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THE EFFECTS OF AGE AND WEATHER ON EGG LAYING IN *DANAUS PLEXIPPUS* L. (LEPIDOPTERA: DANAIDAE)

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INTRODUCTION

The number of eggs laid by a female butterfly over the course of her adult life provides a measure of her reproductive performance. In this paper, the longevity and the effects of physiological age, temperature and solar radiation on egg laying of adult *D. plexippus* under flight cage conditions are examined.

METHODS

The methods and means of analysis used follow closely those of GOSSARD and JONES (1977) working on *Pieris rapae*. Females used in the experiments were all reared from larvae raised on a diet of *Asclepias fruticosa* L. and kept at 25°C in a constant temperature cabinet(12/12 hour light/dark regime).

A large flight cage on the roof of the Environmental Studies building, Griffith University, was used for the egg laying experiment. The cage measured 5×4×2 m and was divided into four equally sized compartments using a fine mesh screen. Each compartment contained three *A. physocarpa*, three *A. fruticosa* and two *A. curassavica* L. plants as well as one or two flowering *Lantana* plants to serve as nectar sources for the butterflies. Additional adult food was provided by three drip bottles per compartment, each containing a 10% honey solution. The drip-point was enclosed by the coloured "corolla" from a plastic flower. Adult *D. plexippus* quickly learned to feed from these. The honey solution in the drip bottles was changed daily.

Five female and three males, nought to one day old were released into each compartment. Eggs laid by these adults were counted and removed from the plants between 6 am and 7 am daily. The number of live males and females was also recorded at this time.

Daily maximum and minimum temperatures were recorded using a thermohydrograph placed in a Stevenson screen on the roof adjacent to the flight cage. Daily solar radiation readings were taken from the records of the Samford Pasture Research Station. This experiment was conducted during November-December, 1978.

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RESULTS

The number of eggs laid daily by *D. plexippus* females was variable (Figure 1) and influenced by age, temperature and solar radiation. The effect of these factors on egg production was investigated by a curve fitting analysis as follows. The effect of any one factor was determined by correcting for all other factors. Solar radiation was taken into account by omitting overcast and rainy days and days immediately following such days. When all variables but one had been corrected for, then a function describing the relationship between the remaining variable and eggs laid was fitted following the technique of GOSSARD and JONES (1977). Subsequently, the individual functions were combined into an algorithm which can predict daily egg production of a female under any given conditions of age and weather.

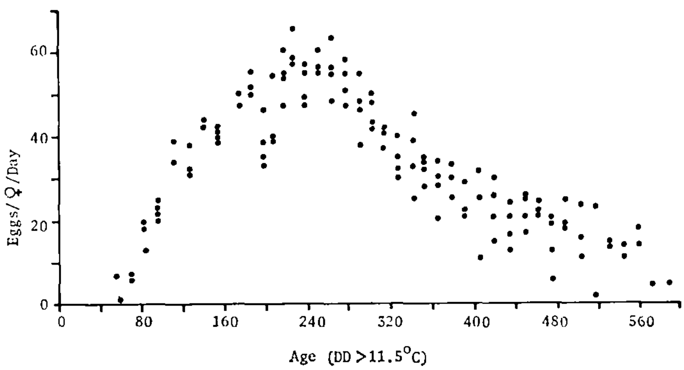

Fig. 1. Age specific fecundities in *D. plexippus* (age measured in DD) before the effects of light and temperature are taken into account.

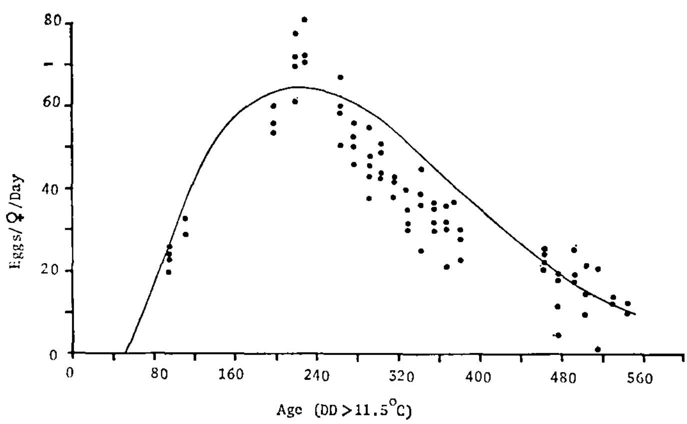

Fig. 2. Age specific fecundities leaving out overcast days and days immediately following them. Each value is corrected to a mean daily temperature of 24.5°C. Correction is done as follows: $E_{\mathrm{observed}}/t = E_{at\ 24.5°C}/(24.5-11.5)$, $\therefore E_{at\ 24.5} = E_{\mathrm{observed}}(13/t)$ where t is temperature in DD.

