

Chew, F. S. & R. K. Robbins. 1984. Egg-laying in butterflies. IN: The Biology of Butterflies. R.I. Vane-Wright & P.R. Ackery. (Eds.). Academic Press, London. Symposium of the Royal Entomological Society of London. No. 11: 65-79 + Lit. Cited.

## 6. *Egg-laying in Butterflies*

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When a female butterfly lays an egg, thereby abandoning her offspring, her behaviour is the result of physiological and ecological factors as well as evolutionary history. In this paper we present a broad overview of oviposition in butterflies with the goal of integrating into an evolutionary framework those factors that influence egg-laying. This is a massive subject; of necessity, we have covered only a few areas in depth. We emphasize multidisciplinary methodologies as the approach yielding the most complete understanding of oviposition. We refer readers to related reviews, emphasizing optimal foraging methods (Rausher 1982a, Stanton 1982b, Miller & Strickler, in press; but see the criticisms of Gould & Lewontin 1979 to this approach) or focusing on the chemical interactions mediating oviposition (Feeny *et al.* 1983). We focus our discussion on four major questions: What factors influence (1) egg production and oviposition rate? (2) specificity of egg-laying site? (3) patterns of egg dispersion? and (4) evolution of oviposition specificity?

### **Patterns of Egg Production**

The gross anatomy of female butterfly reproductive systems is similar to that of other Lepidoptera with two genital openings (Ditrysia): a ventro-posterior copulatory opening for mating and receiving the spermatophore (the bursa copulatrix), and a posterior ovipore for laying eggs (Stern & Smith 1960, Richards & Davies 1977, Hinton 1981). There are two ovaries, each composed of four

ovarioles. Eight oviduct branches connect the ovarioles to a common oviduct that leads to the ovipore. The common oviduct contains openings to the spermatheca, where sperm are stored after they migrate via the ductus seminalis from the bursa copulatrix, and to the colleterial glands, which secrete the cement that glues eggs to the oviposition substrate, and which in some Lepidoptera may cover the eggs with a polysaccharide-rich layer called spumaline. Arnold & Fischer (1977) and de Jong (1978) discuss aspects of the functional anatomy of copulation and oviposition.

Male lepidopterans produce both 'normal' nucleated (eupyrene) sperm and anucleated (apyrene) sperm (Meves 1903). These sperm types undergo different spermatogenetic development and activation (Shepherd 1974a,b, Friedlander *et al.* 1981 and references therein). Apyrene and eupyrene sperm migrate from the corpus bursae of the female to separate spermathecal sacks (Holt & North 1970, Katsuno 1977) although occasionally the 'apyrene sack' is absent (J. G. Shepherd, pers. comm.). Apyrene sperm disintegrate in the spermatheca (Holt & North 1970, Riemann & Gassner 1973), and do not fertilize eggs (Friedlander & Gitay 1972). Although apyrene sperm occur in all lepidopterans tested (butterflies include *Pieris (Artogeia) rapae* and *Papilio polyxenes*, J. G. Shepherd, pers. comm.) as well as snails and rotifers (Friedlander 1975), their function is unclear. Physiological hypotheses are that they facilitate eupyrene migration to the spermatheca (Iriki 1941, Friedlander & Gitay

1972), and that they provide male contributed nutrition for the female (Riemann & Gassner 1973). A proposed evolutionary explanation for apyrene sperm is that they inactivate eupyrene sperm from previous matings (R. E. Silberglied & J. Shepherd, pers. comm.).

The following brief description of oogenesis in butterflies is summarized from a number of sources (Stern & Smith 1960, Telfer 1965, Ehrlich & Ehrlich 1978, Dunlap-Pianka 1979, Hinton 1981, Herman & Dallman 1981). Each ovariole contains a string of progressively enlarging and maturing follicles. Each follicle comprises a primary oocyte and seven nurse cells enclosed in a follicular envelope. As in other insect eggs, lepidopteran yolk protein appears to be synthesized as vitellogenin (probably a glycoprotein—Engelmann 1979, Aldrich *et al.* 1981) by the fat body, and taken up in the oocytes by pinocytosis from the female's haemolymph. As vitellogenesis progresses, nurse cells reach their maximal volume, then transfer all their cytoplasm to the oocyte. After completion of oocyte growth, the follicle cells secrete the chorion, and the mature oocyte ovulates from the follicular envelope into one of the eight branches of the oviduct. From the oviduct branch, the mature chorionated egg passes into the common oviduct. After fertilization, the egg then passes down the common oviduct, past the opening to the colleterial glands and through the ovipore. Recent descriptions of the external morphology of insect eggs include portfolios of scanning electron micrographs of chorion surfaces (Downey & Allyn 1980, 1981 and references therein, and Hinton 1981). Kafatos (1981) reviews developmental and genetic aspects of chorion protein synthesis.

Ovary maturation, oogenesis and vitellogenesis are markedly enhanced by juvenile hormone (Herman 1975, Pan & Wyatt 1971, 1976, Deb & Chakrovorty 1981, Herman & Dallman 1981; cf. Nicholson 1976). Other interactive factors include photoperiod (Herman 1975), temperature (Barker & Herman 1973), diapause (Edwards 1973, Herman 1981), mating (Herman & Barker 1977), and nutrition. Interactions between endocrinological and nutritional factors in butterflies are not well understood (Tojo *et al.* 1981). The nutritional maintenance regimes utilized by some endocrinologists do not seem sufficiently controlled to invite speculation (e.g. Herman & Dallman 1981).

