THE DYNAMICS OF ADULT *DANAUS PLEXIPPUS* L. (DANAIDAE) WITHIN PATCHES OF ITS FOOD PLANT, *ASCLEPIAS* SPP.

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ABSTRACT. Mark-recapture studies of adults of *Danaus plexippus* at four sites in southeast Queensland have been made over a ten month period. Despite unavoidable difficulties associated with non-compliance with the basic assumptions of standard mark-recapture techniques, population trends have been identified, abundance levels having late summer and late autumn peaks, declining to low levels in winter. Longevity of individuals, estimated as the "mean minimum life-span," was 12.4 days overall (13.5 for males, 10.0 for females). These estimates are regarded as conservative. Males predominated in all four sites but a seasonal pattern was evident with the proportion of males declining to below 50% at the end of summer. In the remainder of the sampling period the proportion of males varied from 50 to 75%. Separate estimates of population turnover in a single patch were obtained—within four days, an estimated 50% of the local population had been replaced by "new" individuals about half of which were newly emerged and half, presumably, immigrants.

The male-biased sex ratios are hypothesized to be due, at least in part, to aggressive male-female interactions with resident males, reducing within-patch residence times of females. The overall vagility of the species and the difficulty of studying events occurring between patches makes interpretation of the adult dynamics in this species difficult. Further work, investigating the role of intersexual behavior in determining within patch dynamics is in progress.

The distribution of host plants has been shown to influence the dispersion, abundance and survival of both larval and adult butterflies (Dethier, 1959; Ehrlich, 1965; Singer, 1971; Sharp & Parks, 1973; Zalucki, 1981a). Monarch butterflies (*Danaus plexippus* L.) in Australia lay eggs on introduced *Asclepias* spp. (milkweeds). These plants often grow in large dense patches (Zalucki et al., 1981). In this study we use mark-recapture techniques to investigate abundance, longevity and movement of adult monarchs at and between four milkweed patches in southeast Queensland. The monarch is native to North America and was first noted in Australia around 1871. In southeast Queensland the species breeds throughout the year (Smithers, 1977).

MATERIALS AND METHODS

The four study sites were located southwest of Brisbane (centering on 27°28′S; 153°1′E). The sites were widely spaced (5–16 km apart, Fig. 1) and there were numerous patches of milkweed in the intervening areas (see Zalucki et al., 1981 for a description of patch dispersion).
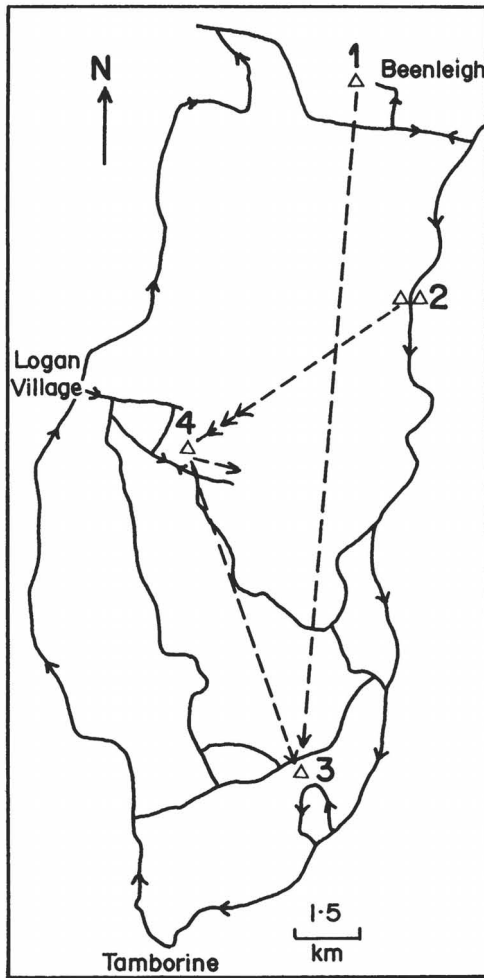
FIG. 1.   Map showing location of study sites 1, 2, 3 and 4 (△), major roads (→) and urban centers. (--) indicates direction of movement and, the number of arrowheads, those butterflies marked at one site and recaptured at another.

