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THE ANALYSIS AND DESCRIPTION OF MOVEMENT IN ADULT *DANAUS PLEXIPPUS* L. (LEPIDOPTERA: DANAINAE)

by

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(With 9 Figures)
(Acc. 10-II-1982)

Non-sessile animals need to search for the many and varied resources they require to survive and reproduce. The fitness of an animal will depend on its movement patterns or searching behaviour. This is the ability to interpret and act upon internal and external pieces of information, so as to minimise the animal's distance from resources and maximise the distance from stress sources such as predators (JANDER's (1975) "orientation fitness").

In this paper we describe the tracks and searching behaviour of male and female *Danaus plexippus* in terms of the so called "rules" of movement as outlined by SMITH (1974a), GILBERT *et al.* (1976), JONES (1977) and KITCHING & ZALUCKI (1982). In a further paper, these descriptions will be built into a simulation model of egg-laying in females.

The direct observation of searching behaviour has been given considerable attention by entomologists and, in general, workers have found that a searching animal, upon locating its quarry, changes its movement patterns so as to remain within, and thoroughly search, the area in which a capture was made. Most authors have suggested that this sort of behaviour is an adaptation to feeding on prey which have clumped dispersions (*e.g.* LAING, 1937; BANKS, 1957; CHANDLER, 1969; MARKS, 1977).

Most studies have been restricted to animals' walking or crawling on plants or in artificial arenas under simplified laboratory conditions. Field

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studies of flying insects are more difficult to make and various simplifications of the animal's track have been employed at the recording stage. LEVIN *et al.* (1971), for instance, used only the angle of arrival at a point (*e.g.* flower) and the angle of departure to define the directionality component of the tracks of various bees and butterflies. One commonly used method of obtaining two-dimensional versions of the tracks of flying insects is to follow the insect from a distance, taking compass bearings at major direction changes and/or drawing the track on a plan view of the area. Such techniques have been used by BRUSSARD & EHRLICH (1970) for the satyrid butterfly, *Erebia epipsodea*; by HEINRICH (1976) for various bumblebees and BAKER (1978) for various British pierid and nymphalid butterflies. A simple extension of this method is to mark out an area of interest into a grid of points using host plants and/or marker poles. An insect's movement through the area can then be defined from point to point. Information is obtained from recorded commentaries by the observer (*e.g.* KAISER, 1976; JONES, 1977). This method is restricted to two dimensions and simplifies the track into a series of directions and step sizes limited by the grid used. ZALUCKI *et al.* (1980) describe an inexpensive means of obtaining records of the tracks of flying insects. The detail provided by this method enables quantitative comparisons of the tracks of various butterflies. This paper presents results obtained using this method applied to adults of the butterfly, *Danaus plexippus* L. moving among various patterns of their host plants, *Asclepias* spp.

Methods

Glasshouse-grown milkweeds (*Asclepias* spp.) were planted out in various patterns at Tanah Merah, Queensland (27°41'S; 153°10'E), between May and June, 1979 (Fig. 1a, b). The study area had been cleared of shrubs and small trees. A few large gums (*Eucalyptus* spp.) remained on the northern boundary of the site, and some young gums and brush box (*Tristania conferta*) were present along the southern border. The land sloped gently to the east (about 1 m in 18 m). The grass surrounding and within the patches was mown every 1-2 weeks. Apart from the milkweeds which were in flower (Fig. 1a, b), other local nectar sources included *Ageratum hortorum* (see map) and some *Lantana* spp. bushes located to the south-east of the area. No supplementary food was provided during the experiments.

The first dispersion pattern used (Fig. 1a) consisted of a large patch of the three milkweed species; *Asclepias fruticosa* L., *A. physocarpa* (E. May) Schlecht and *A. curassavica* L. These were planted in a 9 × 10 m grid, with approximately 1 m between plants. The patch was located at the approximate centre of the area in which tracks were to be recorded. There were also four outlying plants (Fig. 1a). The second pattern consisted of a large patch of older plants in a 10 × 11 m grid (1 m between plants) alongside a patch of younger plants in a 6 × 6 m grid (2 m between plants). There were also small outlying clusters of plants. In each case mixtures of all three *Asclepias* spp. were used.

The butterflies.

Danaus plexippus and its food plant were introduced to Australia. Both have spread throughout eastern Australia (SMITHERS, 1977). General accounts of its biology in North

America can be found in URQUHART (1960) and COMMON & WATERHOUSE (1981) deal with the species in Australia.

Nine male and nine female tracks were obtained during the study period (see below). Butterflies were tracked for periods of from 1 to 26 minutes. All males were wild individuals which entered the study area naturally. Their tracks were collected on the *first dispersion pattern* only (Fig. 1a), during May. Due to the dearth of females, a number were netted at another site, held overnight in a flight cage and released individually at the centre of the study patch at the time they were to be tracked. Of the nine female tracks collected, four were wild specimens and five were introduced in the manner described. On the second dispersion pattern (Fig. 1b) only female tracks were recorded.

Butterflies were tracked until they left the study area (the usual case), or had remained inactive for more than 10 minutes. An attempt was made to net females after their track had been recorded. When successful the specimens were returned to the laboratory, dissected and the number of mature (chorionated) and other unladen eggs counted.

The compass directions at which the butterflies arrived and left the study area were also recorded. If the butterfly was not then netted, the latter reading was taken as that bearing at which the butterfly disappeared from sight — also called the 'extinction' angle or bearing. To overcome the problem of low sample size a further 24 females and 18 male butterflies were caught at a natural milkweed patch. These were released in an open field and their extinction compass bearing recorded.

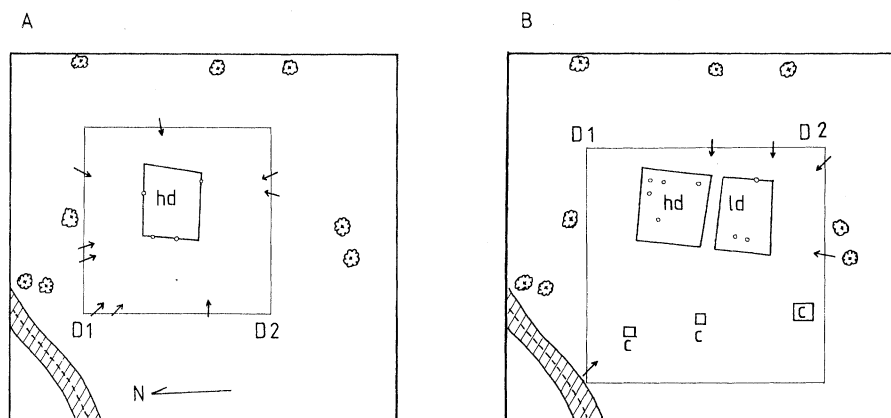


Fig. 1. Location of study sites for males (A) and female (B) butterfly tracking at Tanah Merah. hd = high density patch; ld = low density patch; c = clump; D = tracking device; o = flowering plants. Arrows indicate arrival directions of wild butterflies (Scale 1 cm = 3.6 m).

Tracking the butterflies.

The method of tracking and recording tracks has been outlined in ZALUCKI *et al.* (1980). It employs two fixed recording theodolites focused on the moving butterfly in order to measure changes in angular displacement relative to the theodolites. An ALGOL program written by Mr. D. ABEL (School of Australian Environmental Studies, Griffith University) translated the angular readings into (x, y, z) co-ordinates and calculated distance, horizontal and vertical angles between each successive fix (see Fig. 2), and generated frequency distribution of these distances and angles. Frequency distributions were generated also on the basis of what position in the study area the butterfly happened to occupy; that is, within a patch, around a patch edge (*i.e.* within 1 m of the edge plants), in the open and around single plants.

