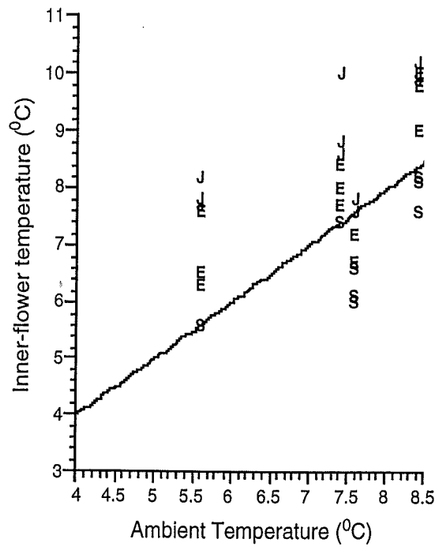

Fig. 1. Comparison of inner-flower temperatures of *Bomarea* flowers (filled circles) compared to inner-flower temperatures of two other species with similar floral morphology (open circles and open triangles). Line represents a flower temperature equal to ambient temperature.

Discussion

Location of patches, selection of vines, and dispersion among flower buds within vines may all be important in influencing the reproductive success of ovipositing Diptera adults. Across patches, Diptera densities were extremely similar, suggesting that Diptera efficiently search the entire population for suitable vines, and all patches have an equal chance of being infested. The bright conspicuous coloration of *Bomarea* sp. may be advantageous in attracting hummingbirds, but may also make *Bomarea* sp. more easily detected by flower parasites.

It may be beneficial for Diptera to expend energy to seek the most favorable vines for increased fitness. Alternatively, Diptera may not be able to distinguish between each flower's potential growth environments. Further research could distinguish between these theories by presenting the larvae with a range of flower phenotypes such as varying nitrogen content, secondary compounds, or those previously having parasitic encounters.

Larval dispersion was random among flowers within vines, indicating a lack of oviposition preference within an individual present. Larval biomass was quite high relative to the flower biomass, and larval success may be reduced in flower buds with multiple larvae. Future studies could test for intraspecific competition by looking for negative correlations between larval size and number. From the vine's perspective, random dispersion is more damaging than clumped dispersion of larvae. More flowers are affected if the same number of larvae are distributed randomly, and it only requires one larva to neuter each flower. Further research could explore the behavioral mechanisms that lead to dispersion of Diptera within and between vines.

Analysis of *Bomarea* sp. flowers suggested toughness, temperature insulation, and moisture retention may set *Bomarea* flowers apart and contribute to the development of Diptera parasites. However, several other local species had similar morphological characteristics. Secondary chemicals in the flower tissue may be another important determinant of host plant quality for the Diptera. Further, analysis of flower characteristics, as well as experimental manipulation, could lead to a better understanding of Dipteran host specificity.

Literature Cited

Green, M. 1986. Effect of guayaba density on fruit fly density. OTS **86** (3): 123-125.

EFFECTS OF POLLINATOR SIZE AND PATCH SIZE ON REPRODUCTIVE SUCCESS IN FOUR SPECIES OF ANGIOSPERMS.

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Abstract. Optimal foraging by pollinators should minimize costs and maximize returns from a flower. Travel represents a cost to pollinators that varies with distance to patches and pollinator size. Plant dispersion patterns and pollinator size should therefore interact to affect plant reproductive success. We compared pod and seed production in two plants with small pollinators and two plants with large pollinators. Plants with large pollinators had proportionally higher reproductive success in solitary vs clumped flowers than plants with small pollinators. Interactions between pollinator size and patch size can exert large effects on plant reproduction, thereby influencing plant dispersion patterns in ecological time, and potentially influencing plant dispersal biology over evolutionary time.

