*, and the interactions of several other combinations of species in these communities (Thomson 1978a, 1980) may constitute mutual facilitation rather than competition for visits. It is by no means certain that an increase in visitation under such circumstances must increase fitness, because the *quality* of visits may be reduced. Heterospecific flower visits may deposit impure loads of pollen on stigmas of limited area (cf. Waser 1977, 1978b) or may result in pollen being lost before getting to proper stigmas (cf. Wissel 1977; Waser 1978b; P. Feinsinger, pers. comm.). Both mechanisms may interfere with seed set, possibly to the extent of cancelling out the gain in visitation. Interference competition of this sort may often be diminished in importance in nature by the tendency of plants to occur in aggregations, which would reduce heterospecific transfers even when the animals displayed no constancy (Levin & Anderson 1970; Waser 1978b; Thomson 1978a). The balance between benefit and detriment will have to be examined in each particular case.

Other reasons for non-correlation between visitation rate and plant fitness include autogamy or apomixis. In such plants, a reduction in visits may be only weakly expressed as reduced seed set if expressed at all. Both *Potentilla gracilis* and *Senecio crassulus* set some seed when insects were excluded by Pollen-tector bags (Carpenter Paper Company, Des Moines, Iowa), although set was lower than in open-pollinated flowers, so these species have a partial requirement for visitation.

Larger implications

Time lags and scale choice characterize foraging in the same sense that more familiar factors such as food preference, habitat choice, and constancy do. The spatial and temporal aspects of resource assessment may have generally escaped attention because so many of the resources used by easily observed animals are difficult to monitor (but see Goss-Custard 1977 and McFarland 1977). The ease with which flowers are seen and counted is one of several characteristics commending their study to zoologists concerned with both the mechanics and the evolution of animal feeding, and these results should interest those scientists directly. I wish to conclude this discussion, however, with some comments on the possible importance of these findings to an understanding of *plant* community structure.

First, the relationship of *Potentilla gracilis* and *P. fruticosa*: although it appeared likely to be competitive, it apparently is not, and *fruticosa* bloom may be helpful to *gracilis* in terms of visits. As a result, divergence in flower morphology or flowering time might be selected against in some cases. This would confound any attempts to see 'resource partitioning' patterns in the ways in which plants share pollinators and time (cf. Pleasants 1977). In other circumstances, temporal and faunal overlap may be deleterious to the plants involved. For example, discrete patches of *Aconitum columbianum* Huth and

Delphinium barbeyi Nutt. (Ranunculaceae) seem to compete for visits (Thomson 1978a). In the other cases where facilitation occurs rather than competition, the plants are intermingled (Thomson 1978a). The pattern suggests that the pollinators are 'summing' densities when the flowers are intermingled a certain amount. The way in which pollinators respond to flower species mixtures probably depends on the concordance of the plants' scale of intermingling and the pollinators' scale of flower assessment. For two plant species served by a particular class of pollinator, then, the scale of their spatial overlap may at least theoretically affect their competitive status, even to the point of determining the sign of the interaction.

CONCLUSION

Patterns of insect visitation rates on flowers demonstrate certain aspects of the insects' perception of and response to variation in resource levels: flower density responses are apparent within a meadow, and show characteristic time lags and spatial scale effects which seem to be different for different insects. These effects may modify competition by plants for pollinators and thus influence the coevolved 'community structure' of plant-pollinator assemblages.

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APPENDIX: RAW DATA

The following Tables summarize the visitation and flower census data used to produce the correlations. Before the correlations discussed in the text were calculated, these raw data were further treated, by (1) converting the fractional visitation measure to a visitation rate expressing the average number of visits received by a flower or head during the experiment, as detailed in the Methods section; and (2) relativizing both the visitation rates and the census data by dividing each value for a day by the total for that day. The flower/head densities for day −1 were computed by taking the arithmetic mean of the densities for day 0 and day −2. The numbers '100, 900, 2500', which appear in the column headings, refer to the area in square m over which the flower density was averaged.