The effect of age

Daily egg production per female with the values corrected to a mean daily temperature of 24.5°C are shown in Figure 2. Adult age was measured in day-degrees above the developmental zero for the larvae (11.5°C, see ZALUCKI, 1981). This, of course, assumes that the developmental threshold for the adults is the same as that for the larvae. The number of day-degrees above 11.5°C accumulated during each calendar day was calculated using the algorithm of ALLEN (1976).

Egg production rises rapidly from no eggs, 45 day-degrees after emergence, to a peak of about 60 eggs/day at about 175 day-degrees, and then declines slowly to 5 eggs/day after 580 day-degrees. The curve used to describe these changes has the form:

$$E = Ax^{B}e^{-Cx} \qquad \text{Equation 1}$$

where E is eggs/female/day; x is age in day-degrees since emergence minus the time before the start of laying and A, B and C are fitted constants (see Figure 2).

The effect of temperature

To show the effect of temperature on egg production, I removed the effect of age by correcting the values in Figure 2 to an age of 175 day-degrees and plotted these against temperature (Figure 3). Daily temperatures were measured in day-degrees accumulated during the day (GOSSARD and JONES, 1977). The effect of temperature can be assumed to be linear ($r^2 = 0.30$, $F(1, 68) = 6.71$, $P < 0.05$) and the predicted intercept is not significantly different from zero ($t = 0.4705$, 68 df, $P < 0.025$). This supports the assumption that the developmental zero used previously for egg production is the same as that for larval development. So, incorporating the effects of temperature, equation 1 becomes:

$$E = A' \, tx^{B}e^{-Cx} \qquad \text{Equation 2}$$

where E, B, C and x are as before; t is the day-degrees above 11.5°C accumulated between daily minima and A' is A adjusted for the temperature effects.

The effect of solar radiation

Solar radiation affects egg laying directly by lowering levels of oviposition on overcast and rainy days and, indirectly, by increasing the number of eggs laid on subsequent sunny days. That is, cloudy days lower the rate of egg laying, but not egg production—eggs are retained and laid subsequently at the earliest possible opportunity. How long *D. plexippus* can retain eggs without resorption and how many can be stored is not known. Overcast periods during the experiment (solar radiation <500 langleys (L.)) did not exceed four days, and some egg laying was possible even on these days.

To take account of solar radiation, egg production for a given day was predicted using Equation 2 and the fraction of this predicted production laid upon any given day plotted against that day's total solar radiation value (Figure 4). Only days on which the previous day had solar radiation>500 L are shown so as to remove the

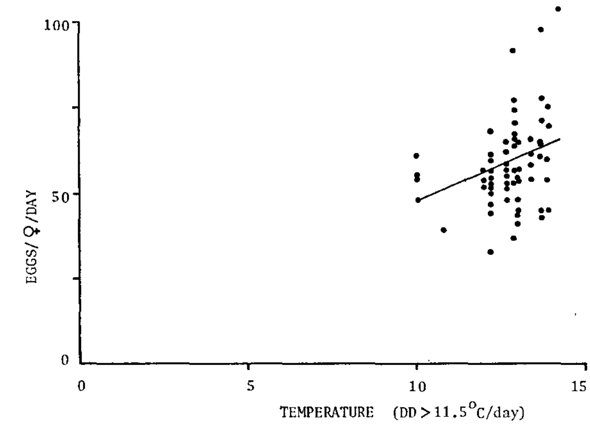

Fig. 3. Effects of temperature on egg production. All values multiplied by (predicted eggs at age 175 DD)/predicted eggs at actual age). Overcast days and days following are excluded. Equation 1 becomes $E=0.0019x^{1.9}e^{-0.0114x}$.

