

SIMULATION OF MOVEMENT AND EGGLAYING IN *DANAUS PLEXIPPUS* (LEPIDOPTERA: NYMPHALIDAE)

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INTRODUCTION

The monarch butterfly *Danaus plexippus* L. and its host plants *Asclepias* sp. (milkweeds) were introduced into Australia around 1870. Both have become established throughout Eastern Australia. In southeast Queensland where average monthly temperatures are above 10°C the butterfly breeds year round (SMITHERS, 1977; ZALUCKI, 1981 b). Two species of host plants are found in this region, *Asclepias curassavica* L. and *A. fruticosa* L.. The latter species predominates and can be found growing in patches—pure stands of plants—of various sizes along roadsides, creek beds, paddock corners and abandoned farms. These patches represent the major ovipositional resource for this butterfly. In this paper I will attempt to answer the question: how should female monarchs fly in order to maximize their fitness?

Recently JONES (1977) has demonstrated the feasibility of observing and modelling the ovipositing movements of *Pieris rapae* L. over short and long distances (see JONES et al., 1980). Here I use a similar approach to model the movements and egg laying of *D. plexippus* over the life time of a female and go further by: (a) using the observed dispersion of host plant patches and (b) including the survival of immatures.

MODEL ASSUMPTIONS AND DATA BASE

The rationale for modelling the movements of an individual female is outlined in Fig. 1 and is similar to the approach used in other movement simulations (KITCHING, 1971; KAISER, 1976; JONES, 1977; SIROTA, 1978; YANO, 1978; ZALUCKI and KITCHING, 1982 c).

The model integrates observations on host plant dispersion (ZALUCKI et al., 1981), female egg production (ZALUCKI, 1982a), immature survival (ZALUCKI, 1981a; ZALUCKI and KITCHING, 1982 a) and adult female movement behaviour (ZALUCKI and KITCHING, 1982 b).

For each day of a butterfly's life the potential number of eggs to be laid is generated. A female's movements, host plant location and oviposition is then simulated using a time step of one (1) second. This generates the actual number and dispersion of eggs laid. These eggs are then survived to the females current age. This whole process (Fig. 1) is then repeated for another day and so on.