#### Nutritional Correlates of Fecundity

Realized fecundity depends upon potential fecundity (the number of primary oocyte cells—e.g. Dunlap-Pianka *et al.* 1977) and various ecological factors, particularly those related to

nutrition. The purpose of this section is to discuss ecological factors that affect actual fecundities. We first note, however, that measures of fecundity in the literature vary. Contents of ovarioles of field-caught females (Ehrlich & Ehrlich 1978), tabulations based on several methods (Hinton 1981) and comparison of various methods for one species (Yamanaka *et al.* 1978) are not equivalent.

Specialization of larvae for assimilation and growth enables them to accumulate limiting nutrients that may be used in the formation of eggs. Herbivorous larvae often assimilate nitrogen preferentially (in the form of amino acids or proteins—Scriber & Slansky 1981). Correlation between adult size and fecundity (Baker 1968a, references in Hinton 1981) suggests that larval nutrition may generally determine reserves available for oogenesis. Female adult insects tend to be heavier than males and often contain greater caloric (fat) content (Scriber & Slansky 1981).

Adult females may supplement larval nutrient reserves. Nutrients and water assimilated by adult females support metabolism for egg maturation (e.g. *Colias eurytheme*, Stern & Smith 1960). Some butterflies discriminate among potential nectar sources, and preferentially visit flowers that produce nectars rich in water, monosaccharides, and nitrogen-rich amino acids (e.g. *Colias* species, Watt *et al.* 1974; DeVries, *in litt.* reports that Costa Rican butterflies feed on parts of rotting fruits that are rich in amino acids). Females of some ithomiines follow army ants, and feed on ant-bird droppings, which are probably rich sources of nitrogen (Ray & Andrews 1980). Amino acids from pollen contribute to adult longevity and oogenesis in *Heliconius* (Gilbert 1975, Dunlap-Pianka *et al.* 1977, Boggs *et al.* 1981; see also Ch.3). Availability of sugars in the adult diet markedly enhances female longevity and number of egg clusters in *Euphydryas editha* (Ch.2); availability of amino acids, however, extends production of maximum-sized eggs in later clutches, in contrast to the otherwise approximate 10% decrease in egg size (Murphy 1981). Murphy's experiments, together with those of Telfer & Rutberg (1960), suggest that age-dependent decreases in egg size in cecropia moths, *Pararge aegeria* and *Pieris rapae* (Jones *et al.* 1982, Wiklund & Persson 1983, see below) reflect depletion of nitrogen stores. For butterflies whose adults eat nitrogen-rich foods, resources for egg production may not be limited by larval reserves (Ch.3).

Adult males may also provide females with nitrogen for vitellogenesis and egg maturation. Spermatophores contain protein that may be absorbed by females and contribute to maintenance and oogenesis (Boggs & Gilbert 1979, Boggs & Watt 1981). Subsequent matings may contribute to

the fitness of later-mating males (because of sperm precedence—Labine 1964, Boggs & Watt 1981), and females, which may obtain a greater supply of protein. Boggs & Watt (1981) and Boggs & Gilbert (1979) suggest that male spermatophores may represent an important nutritional resource for butterflies which do not manipulate pollen sources as supplements of larval nitrogen reserves (e.g. *Colias*, *Danaus plexippus*).

Realized fecundity may be uncorrelated with nutritional status in temperate areas where cold weather unsuitable for flight activity occurs frequently (Douwes 1976a, Gossard & Jones 1977, Courtney 1980, Wiklund & Persson 1983). For example, Wiklund & Persson (1983) found that individual fecundities for *Pararge aegeria* were uncorrelated with adult size or number of spermatophores received, but were strongly correlated with the amount of time a female was able to fly and oviposit.

#### Egg Size

Female age may affect weight or size of eggs produced. Telfer & Rutberg (1960), Murphy (1981) and Jones *et al.* (1982) noted that eggs produced by individuals become smaller as females age. Wiklund & Persson (1983) observed a similar progression in *Pararge aegeria*, but interestingly, demonstrated that egg weight is not correlated with hatchability, mortality, larval growth rate, or eventual pupal weight. For *Euphydryas editha*, however, there appears to be an egg weight threshold below which development is abnormal (D. D. Murphy, pers. comm.).

Egg size varies substantially among butterfly species with comparable adult body sizes. Labine (1968) found a twenty-fold range in egg volume among four species. Egg weights or volumes of congeners, however, apparently differ by less than a factor of two (*Heliconius*, Dunlap-Pianka 1979; *Parides*, *Papilio*, *Siproeta* [as *Victorina*], Young 1972). More approximate estimates, extrapolated from measurements of single dimensions (e.g. egg height) are consistent with this trend. (Such egg measurements are widely scattered in the literature; see e.g. Scudder 1889, Chew 1981.)

Species that produce small eggs can be more fecund, but often produce a smaller total volume or weight of eggs than do species that produce larger eggs (Labine 1968, Young 1972). Because adults of fecund species may be of comparable size to those of less fecund species, smaller total egg volumes or weights may reflect proportionally smaller energy allocation to reproductive effort. However, because measures of reproductive effort must account for possible supplementation of larval reserves by adult nutrient intake (e.g. Boggs 1981a), accurate

estimates of reproductive effort will require additional data on adult feeding habits and energy expenditure.

