

EGG-LOAD ASSESSMENT AND CARRYOVER DIAPAUSE IN *ANTHOCHARIS* (PIERIDAE)

ARTHUR M. SHAPIRO

Department of Zoology, University of California, Davis, California 95616

ABSTRACT. At Gates Canyon, California, *Anthocharis sara* overdisperses its eggs, showing apparent egg-load assessment. *Pieris napi microstriata* at the same site shows a more typical contagious egg distribution. Pupae of *A. sara* frequently carry over into a second or third year of diapause in captivity. Similar phenomena apparently occur in *A. midea* of the eastern U.S. Evolutionary interpretations of such phenomena tend to overestimate "fine tuning" to local environments, but interspecific comparisons may reveal much broader patterns.

The life-history characteristics of insects are receiving increasing attention as theoretical models of such aspects as phenology, diapause and reproductive effort become common (Levins, 1969; Cohen, 1970; Giesel, 1976). The leaf- and inflorescence-feeding guilds of pierid butterflies offer excellent opportunities for studies of life-history phenomena as they affect both population and community ecology. This paper reports upon two ecologically important aspects of the life-history of the Sara Orange Tip, *Anthocharis sara* Lucas, in riparian woodland at Gates Canyon, Vaca Mts. (Inner Coast Range), Solano Co., north-central California (50-600 m).

Egg-load Assessment

"Egg-load assessment" means a female's choice to oviposit or not on a given plant is influenced by whether or not eggs (con- or heterospecific) are already present. The feedback may be negative (leading to overdispersion of eggs) or positive (leading to aggregation); usually the former is meant.

Rothschild and Schoonhoven (1977) obtained laboratory evidence that *Pieris brassicae* (L.), which lays its eggs in large clusters, and perhaps *P. rapae* (L.), which lays them singly, are capable of recognizing conspecific eggs on host plants and adjusting their oviposition behavior, presumably to avoid host overload. This is an appealing idea, although like most density-related factors influencing population density it is bound to be controversial. There is no evidence of such prudence in earlier studies of temperate butterflies (Dethier, 1959). The distribution of *P. rapae* eggs has been studied on field cabbages by Harcourt (1961), Kobayashi (1965 and earlier papers), and Jones (1977); all found contagious (negative binomial) distributions of eggs, arguing strongly against egg-load assessment by that species. Jones (1977) successfully modeled its oviposition behavior while specifically excluding egg-load assessment.

TABLE 1. Distribution of pierid eggs on *Barbarea verna* at Gates Canyon, California, 1973 through 1978 (pooled data), excluding 1977.

Number of eggs/plant	Size class of plant			Totals
	Large	Medium	Small	
<i>Anthocharis sara</i>				
0	154	202	46	402
1	90	138	35	263
2	24	20	2	46
3	1	2	0	3
Totals:	269	362	83	714
\bar{x} (eggs/plant):	0.52	0.57	0.47	0.51
s^2 :	0.45	0.40	0.30	0.41
	Mean eggs/plant with any eggs at all:			1.17
<i>Pieris napi microstriata</i>				
0	198	258	57	513
1	23	35	11	69
2	15	23	5	43
3	12	11	4	27
4	10	17	2	29
5	6	13	3	22
6	1	3	1	5
7	3	1	0	4
8	1	1	0	2
Totals:	269	362	83	714
	\bar{x} (eggs/plant):			0.75
	Mean eggs/plant with any eggs at all:			2.67

Whether or not assessment is a reality in either of these *Pieris*, egg censuses on pierids in California localities which have been under study for several years offer an opportunity to look for statistical evidence of it in others. The best data are for Gates Canyon.

Anthocharis sara deposits its eggs singly near the tops of Crucifers in riparian habitat—usually on stems, pedicels, or the bases of petioles, less often on buds, flowers, or leaves. They are initially creamy white, but rapidly turn orange, becoming conspicuous and easily censused. At Gates the principal host is *Barbarea verna* (Mill.) Asch. Table 1 presents egg counts of *A. sara* and of *Pieris napi microstriata* Comstock on 714 individual plants censused between 1973 and 1978, excluding 1977 (see below). Newly-laid *sara* eggs are distinguishable from *napi* by shape, while older ones are easily recognized by color. These two butterflies are sympatric and synchronic at Gates and feed on the same hosts, but *napi* is a leaf feeder while *sara* consumes

inflorescences and especially green fruit. Numbers of *napi* are more variable from year to year than those of *sara*, and this is reflected in the pooled 1973–78 data in which some 200 *napi* eggs are from its peak year of 1976 alone. The *napi* data are included as a contrast to *A. sara* in the context of their joint use of *Barbarea*.