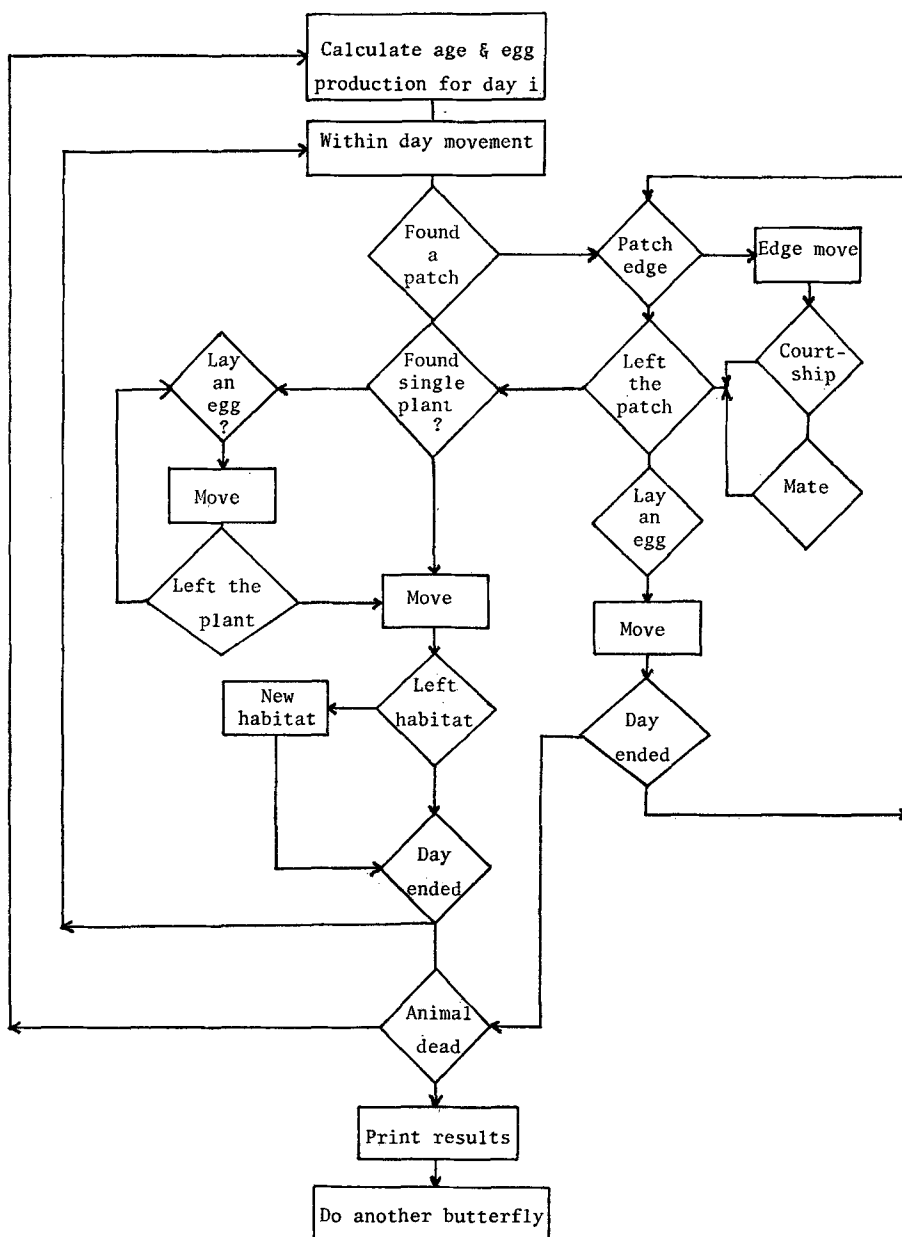


Fig. 1. Flow diagram detailing the logic used to simulate butterfly movement and egg-laying in a patchy environment.

HOST PLANT DISPERSION

The patch locations and sizes used in the model were based on the resource map presented in ZALUCKI et al. (1981). Milkweed patches were clumped maximally at a scale of 3.1 km². This was the size of the area chosen for the simulation of butterfly

movements. Such an area has an average of 6 patches with diameters greater than or equal to 25 m and about 15 patches with diameters less than 25 m. Patches show a clumped dispersion; large patches tend to be well separated and smaller patches tend to be closer together, with smaller patches often surrounding larger patches. The patch dispersion and size classes (Fig. 2) were established to conform with the patterns observed. Single plants (the smallest patch size) do not occur at uniform densities over all areas. In general single plant densities are highest around patches. In the model I assume single plants are at high densities (0.012 plants/m²) within 10 m of the patch edge and low (.00001/m²) elsewhere. The resource dispersion defined in Fig. 2 is a female's basic unit habitat. A butterfly's universe is made up of 'many' contiguous unit habitats.

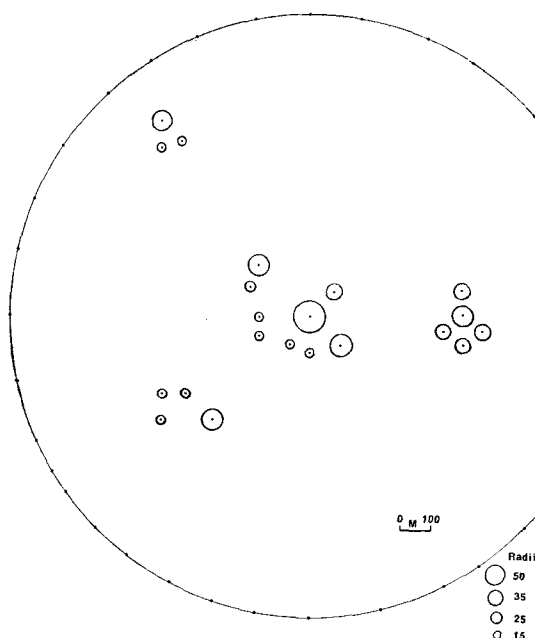


Fig. 2. Unit habitat showing milkweed patch size and dispersion. Single plants not shown.