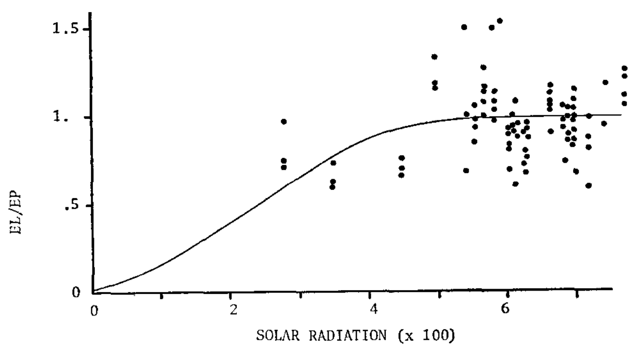

Fig. 4. Effects of solar radiation on oviposition. Days preceded by an overcast day are excluded.

egg-accumulation effect discussed above. This fraction must lie between 0 and 1, if the estimate of production were wholly accounted for by equation 2 (GOSSARD and JONES, 1977). A logistic function with a maximum of one and a minimum of zero was fitted to the observations in Figure 4, and Equation 2 modified according to become:

$$E=sAtx^{B}e^{-Cx} \qquad \text{Equation 3}$$

where $s=1/(1+15.0e^{-0.012\,SR})$ and SR is daily solar radiation in langleys (L.).

The egg accumulation effect was incorporated as follows. There were only two instances when a sunny day ($SR>500$ L) was preceded by a single cloudy day ($SR<500$ L). The number of eggs laid on the sunny day increased on the average by 43% of the previous day's unlaid predicted production (see Table 2), *viz*:

$$E_{\text{laid }i}=s_i\ (E_{\text{prod }i}+0.43\ \text{Unlaid}_{i-1}) \qquad \text{Equation 4}$$

where $E_{\text{laid }i}$ is the number of eggs laid on day i; $E_{\text{prod }i}$ is the number of eggs

Table 1. Final values of parameters shown in Equation 4.

A	0.0019
B	1.90
C	0.0114
s	$\frac{1}{(1+15.0e^{-0.012\ SR})}$
% reduction in eggs remaining unlaid	43

Table 2. Calculation of the % reduction of eggs remaining unlaid.

Day	*SR*	Predicted[a]	Observed[b]				Unlaid[c]	Extra[c]	%Reduction
19	404	50	49	45	47	47	12		
20	611	55	57	61	50	57		5	42
4	296	21	24	21	13	17	9		44
5	668	24	26	25	21	22		4	

[a] using Equation 3.

[b] egg counts for each compartment.

[c] total number of eggs unlaid i.e. $\sum_{i}^{4}$ (P-O) or extra.

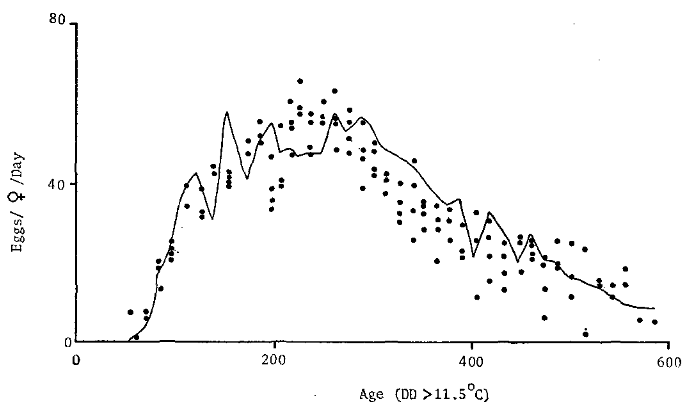

Fig. 5. Age specific fecundities predicted using equation 4, and parameters in Table 1; Actual eggs/♀ also shown.

produced on day i; s_i is as in equation 3; and Unlaid$_{i-1}$, the number of eggs unlaid at the end of day $i-1$. Eggs remaining unlaid at the end of a day are discounted by 43% for each successive day they remain unlaid. That is to say, eggs remaining unlaid are reduced by 43% and added to the next day's eggs. These eggs are treated as though they were identical with newly produced eggs.

The final algorithm for predicting eggs laid per female per day is given by Equation 4 (Table 1). The algorithm accounts for 88% of the variation in egg production (Figure 5).