The *Barbarea* plants have been grouped into three arbitrary size classes which incorporated information on both height and shape of plant (number of stems). Egg dispersion was analyzed statistically for each species on each size class and for the pooled plants. The eggs of *P. napi* are contagiously distributed in all cases, and the statistical properties of their distributions need not concern us here. For *A. sara* the means of the distributions all exceed their respective variances, implying some degree of overdispersion and hence of egg-load assessment. When the distributions are compared to Poisson series by a χ^2 test, medium and small plants both differ significantly ($P < .005$) while large ones do not ($.500 > P > .250$). This suggests that egg-load assessment is on a per-inflorescence, not a per-plant basis and breaks down when many stems are available. Unfortunately, this is not testable with these data as only plant totals were recorded. It is however, definitely occurring in some related species which oviposit in inflorescences (Shapiro, 1981). On the other hand, medium plants are preferred to large ones since about equal numbers of eggs are deposited on both although the biomass of the large plants is much greater. *A. sara* is a more efficient searcher than *P. napi*, since 44% of the plants received at least one *sara* egg vs. 28% with *napi* eggs; *napi*, however, lays more eggs per plant receiving any eggs.

To what extent are these patterns influenced by plant density and dispersion? The spatial distribution and conspicuousness of the host plant may have important, and sometimes subtle, impact on oviposition behavior (cf. Thompson & Price, 1977). The *Barbarea* plants at Gates Canyon are distributed in a nearly linear canyon-bottom environment, and an ovipositing *A. sara* is almost always in sight of other plants. Thus the likelihood of her finding the same plant after her seemingly obligatory interovipositional flight is quite low. Data collected in 1979 from isolated hosts surrounded by unfavorable grassland and chaparral environments (Shapiro, 1981) provide an additional clue. On such plants egg-load assessment seems to occur only by subsequent females after the eggs have darkened. Individual females may oviposit repeatedly on the same plant, with an intervening flight between each oviposition and the next. The overdispersion observed at Gates can then be viewed as a two-part phenomenon: a given female can overdispers her eggs only if sufficient hosts are available nearby, but later females may be obliged behaviorally to

TABLE 2. Distribution of *Anthocharis sara* eggs on *Barbarea verna* at Gates Canyon, California in 1977.

Number of eggs/plant	Size class of plant			Totals
	Large	Medium	Small	
0	4	19	40	63
1	2	9	12	23
2	1	5	1	7
3	0	1	0	1
Totals:	7	34	53	94
			\bar{x} (eggs/plant):	0.43
			Mean eggs/plant with any eggs at all:	0.78

defer to her darkened eggs whatever the host dispersion. The growing literature of egg-load assessment is reviewed and compared to a variety of data on various pierids by Shapiro (1981). It should be explicitly noted that interovipositional flights occur in most or all pierids which do not lay eggs in batches, whether or not egg-load assessment is suspected. The degree to which both phenomena are developed, coupled or decoupled, presumably reflects the relative strength of such selective forces as intra- and interspecific competition, predation, and parasitism, and in particular their spatial and temporal predictability.

Interspecific Interaction

1977 was the second year of severe drought in California, and biomass of *Barbarea* was reduced by an estimated order of magnitude at Gates. The number of plants was reduced, and only seven "large" plants could be found. Faced with this highly atypical host distribution, *A. sara* found only 33% of the plants—but its egg distribution did not change significantly ($.500 > P > .250$) (Table 2). *P. napi* was virtually absent in 1977 (only 1 egg was found). Did this affect *A. sara* in any detectable way? In 1973–78 (except 1977) there was some degree of positive association of the two species on individual plants (Table 3). This is presumably due to similar enough searching behavior to make the same individual plants especially attractive to females of both, rather than to a positive response *per se* to each other's eggs. This interpretation is bolstered by the observation that the same individual plants, or plants in the same locations, receive or do not receive eggs year after year. Due to egg-load assessment, *A. sara* is obliged to spread its eggs more widely, finding many more plants missed by *napi* than the converse. There is no indication that the presence or absence of *napi* affects *sara* at all.

TABLE 3. Measures of association between *Anthocharis sara* and *Pieris napi microstriata* at Gates Canyon, 1973–78 except 1977.

