DESIGN IN NATURE: THE FIERY SKIPPER BUTTERFLY HYLEPHILA PHYLEUS (DRURY) AS AN EFFICIENT FEEDER ON FLOWERS OF LANTANA CAMARA L.

JOSEPH M. REA*

Received 1 August, 1980

The Fiery Skipper butterfly Hylephila phyleus Drury forages efficiently on flowers of Lantana camara L. Hylephila phyleus feeds preferentially from florets of L. camara likely to contain nectar. While foraging on a small artificial patch of flowers of L. camara. H. phyleus chooses the closest flowers 80% of the time. Analysis of foraging bouts on the artificial patch of 3 flower visits in sequence revealed a frequency of revisitation lower than that expected from a random foraging model. This small butterfly demonstrates a neurological program, endowed at the creation, for efficient foraging.

Biological literature is replete with examples of morphological features of animals that contribute to survival. However, structural features alone do not insure survival. Appropriate animal behavior, within each ecological context is also essential for survival.

Since the biosphere was created by an infinitely wise God we can expect that he has programmed the nervous system (via genes) of His creatures with the ability to make decisions that result in incurred benefit. This seems obvious with respect to man, but perhaps not so obvious in insects.

Optimal foraging theory states that animals will make foraging decisions that maximize net intake of food per unit of foraging time. Optimal foraging theory has received much attention in the literature. Experimental tests have been reported by Dixon,¹ Wolf,² Charnov,³ Cowie,⁴ Pyke, Pulliam, and Charnov,⁵ Pyke,⁶ and Waddington,⁷ and models have been proposed by MacArthur and Pianka,⁸ Emlen,⁹ Rapport,¹⁰ Royama,¹¹ and Charnov.¹² Each study and model contain the same basic tenet: animal fitness† is positively related to foraging efficiency, hence foragers that maximize energy intake per unit foraging time should have more surviving offspring.

Nectar in nature is not spatially or temporally uniformly distributed. Because creationists believe God has endowed His creatures with the requisite behavioral repertoire for survival the possibility exists that butterflies can sense the discontinuity of nectar availability in flowering plants and make foraging decisions that increase foraging efficiency. Heinrich¹³ commenting on foraging strategies noted that profits or potential rewards to flower visitors decisively affect their behavior, and that the Lepidoptera acquire a "search image" during foraging as they learn to respond to stimuli associated with their food items. According to Baker¹⁴ flowers visited primarily by butterflies produce copious amounts of nectar and are consistently rich in amino acids. Swihart and Swihart¹⁵ reported on the ability of the butterfly *Heliconius charitonius* Linn. to learn to modify feeding preference through conditioning to feed preferentially at certain colors of artificial flowers that contain honey and the B-vitamins. Dronamraju¹⁶ reported that butterflies preferentially visit yellow flowers of Lantana and Barrows17 reported that yellow flowers of *Lantana* contain nectar, but by the time the flowers turn reddish-orange (a different variety of *Lantana camara* than the present study) they contain no nectar.

The Fiery Skipper Hylephila phyleus feeds at high densities on Lantana camara plants, hence is suitable for a study of foraging behavior. Lantana camara has an indeterminate panicle inflorescence with many salverform, slightly zygomorphic florets per flower head. (See the front cover, which is also Figure 1 of this article.) Maturation is centrifugal with young florets at the center and older florets around the outside of each head. First-day, or newly opened florets are yellow in color with an orange center, second-day florets are lavender in color with an orange center, and third-day florets are all lavender in color.

Within the context of optimal foraging theory I will examine the following questions concerning the feeding behavior of the Fiery Skipper on flowers of *Lantana camara*: 1)Does *H. phyleus* avoid feeding at florets that are void of nectar? 2)How far does *H. phyleus* move when going from flower head to flower head within a patch? 3)Does *H. phyleus* actively avoid visiting flowers at which it has recently fed?

Methods and Material

Data for this study were collected at *Lantana* plants in suburban Phoenix, Maricopa county, Arizona, from 6:00 a.m. to 4:00 p.m. on sunny days with little or no wind during the months of June, July, and August of 1979.

