

Butterflies show flower preferences but not constancy

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ABSTRACT

• Four butterfly species were observed foraging at arrays of manipulated flowers. Each butterfly species showed floral preferences based on color, other floral traits, or the combination. None of the species examined, however, showed evidence of flower constancy.

INTRODUCTION

• The perceptual mechanisms used by flower visiting butterflies are largely unknown. For example, we do not know which visual cues attract butterflies to flowers or if butterflies possess memory limitations that force them to restrict their visits to a few flower types, displaying a flower constant behavior.

• Flower preference refers to the net over-visitation of one flower type over another, whereas flower constancy refers to the propensity to sequentially visit the flower type last visited, bypassing alternative equally rewarding types. These distinct flower visiting behaviors can affect plant reproductive success and gene flow in different ways.

QUESTIONS: Which visual cues (color/morphology) do butterflies prefer?
Do butterflies behave as constant flower visitors?

MATERIALS AND METHODS

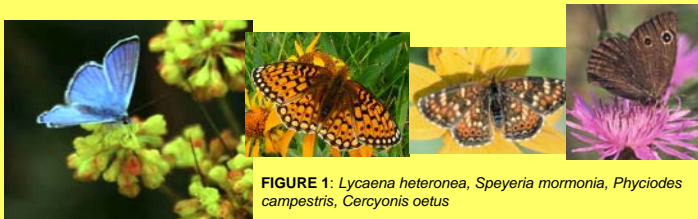


FIGURE 1: *Lycaena heteronea*, *Speyeria mormonia*, *Phyciodes campestris*, *Ceryx oetus*

- We setup artificial arrays of flowers from *Dugaldia hoopesii*, *Wyethia amplexicaulis*, *Erigeron speciosus* and *Achillea alpicola* (Asterales: Asteraceae) and recorded the identity of the series of flowers visited by *Lycaena heteronea* (Lycaenidae: Lepidoptera), *Speyeria mormonia*, *Phyciodes campestris* and *Ceryx oetus* (Nymphalidae: Lepidoptera, FIGURES 1 and 2). All experiments were carried out at the Rocky Mountain Biological Laboratory (RMBL), in Gunnison Co., CO.
- Each array contained 48 flowers, 24 from each of two species or types, randomly distributed.
- *Natural* arrays contained un-manipulated flowers and tested for spontaneous flower preferences. *Color* arrays, designed to test for color preferences, contained flowers from only one species, painted in one of two colors, one resembling the flower's natural hue. *Morphology* arrays contained flowers from 2 different species, all painted the same color, to test for flower preferences not derived from color preferences.
- To test for flower/color/morphology preferences we compared the proportion of visits (whether or not the butterfly fed) made in a foraging bout by individual butterflies to each of the flower species/types with the expected proportion of 0.5 via one sample t-tests. In total we observed 843 foraging bouts.
- To test for flower constancy we analyzed the frequencies of all possible flight transitions using G tests of independence.

RESULTS



FIGURE 2: *Dugaldia hoopesii*, *Wyethia amplexicaulis*, *Erigeron speciosus*, *Achillea alpicola*

- Natural preferences: *L. heteronea* preferred to visit *A. alpicola* over *E. speciosus* ($t = 4.51$, $df=68$, $p<0.001$, FIGURE 3a), whereas *L. heteronea*, *S. mormonia*, and *P. campestris* all preferred *D. hoopesii* over *W. amplexicaulis* ($t=17.07$, $df=187$, $p<0.0001$; $t = 4.65$, $df=22$, $p<0.0001$; $t = 28.95$, $df=35$, $p<0.0001$, respectively, FIGURE 3b).
- Color preferences: *L. heteronea* preferred to visit white over purple *E. speciosus* ($t = 2.05$, $df=30$, $p<0.05$) and white over purple *A. alpicola* ($t = 1.90$, $df=29$, $p<0.05$, FIGURE 4a). *P. campestris* and *S. mormonia* preferred orange over yellow *D. hoopesii* ($t=2.50$, $df=20$, $p<0.05$; $t=3.74$, $df=79$, $p<0.001$), but showed no color preferences when choosing between orange and yellow *W. amplexicaulis* ($t=0.84$, $df=3$, $p=0.46$; $t=1.07$, $df=20$, $p<0.15$). The situation is reversed for *L. heteronea* and *C. oetus*. Both prefer yellow over orange *W. amplexicaulis* ($L. heteronea$: $t=6.93$, $df=24$, $p<0.0001$; $C. oetus$: $t=21.98$, $df=43$, $p<0.0001$), but show no color preferences when choosing between orange and yellow *D. hoopesii* ($t=1.69$, $df=8$, $p<0.13$; $t=1.24$, $df=18$, $p<0.23$) FIGURE 4b.
- Morphology (non-color) preferences: *L. heteronea* preferred white *A. alpicola* over white *E. speciosus* ($t = 2.58$, $df=66$, $p<0.05$, FIGURE 5a). Neither *P. campestris* nor *C. oetus* showed preferences (FIGURE 5b). Both *L. heteronea* and *S. mormonia* had strong morphology preferences. *L. heteronea* preferred *W. amplexicaulis* irrespective of color (orange array: $t=3.20$, $df=16$, $p<0.006$; yellow array: $t=7.42$, $df=11$, $p<0.0001$), whereas *S. mormonia* preferred *D. hoopesii* irrespective of color (orange array: $t=5.00$, $df=59$, $p<0.0001$; yellow array: $t=3.36$, $df=25$, $p<0.005$, FIGURE 5b).
- Flower constancy: None of the butterfly species studied showed flower constancy in any of the arrays employed. The probability of moving to a particular flower type (species or color) was independent from the previous flower type visited (TABLE 1).