Each site was sampled by 30–40 minutes netting once a week. Site 1 was sampled from 8 February to 5 July 1978 and site 3 from 2 February to 28 June 1978, whereas, sites 2 and 4 were sampled from 2 February to 22 November 1978 inclusive. Butterflies were tagged using the alar method outlined by Urquhart (1960), sexed and classified as either fresh (wings soft), old (wings chipped, color very faded) or middle aged (wings slightly chipped, little fading).

Population size, rates of recruitment and losses from a site were

TABLE 1.   Summary of mark-recapture observations by site and sex.

Site	Males			Females			% males
	Marks	Recapt.	% recapt.	Marks	Recapt.	% recapt.	
1	228	18	7.9	142	6	4.2	0.62**
2	249	32	12.9	143	23	16.1	0.64**
3	237	22	9.3	132	8	6.2	0.64**
4	585	113	19.3	422	57	13.5	0.58**
	1299	185	14.2	839	94	11.2	0.61**

** Significantly different from 0.5, P < 0.05.

estimated from the recaptures using the Jolly-Seber method (Jolly, 1965; Southwood, 1966; Seber, 1973). Longevity of marked individuals was estimated as the "mean minimum life-span" (i.e. sum of days survived by all recaptures/total recaptured, see Ehrlich & Gilbert, 1973). The recapture at one site of individuals marked at another provided crude estimates of potential cross-country movements. The sex ratio of the catch was also recorded at each site on each sampling occasion.

In addition on one occasion, virtually all butterflies at site 4 were captured and marked on one day. The purpose of this exercise was threefold: (1) to determine whether the sample sex ratios were accurate; (2) to check population size estimates; and, (3) to check the rate at which a marked population is diluted by unmarked insects.

RESULTS

During the study period a total of 2138 butterflies were netted at the four sites, and of these, 279 (13%) were recaptured at least once; with the exception of site 2, a higher percentage of males was recaptured than females (Table 1).

The populations at the four sites were not isolated from each other. Five marked individuals were recaptured at a site other than the one at which they were marked (recapture distances 6.2, 6.2, 6.2, 7.8, 15.6 km) and one specimen was captured 0.7 km from site 4 (Fig. 1). From these interpatch recaptures we estimated that cross-country moves can proceed at a rate of ca. 1.5 km/day (range 0.7–2.48).

Population Estimates

Due to the low recapture rate at each site each week, male and female recaptures were combined to give weekly population estimates for each site (Fig. 2). The estimated population sizes, dilution and loss rates at each patch were characterized by their large variability. Field experience indicated that the population at each site did not fluctuate to the extent that the estimates suggested. The calculated fluctuations
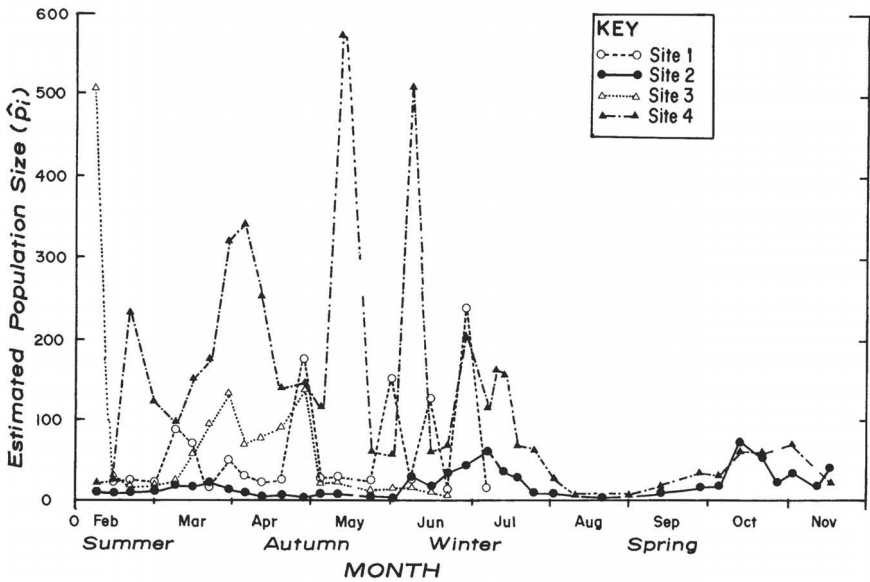
FIG. 2. Estimates of population sizes (P_i given by combining male and female recaptures) for each site.

were due to the failure of some of the assumptions of the method of estimation and the low rates of recapture.