Floret Color Choice

The presence or absence of nectar in yellow and lavender florets was assessed by slicing open the floret with a scalpel and looking for nectar inside with a dissecting microscope. In most cases the nectar, if present, was in sufficient quantity to be seen with the

^{*}Mr. Joseph M. Rea's address is Saratoga Gardens, 7100 Rainbow Drive, #28, San Jose, California 95129.

[†]Fitness here is used by the above mentioned authors in a macroevolutionary context. According to Neo-Darwinism fitness refers to the number of genes an organism contributes to the next generation. However, this definition of fitness does not violate any principle of the creation model of origins. Certainly, survival of creatures is important to the Creator, and macroevolution is not intended by the author. Verifiable, empirical, scientific data cannot contradict the creation model of origins. Creation scientists necessarily disagree with the evolutionists on interpretation and extrapolation, not on observation.

unaided eye. Floret color preferences were documented by observing the number and color of all florets probed (proboscis extended into a floret) per flower head by foraging skippers and recording the number of yellow and lavender florets on each flower head.

Flower Distance Choice

To evaluate flower choice by foraging skippers an artificial patch was constructed to contain flower heads fixed in position in 2 dimensions. The artificial patch was constructed on a 24" square of plywood with 25 holes 3/4" in diameter in 5 rows and 5 columns with 5" between any 2 holes of any row or column. Each hole contained a "flower vase" made of pipe (1/2" inside diameter) 6" long capped at one end with an 1/2" pipe cap on the underside of the plywood. Each "flower vase" position on the artificial patch was given a number (Figure 2). Prior to each foraging bout 1 freshly cut Lantana flower with a 5" stem was placed in each vase. Distances travelled on the artificial patch by foraging skippers are reported in relative units where 5" equals 1 unit. Note that diagonal distances are greater than 1 and are reported as such.



Figure 2. This is a drawing, in plan and front elevation, of the artificial flower patch, with the flower vases. The vases were pieces of halfinch pipe, six inches long, fastened to the piece of half-inch plywood with half-inch pipe caps. The unit distance, e.g. between vases 1 and 6, is 5 inches; note that the diagonal distance between vases, e.g. between 1 and 7, is 1.41 times the unit distance.

Flower Revisitation Frequency

Skippers often visited more than one flower on each visit to the artificial patch. Maps were made from tape recorded verbal records of the number of each flower position visited on the artificial patch to determine the probability of revisiting the initial flower in a 3-stop sequence. One hypothesis of optimal foraging theory is that the efficient forager should not cross its own path during a foraging bout.¹⁸ Thus if insects are foraging efficiently, they should forage in a pattern that reduces the likelihood of revisits to flowers. Heinrich¹³ noted that most bees visit most florets on an inflorescence without revisiting empties, which suggests that they can "remember" florets they have already visited. With this idea in mind, data were collected on 1745 foraging bouts of 3 or more flower stops on the artificial patch.

Results

Description of Behavior of Skippers on Lantana

Skippers arrive at Lantana plants shortly after sunrise. Males arrive first. Activity shortly after arrival at Lantana plants consists mostly of sunning: males rest with the hind wings spread at right angles to incident solar radiation with the forewings nearly closed so as to present minimal surface area to incident solar radiation. Apparently this behavior is common for males in the genus Hesperia.¹⁹ On July 23 and 24, from 7:30 to 8:30 a.m. 10 heads of Lantana received skipper visits from 30 males, 9 females, and 3 sex unknowns. Sex ratios were approximately equal at 11:30 a.m. New florets of *Lantana* begin to open within a half-hour after sunrise. During this time skippers are inactive on Lantana leaves. As soon as the new florets open skippers begin to feed. Skippers land on a head of Lantana and center their heads over a yellow floret. Next, the legs are bent bringing the head closer to the floret in order to push the proboscis into the bottom of the floret tube. There is a short hesitation as nectar is imbibed. The legs are then extended, the proboscis extracted and coiled, and the skipper moves to the next floret. Imbibing duration per head seems to be related to nectar quality and quantity per floret. Yellow florets of Lantana were spiked (solution added to floret via pipet) with distilled water and various concentrations of sucrose. The mean feeding time by skippers in seconds per unspiked head of Lantana was 6.95 ± 4.22 (n = 19). In heads where yellow florets were spiked with distilled water (control) mean feeding time in seconds per head increased only slightly to 8.81 ± 8.18 (n = 14). However, mean feeding time in seconds per head increased to 194.27 ± 181.67 (n = 11) seconds when spiked with 2.0M sucrose. In each case only flower heads with 6 yellow florets were used.