Recording behaviour.

A simple electronic event recorder was used to sum different behaviours. Behaviour states recognised were: (1) basking (both sexes); (2) feeding (both sexes); (3) egg-laying (females only) and (4) visit (a female approaches a plant, occasionally lands, but takes off immediately).

Results

Large scale butterfly movements.

The study areas did not present a uniform environment to the butterflies, there being non-milkweed and milkweed areas. Within the latter areas there were plants of different age, size and condition (*e.g.* defoliated, in flower). For the purposes of this analysis the study area was divided into a grid of 1 m squares and a particular set of (x, y, z) co-ordinates scored as

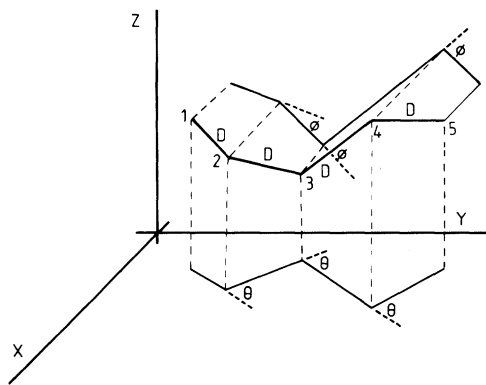


Fig. 2. Interpreting a recorded series of fixes (x, y, z co-ordinates): 1, 2, 3, 4, 5 = fixes; D = distance between fixes. θ = horizontal changes in direction; ϕ = vertical change in direction.

a visit to a grid square if it fell within the square. The row and column totals for the grid squares were tested to see if the butterflies treated the study areas uniformly. Fig. 3 (a, b) show the number of visits made to each grid square for the 9 male (total observation time of 15.2 minutes) and 9 female (110.2 minutes) tracks respectively.

Neither males nor females treated the study area uniformly. Testing the row and column totals in Fig. 3a and b against the null hypothesis of uniformity, there is a significant deviation in all cases (Fig. 3(a), σ , Rows $\chi^2_{17} = 218.21$, $p < 0.005$; Cols $\chi^2_{14} = 295.19$, $p < 0.005$; Fig. 3(b), ϕ , Rows $\chi^2_{21} = 712.47$, $p < 0.005$; Cols $\chi^2_{22} = 1554.76$, $p < 0.005$).

Both males and females tended to visit grid squares containing milkweed plants more than those that did not (Fig. 3a, b). This heterogeneity in the pattern of visits is related to the butterflies' use of the resources available on the site for basking, feeding and ovipositing.

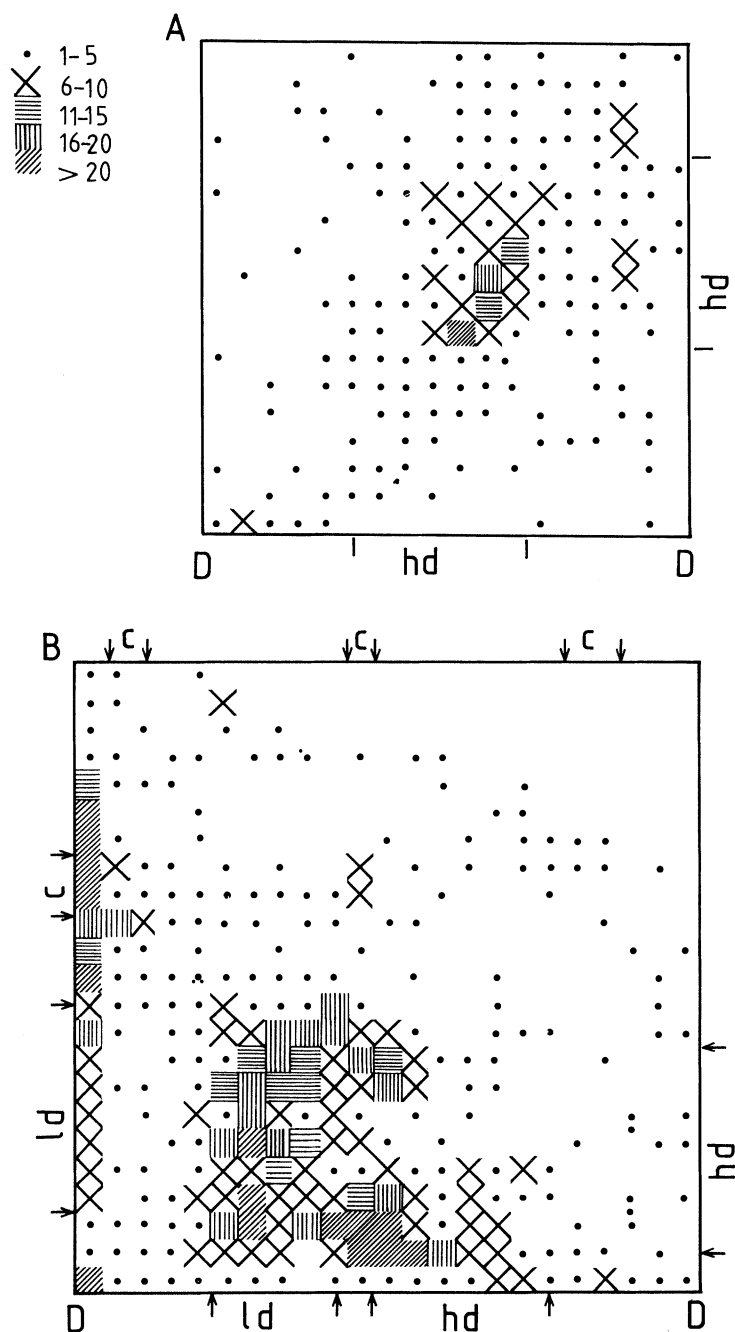


Fig. 3. Total visits/grid square for male (A) and female (B) study sites. Arrows indicate patch boundaries: hd = high density, ld = low density, c = clump, D = tracking device.

The grid squares with the highest number of visits (Fig. 3) were also squares where most behavioural activities (defined above) took place (Fig. 4). Butterflies tended to select basking, feeding and oviposition sites within patches of milkweed.

The butterflies concentrated their activities and flights in certain sections of the study area, particularly around milkweed plants. Visits were not uniformly distributed within milkweed patches. Testing the row and column total for milkweed patch areas only we find that they deviate significantly from uniformity for both males and females (for males, Row $\chi^2_6 = 53.09$, $p < 0.001$; Col $\chi^2_6 = 115.59$, $p < .001$; and, for the females, low density patch, Row $\chi^2_8 = 54.63$, $p < 0.001$, Col $\chi^2_4 = 10.05$, $p < 0.05$; High density patch, Row $\chi^2_7 = 156.88$, $p < .001$; Col $\chi^2_5 = 121.12$, $p < 0.001$).

Males tended to concentrate their activities within the southern section of the patch. Most visits (37) occurred in the single grid square containing a flowering *A. fruticosa*. The moves associated with these feeding and patrolling activities account for most of the unevenness in patch use by males. Females concentrated their visits (Fig. 3b) and activities (Fig. 4b) in the low density patch rather than the high density area. For both patch types, however, visits were concentrated around the eastern and south-eastern margins, although they tended to be more evenly dispersed on the low density patch.