Key words: dispersion patterns, patch size, pollinator size, reproductive success

Introduction

Plants and their pollinators have a mutualistic relationship in which plants rely upon pollinators for pollen dispersal, and pollinators use plant nectar as an energy source. Pollinators will forage to maximize their returns from a flower. Travel costs and benefits will influence optimal foraging strategies of pollinators. The costs of travel for a pollinator decline as body size increases (i.e., the time and energy expenditure for a hummingbird to fly 50 m is generally less than for a small insect flying the same distance). Travel costs vary with distance between patches as well as pollinator size, and travel benefits vary with plant patch sizes. Therefore we hypothesized that pollinator size would interact with patch size to influence plant reproductive success. Specifically, we predicted that reproductive success in solitary vs. clumped flowers would be proportionally higher for plants with large pollinators than for plants with small pollinators.

Methods

We conducted our study on 26 January 1996 at Cuerici Biological Preserve, Costa Rica. We chose two large pollinator flowers and two small pollinator flowers that had countable seeds and seed pods and were distributed in both large and small patches (see Fig. 1 for diagnostic drawings of the four species). We looked at five clumped and five solitary plants for each of the four species. Clumped plants occurred within 0.5 m of at least one conspecific. Solitary plants were a minimum of 3 m from the nearest member of the same species, but the majority of our samples were over 10 m. We counted total flowers and seed pods on at least two branches of each plant, and removed two to five pods or berries from each plant in order to count the number of seeds per pod.

We looked at three ways in which pollinators can affect reproductive success: (1) little or no pollination leads to no fruit development (probability of a flower turning into a pod measured as number of pods per flower); (2) little or no pollination leads to fruit initiation but subsequent abortion (measured as percentage of aborted pods per potential pods); and (3) limited pollination leads to fruit development but reduced seed set (measured as number of seeds per pod). We measured: fruit development in all species, percentage of aborted pods in species A, and seed set for species B, C, and D.

We used a Chi-square to test for effects of patch size on the ratio of pods per flower and a T-test to compare the number of seeds per pod. We used a nominal logistic regression (SAS Institute, Inc., 1995) to test the interactive affects of species, pollinator and patch size on the ratio of pods per flower.

Results

The ratio of pods per flower in species A was almost twice as high for solitary flowers than clumped flowers (Table 1). The proportion of aborted pods did not differ between solitary and clumped flowers: 0.775 vs 0.686 ($X^2 = 0.53$, df = 1, $P > 0.1$). The overall reproductive success was therefore twice as high in solitary versus clumped red hummingbird-pollinated flowers.

Table 1. Comparison of pod per flower ratios and total seeds per pod in solitary and clumped patches of four species of angiosperms.

poll. size	plant species	total # of pods		pod/flower			seed/pod		
		solitary	clumped	solitary	clumped	X^2	solitary	clumped	t
Large	A	69	72	0.233	0.122	15.29***			
	B	11	35	0.440	1.0	5.14**	327	754	2.58*
Small	C	222	214	0.180	0.313	34.84***	1.0	1.0	
	D	13	304	0.046	2.187	562.95***	2.2	14.9	3.15*

*P < 0.05, **P < 0.025, ***P < 0.005

Table 2. Results from nominal logistics regression of pod:flower ratios in clumped and solitary patches of four species of large and small pollinator flowers..

Source	df	X2
Pollinator Size	1	0.42**
Plant Species (Poll. Size)	2	33.04**
Patch Size	1	55.83**
Pollinator Size x Patch Size	1	47.88**
Species x Patch Size (Poll. Size)	2	142.11**

*P > 0.5, **P < 0.001

The ratio of pods per flower in species B was 2.3times higher in clumped versus solitary flowers, and the number of seeds per pod was also 2.3 times higher in the clumped flowers (Table 1), resulting in reproductive success 5.3 times higher for clumped versus solitary *C. talamancensis*.

In species C, the small blue flower, the ratio of pods per flower, and overall reproductive success, was 1.7 times higher for clumped than for solitary flowers (Table 1). The ratio of pods per flower in species D was 52 times higher and the number of seeds 6.7 times higher in clumped versus solitary flowers (Table 1). The overall reproductive success was therefore 351 times higher in the clumped vs solitary in this small, pink, insect-pollinated flower.