APPENDIX TABLE 1. *Potentilla* visitation and flower density. Values (except Fraction visited) are flowers/m^2

Block	Fraction visited	*Gracilis* 100 day 0	*Gracilis* 900 day 0	*Gracilis* 2500 day 0	*Gracilis* 100 day −2	*Gracilis* 900 day −2	*Gracilis* 2500 day −2	*Fruticosa* 100 day 0	*Fruticosa* 900 day 0	*Fruticosa* 2500 day 0	*Fruticosa* 100 day −2	*Fruticosa* 900 day −2	*Fruticosa* 2500 day −2
22 June													
1	0·660	2·125	3·359	2·847	0·625	1·359	1·042	0·0	0·0	0·0	0·0	0·0	0·0
2	0·726	5·922	5·051	3·977	2·068	1·862	1·939	0·0	0·0	0·0	0·0	0·0	0·0
3	0·798	2·735	3·797	3·014	1·503	1·954	1·600	0·0	0·071	0·042	0·0	0·028	0·027
4	0·647	4·180	2·491	1·772	1·004	0·828	0·991	0·0	0·071	0·042	0·0	0·028	0·027
5	0·602	2·473	2·682	2·261	1·443	1·048	1·104	0·0	0·0	0·0	0·0	0·0	0·0
2 July													
1	0·494	11·438	10·219	9·944	9·938	8·891	8·243	0·0	0·0	0·0	0·0	0·0	0·0
2	0·615	9·519	10·574	10·371	11·035	10·491	10·605	0·0	0·0	0·0	0·0	0·0	0·0
3	0·641	14·242	12·774	10·615	12·584	11·736	10·455	7·084	6·813	3·721	6·389	4·801	2·316
4	0·728	17·489	13·909	12·079	14·778	10·728	8·545	0·0	4·542	4·758	0·0	3·023	2·563
5	0·515	14·021	12·064	9·456	9·873	9·543	7·489	0·0	0·0	0·0	0·0	0·0	0·0
7 July													
1	0·575	11·813	9·813	8·681	11·688	10·375	8·646	0·0	0·0	0·0	0·0	0·0	0·0
2	0·620	6·451	10·366	9·639	11·611	11·116	11·464	0·0	0·0	0·0	0·0	0·0	0·128
3	0·932	23·237	12·577	12·273	19·301	13·710	12·873	3·420	7·049	3·832	5·229	6·447	3·586
4	0·715	21·761	13·199	11·734	15·148	13·339	12·361	0·0	4·837	3·592	0·0	4·669	3·458
5	0·681	10·958	11·264	10·058	13·841	14·377	11·848	0·0	0·0	0·0	0·0	0·0	0·0
27 July													
1	0·614	11·000	6·812	5·778	11·000	7·031	7·222	0·0	0·0	0·0	0·0	0·0	0·0
2	0·591	3·388	4·363	5·525	4·931	5·176	8·055	0·0	0·0	0·0	0·0	0·0	0·0
3	0·745	7·654	6·353	7·403	10·621	10·999	10·972	1·046	1·110	0·578	0·975	1·510	0·880
4	0·701	10·498	9·644	8·992	15·660	8·972	9·305	0·0	0·689	0·542	0·0	0·992	0·787
5	0·705	8·198	9·300	7·331	11·000	9·749	9·120	0·0	0·0	0·0	0·0	0·0	0·0

APPENDIX TABLE 2. *Senecio* visitation and head density. Values (except Fraction visited) are heads/m^2

Block	Fraction visited	*Senecio* 100	*Senecio* 900	*Senecio* 2500	*Senecio* + *Helenium* + *Helianthella* 100	*Senecio* + *Helenium* + *Helianthella* 900	*Senecio* + *Helenium* + *Helianthella* 2500	*Senecio* + *Helenium* + *Helianthella* + *Agoseris* 100	*Senecio* + *Helenium* + *Helianthella* + *Agoseris* 900	*Senecio* + *Helenium* + *Helianthella* + *Agoseris* 2500
Day 0										
1	0·456	0·750	0·375	0·367	1·563	1·081	0·917	2·751	1·878	1·563
2	0·422	0·145	0·142	0·245	2·031	1·048	0·440	2·067	1·995	2·345
3	0·385	0·314	0·047	0·009	1·661	0·438	0·073	2·751	2·647	2·559
4	0·661	1·221	0·266	0·031	3·151	2·308	0·367	1·694	2·869	2·987
5	0·889	1·393	0·500	0·245	3·889	2·421	2·274	6·279	3·665	3·151
Day −2										
1		0·770	0·375	0·380	1·600	1·116	1·004	2·700	1·625	1·447
2		0·240	0·156	0·292	2·215	0·744	0·415	4·934	1·507	1·054
3		0·240	0·027	0·010	1·285	0·175	0·124	5·228	2·079	1·527
4		1·013	0·240	0·071	3·009	1·201	0·357	1·692	1·271	0·960
5		1·160	0·467	0·330	5·566	2·078	2·344	4·762	2·596	2·283