Both sexes avoided the northern section of the study area. This section was shaded from mid-morning to mid-afternoon, and the butterflies preferred to concentrate their activities in the sunny, exposed, section of the study site. This is not the only reason why females preferred the low density patch (544 visits) to the high density patch (293 visits). The former also contained younger plants which were preferred as oviposition sites (ZALUCKI & KITCHING, 1982).

There seems to be a separation of feeding and basking sites in males, but this is not the case in females (Fig. 4). Males tend to bask outside or on the fringe of a patch, females tend to bask within and outside patches, as well as ovipositing on plants. Both sexes feed on suitable flowers wherever they are encountered.

Preferred direction.

Although there was heterogeneity in the use of the study area, there was no bias in the overall straight-line heading of the tracks (that direction joining the first and last points of a recorded track). The headings did not deviate significantly from the assumption of uniformity (Fig. 5(a); $\chi^2_5 = 0.917$, $p < 0.25$). However the incident angle at which females ar-

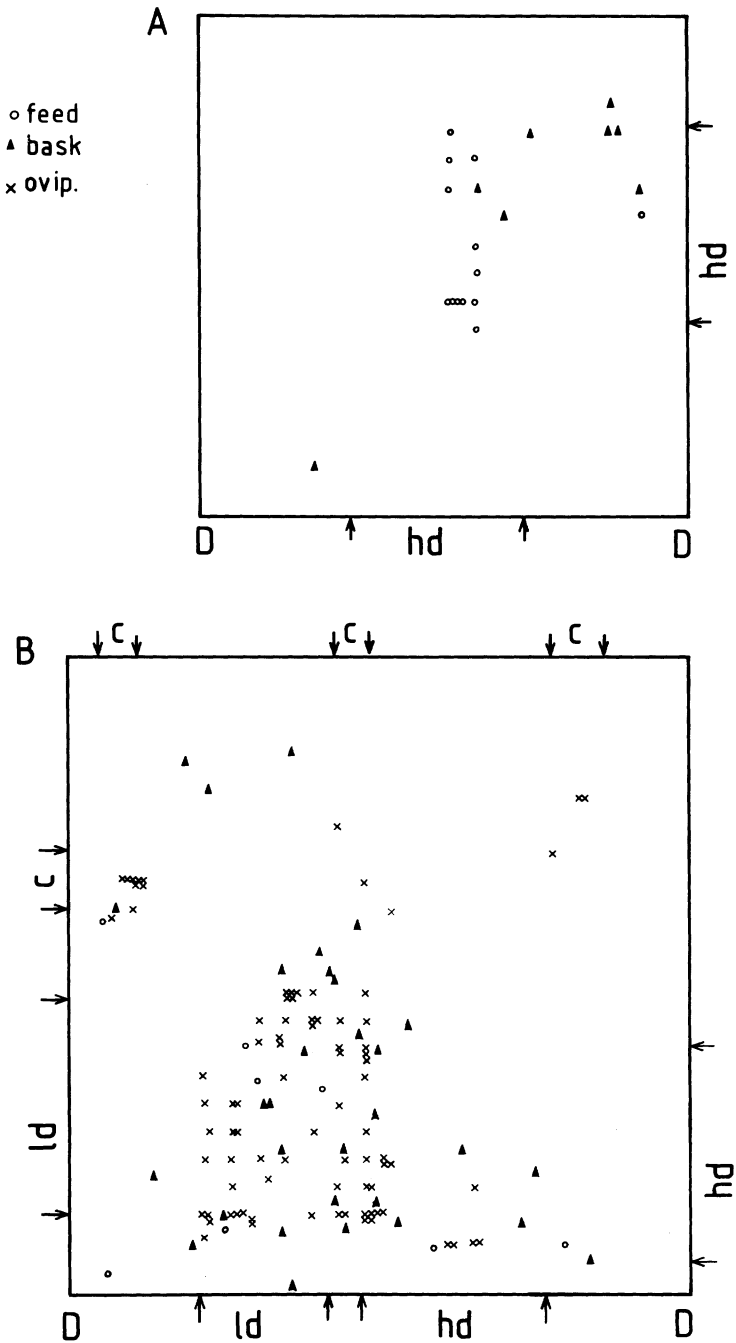


Fig. 4. Location of activities within study areas for males (A) and females (B) Arrows indicate patch boundaries as in Fig. 3.

rived tended to be in the south and east (Fig. 1b) and the concentration of visits in that section of the study area may be due to the females arriving here first. Two observations, however, argue against this: (1) females that started toward the centre also concentrated activities around the eastern and southern patch corners, and (2) most females ranged over most of the study area, but seemed to prefer to return to the southern and eastern sections. Males on the other hand arrived from all directions (Fig. 1b) but the sample size (9♂ and 9♀) is too small to be able to test for a preferred direction.

To overcome this shortcoming and test for a preferred direction of bearing in the local population of monarchs a further sample of male and female extinction angles were added to those collected over the study site (see Fig. 5b). Males and females showed no difference in their mean angle of heading (taking north as an arbitrary 0°, these angles were 66.2° for ♀ and 67.9° for ♂; $F_{58}^1 = 0.0023$, $p < 0.001$, BATSCHLET (1965) pg.

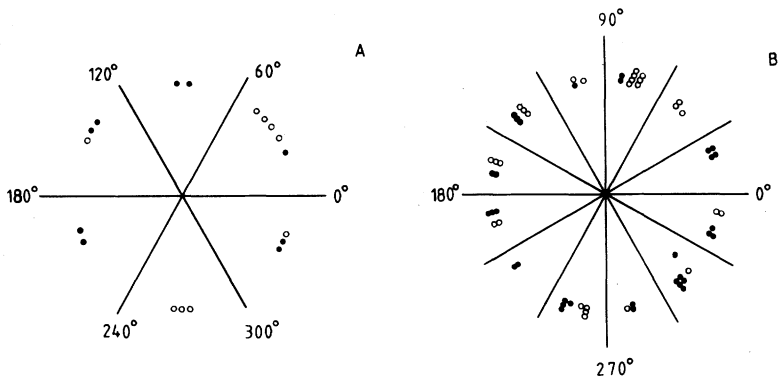


Fig. 5. Frequency distribution of beeline headings (A) and extinction angles (B, see text) in a sample of male (♂) and female (♀) butterflies.

33), so both sexes were combined to test whether the extinction angles are uniformly distributed over 360°. Using Rayleigh's test for randomness (BATSCHLET, 1965, pg 28) we find $Z = 0.1047$, which is less than the critical value given in BATSCHLET (1965, Table 20.1). The directionality for the population can be taken as zero (calculated at 0.04). We conclude there is no preferred direction in *D. plexippus* at that time of the year (May-June) in this area. Accordingly we suggest the uneven use of the study sites is due to the response of butterflies to factors such as light, temperature, plant dispersion, plant age and condition with butterflies concentrating their search paths in preferred areas.

Detailed analysis of butterfly tracks.

Duration of different behaviours.