Egg size may be related to number of larval instars and adult size. Dyar (1890) noted that larval head capsule widths of some 28 lepidopteran species increase 1.2 to 1.4 times between instars; this increase approximates a doubling of volume in each instar. The significance of this finding is that doubling egg size theoretically allows a species to eliminate one instar while producing the same sized adult. To the extent that Dyar's law is valid (see Richards & Davies 1977 for exceptions, Richards 1949 and Wright & Clarke 1981 for factors affecting size changes between instars), this theoretical deduction may provide a convenient 'rule of thumb' for investigating the relations among egg size, number of instars, and adult size. Species with variable numbers of instars, such as some brassolids (Aiello & Silberglied 1979), would be particularly appropriate experimental animals for such a study. To our knowledge, these relationships have not been explored, but the foregoing discussion on nutritional influences suggests that the relationships may be complex.

#### Rate of Oviposition

Reproductive patterns involve consideration not only of the number and size of eggs, but also egg distribution over time and space (onset of oviposition, oviposition rate, cluster size—Labine 1968). We consider here factors that influence egg distribution over time and defer to a later section discussion of spatial aspects of egg distribution. Gossard & Jones (1977) distinguish between factors affecting the rate of oogenesis and those affecting the rate at which eggs are laid. Butterflies with different egg-laying rates may require about the same amount of time to mature single eggs, but have different numbers of simultaneously maturing oocytes (Dunlap-Pianka 1979).

Available data on rate of oviposition (records of eggs produced by individual females per unit time under various conditions—e.g. Yamanaka *et al.* 1978, Yamamoto & Ohtani 1979) during adult lifespans appears to form three general categories. We describe them as distinct patterns but they may well be modes of a continuum. First, females may eclose with large numbers of mature eggs in their oviducts, and begin laying eggs very soon after mating (e.g. *Euphydryas editha*, Labine 1968). The presence of a very large egg load in the oviducts at the time of eclosion would probably preclude much pre-oviposition dispersal by females (Labine 1968). Second, females may eclose with few mature eggs, but oocytes quickly mature after the female mates and begins to nectar, e.g. *Pieris rapae*, *Colias*

*eurytheme*, *Agraulis vanillae* and *Anartia fatima* (respectively, Gossard & Jones 1977, Yamamoto & Ohtani 1979, Stern & Smith 1960, Dunlap-Pianka *et al.* 1977; R. E. Silberglied, pers. comm.). These butterflies, which are often widely-dispersing, produce relatively few eggs during the first few hours or days of adult life, but oviposition rates quickly rise to a peak and then sharply decline after a few days. The third pattern is characterized by oviposition rates that remain constant for comparatively long periods. These butterflies, e.g. *Heliconius*, produce fewer, usually somewhat larger eggs during their lives than those in the first two patterns, and tend to have longer active lives.

These generalized oviposition patterns may vary among congeners. For example, while *Pieris rapae* exemplifies the second grouping, *P. napi nesis* produces eggs in a pattern that more closely resembles that of *H. charitonius* in the third grouping (Dunlap-Pianka 1979, Yamamoto & Ohtani 1979).

#### Scales on Eggs

Females of some lycaenid and hesperiid species have tufts of scales (at the posterior end of the abdomen) that adhere to eggs as they are laid. Lycaenid records include *Chaetoprocta odata*, *Nordmania acaciae*, *N. myrtale*, *Crudaria leroma*, *Phasis wallengrenii* and *P. argyrophaga* (de Nicéville 1890, Clark & Dickson 1971, Nakamura 1976). Females of *Pseudaletia* have large tufts of anal scales that presumably adhere to eggs (Stempffer 1967). Scales and dust accumulate on the eggs of *Japonica lutea* and *J. saepestriata* (Shirôzu & Hara 1960-1962, Nakamura 1976), but the females lack conspicuous tufts of abdominal scales. Hesperiid records include *Daimio tethys*, *Tagiades trebellius*, *T. litigiousus*, and *Matapa aria* (Shirôzu & Hara 1960-1962, Johnston & Johnston 1980). These species represent several thecline tribes and two hesperiid subfamilies, indicating repeated evolution of the phenomenon. Hinton (1981) summarizes records among moths.

Proposed explanations for the occurrence of adherent scales on butterfly eggs include protective and nutritive functions. The scales might shield the egg like armour, camouflage it, or emit a chemical that deters parasitoids (de Nicéville 1890, Nakamura 1976, Downey & Allyn 1981). Alternately, these scales may be nutritionally important to newly hatched larvae. Downey & Allyn (1981) state that larvae of lycaenid species with adherent scales generally consume the entire eggshell after hatching, in contrast to the usual lycaenid behaviour of eating only a small exit hole. Larvae of *C. leroma*, however, do not eat their eggshells (Clark & Dickson 1971). As mentioned by Downey

& Allyn (1981), removal and addition experiments are required to determine the functions of these specialized scales.