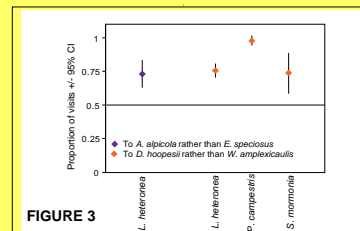


FIGURE 3

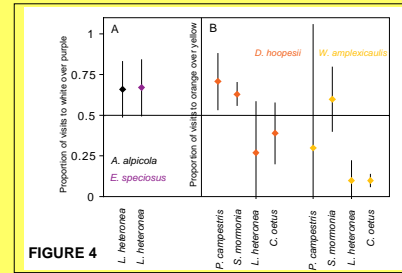


FIGURE 4

	Natural array			All <i>Wyethia</i>			All <i>Dugaldia</i>			All Orange		
	G	N	P	G	N	P	G	N	P	G	N	P
<i>P. campestris</i>	0	57	1	0.68	4	0.41	3.60	37	0.06	0.35	12	0.56
<i>S. mormonia</i>	1.64	31	0.20	0.11	42	0.74	2.39	360	0.12	0.60	189	0.44
<i>C. oetus</i>	---	---	---	1.50	229	0.22	1.85	35	0.17	0.18	106	0.68
<i>L. heteronea</i>	1.55	245	0.21	3.51	9	0.06	0.17	12	0.68	1.83	13	0.18
	Natural array			All <i>Erigeron</i>			All <i>Achillea</i>			All white		
<i>L. heteronea</i>	0.50	20	0.48	0.001	6	0.98	0.002	117	0.96	0.57	76	0.45

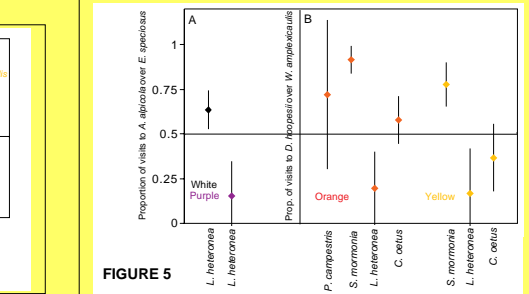


FIGURE 5

DISCUSSION AND CONCLUSIONS

- Butterflies choose flowers to land on based on both color and flower morphology. Different butterfly species utilize visual cues in different ways when choosing which flowers to visit.
- *P. campestris* has no significant morphology preferences and appears to choose *Dugaldia* on the basis of its orange color. One possibility is that it chooses familiar combinations of flower visual traits (associating orange with the morphology of *Dugaldia*).
- *C. oetus* prefers the color yellow, has no significant morphology preferences and could also be choosing familiar combinations of traits.
- *S. mormonia* prefers *Dugaldia* based on both color (orange) and morphology.
- *L. heteronea* prefers *Dugaldia* over *Wyethia*, but this natural preference did not coincide with preferences for color and morphology when traits were manipulated. This change in behavior could be due to learning over the season since the arrays with un-manipulated flowers were setup at the beginning of the field season, followed by the painted arrays. *L. heteronea* prefers *A. alpicola* over *E. speciosus* based on a preference for white over purple.
- Despite the existence of color and morphological preferences, none of the studied butterflies displayed flower constant behavior in any of the arrays employed. Our results contradict the few studies in the literature, which advocate for the existence of flower constancy in butterflies. However, none of these other studies used rigorous methodologies and natural flowers to test for constancy.
- The absence of constancy can be disadvantageous for plant species that rely mostly on butterfly pollinators, if there are fitness costs associated with the loss of pollen to other flowering species.