One assumption is that recaptures be random. Marked females were recaptured randomly ($z = 0.3588$, $P > 0.5$); whereas, males were not ($z = 2.3294$, $P < 0.05$). The other assumption that is violated is that migration be permanent. Direct evidence for this occurred during the patch clearing exercise. Two tagged specimens where recaptured at site 4 before and after but *not* during the patch clearing exercise (see below).

Despite these problems, population trends over the sampling period are apparent (Fig. 2). Populations are high in late summer (100–200 butterflies per patch in February, Fig. 2), declining in early autumn (to around 50/patch in March), increasing again in late autumn to about 100/patch (April, May) and declining to low levels (10–50/patch) in winter. Populations increase in spring to achieve the high levels observed in summer.

Due to the variability of the various estimates obtained using the Jolly-Seber methods, the associated estimates of survivorship are unreliable. For these reasons we have analyzed longevity (survivorship) using a different method.

TABLE 2. Longevity[a] of marked *D. plexippus*.

	This study			North America[b]				Australia[e]	
Min. days survival	♂	♀	T	Min. days[c] survival	July–Aug 16[d] Summer	All months	T	Min. days survival	♂ + ♀
				0–5	4	33	37	3.5	720
7	93	67	160	5–10	5	20	25	10.5	360
				10–15	7	13	20	17.5	214
14	47	20	67	15–20	4	6	10	24.5	133
				20–25	4	5	9	31.5	76
21	23	5	28	25–30	2	4	6	38.5	57
				30–35		4	4	45.5	53
28	16	1	17	35–40		3	3	52.5	52
				40–45	1	3	4	59.5	22
35	4		4	45–50		1	1	66.5	20
				50–55		4	4	73.5	15
49		1	1	55–60				80.5	9
				60–65		2	2	87.5	17
56	1		1	65–70		1	1	94.5	7
				70–75				101.5	8
70	1		1	75–80				108.5	7
				>80		6	6	>115.5	85
Total	185	94	279	Total	27	105	132		1806
Mean min. life-span (days)	13.5	10	12.4		14.5	21.6	20.2		19.9

[a] Based on Ehrlich and Gilbert (1973). [(No. known age × days since capture)/Total recaptures] = Mean minimum life-span.
[b] Taken from Urquhart (1960, table II, p. 291).
[c] Calculations based on the midpoint of the interval. Those recaptured on the same day have been ignored.
[d] Marked and recaptured during summer months.
[e] Taken from Smithers (1973, table II).

Longevity

The "mean minimum life-span" for all individuals is about 12.4 days; 13.5 days for males and 10 days for females (Table 2). These values greatly underestimate longevity, reflecting as they do, the time spent in a patch (see below). This is determined by movements into and out of patches rather than by permanent removal due to death. Our estimates of life-span are similar to those calculated for the summer breeding population of *D. plexippus* in North America (Table 2). This presumably reflects a similar underlying population structure. The estimated life-spans are consequently less than the 40 days recorded for adults in captivity (Urquhart, 1960; Munger & Harriss, 1970; Zalucki, 1981b) and of adults marked and recaptured over the years in North America (Table 2). The estimated longevities based on Smithers (1973, table II) are also longer than our estimates. Smithers' recaptures are based mainly on butterflies from around Sydney, N.S.W., where

TABLE 3.   Mean minimum life-span (in days) estimates[a] for sites 1-4 by sex and age.

Site	Males		Females	
	Fresh[b]	Other[c]	Fresh[b]	Other[c]
1	8.8	11.5	[d]	8.2
2	9.4	14.9	7.0	10.1
3	9.5	10.0	[d]	11.4
4	15.9	13.7	7.0	10.3
Pooled estimate	13.0	13.7	7.0	9.9

[a] Formula as in Table 4.
[b] Newly emerged, wings soft.
[c] Not newly emerged.
[d] None caught in this category.

adults hibernate. That adults lived longer than indicated by recapture data is evidenced by the good condition of most adults (even the longest-lived) when they were last captured compared with their condition at the time of first capture.