The effect of patch size on reproductive success differed for plant species pollinated by different size classes of animals (Pollinator size x Patch size interaction in Table 2). Reproductive success tended to increase in solitary vs. clumped patches for plant species pollinated by hummingbirds, while decreasing for plant species pollinated by insects. The effect of patch size on reproductive success differed between species in the same size pollinator class as well (Species x Patch size (Pollinator size) interaction in Table 2). Within pollination size classes, species A had greater reproductive success in solitary vs. clumped patches than those of species B, and species C had greater reproductive success in solitary vs. clumped patches than species D. Significant effects of patch size and plant species within pollinator size (Table 2) are probably artifacts of different plant species having different flower longevities, and have little biological meaning here.

Discussion

Results support the hypothesis that pollinator size may interact with patch size to influence plant reproductive success. The solitary flowers that depended upon small pollinators clearly suffered the greatest limitations to reproduction, presumably because the energetic costs of flying to solitary flowers are too great for small insects. Conversely, the large-pollinator flowers did nearly as well (species B) or even better (species A) when they occurred as solitary plants compared to when they were in clumps. This suggests that large pollinators may be more likely than small pollinators to visit a solitary plant because the costs of travel are low.

Species A actually did better when it was solitary than when it was clumped. This flower always occurred in a field with high flower densities, which should increase the odds that hummingbirds will forage on or near any given plant because of the high returns in that area. Once a plant or patch is included in a pollinator's foraging pattern, the chance of an individual being visited is higher for a flower on a solitary plant than for a flower growing with several hundred other flowers in a clumped patch. Compared to species A, reproductive success of species B was proportionally lower in solitary flowers than for species A, which may be due to low overall flower densities in the forest where species B grew. Pollinators may alter their foraging pattern to include fewer solitary flowers if the returns are lower in the forest.

Solitary plants of species C and D had approximately double the number of flowers on the clumped plants, however the number of pods remained relatively equal. This suggests that pollinator limited

flower production to compensate for a reduced probability that any one flower will be pollinated. If there are meaningful costs to flower production, the fitness differential between solitary plants and clumped plants is even greater than indicated by Table 1 for small-pollinator species.

Our conclusions rest on several untested assumptions. (1) We did not specifically know what animals pollinated species C and D; we made assumptions based on flower morphology and limited observations of visitors. (2) The ratio of pods per flower estimates the probability that a flower will turn into a pod, assuming that the pools of flowers and pods were in a dynamic steady state (that flowers were being produced at the same rate during our study as a few weeks earlier when the pods we observed were flowers). If instead, rates of flower production had changed, the ratio of pods per flower still allows valid related comparisons within species between large and small flower patches (provided that intraspecific flowering phenology did not differ between patches). It would be important for further studies to observe visitations as well as conduct the study over a longer period of time so as to observe different reproductive peaks that may occur throughout the year.

Results suggest that optimal patch size for plant reproductive success varies with pollinator size. In fact, reproductive success may have markedly varied affects over time on the abundance, dispersion, and patch size of plants with different sized pollinators. In small-pollinator species with limited seed dispersal, small patches would tend to remain small patches or even decrease in size over time, while large patches should tend to grow even larger. Conversely, in large-pollinator species, small patches would differ less in reproductive success. This verbal model implies that plants with large pollinators should have less variance in patch size than plants with small pollinators. Future study could explore the mechanisms by which pollinator size and pollinator foraging patterns can influence plant dispersion.

Literature Cited

JMP® Statistics and Graphics Guide, Version 3.1. The SAS Institute, Inc. 1995. Cary, North Carolina.

Figure 1. Upper right: Species A is a hummingbird pollinated flower that grows on a vine. Photo unavailable: Species B is a hummingbird pollinated flower, *Centropogon talamancensis*. Lower right: Species C has insect pollinated flowers and grows on a 2-3 m tree. Photo unavailable: Species D grows on a 1 m shrub. Flowers were found primarily in a large field 500 m east of the field station, except for species B which grew along the loop trail near el Albergue, 200 m west of the field station. All flowers are drawn to scale.