DAILY EGG PRODUCTION

The number of eggs available (E_i) to be laid on any day i is given by:

$$E_i = S_i (0.0019t_i \lambda^{1.9-0.0114\lambda} + 0.43 \text{ Unlaid}_{i-1})$$

where where S_i is the effect of light intensity and is given by:

$S_i = 1/(1 + 15.0e^{-0.012SR_i})$, λ is age in day-degrees (D^0) above a threshold of 11.5°C, t_i is $D^0_{11.5}$ accumulated for day i , SR_i is solar radiation in langleyes and Unlaid_{i-1} is eggs remaining unlaid from the previous day. (ZALUCKI, 1982 a).

In the model daily solar radiation and day-degrees accumulated per day were made

constant ($600L$ and $10D^0$ respectively). The number of eggs to be laid on any day was generated at the beginning of the day. This batch of eggs was then decremented depending on the number of patches and/or single plants encountered on that day.

IMMATURE AND ADULT SURVIVAL

Survival of immatures was defined from life-tables presented in ZALUCKI and KITCHING (1982 a). In the model only patches and single plants were distinguished, otherwise patch size played no part in immature survival. Eggs laid on patch plants were reduced by 98% to give the numbers of newly emerged adults. For single plants the equivalent mortality was 90%. The number of teneral adults was reduced using the relationship:

$P = 1/(1 - 0.012e^{0.0104x})$, where P is the proportion surviving to age λD^0 , the age of the female which produced them (ZALUCKI, 1982 a). The resulting number was reduced by half to account for the sex-ratio (50:50) at birth. This also assumes male and female survival is equivalent (ZALUCKI and KITCHING, unpublished).

MOVEMENT AND RESOURCE USE

Movement from any cartesian co-ordinate (X_i, Y_i) to any other point (X_{i+1}, Y_{i+1}) can be defined by:

$$X_{i+1} = X_i + d_i \cos \theta_i$$

$$Y_{i+1} = Y_i + d_i \sin \theta_i$$

where d_i and θ_i are the distance (in ms^{-1}) and direction of movement (in radians) respectively. In the model I need to specify a mechanism for generating d_i and θ_i . Following ZALUCKI and KITCHING (1982 b) I distinguish four spatial locations which may influence *Danaus* movements, viz. (a) within patches; (b) around patch edges; (c) around single plants (a special case of (a) and (b)); and (d) non-milkweed areas.

The d_i and θ_i for each situation were chosen as follows:

(a) Within patches d_i was set to 1 m the average movement distance/second observed under field conditions (ZALUCKI and KITCHING, 1982 b) and θ_i was determined by current fecundity via the relationship:

$\theta_i = \mp \pi R (1 - D)$, where \mp can be either positive or negative with probability 0.5; R is a uniform random number, $0 \leq R \leq 1$, π is the constant P_i and D is directionality, $0 \leq D \leq 1$ and is given by:

$D = 0.40 - 0.005x$, where x is current fecundity, $0 \leq x \leq 65$ eggs (ZALUCKI, 1981 b). If D were equal to 0 then θ would be uniformly distributed on the interval $-\pi \leq \theta \leq \pi$, if D were equal to 1 then θ would be 0, that is the animal moves in a straight line with a direction set by the initial direction (see below).

(b) Around a patch edge d_i was set to 1.7 m (ZALUCKI and KITCHING, 1982 b) and θ_i for the *first* move on encountering an edge was such that the animal turned parallel

to the edge. All subsequent θ_i were determined as in a patch (*a* above). The edge was defined as being 1 m either side of the physical patch boundary.

(c) Single plants were treated as single plant patches with d_i and θ_i determined as in *a* above. If after finding a single plant a butterfly moves away and is still within perceptive distance (2 m see JONES, 1977; IVES, 1978), then if the plant is deemed attractive (see below) the next move takes the butterfly back to the plant, and so on.

(d) Under open conditions d_i was set to 2.4 m (ZALUCKI and KITCHING, 1982 b) and θ_i was determined as in *a* above except that now various values of D $0 \leq D \leq 1$ were tried in the model. A directionality (D) was specified for non-patch (low single plant density) and areas within 10 m of a patch (high single plant density).