The mean minimum life spans were calculated for each patch site with individuals categorized by age on the basis of wing wear (Table 3). These estimates are an indication of residence time in a patch. Females, both fresh and otherwise, have lower residence times than males (Table 3). We interpret this as being because females are more likely to leave a patch (i.e., have a shorter residence time) than males.

Sex Ratios

Males predominate at all patch sites (Table 1) and show similar changes in relative abundance over the study period across all four sites (Fig. 3; Spearman rank correlation coefficients: S1 × S3, 0.367, $0.01 < P < 0.05$; S1 × S4, 0.224, $P > 0.005$; S3 × S4, 0.728, $P < 0.001$; site 2 was ignored due to low sample sizes as were all samples with <10 individuals). All sites show a change from significantly more than 50% males, to significantly less than 50% males around early autumn (March, April). At other times of the year the sex ratio fluctuates from 75% to 50% males (Fig. 3). These changes may be due to sampling bias, changes in the sex ratio at birth, changes in male/female migration rates or male/female death rates.

To test if samples were biased we compared the estimates of sex ratio before and after the patch clearing exercise. This exercise gave the actual sex ratio in the patch on 8 July as 61% males. This does not differ from the sex ratio estimated by samples taken before (66%) and after this date (69%). On the strength of this result we feel that the sample estimates of the sex ratio probably indicate real fluctuations in the percentage of males. These fluctuations are not due to the produc-
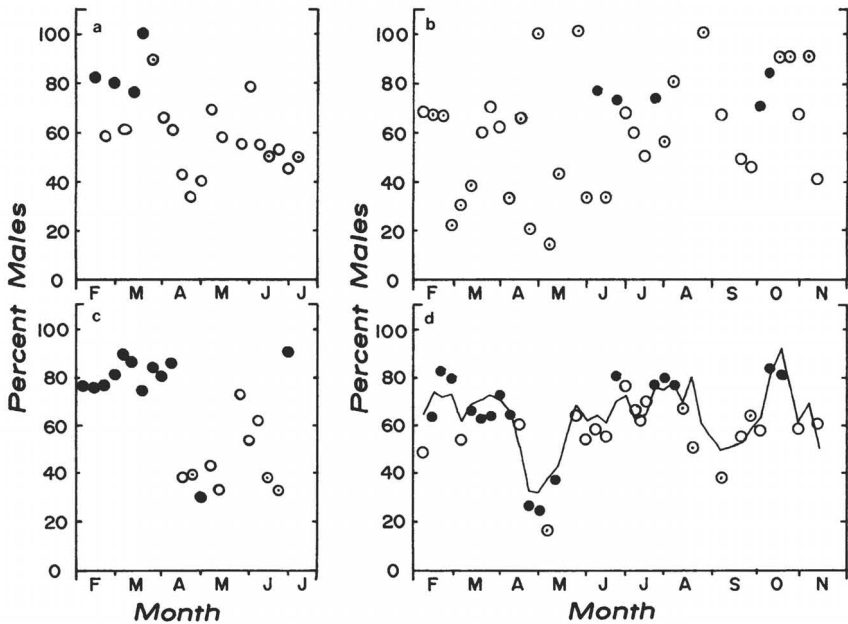
FIGS. 3a–d.   Percentages of males for each site plotted against time: site 1 (a), site 2 (b), site 3 (c) and site 4 (d). Solid symbols indicate significant deviation from 50% (P < 0.01). Open symbols denote non-significance. Double symbols indicate sample size small (<10). — average percent males across all sites shown in (d).

tion of all male broods—the sex ratio of newly emerged butterflies pooled over time for each site and the changes in the sex ratio at birth over time (pooled across sites) do not differ significantly from 50/50. This agrees with the sex ratio of laboratory reared adults (Zalucki, 1981c).

Population Turnover

Since, as far as we could tell, every adult was marked at site 4 on 8 July, a sample taken on the 12th should reveal what fraction had left, how many migrants had arrived and how many had emerged from around the patch (Table 4). Assuming that the population was about the same size on the 12th as on the 8th, then the sample taken on the 12th represents about half the population. On this basis multiplying the sample values on the 12th by two gives an estimate of the various marked and unmarked fractions in the population on that date.