	Size class of plant		
	Large	Medium	Small
Expected # plants jointly occupied if independent	31.1	46.2	11.6
Observed # plants jointly occupied	39	63	10
χ^2	5.84	15.87	0.57
P	.025 > P > .010	P < .005	.500 > P > .250 (N.S.)
Cole's index of association (Cole, 1949) ^a	+0.285	+0.371	-0.050
Mean # eggs laid by <i>sara</i> on plants without <i>napi</i>	0.477	0.418	0.492
Mean # eggs laid by <i>sara</i> on plants with <i>napi</i>	0.690	0.731	0.500
Significantly different? ^b	yes	yes	no
Mean # eggs laid by <i>napi</i> on plants without <i>sara</i>	0.474	0.475	0.848
Mean # eggs laid by <i>napi</i> on plants with <i>sara</i>	1.052	1.125	0.622
Significantly different? ^b	yes	yes	no

^a Values range from +1 (completely associated) to -1 (completely negatively associated); 0 is independent.

^b Student's t-test.

Egg-load assessment is a form of contest competition akin to territoriality. The first female to oviposit on an inflorescence reserves it for her young, excluding any other individual which participates in assessment. The shortage of oviposition sites in 1977 could have led to at least three different responses by *A. sara*, or combinations of them: (1) longer-range dispersal of females beyond the study area; (2) increased searching efficiency with more use of normally unused plants; (3) increased willingness to oviposit multiply on normally used plants. There is no direct evidence that any of these occurred; the egg data argue strongly against (3) and give no support to (2), while there are no adult data bearing on (1). The total egg output in 1977 was somewhat lower than in some preceding and following years, but this could be due to decreased fecundity or life-span rather than to dispersal. The 1979 data on isolated plants supported alternative (3) above, at least for individual (but not subsequent, post-egg-darkening) females, but here the host density was very much lower than at Gates even under the severe stress of 1977. The ratio of females to plants apparently did not pass the threshold at which same-day multiple ovipositions would at least partly nullify egg-load assessment.

TABLE 4. Developmental times of *Anthocharis sara* pupae from Gates Canyon, reared *ex ovo* on continuous light at 25°C, stored at 3°C. All were in diapause.

Year	Number of hatching after time at 3°:		
	Following spring	Second	Third or more ^a
1973	3	5	3
1974	6	8	5
1975	0	4	2
1976	0	9	3
1977	3	5 ^b	—
Totals:	12	31	13

^a Includes pupae which died after 2 years of storage.

^b Includes all pupae unclosed as of spring, 1978.

Carryover Pupae

Most uni- or bivoltine pierids have a mandatory chilling requirement to break pupal diapause, and will not eclose without a period of refrigeration. If held at room temperature they may live several years before expiring. Most pupae will eclose if held near 0°C for 9–10 months, but in any brood some may require a second or even a third year of chilling. The incidence of such carryover pupae, and their relation to environmental conditions during rearing, are uninvestigated. They are of interest because they may provide a “hedge” against population extinction due to a single catastrophic season, analogous to the “seed bank” of the plant ecologist (Harper, 1977). Facultative bi- or trienniality in normally annual species is on its face highly adaptive in uncertain environments. Insofar as it lengthens the mean generation time it reduces r , the intrinsic rate of natural increase, and it should therefore carry a selective tradeoff. The higher the environmental uncertainty, the easier it becomes to account for pupal carryover in terms of individual, rather than group, selection. Its taxonomic distribution in Lepidoptera is reviewed by Powell (1974).

In multivoltine pierids generally, diapause can be inhibited by rearing on long days or continuous light at temperatures of 25°C. This does not work on the spring univoltines. Since 1973 several eggs of *A. sara* have been collected each year at Gates for lab rearing on this regime. All the resulting pupae have diapaused, despite the facultative bivoltinism of the population, and 76% have carried over beyond the first year (Table 4). The tendency to produce carryover pupae is thus great in this population.

Between 1973 and 1978 rainfall at Vacaville, at the mouth of Gates Canyon, varied between 95.78 and 23.32 cm/water year (July 1–June 30). As noted above, *Barbarea* biomass fluctuated by an order of mag-

nitude, and in one year *P. napi* was virtually absent. Yet numbers of adult *sara* were surprisingly constant, and so were egg counts. Do carryover pupae provide a buffer against environmental uncertainty for this species?