#### Specificity of Oviposition Site

The idea that taxonomic specificity of butterfly-angiosperm associations is mediated by plant secondary compounds (e.g. Fraenkel 1959) has strongly influenced studies of determinants of oviposition specificity. Because many studies on larvae implicate plant secondary compounds as important determinants of larval taxonomic specificity, for physiological (e.g. Erickson & Feeny 1974) as well as behavioural reasons (e.g. Waldbauer 1968), the conspicuous, 'characteristic' compounds associated with individual plant families have been the focus of many investigations of oviposition cues. However, determinants of larval foodplant suitability and determinants of oviposition specificity need not be the same (see e.g. Courtney 1981, 1982a, who suggests that foodplant suitability of the crucifer *Hesperis matronalis* (Brassicaceae) for *Anthocharis cardamines* larvae is determined primarily by mechanical defences while ovipositing females are attracted to visually conspicuous, blooming flowers). Ovipositing females perceive plants using many sensory modalities. Any stimulus, if correlated with first instar larval success in locating suitable foodplants, may provide a cue for oviposition sites.

Oviposition sites are not equivalent to larval foodplants because some apparently 'mistaken' choices are normal behaviour, even if they are imprecise assessments of what is suitable for larval development. Examples of apparent 'mistakes' include oviposition on the following: non-plant substrates (Dethier 1959a and references therein; Singer *et al.* 1971); withered, or otherwise unsuitable plant parts (Tutt 1899, Wiklund 1977b); plants that do not support larval development and that are taxonomically and phytochemically unrelated to suitable larval hostplants (Dethier 1959a, Singer 1971, Chew 1977); plants that do not support larval development, but which are taxonomically and phytochemically related to suitable larval hostplants (Hefley 1937, Straatman 1962, Sevastopulo 1964, Smiley 1978a, Rodman & Chew 1980, Berenbaum 1981); failure to discriminate among plants suitable for larvae, but whose ingestion results in significantly variable developmental times or adult weights (Dolinger *et al.* 1973, Chew 1975, 1977); suitable plants of insufficient size to support complete larval development (Dethier 1959a, White 1974, Chew 1977); ignoring specific habitats in which suitable

larval hostplants grow (Petersen 1954, Owen 1959 and references therein, Shapiro & Cardé 1970, Singer 1971, Benson 1978 and references therein, Smiley 1978a, Ohsaki 1979, Courtney 1980, Chew 1981, Jordan 1981); ignoring plant species suitable for larval growth that occur in habitats where adults fly (Emmel & Emmel 1969, Gilbert & Singer 1975 and references therein, Neck 1973, 1977). But many 'mistakes' do not necessarily have dire consequences, and many represent normal oviposition behaviour for the specific butterfly species involved (see Tutt 1899; Ch.7). They do, however, provide a tool for probing oviposition processes in much the same way that mutations are routinely used to reveal genetic processes. They also emphasize the necessity of studying other life-history stages to assess the role of adult choice in the nutrition of larval offspring.

#### Measuring Preferences

To study oviposition specificity, we must be able to assess butterfly preference among potential oviposition sites. Methods for detecting and quantifying preference are extensively discussed in literature on foraging behaviour (e.g. Pyke *et al.* 1977). These methods usually compare the frequency with which potential resources are chosen (Berube 1972, Chew 1977, Jaenike 1980) or observe how encounters with particular resources affect subsequent searching behaviour (Jones 1977b, Stanton 1982a). We refer readers to discussions of specific methodologies (e.g. Stanton 1982a, Singer 1982a).

Sampling procedures may bias measures of oviposition preferences. Variation in the plant species chosen by individuals has been documented in laboratory or cage tests (Singer 1971, Wiklund 1981, Tabashnik *et al.* 1981) and in the field (Singer 1982a, Chew 1977, Rausher 1978). These observations are based on obtaining a limited sample of behaviour from many 'randomly chosen' individuals rather than obtaining a large sample of behaviour from each chosen individual (cf. Douwes 1968; Tabashnik *et al.* 1981, Wiklund 1981). This procedure may underestimate the variance in an individual's behaviour and correspondingly overestimate the variance among individuals. For example, the number of crucifer species chosen by ovipositing *Pieris* increases with the length of the observed oviposition sequence; differences among individuals are probably artifacts of the small number of oviposition choices recorded for each individual (Chew 1977).

Observed preferences may vary with the motivational state of females, season, or geographic location. Females that carry heavy egg loads or have not recently oviposited, may more readily

accept a variety of oviposition substrates (Singer 1971, 1982a, Jones 1977b, Wiklund 1981). Oviposition preferences may vary within a season or between seasons (Rausher 1978, 1981a, Stanton 1980, 1982a). Geographic variation in flight behaviour and oviposition choice has been documented in *Euphydryas editha* (Singer 1971, Gilbert & Singer 1973, White & Singer 1974). This variation suggests that care is necessary in generalizing results from studies of single populations.

#### Secondary Plant Compounds as Determinants of Specificity

Although the clear roles prematurely ascribed to secondary plant compounds in herbivore-plant interactions by early work (e.g. Verschaffelt 1911) have now been rendered more complex by subsequent findings, they nonetheless provided impetus for examining butterfly phytochemical specificity. Many papers written since 1950 on foodplant choice by butterflies and other herbivores are steeped in corollaries of insect-plant coevolution and spiced with the diverse flavours and aromas that angiosperms produce (Dethier 1970, Feeny 1975). As a result, we know more about butterfly response to secondary plant compounds than about other determinants of specificity. However, although some butterflies oviposit in response to single compounds (or classes of compounds, e.g. *Pieris brassicae* in response to glucosinolates, David & Gardiner 1962), such unequivocal results probably represent isolated cases.