On the basis of these calculations we suggest that about half the individuals marked on the 8th had left, and this was similar to the

TABLE 4.   Mark-recapture history of adults netted on 8 and 12 July.

Date	Total netted	Marks	Un-marked	Fresh	Date of first capture for marked insects				
					8 Jul	5 Jul	28 Jun	21 Jun	14 Jun
8 July[a]	119	28	91	13		14	6	4	4
12 July[b]	52	37	15	6	23	6[e]	4[d,e]	2[e]	2[e]
12 July[c]	104	74	30	12					

[a] Patch completely cleared.
[b] Twice normal sampling effort (about 1 hour).
[c] 12 July values multiplied by 2.
[d] Includes 2 individuals *not* captured on the 8th.
[e] Also caught on the 8th.

situation with the marked individuals first captured on the 5th and then recaptured on the 8th. Individuals marked earlier (e.g., 28, 21 and 14 June) seem to be "resident"; that is, captured on both the 8th and 12th. Of the 30 "new" individuals, 12 (about 50%) were born within the patch (wings were in perfect condition, no scale loss or still soft) and 18 had immigrated into the patch, as had two individuals marked on 28 June. These were *not* present on the 8th but were caught again on the 12th.

Discussion

The present study of adult *D. plexippus* was conducted in a region where the insect breeds continuously throughout the year. The host plants of *D. plexippus*, milkweeds, represent a discontinuous, heterogeneous resource for adults and larvae. Milkweeds grow in dense, relatively well defined stands or patches. Patches vary greatly in area, plant density, age, condition and dispersion. The number of adults within any one patch varies through the year, the fluctuations representing changing birth, death and movement rates. Adult monarchs are highly vagile and have the potential to range widely during the course of their lifetime. The evidence for monarch movement is extensive and consists of: (1) the recapture of marked individuals at a patch other than the site of first capture—although the number of these in this study was small (due mainly perhaps to low sampling intensity), they indicate that monarchs can move between patches; (2) over half of the "new" individuals entering a patch population were not necessarily born there; (3) monarchs can be observed flying in all types of habitat and new milkweed patches are rapidly colonized (see Zalucki & Kitching, 1982a, b, c); and (4) various studies in North America in all seasons (e.g., Gibo & Pallett, 1979; Urquhart, 1960; Urquhart & Munger, 1970; Urquhart & Urquhart, 1976).

The monarch's vagility makes it difficult to study patch populations

using techniques of mark-recapture. One difficulty is that in sampling a patch one is sampling a sub-population of a much larger population. Individuals in the sub-population move over a much wider area than is contained by a patch. For this reason marked individuals are not equally available for recapture in the sub- and parent populations. Movement into and out of the patch will cause fluctuations in the proportion of recaptures leading to large fluctuations in estimates of population size and large variances in associated vital rates (see also Brussard & Ehrlich, 1970).

Movement into and out of patches seems to depend partly on the interactions between males and females as evidenced by changing sex ratios. The changing sex ratios could also be due to differential male-female mortality. The mark-recapture method does not distinguish between losses due to death and those due to emigration. However, from laboratory studies, male and female survivorship curves are identical (fig. 6 in Zalucki, 1981b; $\chi^2_{21} = 0.908$). This leaves differential movement rates and consequent patch residence times (see Table 3) as the most likely explanation for changing sex ratios. Certainly, male-female interactions are dramatic. Males pursue any flying object within range. Females will attempt to evade males, and high speed chases usually ensue (see Pliske, 1974, for detailed description of courtship behavior). We suggest these sexual interactions between males and females could provide a mechanism whereby females are differentially dispersed from a local population, such as exists within a patch. Shapiro (1970) provides evidence for a similar dispersal mechanism in pierids.

The change in sex ratio towards females in early autumn (Fig. 3) is presumed to be due to the movement of females from around the countryside in towards large patches. It may even represent the return of individuals from inland areas, as the monarch's summer range contracts (Smithers, 1977). (Eanes & Koehn, 1978 note a similar change in sex ratios for migratory populations in North America.) However, this would imply that the inland population has a skewed sex ratio, for which there is no evidence.