Having specified the movement rules I need to include how host plants were found and used (i.e. eggs laid). Within patches plant densities are high (17 to 40 plants/m², ZALUCKI and KITCHING, unpublished). I therefore assume a host plant is present whenever a movement ends. The decision to lay was determined by host attractiveness and current fecundity. For simplicity I assume all plants are equally attractive, and have 1 chance in 4 of being accepted. In practice attractiveness is a function of plant species, age, size and condition (ZALUCKI and KITCHING, 1982 d). If a plant is attractive then the probability of laying is given by: $p = 1 - 0.015\lambda$, λ is current fecundity $0 \leq \lambda \leq 65$ and the constant was determined by trial and error until the ratio of eggs/visit in trial simulations corresponded to observed values (ZALUCKI, 1981 b). The time taken to lay an egg was 10 s. (It takes 7 s to lay (ZALUCKI and KITCHING, 1982 b) and 3 s say for within plant movements i.e. leaf selection). Single plants (i.e. outside a patch) were located randomly, but were otherwise treated as single plant patches, with the decision to land and lay being determined as for a plant within a patch.

Basking and feeding behaviour were not explicitly included in this model. Instead it was assumed that basking and feeding sites are always available and do not have to be sought. The effect of these behaviours is to shorten the time available for searching and laying. As noted in ZALUCKI and KITCHING (1982 b) 75% of a female's time was spent either basking or feeding. Subsequently the time available for moving and laying in the model was set to 6300 s.

An attempt was made to mimic the interactions of male and female butterflies. Encounters with males are more likely to take place along edges as male densities are often highest on the edge of patches (ZALUCKI and KITCHING, unpublished). Encounters with males (and mating) represent further delays in egg laying. These effects have been included in the model explicitly (Fig. 1). Along edges there is a low probability (arbitrary, set to 0.03) of encountering a male. If this occurs the female is diverted from egg laying for 2 min (average courtship time; PLISKE, 1974) and is displaced by 10 m from its current location using the current bearing angle. The latter distance is arbitrary and attempts to *mimic* the displacement and avoidance often exhibited by females when they contact males. This behaviour may result in a female

"losing" a patch. If a male-female encounter occurs there is also a low probability (see PLISKE, 1974) that mating can occur, if this is the case then the rest of the day is lost (mating times up to 14 h; PLISKE, 1974).

MODEL IMPLEMENTATION

Having specified all behavioural, movement and survival rules the model sought that combination of directionalities in low and high milkweed density areas which would maximise egg laying and/or fitness. Directionalities were chosen in the range $0 \leq D \leq 1$, in steps of 0.25. For each combination of directionality 25-50 females were "flown over" the unit habitat (Fig. 2). If a butterfly leaves a unit habitat she immediately enters an identical habitat. Each female started her egg laying in the central cluster of patches. The initial bearing angle on any one day was chosen uniformly on the interval $(-\pi, \pi)$. Egg laying and movement continued for 16 days. The model was programmed in FORTRAN by the author for a VAX computer system, (Prentice Computer Centre University of Queensland. A copy of the program is available on request to the author).

Output for each simulated butterfly consisted of the patches found and the associated frequency, the eggs produced and laid, the distance moved from birth to death and the number of adults surviving to the age of the female when she laid those eggs (a measure of fitness).

RESULTS

The proportion of a female's egg production laid and the returns on this egg laying are plotted against directionality in favourable (patch and high single plant density areas) and unfavourable (low single plant density) areas (Fig. 3). Both the proportion of eggs laid (Fig. 3a) and returns on these eggs (Fig. 3b) show similar trends. As the directionality of movement in areas of high milkweed density increases the proportion of eggs laid and fitness declines; whilst both increase with increasing directionality in areas of low milkweed density. Maximal fitness occurs when directionality is low (in the range 0-0.25) in high density areas and high (1) in low density areas (Fig. 3b). Similarly with egg laying except that the maximum is more clearly defined at the point (0, 1) (Fig. 3a). An explanation for this is that butterflies with a directionality of 1 in low density areas find new patch clusters rapidly. If such butterflies also have a very low (i.e. 0) directionality just outside a patch (i.e. in high density areas) then they also readily relocate patches. Such butterflies lay a large fraction of their potential egg production (Fig. 3a). A butterfly with a higher directionality outside patches, will not relocate patches as often but will locate more single plants in these areas. The differential survival between patch and single plants accounts for the higher fitness of the latter movement