#### Perception of secondary compounds

In adults and caterpillars, peripheral chemoreceptors may respond to specific compounds or to a variety of stimuli. Specialized receptors appear to be restricted to a few types, which vary among species and which are correlated with the known feeding habits of particular species. For example, *P. brassicae* has specialized receptors for glucosinolates (Ma & Schoonhoven 1973; Dethier 1978, 1980a gives other examples).

Most contact chemoreceptors and antennal olfactory receptors, however, respond to a wide variety of stimuli. Individuals possess many generalized receptors that differ in their sensitivities and electrophysiological responses to given stimuli. The greater number of these different receptor types in herbivorous caterpillars and their adults enables these insects to perceive a large diversity of compounds, so giving them an expanded sensitivity when compared, for example, with the carnivorous dipteran *Phormia* (Dethier 1980a)—whose limited receptors make it 'blind' to many stimuli. A similar

positive correlation exists between number of receptor types and diet breadth in grasshoppers (Chapman & Blaney 1979 and references therein).

Females may perceive foodplants chemically before alighting (Minnich 1924). Various lepidopterans respond differentially to potential larval foodplants before contact (Hovanitz & Chang 1964, Douwes 1968, Vaidya 1969a,b, Berube 1970, Rothschild & Schoonhoven 1977, Mitchell 1978); the chemical basis for differential response, however, is little explored (see further below). Female *P. brassicae* have olfactory sensilla on most distal flagellar segments of the antennae (Behan & Schoonhoven 1978; Den Otter *et al.* 1980).

Once a female alights, contact chemoreceptors respond to plant compounds that may stimulate or inhibit oviposition (e.g. Lundgren 1975). Females may tap or 'drum' the plant surface with their foreleg tarsi (Ilse 1956, Fox 1966, Myers 1969, Vaidya 1969b, Calvert 1974; see also Calvert & Hanson 1983). Fox (1966) suggested that combinations of leaf-abrading spines and chemosensory hairs on foretarsi permit females to detect plant compounds. Both 'B-type' chemosensory hairs of the Pieridae (Ma & Schoonhoven 1973) and clustered trichoid sensilla found in the Nymphalidae, which Calvert (1974) believes are chemosensory, are paired with spines on proximally adjacent tarsomeres. A female may also probe plant surfaces using her proboscis (Platt 1979, DeVries, 1983). Trichoid sensilla have been described on the proboscis of lepidopterans (Frings & Frings 1949).

Homologies between tarsal sensory receptors in different species are unclear. Sensory receptors in *Chlosyne lacinia* include clustered trichoid sensilla, approximately 13 pairs of other structures that show chemoreceptor-like activity as determined by electrophysiological responses, and 'pit setae', which point towards the terminus of the foretarsus (Calvert 1974). In *P. brassicae*, 'A-type' tactile bristles are oriented distally, and may be homologous to Calvert's 'pit setae'. 'B-type' chemosensory receptors in *P. brassicae* are similar in size to the 13 paired 'chemosensory' hairs in *C. lacinia* (Ma & Schoonhoven 1973).

Prior to oviposition, some butterflies curl their abdomens (Saxena & Goyal 1978) and/or dip their antennae towards the plant (Calvert 1974). Contact receptors occur on antennal tips and on ovipositors of pyralids (e.g. *Chilo partellus*, Chadha & Roome 1980). Functionally similar sensilla on the ovipositor valves of *P. brassicae* respond electrophysiologically to oviposition deterrent pheromone (Klijnstra 1982).

Compared with the large number of phytochemical compounds to which female butterflies are potentially exposed, the actual number of

chemoreceptor sensilla is relatively small. This limited number involves redundancy, however, because removal of antennae, fore-, meso-, or meta-thoracic tarsi (but not all tarsi simultaneously) does not inhibit oviposition in *P. brassicae* (Ma & Schoonhoven 1973); Myers (1969) obtained similar results for tarsi of *Danaus gilippus berenice*. Whether such removal compromises the butterfly's ability to differentiate among potential oviposition substrates is not clear.

Deciphering the gustatory and olfactory 'coding' of complex response profiles of lepidopterans has proved difficult. Specialized cells, for example the G (glucosinolate) cells in tarsal chemoreceptors of *P. brassicae*, respond to increasing concentrations of glucosinolates by increasing their firing rates (Ma & Schoonhoven 1973). However, mixtures stimulate responses that are difficult to interpret. Plants that are behaviourally rejected or accepted (by lepidopteran larvae) induce no standard electrophysiological responses correlated with acceptance or rejection. Further, plants accepted by two caterpillar species stimulate different electrophysiological responses in each (Dethier 1973). Failure to find universal modalities for rejection (or acceptance) is not surprising given the variety of reasons for which a plant might be rejected (e.g. presence of deterrent, lack of attractant—Dethier 1973). When responses to chemically-similar compounds are studied, electroantennograms (which represent summations of responses of many antennal olfactory cells) may be useful in comparing receptor sensitivities (Behan & Schoonhoven 1978, Den Otter *et al.* 1980). However, the variation among responses of individuals (Ma & Schoonhoven 1973, Schoonhoven 1977) does not encourage us that this 'coding' in peripheral receptor output will be easily solved. On the other hand, to the extent that the wide variation observed in electrophysiological responses correlates with variation in individuals' behaviours, these inconsistencies may reflect ecologically and evolutionarily significant differences among individuals.