Time spent in each behavioural state (as defined above) is summarised for both sexes in Fig. 6. Two limitations must be borne in mind when comparing males and females. One is that the sample size for males is small (total observation time of 15.2 minutes on nine individuals). The other is that the records were collected at different times and with different plant dispersion patterns (see above). Table 1 compares the times in each behavioural state for males and females. Average move duration

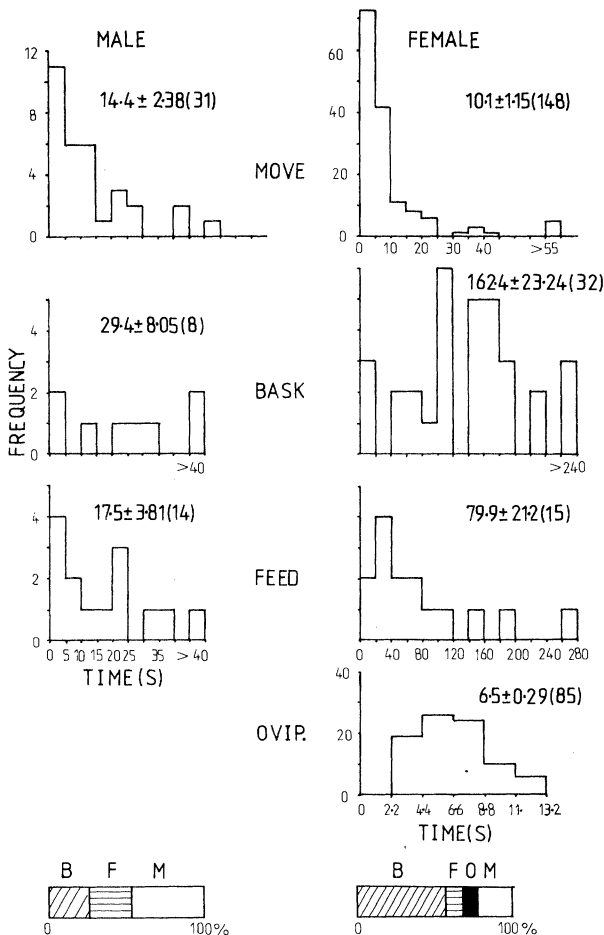


Fig. 6. Frequency distribution of time (in secs) spent in different behavioural states (see text) by males and females (top) and % total time spent moving (M), basking (B), feeding (F) and ovipositing (O) (Bottom). Mean time ± SE (sample size) shown on each distribution.

in males (14.4 s) was not significantly larger than in females (10.1 s). Bask and feed durations were significantly different (Table 1). On average females spent longer basking (162.4 s *vs* 29.4 s) and feeding (79.9 s *vs* 17.5 s) than males.

The percentage of the total time spent in each activity is shown in the bar graphs at the bottom of Fig. 6. Males divided their time equally between moving (7.2 min) and pausing (8.0 min) and the latter was divided equally between basking (3.9 min) and feeding (4.1 min). Females spent 25% of their time moving (27.1 mins) and 75% (93.4 min) pausing; 75% of the pause time being spent basking (68.9 min) and the remainder being divided up between laying (9.9 min) and feeding (14.6 min).

TABLE 1. Comparison of male and female durations in different behavioural states

	F ratio	df	p	t ¹	df	p
Move duration						
♀ <i>vs</i> ♂	1.137	147/30	> 0.10 ^{NS}	-1.579	177	0.2-0.10 ^{NS}
Bask duration						
♀ <i>vs</i> ♂	36.87	31/7	< 0.001**	5.523	36.2	< 0.001**
Feed duration						
♀ <i>vs</i> ♂	33.29	14/13	< 0.001**	2.999	14.9	< 0.01**

¹ = t-test when variances unequal (BROWNLEE, 1965). NS = not significant, ** = significant.

TABLE 2. Sequence of behavioural states in female monarchs for all 9 tracks (*e.g.* a basking state followed the laying of an egg on 22 occasions)

		Following state			
		Lay	Bask	Feed	Total
Preceding state	Lay	39	22	8	69
	Bask	22	7	7	36
	Feed	11	7	3	21

Females take on average 6-7 s to lay an egg (range 3-15 s). This is the time taken from when the butterfly alights on the plant, arches her abdomen, deposits an egg and takes off again. URQUHART (1960, p. 164) estimated the time to oviposit as 3.2 s, although he was measuring from when the tip of the abdomen came into contact with the leaf.

The sequence of switches from one behavioural state to another are summarised in Table 2 for females only. Because there were too few transitions in any one track, the table summarises all available tracks. The

transitions between basking, feeding and laying are not all equally likely. An ovipositing state tends to be followed by the same or a bask, and the latter tend to be followed by oviposition. How females allocate their time when both sexes are present and interacting was not measured.

Analysis of moves and turns.

The frequency distribution of distances between 0.75-second fixes for males and females (Fig. 7) have similar shapes. Both are skewed slightly to the left (skewness 4.5♂; 5.3♀). Although the sample size is small (9♂; 9♀), we will treat the distribution of mean move lengths for each

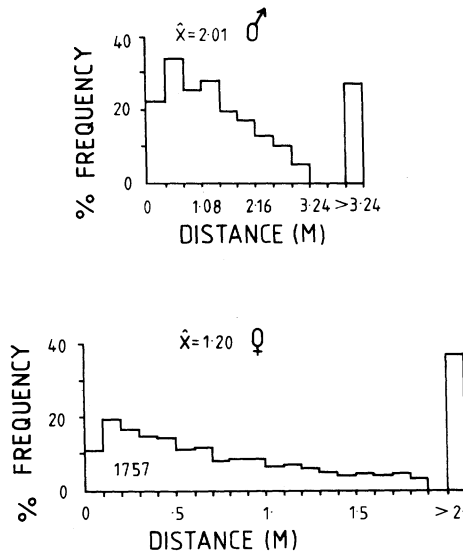


Fig. 7. Percent frequency distribution of distances between successive fixes for males (♂) and females (♀). \bar{x} = average distance moved.

track as approximately normal and compare the male and female group averages using a t-test (see SMITH, 1974a). Table 3 shows the mean distance between fixes for males and females and the results of the test. Males move further on average between fixes than females. Male move lengths are also more variable than those for females.

The frequency distributions of angles turned through between successive fixes in the horizontal and vertical planes for both sexes are shown in Fig. 8. Each angle turned through is taken relative to the previous direction of heading (Fig. 2), a convention of turns to the left being allocated a negative sign and those to the right, a positive sign was adopted. The horizontal angles are distributed between -180° to 180° ,

peaking at 0° (*i.e.* successive moves between fixes are in the same direction). We have calculated the *mean vector* for each of the horizontal angle distributions. The mean vector has two components, its length (R_1) and direction or mean angle (ξ); R_1 provides a measure of the concentration about the mean angle and ranges from zero (no concentration, bearings uniformly distributed on the circle) to one (maximal concentration, all bearings in the same direction). A better measure of the spread of the distribution is provided by the mean angular deviation (S_1) which is analogous to the standard deviation of normal statistics. A measure of symmetry is provided by the skewness coefficient (G). Symbols and formulae for calculating these parameters are taken from BATSCHULET (1965).

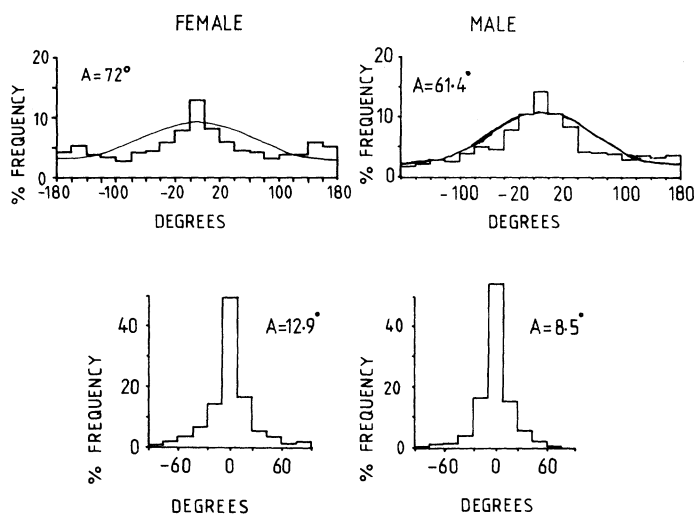


Fig. 8. Percent frequency distribution of angles turned in the horizontal (top) and vertical planes (bottom) by male and female butterflies. (A = mean absolute angle turned: — = circular normal distribution, see Table 4 for parameters).