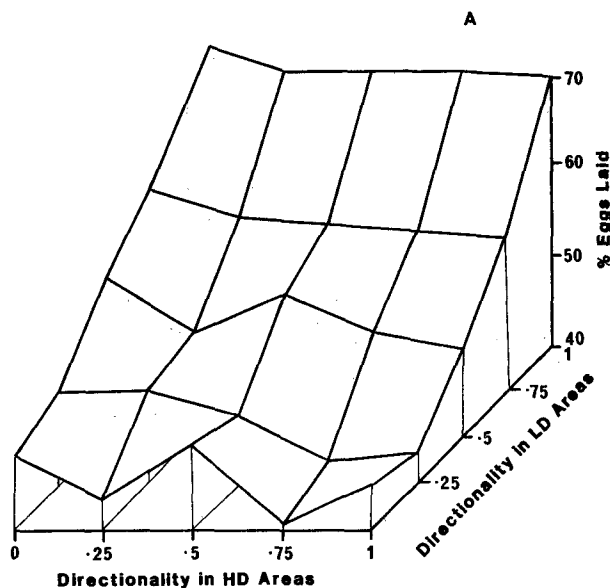


Fig. 3A. Percentage eggs laid plotted against directionality in low density (LD) and high density (HD) milkweed areas.

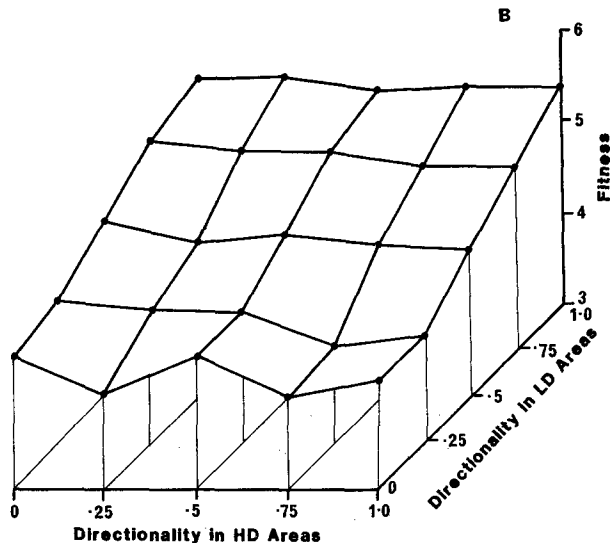


Fig. 3B. Fitness plotted against directionality in low density (LD) and high density (HD) milkweed areas.

strategy. The predicted optimal movement behaviour does make sense intuitively. To summarise, it is optimal to move rapidly and with a straighter course in unsuitable or low density areas; and, to move more slowly with a lower directionality around patches of host plants.

There is some evidence to support these predictions. Observations on butterfly directionalities in areas just outside patches gave a value of about 0.27 (ZALUCKI and KITCHING, 1982 b). This value was recorded in what might be considered a high density area and is close to the predicted range of values (0 to 0.25). I have not tracked butterflies in 'unsuitable' areas, but my own casual observations and BAKER's (1978) work on other species suggests that butterflies in such areas maintain high directionalities. The model generates realistic birth-death distances (Fig. 4). Based on my own observations (ZALUCKI and KITCHING, unpublished) SE Queensland monarchs move at an average rate of about 0.76 km d^{-1} ($\text{SD}=0.298$; $N=6$; Range; 0.35-1.24). In the model movements were over a period of 16 days. This gives a birth-death distance of between 5.6 to 19.8 km. At the optimal combination of directionalities (above) the model predicts a birth-death distance of around 10 km, well within the observed range of values.