Floret Color Choice

Eighty percent (n = 50) of yellow florets that were examined contained nectar, whereas only 19% (n = 50) of lavender florets contained nectar. Skippers probed nearly 75% (n = 84) of yellow florets per head but probed less than 2% (n = 84) of lavender florets per head Skippers preferred yellow over lavender florets.

Distances Travelled Within the Artificial Patch

Figure 3 is a histogram of the results of data on flower distance choice from maps of tape recorded verbal accounts of foraging paths of skippers on the artificial patch (see figure 4). More than 60% of all visits on the artificial patch were to adjacent (distance = 1) flowers. Over 80% of all visits on the artificial patch were to flowers either adjacent (distance = 1) or adjacentdiagonal (distance = 1.414).

Flower Revisitation Frequency on the Artificial Patch

Figure 4 shows a few typical foraging patterns of skippers on the artificial patch. Examination of these patterns suggested that foraging skippers pursue a nonrandom foraging "strategy" to reduce revisitation frequency. Sequences of 3 consecutive flower visits were examined to compare expected vs. observed revisitation frequencies. In a 3-stop sequence, what would be the probability that the third flower visit was the same as the first in the sequence? The expected frequency is a function of where the skipper is at the second stop. If at a corner the skipper has only 3 choices assuming adjacent or adjacent-diagonal visits only: to the first flower visit in the 3-stop sequence (a revisit) or to one of the



relative distance

Figure 3. This shows the frequency of occurrence of flights of various lengths, from one flower to the next visited, in the artificial patch.



Figure 4. Some of the foraging patterns of *H. Phyleus* observed on the artificial patch are shown here.

other 2 flowers (not a revisit). If skippers are foraging randomly it is expected that 1/3 of all 3-stop sequences in which the second visit is to a corner will involve a revisit. By similar reasoning, it is expected that 1/5 of all 3-stop sequences in which the second visit is to an edge flower will involve a revisit. Similarly, assuming random foraging, it is expected that 1/8 of all 3-stop sequences in which the second visit is to a central (nonedge, non-corner) flower will involve a revisit.

Table I compares expected and observed foraging revisit frequencies for 3-stop sequences on the artificial patch. The data summary is based upon 467 foraging bouts involving all 3 of the previously discussed locations. Revisitation frequency was significantly less than expected for all 3 foraging locations.

Conclusions Floret Color Choice

H. Phyleus appears to feed preferentially at florets likely to contain nectar. It is clearly to the advantage of foraging skippers to major on yellow florets in terms of

VOLUME 18, JUNE, 1981

an energy budget, maximizing return per unit foraging time. It is most likely skippers "choose" yellow florets over lavender florets based upon a visual perceptual system. Color vision in butterflies has been demonstrated in *Heliconius erato hydara* by Crane.¹⁰ Floret color change within 20 hours in *L. camara* induced by pollination was reported by Mathur and Mohan Ram²⁰ and Schemske.²¹ According to Heinrich¹³ insect pollinators avoid flowers void of nectar based upon corolla color change. These observations suggest that corolla "choice" by pollinators is color mediated.

Foraging on the Artificial Patch

Given the artificial foraging situation of non-random spatial distribution of flowers fixed in 2 dimensions *H. phyleus* usually "chooses" the closest flower heads of *L. camara*. Observation of *H. phyleus* foraging at *L. camara* bushes suggest the presence of this same behavioral trait. The design advantage is obvious: shorter flight distances require less energy.

With regard to spatial foraging patterns Heinrich¹³ noted that visiting flowers in a sequence rather than at random reduces the possibility of revisiting empty florets and that foraging along specific paths occurs in butterflies. Analysis of foraging patterns of *H. phyleus* on the artificial patch suggested that this insect forages efficiently by actively avoiding previously visited heads of *L. camara*.

Pyke²¹ has formulated a model of movements for foraging bumblebees. The model supposes that bumblebees choose the next flower to fly to by aiming their departure in some direction relative to the direction of arrival at the present flower. Von Frisch²² reported the use of the sun as a compass by foraging honeybees. Crane¹⁹ noted that the butterfly *Heliconius erato*

TABLE I. Results of analysis of expected vs. observed foraging revisit frequency, 3-stop sequence, on the artificial patch.