For angular deviations distributed between 0 - 180° (or -90° to $+90^\circ$), such as in the case of the vertical angular deviations, normal descriptive statistics apply (BATSCHULET, 1965). For the vertical angles, we have calculated the mean absolute angle turned through (disregarding sign) and its standard deviation. Although normal descriptive statistics do not apply to circularly distributed measures, we have also calculated the mean absolute angle turned for horizontal angles, mainly because this gives a rough indication of the size of the angle turned through and can be compared with that for the vertical angles.

These descriptive measures are summarised for males and females in Table 4. The calculations were made by pooling the tracks, so they are based on all the angles turned through. Neither male nor female horizontal turn angles are uniformly distributed between -180° & 180° (assessed using Rayleighs Z test, see Table 4), both R_1 values deviating significantly from zero. Males are more directional, turning less than females (mean absolute turn angle is 72° in ♀ compared with 61.4° in ♂). The mean horizontal angles turned through (ξ) do not differ significantly from zero or from each other (Table 4), which is also indicated by the symmetry of the distribution ($G = 0$) about the modal frequency class of zero (Fig. 8).

TABLE 3. Comparison of the mean distance between fixes (see Fig. 2) for 9 male and 9 female tracks

Sex	n	x(m)	S.E.	VAR	F	df	p	t	df ¹	p
♂	9	1.85	0.30	0.72	7.91	8/8	0.01	2.364	10.01	0.025-0.01
♀	9	1.14	0.11	0.091						

¹ = t-test when variances unequal (BROWNLEE, 1965).

TABLE 4. Summary of horizontal and vertical turn angle statistics

N	Males 539	Females 1756
<i>Horizontal angles</i>		
Mean direction ($R\hat{1}$)	0.37 ^(a)	0.22 ^(a)
Mean angle (ξ)	0.98 ^{o(b)}	1.04 ^{o(b)}
Angular deviation ($S\hat{1}$)	64.17 ^o	71.62 ^o
Skewness (G)	-0.01	0.0002
Mean absolute angle	61.4 ^o	72.0 ^o
Circular normal parameters $K^{(c)}$	0.80	0.50
Circular normal parameters $\theta^{(c)}$	0.0	0.0
<i>Vertical angles</i>		
Mean absolute angle	8.5 ^o	12.9 ^o
S. Dev.	13.75 ^o	19.64 ^o
F ratio (♀ / ♂)		2.04 ^(d)
t-test (♀ v ♂)		5.8258 ^(e)

^(a) = $R\hat{1}$ significantly different from 0.0 by Raleigh's test, $p < 0.001$ (see BATSCHULET, 1965). ^(b) = Male and female mean angles the same using a parametric two sample test, $p < 0.01$ (see BATSCHULET, 1965). ^(c) = K value taken from table C in BATSCHULET (1965) and θ given by the mean angle which in each case can be taken as 0.0. The fitted distribution has the density function: $f(\alpha) = \frac{1}{2 \pi I_0(K)} e^{K \cos (\alpha-0)}$.

^(d) = ♀ df = 538; $p < 0.001$. ^(e) = df = 1270; $p < 0.001$.

The above tests are based on the assumption that the observed distributions are unimodal and circular normal. Circular normal distributions with parameters, $K = 0.8$, $\theta = 0$ for σ and $K = 0.5$, $\theta = 0$ for φ , were fitted to the observed distribution of horizontal angles of turn (Fig. 10). For both males and females the expected distribution differed significantly from the observed ($\chi^2_{15} = 45.57$, $p < 0.005$ σ ; $\chi^2_{15} = 244.51$, $p < 0.005$ φ). The observed distribution in each case exceeded the expected distribution around the mean angle (0°) and tails ($\pm 180^\circ$), and fell below the expected in intermediate angles. These deviations are more pronounced for females than males. In fact for females there is the suggestion of more than one mode (one at 0° and the other at $\pm 180^\circ$). Accordingly, the observed distribution may be a composite of two distributions — a circular normal and a binomial distribution, both symmetrical around 0° . This question will be pursued further in examination of the movement path and its form in different sections of the study area (see below).

The angles turned through in the vertical plane between successive fixes, are also shown in Fig. 8. They range from -90° to 90° and show a pronounced peak around zero degrees. Females show a larger vertical turn angle (12.9°) than do males (8.5°), although both are small relative to the large absolute angle of turn in the horizontal plane. In fact the butterflies showed little variation in their vertical position, flying at about the height of the tops of the plants (1-2 m). The larger angular turns and associated variability in females is due to their behaviour around plants when they search up and down a plant for a suitable leaf.

Before a synthesis of the movement patterns in *D. plexippus* can be attempted, we need to consider the sequential relationships between moves and turns, and the effect of environmental factors on the track. From the analysis so far it seems neither males or females exhibit a classical random walk (JONES, 1977). Both have directionalities greater than zero.

Speed of movement.

As both males and females differed in the distance between successive fixes and allocated different proportions of their time to moving and pausing we might expect their speeds of movement to differ. Speed was calculated for each butterfly by dividing the total path length by the total time spent flying.

Males moved significantly faster than females (Table 5), as well as spending a larger proportion of their time moving during the observation period.

Sequence tests on move lengths and horizontal turn angles.

Successive moves were classified as falling above or below a certain value and successive turns as being left or right. Sequences of pairs of such

values (1st order test) and triplets (2nd order test) were placed into contingency tables depending on their order. These could then be tested to see if moves or turns occurred in random sequence or if any regularities existed in the sequences.

Since each track contains little sequential information, these tests were applied to all male tracks combined and to all female tracks combined. The first order sequence test consisted of taking successive pairs of angles and moves and classifying them as L (left) or R (right) for angles or as above (A) or below (B) a set value for move lengths. The latter was set at

TABLE 5. Comparison of average search speed in male and female *D. plexippus*

	n	Mean speed (m/s)	Variance	F Ratio	df	t	df ¹
♂	9	2.38	1.325	4.417**	8/8	2.2357**	11.45
♀	9	1.43	0.30				

** = 0.01 < p < 0.025; ¹ = t-test for unequal variances (BROWNLEE, 1965).

1 m which is around the mean move length for males and females (Table 3). Once a pair had been classified it could be added to the appropriate cell in a table of the form:

Preceding move		Following moves	
		Above or Right	Below or Left
	Above or Right	AA or RR	AB or RL
	Below or Left	BB or LR	BB or LL

The Chi squared test based on this table, has one degree of freedom and asks whether move lengths that are above or below 1 m alternate (*i.e.* AA and BB fall below expectation) or group in like pairs (*i.e.* BA and AB fall below expectation). Similarly for turns, do either Left (L) and Right (R) turns alternate or do they occur in pairs.