#### *Isolating biologically active compounds*

Correctly identifying the chemical group responsible for behavioural variation can be a problem in research on secondary compounds. Although early work with *Pieris brassicae* suggested that single compounds could attract butterflies and elicit oviposition (David & Gardiner 1962), compounds that stimulate oviposition need not be the same ones that attract females (Rothschild & Fairbairn 1980, Feeny *et al.* 1983). For example, the Apiaceae and families related to these umbels contain essential oils, some of which are attractive to larval *Papilio* (Dethier 1941). However, attempts

to isolate and identify the oviposition stimulant in foodplants of *Papilio* species suggests that active fractions do not contain essential oils, although essential oils may initially attract females to the plants (Feeny *et al.* 1983; see also Rothschild & Fairbairn 1980). Feeny *et al.* (1983) suggest that the active components of biologically active fractions may be compounds that are widely distributed botanically, rather than unique secondary compounds (see also Jones *et al.* 1970, who suggest this is the case for the moth *Heliothis zea*). The oviposition 'mistakes' observed by Berenbaum (1981) suggest that coumarins or biosynthetically related compounds, rather than the somewhat more conspicuous essential oils, may be responsible for variation in *Papilio* responses to these plants. At issue are problems of separating correlative from causative relationships, and testing possible synergistic interactions among compounds. These observations warn us against uncritically assuming, without appropriate evidence, that specific, conspicuous compounds are involved in choice behaviour by particular butterflies.

#### *Response to variation within chemical classes*

Of primary interest is the hypothesis that variation among compounds belonging to a single class (i.e. sharing the same chemical functional group, with many R-group substituents) are the bases for differentiation of potential foodplants (e.g. Chew & Rodman 1979). Evidence for this hypothesis rests on a relatively small number of cases in which both behavioural and chemical aspects of oviposition choice have been examined.

The most extensive evidence that butterflies respond to variation among members of a single class of secondary plant compounds concerns pierids and their cruciferous foodplants. Hovanitz & Chang (1963) provided early evidence that in laboratory tests, *Pieris rapae* females respond differentially to extracts of different Brassicaceae. These observations suggested that *P. rapae* females detect variation in both glucosinolates (mustard oil glucosides) and isothiocyanates (mustard oils, one of the aglycone products of enzymatic degradation of glucosinolates) in extracts of crushed plants. However, Ma & Schoonhoven (1973) detected electrophysiological responses in the tarsal chemoreceptors to individual glucosinolates, but not to isothiocyanates. These electrophysiological observations do not exclude the possibility that olfactory receptors (Behan & Schoonhoven 1978) respond differentially to R-group substituents of isothiocyanates, but to our knowledge, the possibility has not been pursued. Chew and Rodman (Chew 1975, 1977, 1980, Rodman & Chew 1980) have provided correlational evidence that *Pieris occidentalis* and *Pieris napi macdunnoughii*

respond to variation among glucosinolates in the field.

Another set of data on responses to secondary plant metabolites comes from work on pierids and lycaenids that use leguminous foodplants. Stanton (1979) tested the behavioural responses of *Colias* butterflies in the laboratory to extracts of various legumes. The butterflies distinguish among legumes and legume extracts at contact range (i.e. stimulation was gustatory rather than olfactory). Females of *Glaucopsyche lygdamus* distinguish among perennial *Lupinus* species (Breedlove & Ehrlich 1968, 1972, Dolinger *et al.* 1973) in localities where plant species are characterized by invariant species-specific alkaloid profiles. However, where plant populations are characterized by considerable intraspecific variation, butterflies seem unable to distinguish those species that support larval survival from those that do not. It is not clear whether these butterflies sometimes are unable to detect differences among R-group substituents of the alkaloids, or whether their perceptual ability to distinguish these compounds sometimes was rendered useless by the low correlation between alkaloid profile and larval foodplant suitability.

#### Other Cues as Determinants of Specificity

Because ovipositing butterflies possess a number of sensory modalities, they may utilize different plant characteristics as oviposition cues at different distances from the plant, or during successive parts of an oviposition sequence (Courtney 1980, Stanton 1980). Many authors (e.g. Ives 1978, Wolfson 1980, and Jordan 1981 and references therein) show that ovipositing pierids discriminate among plants and plant parts on the basis of factors such as water content of leaves (important for larval growth efficiency—Scriber & Slansky 1981). The presence of ants may stimulate myrmecophilous species to oviposit (Atsatt 1981a). Colour and shape of plants, particularly leaves, are conspicuous distinguishing features. Ilse (1937) provided early evidence that ovipositing *Pieris brassicae* are attracted to certain shades of green, a finding corroborated for *Papilio demoleus* (Vaidya 1969a,b, Saxena & Goyal 1978).

Recent work has established the importance of leaf shape as an oviposition cue. In *Heliconius*, ovipositing butterflies select larval foodplants for their offspring by leaf shape, which varies substantially among *Passiflora* species in each community. The butterflies thus exploit, and possibly engender, the diversity of leaf shapes that characterize *Passiflora* (Gilbert 1975, Benson 1978).