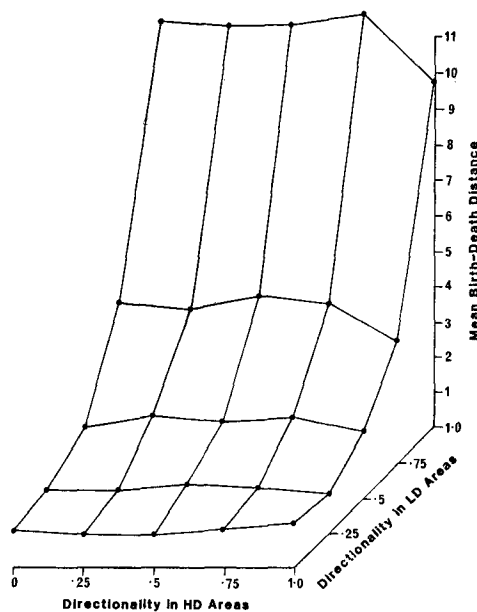


Fig. 4. Mean distance (km) from birth site to death site plotted against directionality in low density (LD) and high density (HD) milkweed areas.

The model also predicts that a female should lay about 50% of her egg production (Fig. 3 a). I have not estimated this proportion in the field. However, in qualitative terms the model suggests that females should contain a large number of unlayed eggs. A female is capable of maturing around 70 eggs a day during peak production (ZALUCKI, 1982 a). In the event that she spends an entire day in one patch then all these eggs will be laid. However she is more likely to leave a patch and on average lay about half her daily egg complement. Therefore we can expect captured wild females (if they are around peak egg production age) to have mature egg numbers

in the range 70 to 30. Five females caught and dissected did in fact have egg numbers in this range (eggs counted were: 64, 48, 46, 40, 32). These females were not old (based on wing condition).

If the model is to be accepted it must not only generate reasonable numbers of eggs laid, movement patterns and birth-death distances it must also generate realistic egg dispersions. ZALUCKI and KITCHING (1982d) have shown that monarchs lay more eggs on single isolated plants than on plants in a patch, and more eggs are found on edge plants than on plants within a patch (see also Table 1). Both these phenomena are "edge effects" (JONES, 1977), determined by the females responses to plants, her directionality and perception of edges. Egg dispersions observed in the field are compared with model predictions under similar conditions (e.g. patch size, total eggs laid) in Table 1. Again the model's predictions agree well with observed values.

Table 1. Comparison of observed and predicted egg dispersions.

Patch Size	Observed					Predicted						
	1 ^{a)}	90 ^{b)}		110 ^{b)}		Large ^{a)}	1 ^{c)}	100 ^{d)}				Large ^{c)}
Total Eggs Counted		21	44	43	55			23	40	48	55	
Egg/Plant Overall	6 (0-22)	0.23	0.49	0.39	0.5	2 (0-9)	1.41	0.23	0.40	0.48	0.55	0.13
<i>Within patch dispersion</i>												
Outer Edge	NA	0.38	0.65	0.45	0.76	NA	NA	0.42	0.47	0.53	0.58	NA
Next Ring	NA	0.23	0.65	0.47	0.30	NA	NA	0.25	0.43	0.50	0.68	NA
Remainder	NA	0.07	0.17	0.29	0.40	NA	NA	0.03	0.31	0.42	0.42	NA

^{a)} Based on all counts to date of eggs on single isolated plants and patch plants (range of counts). ^{b)} Egg counts on single sample occasions from an unknown number of females. ^{c)} Based on 4 females life time ovipositions. Ratios are for plants found acceptable. ^{d)} Simulations on a patch of 100 plants. Total eggs laid comparable to those laid for real patches of 90 and 110 plants. NA: Not applicable or assessed.

The model also predicts that butterflies behaving in an optimal fashion should have fitness values around 4 to 5 (Fig. 3b). The fitness measure used will be analogous to (but not equal to) the intrinsic rate of increase (r) since it is based on age specific fecundities, and survival rates for immatures and adult females. The predicted values will be an overestimate as the model does not take into account fluctuating weather conditions, the occurrence of patch (and plant) destruction. The former will reduce the time available for oviposition and the latter will reduce offspring survival. Both factors will reduce the fitness value calculated. If these two factors were added then the model would be better able to make predictions concerning population changes. (The effects of monarch-monarch interactions would also need to be included.).

DISCUSSION

This study has looked at movement in a 'model' system consisting of female monarch butterflies and milkweeds. In doing this I attempted to answer the question: Is there a best way for monarchs to move around, locate host plants and lay eggs in order to maximize their fitness? I could relate behaviour to fitness in one of two ways, either by (a) assuming it to be the maximization of eggs laid, which will be related to inclusive fitness, or (b) taking it to be the maximization of the number of female offspring surviving to replace the laying female. The latter will more nearly approximate inclusive fitness.