For males and females the subsequent direction of turn are independent of preceding turns (Table 6, $\chi^2_1 < \chi^2_{.1}$, $\alpha = 0.10$). That is, a left hand turn is equally likely to be followed by a left or a right hand turn. On the other hand, move lengths show a distinct pattern in both males and females; the length of the second move depending on the length of the previous one ($\chi^2_1 > \chi^2_{.001}$, $\alpha = 0.001$). Moves above 1 m tend to be followed by similar moves and moves of shorter length also tend to co-occur. The AA

TABLE 6. Comparison of 1st and 2nd order move and angle sequence for male and female butterflies (see Text for explanation)

Male						Female					
<i>Angle sequence</i> 1st Order											
	R	L	CT				R	L	CT		
R	125	126	251			R	373	348	721		
L	121	118	239			L	353	338	691		
RT	246	244	490	$\chi^2_1 = 0.0333$ NS		RT	726	686	1412	$\chi^2_1 = 0.0595$ NS	
2nd Order											
	S	F	CT				S	D	CT		
S	114	121	235			S	330	311	641		
D	120	116	236			D	318	316	634		
RT	234	237	471	$\chi^2_1 = 0.2569$ NS		CT	648	627	1275	$\chi^2_1 = 0.2235$ NS	
<i>Move sequence</i> 1st Order											
	A	B	CT				A	B	CT		
A	263	68	331			A	446	247	693		
B	64	95	159			B	212	507	719		
RT	327	163	490	$\chi^2_1 = 74.3708$ **		RT	658	754	1412	$\chi^2_1 = 175.2398$ ***	
2nd Order											
	AA	BA	BA	BB	CT		AA	AB	BA	BB	CT
A	209	44	38	29	320	A	296	131	78	146	651
B	44	20	25	62	151	B	108	94	99	323	624
RT	253	64	63	91	471	RT	404	225	177	469	1275
$\chi^2_3 = 81.9753$ ***						$\chi^2_3 = 162.3633$ ***					

R = Right; L = Left; A = Above; B = Below; S = Same *i.e.* LL or RR; D = Different *i.e.* RL or LR; RT = Row Total; CT = Column Total; NS = Not Significant; $p < 0.01$; ** = $p < 0.01$; *** = $p < 0.001$.

category is perhaps overinflated in males as 1 m is below the average move length in males (1.85 m).

The χ^2 test of second-order heterogeneity took triplets of moves and turns and classified each of these as being either A or B and R or L as before. For move lengths the χ^2 test had 3 degrees of freedom and was calculated from a contingency table of the form:

		Second and third move			
		AA	AB	BA	BB
First move	A	AAA	AAB	ABA	ABB
	B	BAA	BAB	BBA	BBB

For horizontal angles turned, the χ^2 test had one degree of freedom, being based on a contingency table of the form:

		Second pair of triplet	
		Same	Different
First pair of triplet	Same (LL or RR)	LLL	LLR
		RRR	RRL
	Different (LR or RL)	LRR	LRL
		RLL	RLR

There was no second order heterogeneity in angles turned, suggesting that the turn angle is "decided" independent of the previous two moves, in males and females (Table 6). The χ^2 -tests for second order heterogeneity in move lengths were significant (Table 6) in both males and females. As with the first order tests moves longer and shorter than 1 m tend to co-occur.

The results of these chi squared tests can only be taken as a rough indication of the relationships among sequences of moves and turns. The chi squared test assumes that entries in the contingency table are independent of one another. As the entries are based on successive moves and turns in an animal's track, the existence of any higher order dependency would violate this assumption (see SMITH, 1974a, for a similar treatment of this problem).

Analysis of tracks by position in the study area.

The analysis carried out previously for the male and female tracks was repeated but with fixes classified by where they occurred in the study

TABLE 7. Comparison of male and female horizontal angular distribution parameters R_1 , ζ_1 , S_1 plus mean distance (\bar{X}) between fixes, the latter classified by where in the study area they occur (symbols explained in Table 4)

Position	R_1	ζ_1	S_1	\bar{X}	SE	N
Males						
Open	0.38	0.05°	63.91°	2.95	0.22	248
Patch	0.32	0.05°	66.66°	1.12	0.08	77
Edge	0.31	0.04°	67.42°	1.17	0.37	172
Singles ^(a)	0.11	0.85°	76.42°	1.07	0.23	12
Females						
Open	0.27	0.08°	68.21°	1.79	0.09	565
Patch	0.07	5.26°	78.01°	0.80	0.06	132
Edge	0.03	21.70°	80.01°	1.25	0.11	459
Singles ^(a)	0.07	19.78°	78.24°	0.85	0.06	406

^(a) = Note very small sample size.

area. Fixes were classified as having occurred in one of the following: (1) in the open, *i.e.* milkweed > 1 m away; (2) around an edge, *i.e.* within 1 m of the edge plants in a patch; (3) within a patch, *i.e.* more than 1 m inside a patch; and (4) around single plants, *i.e.*, within 1 m of an isolated plant or within the low density patch (Fig. 1b). Plants in the low density patch were 2 m apart and each was treated as a 'single' plant.

Table 7 summarises the track description for both sexes in different subsections of the study area. The frequency distributions of the horizon-

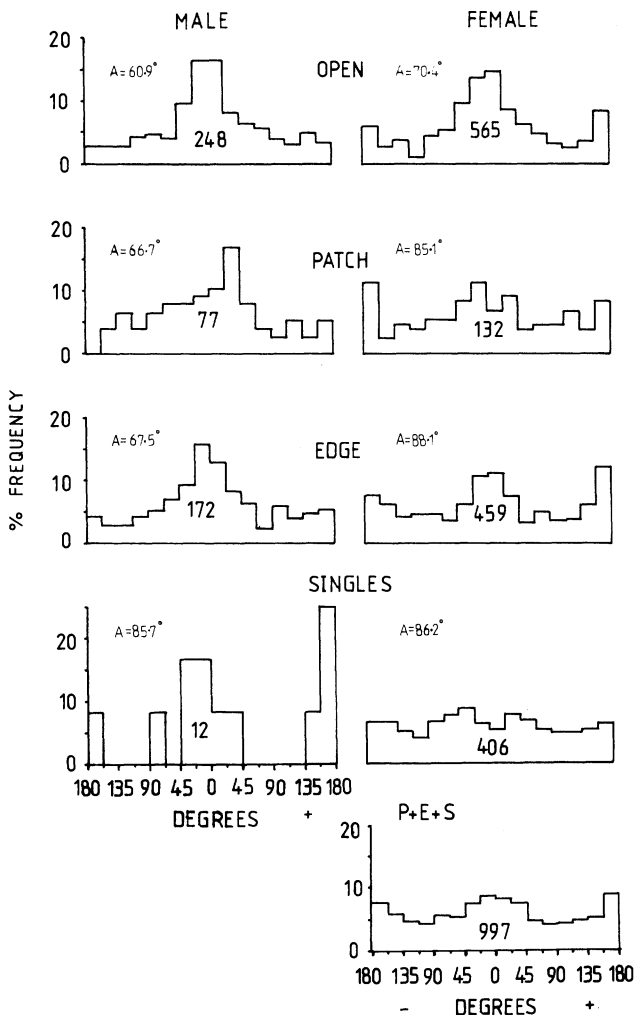


Fig. 9. Percent frequency distribution of angles turned in the horizontal plane for males and female butterflies in different sections of the study area (see text for definition). (A = mean absolute angle; P = patch; E = edge; S = singles).