Longevity

The proportion of males and females used in these experiments surviving each day

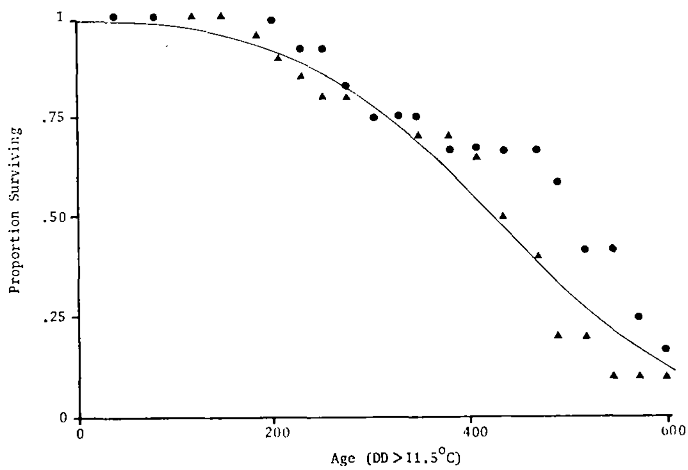

Fig. 6. Proportion of *D. plexippus* adults surviving against age (Males●; Females▲) curve fitted to all data.

is plotted against physiological age in Figure 6. The curve fitted to the data is:

$$S = 1/(1+0.012\, e^{0.0104x}) \qquad \text{Equation 5}$$

where S is the proportion of males and females surviving to age x, where x is age in day-degrees.

On the average, adult *D. plexippus* live 330 day-degrees, with some individuals surviving to 580 day-degrees and above. In calendar time this mean life-span represents about four weeks of normal Brisbane summer temperatures and about three months at winter temperatures.

Discussion

The life-time fecundity of *D. plexippus* is strongly influenced by age, temperature and light conditions. These effects, summarised by equation 4 and Table 1, together with Equation 5 which describes longevity, specify an age-specific life-table for the species. It should be stressed that these equations are descriptive and do not necessarily imply causal mechanisms underlying the physiology of egg laying.

The pattern of egg laying in *D. plexippus* is similar to that recorded for other Leipdoptera. These include the moth *Panaxia dominula* (L.) (Sheppard, 1951), and two pierids, *Pieris brassicae* (L.) (David and Gardiner, 1962) and *P. rapae* L. (Gossard and Jones, 1977). Comparisons among these are not fully appropriate as some authors have used calendar time (Sheppard, 1951; David and Gardiner, 1962) and others, physiological time (Gossard and Jones, 1977; and this work). With this caveat the pattern throughout consists of a period following emergence in which no eggs are laid—about a day in *P. dominula*; 2—3 days in *P. brassicae*: 10 day-degrees in *P. rapae* which at 8 degrees per day (see Gossard and Jones, 1977) represent 1—2 days and, 45 day-degrees in *D. plexippus* (about 6—7 days).

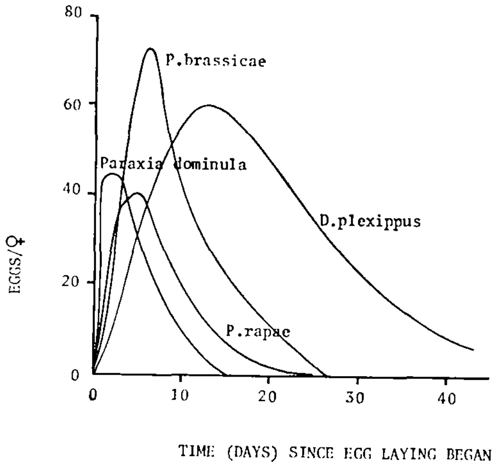

Fig. 7. Eggs/♀ plotted against time. *P. dominula* taken from Table 1, SHEPPARD (1951), *P. brassicae* from Table V, DAVID and GARDINER (1962) *P. rapae*, equation 4 from GOSSARD and JONES (1977), $t=13$/day, $SR=600L$. *D. plexippus* this work, $t=13$/day, $SR=500L$.

URQUHART (1960, page 165) reports a similar value before oviposition begins. The rate of oviposition by females increases rapidly to a peak and then declines more slowly to low values at older ages. The species listed above differ only in the magnitude and timing of their peak reproductive efforts (Figure 7). SHEPPARD (1951), DAVID and GARDINER (1962) and GOSSARD and JONES (1977) report similar effects of temperature and light on egg laying as found here for *D. plexippus*. Overall, the rate of oviposition increases with temperature and declines with decreasing light intensity (see also BARKER and HERMAN, 1976). All the above species show an increase in the rate of oviposition after being deprived of an opportunity for laying and, indeed, a similar response has been noted in *Heliconius ethilla* (EHRLICH and GILBERT, 1973).