Third stop to head: a revisit	previously visited	Third stop to other than pre- viously visited head: not a re- visit
corner. 3 altern	natives	
observed	3	34
expected*	12.3	24.7
n = 37		
$X^2 = 10.53**$		
edge, 5 alterna	tives	
observed	20	211
expected	46.2	184.8
n = 231		
$X^2 = 18.57$		
central, 8 alter	natives	
observed	5	194
expected	24.9	174
n = 199		
$X^2 = 18.2$		

For corner location expected frequency based on 1/3 n. For edge location 1/5 n. For central location, 1/8 n.
0.05 level of significance at (r-1) (c-1) = 3.841

hydara would not feed on cloudy days, and that butterflies became inactive in dull weather. If foraging skippers use the sun as a point of orientation for foraging directionality within a patch, this would in part explain observations of the curious behavior of skippers when a cloud suddenly obscures sunlight: skippers either cease to forage and remain motionless or seek the cover of low vegetation until the sun reappears. In both cases skippers are much less easily provoked to a flying departure by a human hand. However, there are possible alternative explanations for the lull in foraging activity by skippers when clouds obscure the sun. Clouds frequently portend inclement weather. Also, there is some evidence that nectar flow in flowers decreases with reduced sunlight.^{23, 24} The behavioral trait of skippers to avoid previously visited heads of L. camara is clearly advantageous in that it results in an increase in nectar obtained per unit foraging time.

I believe that the behavior of the Fiery Skipper with respect to color choice, distance choice, and foraging pattern demonstrate part of the neurological program of this insect, endowed at creation, to insure increased foraging efficiency. It is my hope that this paper will be an inspiration to creation biologists to further expound upon design in nature, and God's wisdom as expressed in animal behavior.

References

¹Dixon, A. F. G., 1959. An experimental study of the searching behavior of the predatory coccinellid beetle Adalia decempuctata (1.). Journal of Animal Ecology 28: 259-281.

- ²Wolf, L. L., 1975. Energy intake and expenditure in a nectar feeding sunbird. *Ecology*. 56: 92-104.
- ³Charnov, E. L., 1976. Optimal foraging: attack strategy of a mantid. American Naturalist. 110: 141-151.
- ⁴Cowie, R. J., 1977. Optimal foraging in great tits (*Parus major*). Nature 268(5616): 137-139.
- ⁵Pyke, G. H., H. R. Pulliman, and E. L. Charnov, 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review* of *Biology*. 52:137-155.
- ⁶Pyke, G. H., 1978. Optimal foraging: movement patterns of bumblebees between inflorescences. *Theoretical Population Biology*. 13:72-98.
- ⁷Waddington, K. D., 1979. Quantification of the movement patterns of bees: a novel method. *The American Midland Naturalist*. 101(2): 278-185.
- ⁸MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist*. 100: 603-9.
- ⁹Emlen, J. M., 1968. Letters to the Editor. Optimal choice in animals. *American Naturalist*. 100: 611-617.
- ¹⁰Rapport, D. J., 1971. An optimization model of food selection. American Naturalist. 105:575-587.
- ¹¹Royama, T., 1971. A comparative study of models for predation and parisitism. *Res. Population Ecology Supplement*, 1:1-91.
- ¹²Charnov, E. L., 1976. Optimal foraging: The marginal value theorem. *Theoretical Population Biology*. 9: 129-36.
- ¹³Heinrich, B. 1975. Energetics of pollination. Annual Review of Systematics and Ecology. 6:139-170.
- ¹⁴Baker, I., 1973. Amino-acids in nectar and their evolutionary significance. *Nature*. 241: 1-23-73.
- ¹⁵Swihart, C. A., and S. L., 1970. Color selection and learned feeding preferences in the butterfly *Heliconius charitonius* Linn. *Animal Behavior.* 1970. 18:60-64.
- ¹⁹Dronamraju, K. R., 1958. The visits of insects to different colored flowers of *Lantana camara* L. Curr. Sci. 27: 452.
- ¹⁷Barrows, E. M., 1976. Nectar robbing and pollination of Lantana camara (Verbenaceae). Biotropica 8(2): 132-135.

(Continued on page 26)