TABLE 8. χ^2 values for male and female angle and move length sequences. Tracks classified by position in study area (see text for explanation)

	1st Turns ¹	2nd Turns ¹	1st Move	2nd Move ³
Males				
Open	0.1243 ^{NS}	0.4972 ^{NS}	31.7579**	28.036***
Patch ⁴	1.0747 ^{NS}	1.3398 ^{NS}	4.1365 ^{NS}	5.8632 ^{NS}
Edge	0.5092 ^{NS}	2.1532 ^{NS}	27.2094***	15.7812***
Singles ²	—	—	—	—
Females				
Open	0.01555 ^{NS}	2.0071 ^{NS}	68.795***	60.4905***
Patch ⁴	2.9372 ^{NS}	1.7097 ^{NS}	20.3752***	23.6367***
Edge	0.5927 ^{NS}	0.0415 ^{NS}	45.635***	32.5401***
Singles	0.0743 ^{NS}	0.3681 ^{NS}	37.3526***	27.1153***

¹ = degrees of freedom equal 1; ² = too few in sequence to be meaningful (N = 2-6);

³ = degree of freedom equal 3 (** = $p > 0.05$; *** = $p > 0.001$; NS = not significant);

⁴ = move sequence may be non-significant due to small number of sequence, N = 53 for 1st order, and N = 37 for 2nd order sequences.

tal angles turned through are plotted in Fig. 9, and Table 8 contains the results of the χ^2 sequence tests for turns and moves in the different subsections.

The pattern of movement is similar in form in both sexes in the various subsections although there are important differences. Both sexes are most directional when flying in the open (R_1 large, Abs. Angle small – Table 7) and move in large step sizes (\bar{x} large with small variance – Table 7). Males, however, are more directional (that is, they fly in straighter lines, R_1 is larger) throughout all sections of the study area. The differences are particularly marked when comparing within patch, edge and single plant subsections (Table 7). The distribution of horizontal angles turned through has a mode around zero for males in all instances (Fig. 9, disregarding singles), whereas females display bimodality in patch and edge subsections (peaks at 0° and $\pm 180^\circ$, Fig. 9) and practically have a uniform distribution around single plants.

The reason for the larger number of turns around $\pm 180^\circ$ in females is their responses to plants. Often when a plant is visited the female butterfly leaves, turns through a large angle and returns to the plant, either to visit again or lay an egg. Plant to plant moves tend to have smaller turn angles and larger step sizes. Movements around plants tend to be small in size with larger turn angles and the same is true around edge plants, although females (and males) will occasionally fly in a straight line up

along an edge, turn 180° and fly down again. Hence the large step size around edges (Table 7). Around single plants females not only show a responsiveness to plants (turns of $\pm 180^\circ$), but also turn more when moving away from the plant (turns much larger than zero, Fig. 9).

The results of tests for turn and move sequences are similar to those for the overall track (Table 8). For males and females in all sections of the study area there was no pattern in either first or second order turn-sequences. A turn to the right is just as likely to be followed by either a turn to the right or left. There were, however, very distinct patterns in move length sequences (Table 3). In males long moves (> 1 m) tend to be followed by the same in open and patch areas. Around edges short and long moves are equally likely to co-occur in series. In females long follows long in open areas. Around patches, edges and single plants there are many short moves and these tend to follow one another.

Discussion

The information and analysis in this paper permits a partial formulation of the rules of movement in adult *D. plexippus*. As males and females differ in most measures we will describe each separately.

Males.

Males move around the milkweed patch and open fields in step sizes of about 2 m (per 0.75 s). Step sizes in the open (2.95 m) are larger than those around a patch (1.12 m). Long moves in the open and moves of similar length within a patch tend to occur in runs which extended back at least two moves. Turns are symmetrical about the zero direction, with 67% falling within $\pm 61^\circ$ of this direction. A small turn angle tends to be associated with a large move length, although larger moves also occur with very large turns angles ($\pm 180^\circ$). Males tend to fly in straight lines ($R_1 > 0$) or at least maintain their "present" heading under all local conditions. They turn slightly more (67% of turns within $0^\circ \pm 67^\circ$) and move with smaller steps within patches and along edges. Turn signs for successive moves are independent of each other.

Females.

Females have an average step size of 1.2 m, but this varies from 1.8 m in the open to 0.8 m around plants. Moves of similar length also occur in runs extending back up to two moves. Turns are symmetrical about the zero direction, with 67% lying within $\pm 72^\circ$ of this heading. As with males larger steps are associated with smaller angles, step sizes being more variable with larger turn angles. Females are directional in the

open, but turn much more within patches and around single plants (67% of the distribution within ± 85 - 88° of the zero direction). The distribution of turns sizes around patches has two modes, one at zero and the other around $\pm 180^\circ$. Turn sign is again independent of previous sign.

JONES (1977) presented movement rules for Australian and Canadian demes of *Pieris rapae* on different plant dispersion patterns. As the method used to record and analyse tracks differed from the present study no direct comparison is possible. However, there do seem to be some similarities between female *D. plexippus* and Australian *P. rapae*. Both have similar values for Batschelet's directionality (0.10-0.28 for *Pieris* and 0.07-0.27 for *Danaus*), and both species tend to fly through patches of host plants investigating certain plants and then either returning to the patch, leaving or flying along the edge before moving through the patch again.

The biological significance of the movement patterns recorded for *Danaus* must be interpreted cautiously. Although the tracks were collected over milkweeds, in nature the latter rarely occur in regularly planted rows! Field patches are usually at a much higher density, are larger and contain more conspecifics than those arranged at the study site. Despite this the form of the tracks around individual plants, within patches and around edges seem to be characteristic of these butterflies in nature, at least as far as can be confirmed by casual observations. The length of a move and size of turn are determined at any particular time, in part, by local stimuli, both internal and external. Where the butterfly is, spatially, in relation to these stimuli greatly influences its movement path. Around plants short moves and large turns predominate. In the open small turns and larger moves are the norm. The question arises, to what extent are the moves and turns made according to some overall movement strategy, as opposed to being made solely according to local stimuli?

On a qualitative level, the strategy of moving in straight lines over open areas should take the butterflies out of one patch and allow them to locate another, new, patch most effectively (CODY, 1971; BAKER, 1978). By taking small steps and turning more around a patch the butterfly will: (1) search the patch thoroughly and (2) remain within and around the patch. In fact the larger turns and small steps are made so as to return to suitable plants. Where a resource is abundant and not being rapidly depleted it costs little to find and use the same plant more than once. In fact this strategy probably pays if the plants' qualities (age, size, condition, species) enhance offspring survival (see JONES, 1977). Once a butterfly has flown through and out of the patch it can either turn back, fly along the edge or leave. For males it also costs little to re-search a patch — they often fly through a patch rapidly many times and 'patrol' the edges — as their resources, mates, are highly mobile or rapidly renewing.

An empty area can very readily gain a female. The habit of patrolling edges exploits the fact that females must also make use of an edge when arriving, leaving and laying.