A counterpoint: *Anthocharis midea*

The eastern Falcate Orange Tip, *A. midea* (Hbn.), belongs to a different subgenus than *A. sara* and occurs in a region of much less climatic uncertainty. Like *A. sara*, however, it is a spring-univoltine Crucifer feeder (perhaps locally facultatively bivoltine southward, but this is disputed), even including *Barbarea verna* in its diet (dos Passos & Klots, 1969; Shapiro, unpubl.).

Clark (1932, p. 165–166) reviews H. F. Schönborn's correspondence with W. H. Edwards regarding this species. He "never found a larva in open fields, although the plant grows there in abundance in large patches. I always found them on isolated plants growing in places sparingly covered by . . . trees." This is familiar to Californians who recognize the limitation of *A. sara* to riparian woodland and its failure, after 150 years, to colonize the immense stands of weedy mustards on the broad valley floors. Schönborn moreover "never found more than one egg on a plant," nor have I in eastern Pennsylvania and New Jersey ($N \approx 100$). These egg distributions carry no statistical force, but their implications are obvious.

Dos Passos & Klots (1969) provide some data on carryover pupae. Of thirteen 1953 pupae, 6 emerged in 1954 and 7 in 1955. They quote C. E. Rummel as having reared a 3-year individual. Photoperiods and temperatures are not specified. In 1966 I reared 4 larvae from Brown's Mills, Burlington Co., N.J. under uncontrolled photoperiod and temperature, and all gave carryover pupae.

These fragmentary data are included to emphasize the danger inherent to inferring causality from apparent adaptation. Stearns (1977) reviewed the epistemological pitfalls of life-history theory and concluded that many of its "validations" are spurious. Pitelka & Van Valen (1974) said the same thing, adding that "many theories are true when their assumptions are not, but this can never be taken for granted."

Both egg-load assessment and pupal carryover, considered uniquely as attributes of the Gates Canyon population of *A. sara*, appear as good candidates for "finely-tuned" adaptations to host dispersion and climatic uncertainty in that particular locality, and the temptation to interpret them thus in the terms of current theory is strong. When *A. midea* is also considered, the "fine-tuning" hypothesis becomes less appealing: the ecologies of the two species are quite different, while

their obvious commonality is genetic. Both egg-load assessment and pupal carryover may be derived by both species from a common ancestor; both *may* be preadaptive in current ecological contexts, but perhaps not. (One need not belabor the difficulties in establishing that X is *the* function of some attribute of an organism.) The subgenus *Falcapica*, which includes *midea* and *lanceolata* Lucas of the Pacific slope and is not really distinguishable from *Paramidea* of East Asia (*scolymus* Butler and *bieti* Oberth.), shows a classic Arcto-Tertiary relict distribution. The subgenus *Anthocharis*, to which *sara* belongs, is disjunctly distributed in western North America and the Palearctic region (mostly western) and is also probably Arcto-Tertiary. We are beginning to talk about common ancestors of no small antiquity. Moreover, the related genus *Euchloe*, which also shows an Arcto-Tertiary pattern of dispersion, assesses egg load and has carryover pupae as well (Shapiro, in prep.), pushing the common origin of these phenomena back even further in time.

ACKNOWLEDGMENTS

Field work was funded through 1976 by grant D-804 from the Committee on Research, University of California, Davis. I thank H. Carey and R. Davis for forcing epistemological questions on me without relief.

LITERATURE CITED

- CLARK, A. H. 1932. The butterflies of the District of Columbia and vicinity. Bull. U.S. Natl. Mus. 157: 1-337.
- COHEN, D. 1970. A theoretical model for the optimal timing of diapause. Am. Nat. 104: 389-400.
- COLE, L. C. 1949. The measurement of interspecific association. Ecology 30: 411-424.
- DETHIER, V. G. 1959. Egg-laying habits of Lepidoptera in relation to available food. Canad. Entomol. 91: 554-561.
- DOS PASSOS, C. F. & A. B. KLOTS. 1969. The systematics of *Anthocharis midea* Hübner (Lepidoptera: Pieridae). Entomol. Amer. 45: 1-34.
- GIESEL, J. T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. Annu. Rev. Ecol. Syst. 7: 57-79.
- HARCOURT, D. G. 1961. Spatial pattern of the imported cabbageworm, *Pieris rapae* L., on cultivated Crucifers. Canad. Entomol. 93: 945-952.
- HARPER, J. L. 1977. Population Biology of Plants. Academic Press, London. 892 pp.
- JONES, R. E. 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 46: 195-212.
- KOBAYASHI, S. 1965. Influence of parental density on the distribution pattern of eggs in the common cabbage butterfly *Pieris rapae crucivora*. Res. Popul. Ecol. (Kyoto) 7: 109-117.
- LEVINS, R. 1969. Dormancy as an adaptive strategy. Symp. Soc. Exptl. Biol. 23: 1-10.
- PITELKA, F. & L. VAN VALEN. 1974. Intellectual censorship in ecology. Ecology 55: 924-925.
- POWELL, J. A. 1974. Occurrence of prolonged diapause in Ethmiid moths. Pan-Pac. Entomol. 50: 220-225.
- ROTHSCHILD, M. & L. M. SCHOONHOVEN. 1977. Assessment of egg load by *Pieris brassicae* (Lepidoptera: Pieridae). Nature 266: 352-355.