In *Battus philenor*, ovipositing females utilize leaf shape to distinguish *Aristolochia* species, whose

suitability for larvae varies seasonally (Rausher 1978, 1979a,b, 1980). Females that consistently oviposited on *Aristolochia* plants, whose leaves were a particular shape, more frequently approached leaves (of any plant species) of similar shape. Upon alighting on visually chosen plants, however, females may reject the plant, presumably after assessing phytochemical cues.

*Colias* butterflies similarly utilize leaf shape to distinguish potential larval foodplants (Stanton 1980, 1982a). Females sometimes were confused by legumes of similar leaf shape (but of differing suitability for larval development) during approaches to plants. However, gustatory and olfactory stimuli at close range are probably responsible for differences in acceptance after alighting (Stanton 1979).

Behavioural responses to leaf shape may vary with vegetational characteristics of the habitat, and may depend on the degree of size, shape, colour, or textural contrast between foodplant species and the surrounding vegetation (Rausher 1982a, Stanton 1982b). Ovipositing *Euphydryas editha* display different behaviours in adjacent habitats with different densities and species of potential foodplants. In one habitat, searching behaviour resembles that of *B. philenor* and *C. alexandra*: females encounter preferred plant species more frequently than expected on a random basis by flying to areas where the preferred species is more abundant. In the other, females encounter potential foodplant species in proportion to their relative abundance (Mackay, *in litt.* 1982).

That the preferences of females for plants with different leaf shapes can change within seasons (Rausher 1978, 1981a) or between seasons (Stanton 1982a) or localities (Stanton 1980), suggests that female butterflies learn to associate leaf shape with other plant characteristics. They may then use these conspicuous visual cues to increase searching efficiency in diverse natural communities. Such associative learning (Traynier 1979) may enable butterflies to locate larval foodplants more efficiently, while retaining ability to later reassess the suitability of potential foodplants in a community. Visual cues (involving leaf shape) appear to enhance the rates at which *Battus philenor* and *Colias alexandra* encounter potential foodplants (Rausher 1978, Stanton 1982a); similar results involving flowers were obtained for *Anthocharis cardamines* (Courtney 1980). Similar responses have been observed in nectaring butterflies, which exhibit flower constancy, and for which visual cues of floral colour and morphology are strongly associated with nectar of given composition (see e.g. Watt *et al.* 1974, Levin & Berube 1972).

Further evidence for specificity based on visual

cues involves female recognition of previously laid conspecific eggs, and plant 'egg-mimics'. Pierids (Rothschild & Schoonhoven 1977, Shapiro 1981c,d), heliconiines (Gilbert 1975), and papilionids (Rausher 1979a) avoid ovipositing on plants carrying confamilial or conspecific eggs (see also Ch.3). Some of this response is chemically mediated (Behan & Schoonhoven 1978, Schoonhoven *et al.* 1981), but the presence and efficacy of similarly shaped and coloured 'egg-mimics' in preventing oviposition on plants (Shapiro 1981c, d, Williams & Gilbert 1981) indicates the importance of visual stimuli.

Female preference may be influenced by the presence of plant parts on which larvae preferentially feed. Plant parts include leaves of a specific age (Jordan 1981), apical meristems (Benson *et al.* 1976) and reproductive organs (Downey 1962a, Breedlove & Ehrlich 1968). An unusual example is two lycaenids, *Azanius jesous* (Clark & Dickson 1971) and *Celastrina lucia* (Robbins unpublished), that occasionally oviposit on galls on their normal foodplants; the larvae feed on the galls.

The predilection of butterflies for ovipositing in specific habitats has been widely observed and, in some cases, is attributable to specific causes. Among these are adequate density of larval foodplants (Courtney 1981, Smiley 1978a), avoidance of predators (Singer 1971 and references in Gilbert & Singer 1975), and adult preference for specific environmental conditions (Petersen 1954, Singer 1971, Cromartie 1975b, Williams 1981). In other cases, however, the sighting of butterflies is not necessarily reliable information on where eggs are deposited (Chew 1981). Habitat selection (Ch.8), rather than partitioning of potential larval foodplants, appears to be responsible for maintaining reduced potential competition between closely related butterfly species (Gilbert & Singer 1975, Shapiro & Cardé 1970, Chew 1981). In other cases, however (e.g. Emmel & Emmel 1969 on *Papilio* species), butterflies that fly in the same habitats partition larval foodplant species even though larvae of both species develop normally on all potential foodplants. Larvae compete for the same foodplants only in years when environmental deterioration renders a large proportion of the foodplants unsuitable for larval growth.

#### Oviposition Cues and Larval Polyphagy

Although conspicuous plant secondary compounds stimulate oviposition behaviour in some butterflies, these chemicals may lack a stimulatory role in species whose larvae exhibit extreme taxonomic polyphagy. In some cases where insects have restricted feeding habits, such as leaf mining or

boring into buds, plant anatomy rather than plant phytochemistry or phylogenetic relationships may primarily determine which plant tissues are acceptable as food (van Emden 1978, Powell 1980). In other cases, chemicals present in virtually all plants may stimulate oviposition (Jones *et al.* 1970), but deterrents distributed more or less at random among plant taxa determine the range of foodplants that are used (Thorsteinson 1960). Perception of deterrent compounds by larvae (and presumably by ovipositing females) is postulated to occur in central processing, not in peripheral sensory receptors (Dethier 1980a). As a result, restriction of the range of foodplants might evolve more quickly than if specific receptors were needed to perceive each potential deterrent.