Our observations indicate strongly that populations of monarchs around patches exhibit high rates of turnover. Our data on how far monarchs fly, given they leave a patch, are scant. Only five individuals were caught at sites other than the site of marking. These indicate the potential for cross-country movements but *not* what percentage of individuals undertake such movements. Of the butterflies netted, 87% are not recaptured (Table 1). Where do they go? Either monarchs "loiter" outside milkweed patches, moving in and out of local patches with some unknown percentage undertaking longer movements; or

most monarchs range widely if only by diffusion among many clumps of patches. Further intensive studies, some of which are in progress, will be needed to distinguish among these and other hypotheses.

ACKNOWLEDGMENTS

LITERATURE CITED

BRUSSARD, P. F. & P. R. EHRLICH. 1970. The population structure in *Erebia epipsodea* (Lepidoptera: Satyrinae). Ecology 51:119–129.
DETHIER, V. G. 1959. Food plant distribution and density and larval dispersal as factors affecting insect populations. Can. Entomol. 91:581–596.
EANES, W. F. & R. K. KOEHN. 1978. An analysis of genetic structure in the monarch butterfly *Danaus plexippus* L. Evolution 32:784–797.
EHRLICH, P. R. 1965. The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. Evolution 19:327–336.
—— & L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5:69–82.
GIBO, D. L. & M. J. PALLETT. 1979. Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. Canad. J. Zool. 57:1393–1401.
JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. Biometrika 52:225–247.
MUNGER, F. & T. T. HARRISS. 1970. Laboratory production of the monarch butterfly *Danaus plexippus*. J. Res. Lepid. 8:169–176.
PLISKE, T. E. 1974. Courtship behaviour of the monarch butterfly, *Danaus plexippus* L. Ann. Entomol. Soc. Am. 68:143–151.
SEBER, G. A. F. 1973. The Estimation of Animal Abundance. Griffin and Co. Ltd., London. 506 pp.
SHAPIRO, A. M. 1970. The role of sexual behaviour in density related dispersal of pierid butterflies. Amer. Nat. 104:367–372.
SHARP, M. A. & D. R. PARKS. 1973. Habitat selection and population structure in *Plebejus saepiolus* Boisduval (Lycaenidae). J. Lepid. Soc. 27:17–22.
SINGER, M. C. 1971. Evolution of food-plant preferences in the butterfly *Euphydryas editha*. Evolution 25:383–389.
SMITHERS, C. N. 1973. A note on length of adult life of some Australian butterflies. Aust. Entomol. Mag. 1:62–66.
—— 1977. Seasonal distribution and breeding status of *Danaus plexippus* in Australia. J. Aust. Entomol. Soc. 16:175–184.
SOUTHWOOD, T. R. E. 1966. Ecological Methods. Methuen, London.
URQUHART, F. A. 1960. The Monarch Butterfly. Univ. Toronto Press.
—— & F. MUNGER. 1970. A study of a continuously breeding population of *Danaus plexippus*. J. Res. Lepid. 7:169–181.
—— & N. R. URQUHART. 1976. A study of the peninsular Florida populations of the Monarch butterfly (*Danaus p. plexippus*; Danaidae). J. Lepid. Soc. 30:73–87.
ZALUCKI, M. P. 1981a. Temporal and spatial variation of parasitism in *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae: Danainae). Aust. Entomol. Mag. 8:3–8.
—— 1981b. The effects of age and weather on egglaying in *Danaus plexippus* L. (Lepidoptera: Danaidae). Res. Pop. Ecol. 23:318–327.
—— 1981c. Animal movement and its population consequences with a case study of *Danaus plexippus* L., Ph.D. Thesis, Griffith University, Australia.
——, A. CHANDICA & R. L. KITCHING. 1981. Quantifying the distribution and abundance of an animal's resource using aerial photography. Oecologia (Berl.) 50: 176–183.

———— & R. L. KITCHING. 1982a. The dynamics of oviposition of *Danaus plexippus* (Insecta: Lepidoptera) on milkweed (*Asclepias* spp.). J. Zool. Lond. 198:103–116.

———— 1982b. Temporal and spatial variation of mortality in field populations of *Danaus plexippus* L. and *D. chrysippus* L. larvae (Lepidoptera: Nymphalidae). Oecologia (Berl.) 53:201–207.

———— 1982c. The analysis and description of movement in adult *Danaus plexippus* L. (Lepidoptera: Danainae). Behaviour 80:174–198.