- SHAPIRO, A. M. 1981. The Pierid red-egg syndrome. *Am. Nat.*, in press.
- STEARNS, S. C. 1977. The evolution of life-history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8: 145-171.
- THOMPSON, J. N. & P. W. PRICE. 1977. Plant plasticity, phenology, and herbivore dispersion: wild parsnip and the parsnip webworm. *Ecology* 58: 1112-1119.

Journal of the Lepidopterists' Society
34(3), 1980, 315

NEW LOCALITY RECORDS FOR THE SALT MARSH COPPER,
EPIDEMIA DORCAS DOSPASSOSI (LYCAENIDAE)

Since its discovery in 1939 (McDunnough, 1940, *Canad. Ent.* 72: 130-131) *Epidemia dorcas dospassosi* (McDunnough) has been recorded only from its type locality, Bathurst, New Brunswick (Ferris, 1977, *Bull. Allyn Mus.* 45: 1-42). In late July and early August 1979 I briefly searched every easily accessible salt marsh from Bartibog Bridge, Northumberland Co., New Brunswick to Campbellton, Restigouche Co., New Brunswick; and several salt marshes on the Gaspé Peninsula, Quebec, from Oak Bay on the Bay of Chaleur to Ste.-Anne des Monts on the south shore of the St. Lawrence River. *E. d. dospassosi* was collected in the following 9 localities, including 3 separate localities within the city limits of Bathurst.

- 1) Hay Island, 2 km south of Neguac, Northumberland Co., New Brunswick; 30 July 1979. 9 ♂ seen and collected, individuals were scarce and present only on the western tip of the island.
 - 2) Wishart Point, mouth of Tabusintac River, Northumberland Co., New Brunswick; 31 July 1979. Adults numerous, 7 ♂ and 11 ♀ collected.
 - 3) Village-des-Poirier, 4 km SW of Maisonnette, Caraquet Bay, Gloucester Co., New Brunswick; 2 August 1979. Adults scarce, 3 ♂ and 4 ♀ collected.
- The following 3 localities are within the city limits of Bathurst, Gloucester Co., New Brunswick. These populations seem to be separated from each other by unsuitable habitat.
- 4) Carron Point, NE point of Bathurst Harbour; 1 August 1979. Adults very common in association with *Coenonympha nipisiquit* McDunnough.
 - 5) East Bathurst, SE corner of Bathurst Harbour, mouth of Nepisiquit River; 28 July 1979. Adults very common.
 - 6) Youghall Beach, NW corner of Bathurst, marsh bordering Peters River; 27 July 1979. Adults scarce, possibly just emerging, 3 ♂ and 1 ♀ collected, in association with *C. nipisiquit*.
 - 7) Beresford, Gloucester Co., New Brunswick; 27-28 July 1979. Adults scarce, 5 ♂ and 8 ♀ collected. This locality is 5 km NW of Youghall Beach with a continuous salt marsh habitat between the two localities.
 - 8) St.-Siméon, Bonaventure, Gaspé Peninsula, Quebec; 26 July 1979. A cool windy evening, 1 fresh ♂ collected resting on *Carex*.
 - 9) Penouille, Gaspé, Gaspé Peninsula, Quebec; 24 July 1979. About 20 adults seen, 2 ♂ and 2 ♀ collected.

ANTHONY W. THOMAS, *Maritimes Forest Research Centre, P.O. Box 4000, Fredericton, New Brunswick, E3B 5P7, Canada.*