Although both measures are related to inclusive fitness, what is maximized depends on what evolution is capable of optimising. If selection acts on egg laying then the proportion (and number) of eggs laid should be maximal. The model predicts that in this case directionality around milkweed regions should be zero. If selection acts on offspring production then the proportion surviving should be maximal. In this instance the model predicts a higher directionality in milkweed regions (around 0.25). The question then arises, how significant is the difference between these two results? The model rests on the assumption that the behaviour of a female over the course of her adult life is simply the sum of behaviours over a short period of time. The latter we can observe and describe. The model's predictions of low directionalities around milkweed areas and a high directionality in unsuitable areas being optimal in terms of "fitness" agrees well with what information is available on monarch behaviour. The model's other predictions also accord well with what is known about monarchs.

The approach I have taken is a general one and can be applied to any animal searching for resources in a heterogeneous environment. The simulation model not only summarises our observations on components of the animal's life system, but also becomes a predictive tool indicating those behaviours which optimise fitness. These predictions may then be compared with observed behaviour.

There are other approaches to the question of optimal movement (foraging, searching) behaviour (e.g. CHARNOV, 1976; CODY, 1971; PYKE, 1978 a,b). These have two limitations: (1) they assume organisms move to maximise net energy gain (this may or may not be correlated with fitness) and (2) they are short-term studies, and no attempt is made to apply this energy foraging behaviour to the organism over its life time, and include reproduction (but see COOK and HUBBARD, 1977; PYKE, 1978 b) under realistic environmental heterogeneity. By dealing with an organism whose movements and resource location result directly in reproduction (egg-laying) I avoid the first limitation (also by including the survival of these eggs I can estimate fitness). It then becomes a simple matter to overcome the second limitation; movement and reproduction are allowed to continue over the course of a female's life time and in an environment whose resource heterogeneity I have recorded. Note,

however that I have to make two assumptions: (i) energy resources are never limiting and (ii) movement behaviour over a life time is simply the sum of movements over short time periods. (The latter implies no effects of age and experience, which is probably wrong.). Given these assumptions however I can predict that movement behaviour which will maximise the number of offspring produced by an individual. Such an approach has other advantages. Firstly, it generates movement distances; these are a consequence of an individual's directionality and patch responses. It is these movement distances that "simple" empirical models attempt to describe and explain! (e.g. TAYLOR, 1978; TAYLOR and TAYLOR, 1977). Secondly, an individual's behaviour can be directly related to its population performance. This provides one means of including the individual (see PRICE, 1975; WELLINGTON, 1977; KAISER, 1979) and spatial heterogeneity into population dynamics.

SUMMARY

A model simulating the movement and oviposition of monarch butterflies over a female's life time is presented. The model's predictions compare favourably with observed data and suggest that females who lay eggs in an optimal fashion should have low directionalities in areas with high host plant density (patches and single plants) and high directionalities in areas with low host plant density. The model also provides one means of combining individual animal processes and spatial heterogeneity into population dynamics.

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REFERENCES

- BAKER, R. R. (1978) *The Evolutionary Ecology of Animal Migration*. Hodder and Stoughton, London.
- CHARNOV, E. L. (1976) Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.* 9: 129-136.
- CODY, M. L. (1971) Finch flocks in the Mohave desert. *Theor. Pop. Biol.* 2: 142-158.
- COOK, R. M. and S. F. HUBBARD (1977) Adaptive searching strategies in insect parasites. *J. Anim. Ecol.* 46: 115-125.
- IVES, P. M. (1978) How discriminating are cabbage butterflies? *Aust. J. Ecol.* 3: 261-276.
- JONES, R. E. (1977) Movement patterns and the egg distributions of cabbage butterflies. *J. Anim. Ecol.* 46: 195-212.
- JONES, R. E., N. GILBERT, M. GUPPY and V. NEALIS (1980) Long distance movement in *Pieris rapae*. *J. Anim. Ecol.* 49: 629-642.
- KAISER, H. (1976) Quantitative description and simulation of stochastic behaviour in dragon flies (*Aeschna cyanea*, Odonata). *Acta Biotheoretica* 25: 163-210.