One of us (ZALUCKI, 1981a) has used the rules of movement described herein for female monarchs and their observed egg laying behaviour (ZALUCKI, 1981a, b; ZALUCKI & KITCHING, 1982) to simulate egg laying movements over the course of an adult's life-time. The model "tried" different movement rules in areas outside milkweed patches. Once a patch was found movements were simulated using the observed rules reported in this paper. Using realistic patch dispersion patterns (as described in ZALUCKI *et al.*, 1981) the model predicts that, in order to maximise the number of eggs laid, a female should have low (non-zero) directionality around host plant patches (the latter occur in clumps) but should move with high directionality in non-patch areas. The observed directionality in open areas outside patches (Table 7) was around 0.27 which agrees with the model's predictions. We have not recorded female monarch directionality in non-patch areas but casual observations suggest that it is high. These results suggest that monarchs may have an overall movement strategy for maximising the location of host plant patches. Once a patch is found movements are determined by local environmental stimuli (*e.g.* host plants spacing, flowering plants, edges) and physiological condition (see ZALUCKI, 1981a and JONES, 1977). These movements determine patch use and how quickly a patch is "lost" — viz. the butterfly wanders out of a patch. Her low directionality in this case (above) means she may relocate the "lost" patch or any nearby patches. The question then arises, what determines the switch from low to high directionality? Could it be prolonged lack of contact with host plants? Or a "decision" to abandon one microhabitat and seek another (in order to spread risk for instance)? We leave these questions to a later date.

Summary

1. Interactions among flying butterflies, *Danaus plexippus*, and various densities and dispersions of their milkweed food-plants, *Asclepias* spp., have been studied using a continuously recording tracking device.

2. Study areas comprising within-patch and edge plants and areas with no plants were not treated uniformly by the butterflies. Regions with plants were visited more frequently than those without and the greatest range of behavioural activities, basking, feeding and ovipositing, occurred about the plants themselves. There was also a geographical bias in usage by both sexes.

3. Distributions of straight line headings of butterfly tracks (*i.e.* lines joining the first and last points of a recorded track) did not differ from uniformity for either males or females.

4. Incident angles for females but not for males were significantly biased geographically.

5. Males divided their time equally between flying and pausing and their pauses were made up equally of feeding and basking.

6. Females spent 25% of their time flying and 75% pausing, these pauses comprising approximately 75% basking, 10% egg-laying and 15% feeding.

7. Transitions between particular behavioural states were not all equally likely for females. An oviposition was most likely to be followed by another oviposition or basking; a bask by an oviposition.

8. The mean vectors of tracks in the horizontal plane based on an analysis of 0.75 s fixes along the continuous tracks had a mean direction (R_1) of 0.37 for males and 0.22 for females with associated mean angle (ξ) values of 0.98 and 1.04 respectively (statistics after BATSCHELET, 1965).

9. There was much less movement in the vertical plane with a mean absolute angle of turn of 8.5° ($SD = 13.75$) for males, and 12.9° ($SD = 19.64$) for females.

10. Speed of movement based on the distances moved between successive fixes was 2.38 m/s ($SD = 1.15$) for males and 1.43 m/s ($SD = 0.54$) for females. Males moved significantly faster than females.

11. The signs of angles turned through (*i.e.* left hand *vs* right hand turns) in successive segments of track were independent both at the first order (two segments) and third order (three segments) level, in both sexes.

12. Move lengths showed significant differences from homogeneity at both first and second order level when the moves were classified as above or below average for each sex.

13. Both sexes were more directional and faster when flying in the open than when within patches of food-plants. Differences in directionality among patch edge, patch centre, and single plant situations occur. The distribution of angles turned through is centred on 0° for males in all areas and is bimodal about 0° and $\pm 180^\circ$ for females. This difference between sexes is ascribed to specific, food-plant related activities on the parts of the females. Other minor differences in flight patterns in different parts of the study area are noted.

14. The results of this work are used to draw up the 'rules of movement' for male and female adult *D. plexippus* and the biological significance of these rules for the resulting patterns of movement and resource usage are discussed.

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Résumé

1. On a étudié les interactions du vol des papillons, *Danaus plexippus*, avec les plantes qui leur servent de nourriture (*Asclepias* spp.) à l'aide d'un appareil d'enregistrement continu. Les distributions et les densités des plantes variaient.

2. Les sites d'étude comprenaient des régions avec et sans plantes. Les papillons se comportaient différemment envers ces régions ainsi qu'envers des plantes à l'intérieur ou au bord d'un lopin. Les papillons visitaient plus souvent les régions avec que celles sans plantes. On a aussi observé un plus grand nombre de comportements (réchauffement, prise de nourriture, ponte des œufs) dans le premier cas. On a observé un biais par rapport à la position géographique chez les deux sexes.

3. Les distribution des directions rectilignes des vols des papillons (*i.e.* les lignes tirées entre la première et la dernière position d'un vol enregistré) n'étaient pas différentes d'une distribution théorique uniforme dans les deux sexes.

4. Les angles incidents du vol des papillons n'étaient pas aléatoires par rapport aux directions du compas dans les femelles, mais bien dans les mâles.

5. Les mâles partageaient leur temps de façon égale entre les activités de vol et de repos; ces dernières étaient aussi partagées également entre la prise de nourriture et le réchauffement.

6. Les femelles passaient 25% de leur temps au vol et 75% au repos. Leur repos fut partagé en 75% de réchauffement, 10% de ponte et 15% de prise de nourriture.

7. Les probabilités de passage d'un comportement à l'autre variaient pour les femelles. On a trouvé que la ponte était plus souvent suivie d'une autre pont ou de réchauffement, et une période de réchauffement d'une ponte.

8. Les vecteurs moyens des vols enregistrés dans un plan horizontal, basés sur les positions prises à 0.75 s d'intervalle, avaient une direction moyenne (R1) de 0.39 pour les

mâles et 0.22 pour les femelles et une valeur moyenne d'angle (ξ) de 0.98 et 1.04 respectivement (après BATSCHLET, 1965).

9. Le mouvement dans le plan vertical était moins considérable. La valeur absolue de l'angle moyen de changement de direction était de 8.5° (Écart type = 13.75) pour les mâles et de 12.9° (Écart type = 19.64) pour les femelles.

10. La vitesse basée sur la distance parcourue durant des intervalles de 0.75 s était de 2.38 m/s (Écart type = 1.15) pour les mâles et de 1.43 m/s (Écart type = 0.54) pour les femelles. La vitesse de déplacement des mâles était donc plus élevée que chez les femelles de manière significative.

11. La valeur du signe des angles de changement de direction (*i.e.* virage à droite ou à gauche) dans des intervalles contigus de l'enregistrement était en accord avec une distribution aléatoire aux deux niveaux (*i.e.* deux ou trois intervalles) chez les deux sexes.

12. Une classification de la distance parcourue par rapport à la moyenne (*i.e.* au dessus ou en dessous de la moyenne) indiquait un manque d'homogénéité aux deux niveaux chez les deux sexes.

13. Chez les deux sexes, on a trouvé que la direction du vol était plus prononcée et sa vitesse plus considérable lorsque les papillons se déplaçaient en terrain ouvert par rapport aux lopins implantés. On a aussi trouvé des différences significatives dans la direction du vol au bord ou au centre d'un lopin, ainsi que sur des lopins avec une seule plante. La distribution des angles de changement de direction a pour moyenne 0° chez les mâles pour tout le site, et est bimodale chez les femelles avec des modes de 0 et $\pm 180^\circ$. Cette différence entre les sexes est attribuée aux activités particulières des femelles liées aux plantes qui leur servent de nourriture. D'autres différences secondaires dans les types de vol des papillons entre les régions différentes de notre site sont mentionnées.

14. On utilise les résultats obtenus pour décrire de façon empirique les "règles de déplacement" des adultes de *D. plexippus* des deux sexes. L'importance biologique de ces règles est considérée par rapport aux types de déplacement observés et par rapport à l'exploitation de leur ressources naturelles.