A distinction can be made between factors which affect egg production and those that affect egg laying. The former include: age, temperature (GOSSARD and JONES, 1977), size (BAKER, 1968) and energy sources for adults (DAVID and GARDINER, 1962). Egg laying, on the other hand, is influenced by temperature and light (GOSSARD and JONES, 1977; DAVID and GARDINER 1962), host availability and time spent finding hosts (JAENIKE, 1978)—in fact anything that interferes with a butterfly laying, such as courtship and mating time. Butterflies can compensate for delays in egg laying caused by the latter influences. This compensation, a spurt in egg laying as soon as it is possible, is not perfect however, there being a 22% reduction in *P. rapae* and 57% reduction in *D. plexippus* in eggs remaining unlaid. Consequently these delays may constitute an important means of decreasing reproduction in *D. plexippus* (see also KITCHING, 1977). The importance of delays is shown in Figure 8, which compares egg laying in *D. plexippus* under constant and varying light

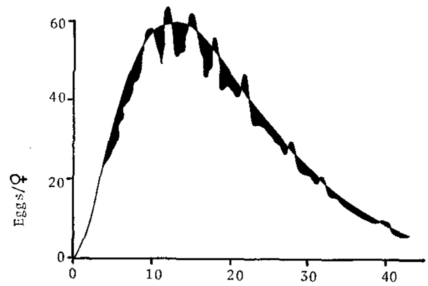

Fig. 8. Eggs/♀ plotted against time using equation 4 and constant conditions, $t=13$/day, $SR=500L$. Other curve with $t=13$/day and $SR=500L$ or $350L$ depending on random number. If Ran<0.5, $SR-350$; if Ran≥ 0.5 $SR=500L$. Shaded area represents difference between the two.

conditions. The shaded area indicates egg production lost. Although females compensate for some of this lost production there is a shortfall (Figure 8).

Under field conditions factors such as the time taken to find a host plant and male interference will also delay egg laying and reduce life-time fecundity. The effects of host plant dispersion and searching on egg laying is discussed further in ZALUCKI (1981). Female *D. plexippus* can mate many times; up to 4 spermatophores having been removed from the bursae copulatrices of an old individual;and a single mating can last from 2—14 hours (PLISKE, 1974). How many times a female has been courted during her life time is not known, but will be much larger presumably than the number of matings. Such courtship can last from 0.2 —2 minutes (PLISKE, 1974). Thus male-female encounters and mating time will represent yet another factor diverting females from egg laying.

All the butterflies studied under flight cage conditions show a similar shaped survivorship curve with low mortality during early adulthood, increasing greatly at older ages (Figure 6; and SLOBODKIN, 1962, "Type I" curve). With bird predation one might expect an overlaid constant rate of mortality with age under field conditions, that is a"Type II". In *D. plexippus* the bright warning colouration together with the contained toxic cardiac glycosides (e.g. BROWER *et al.*, 1968) confer a certain amount of immunity to bird predation. Flight cage and field survivorship may therefore be similar.

URQUHART (1960, page 165) reports a survivorship of 40 days for monarchs under flight cage conditions, which is comparable with the 47 days in this study. However 'days' is a misleading unit in which to measure survivorship, as ageing in poikitotherms is closely related to temperature. The number of days survived will therefore depend on the time of the year.

SUMMARY

The effects of age and weather conditions on egg laying in *D. plexippus* were determined for caged females. Age (measured in physiological time), temperature and solar radiation influence egg laying in this species of butterfly. An algorithm taking these factors into account is presented and accounts for 88% of the daily variation in egg laying. Caged *D. plexippus* begin to lay eggs six— seven days after emergence, peak egg production (about 60 eggs/♀) occurs about 15 days later. Females continue to lay eggs throughout their adult life, which in a flight cage was about 40 days. This egg laying pattern is compared with other published fecundity schedules. The effect and importance of a female being prevented from laying her eggs, on her life-time egg production, is also discussed.

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マダラチョウの1種 *Danaus plexippus* の産卵における年令と天候の影響

M.P. Zalucki

マダラチョウの1種 *Danaus plexippus* の産卵における年令と天候条件の影響をケージに入れた雌で調べた。年令（生理的時間（日度）測定），気温および太陽の輻射はこの蝶の産卵に影響を及ぼした。これらの要因を考慮に入れて計算を行なったところ，産卵の日変化の88%を説明できた。ケージ内の蝶は羽化後6～7日で産卵を開始し，約15日後に卵生産のピーク（1雌あたり約60卵）に達した。雌はケージ内で，約40日間の寿命を全うするまで産卵を続けた。この産卵パターンを他の蝶類の蔵卵数と比較した。また，産卵を妨げられた雌の影響とその重要性について考察した。