- KAISER, H. (1979) The dynamics of populations as a result of the properties of individual animals. *Fortschr. Zool.* 25: 109-136.
- KITCHING, R.L. (1971) A simple simulation model of dispersal of animals among units of discrete habitat. *Oecologia* 7: 95-116.
- PLISKE, T.E. (1974) Courtship behaviour of the monarch butterfly. *Danaus plexippus* L. *Ann. Ent. Soc. Am.* 68: 143-151.
- PRICE, P.W. (1975) *Insect Ecology*. Wiley-interscience, New York.
- PYKE, G.H. (1978 a) Are animals efficient harvesters? *Anim. Behav.* 26: 241-250.
- PYKE, G.H. (1978 b) Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor. Pop. Biol.* 13: 72-98.
- SIROTA, Y. (1978) A preliminary simulation model of movement of larvae of *Culex pipiens molestus* (Diptera: culicidae). *Res. Popul. Ecol.* 19: 170-180.
- SMITHERS, C.N. (1977) Seasonal distribution and breeding status of *Danaus plexippus* in Australia. *J. Aust. Ent. Soc.* 16: 175-184.
- TAYLOR, L.R. and R.A.J. TAYLOR. (1977) Aggregation, migration and population mechanics. *Nature* 265: 415-421.
- TAYLOR, R.A.J. (1978) The relationship between density and distance of dispersing insects. *Ecol. Entomol.* 3: 63-70.
- WELLINGTON, W.G. (1977) Returning the insect to insect ecology. *Env. Entomol.* 6: 1-8.
- YANO, E. (1978) A simulation model of searching behaviour of a parasite. *Res. Popul. Ecol.* 20: 105-122.
- ZALUCKI, M.P. (1981 a) Temporal and spatial variation of parasitism in *Danaus plexippus* (L.) (Lepidoptera). *Aust. Ent. Mag.* 8: 3-8.
- ZALUCKI, M.P. (1981 b) Animal movement and its population consequences with a case study of *Danaus plexippus* L. Ph. D. Thesis, Griffith University.
- ZALUCKI, M.P., A. CHANDICA and R.L. KITCHING (1981) Quantifying the distribution and abundance of an animal's resource using aerial photography. *Oecologia* 50: 176-183.
- ZALUCKI, M.P. (1982 a) The effects of age and weather on egg-laying in *Danaus plexippus* L. (Lepidoptera: Danaidae). *Res. Popul. Ecol.* 23: 318-327.
- ZALUCKI, M.P. (1982 b) Temperature versus rate of development in two species of *Danaus*, *D. plexippus* L. and *D. chrysippus* L. *J. Aust. Ent. Soc.* 21: 241-246.
- ZALUCKI, M.P. and R.L. KITCHING (1982 a) Temporal and spatial variation of mortality in field populations of *Danaus plexippus* L. and *D. chrysippus* L. larvae (Lepidoptera: Nymphalidae) *Oecologia* 53: 201-207.
- ZALUCKI, M.P. and R.L. KITCHING (1982 b) Movement patterns in *Danaus plexippus* L. *Behaviour* 80: 174-198.
- ZALUCKI, M.P. and R.L. KITCHING (1982 c) Component analysis and modelling of the movement process: the simulation of simple tracks. *Res. Popul. Ecol.* 24: 239-249.
- ZALUCKI, M.P. and R.L. KITCHING (1982 d) The dynamics of oviposition of *Danaus plexippus* L. on *Asclepias* spp. *J. Zool. Lond.* 198: 103-116.

オオカバマダラ雌成虫の動きと産卵行動のシミュレーションモデル

M. P. ZALUCKI

オオカバマダラの雌が適応度を最大化するのにどのように飛翔し、産卵するかを示すシミュレーションモデルを作成した。モデルには寄生植物の分布パターン、産卵パターン、幼虫の生存、および雌成虫の動きという要素を組みこんだ。モデルは観測値をよくあらわし、最適適応度は雌が好適な場所（寄主植物の高密度区）では低い指向性を示し、不適な場所（低密度区）では高い指向性を示すときに得られることが示唆された。