Butterfly oviposition and larval feeding on plants in more than three or four taxonomically disparate families apparently only occurs with regularity among the species-rich (over 1000 species) primarily Neotropical eumaeine hairstreaks (Lycaenidae). Many eumaeines are strikingly more polyphagous than other butterflies (Robbins & Aiello 1982; an extensive list of records is in preparation) with the exception of some true nymphalids (Ehrlich & Raven 1965). This taxonomic polyphagy is correlated with oviposition on and larval boring into plant reproductive tissues (especially flower-buds and flowers) rather than feeding on foliage. It is not correlated with the presence of ants; obligate myrmecophily is unrecorded among eumaeines (Robbins unpublished).

Lycaenids that feed on buds, flowers, developing seeds and fruits eat food with a greater ratio of amino acids and protein to alkaloids or other secondary compounds than if they fed on foliage. Developing ovules and reproductive structure generally contain higher concentrations of proteins and amino acids than do leaves (McNeill & Southwood 1978, Mattson 1980). The higher assimilation efficiencies documented for insects feeding on plants with high nitrogen levels (e.g. McNeill & Southwood 1978) suggests that lycaenid larvae feeding on such tissue might require smaller quantities, and complete development with less exposure to alkaloids in their diets. Also, meristematic tissues often contain no or small vacuoles rather than large, well-organized vacuoles often found in foliage (Esau 1965, Matile 1976). Very young cells that have not yet become vacuolized contain small concentrations of compounds such as alkaloids than do more mature tissues (Robinson 1979). We consider it likely that a broad-range stimulant (such as the shape of buds or flowers), or a chemical or chemical composition common to young reproductive tissues (cf. Feeny *et al.* 1982, Jones *et al.* 1970), combined with an

absence of deterrent compounds that might be sequestered in well-organized vacuoles, make these reproductive plant parts attractive to ovipositing lycaenid females.

### Spatial Distribution of Eggs

#### Dispersion of Eggs

Distribution of eggs on foodplants may be classified as clumped, random or regular based upon the ratio of the variance to the mean in numbers of eggs per plant, branch or quadrat (see Myers 1978 for measures of dispersion). These patterns may result from female assessments of foodplant quality or of 'egg load', or may be a statistical result of female movements and plant spatial distributions. Some of the most detailed knowledge of oviposition patterns comes from work on *Pieris rapae* in agricultural plots (Harcourt 1961, Kobayashi 1965, 1966, Jones 1977b, Ives 1978, Jones & Ives 1979). Egg distributions in agricultural plots are clumped, and can be fitted rather well to negative binomial distributions (but see Myers 1978). Jones (1977b) successfully modelled oviposition behaviour of *P. rapae*. Her model shows that egg distributions, including 'edge effects' (more eggs on peripheral plants) can be explained for this species in agricultural plots as a statistical result of female movement patterns.

Eggs of *Pieris napi microstriata*, *Euphydryas editha*, and *Euptychia libye* also have clumped distributions (Shapiro 1980c, Rausher *et al.* 1981, Singer & Mandraccia 1982, respectively). These distributions are the result, in part, of a preponderance of eggs being laid on peripheral and isolated plants. Several explanations may account for this phenomenon (see also Ch.3). When a female butterfly picks the nearest plant from a random point (her location), this choice process results in isolated plants being chosen more frequently than would be expected on a random basis (Pielou 1969, Mackay & Singer 1982). Isolated plants may also be easier to see from a distance (e.g. Cromartie 1975a,b). Additionally, the preponderance of eggs on peripheral or isolated plants may result from female movements as they cross from nectaring to oviposition areas, or from one habitat to another (Kobayashi 1965, 1966, Gilbert & Singer 1973, Wiklund 1977a, Courtney & Courtney 1982).

Eggs or other immature stages on a particular plant inhibit oviposition of some species (Urquhart 1960, Gilbert 1975, Rothschild *et al.* 1975a). This assessment behaviour usually results in a regular distribution of eggs. Gilbert (1975) reported that some heliconiines do not oviposit if they see an egg

on a potential foodplant. Rothschild & Schoonhoven (1977) supplied laboratory evidence that visual cues, olfactory stimuli, and tactile chemosensory input from previously laid clusters inhibit female *Pieris brassicae* from ovipositing. They found similar patterns for *Danaus plexippus* and *P. rapae*, but egg distributions of *P. rapae* on other continents and *P. napi* in North America show no evidence of egg-load assessment (Jones & Ives 1979, Chew, unpublished data). Larval frass and macerated larval foodplant (cabbage) are reported to deter oviposition in some lepidopteran pests (e.g. *Trichoplusia ni*, Renwick & Radke 1980, 1981). Shapiro (1980c, 1981c,d) has shown that some pierids assess egg loads visually, and that the resultant egg distributions are statistically regular. He experimentally demonstrated that those species that lay visually conspicuous red eggs, or whose eggs turn red a few hours after oviposition, are inhibited from ovipositing on plants or branches with red eggs. Dispersion of eggs may ensure adequate larval food supply and prevent cannibalism.

Some plants have evolved 'egg-mimics' to deter females from ovipositing (see Gilbert 1975, Shapiro 1981d, Williams & Gilbert 1981, and Ch.3).

#### Cluster Laying

Females of many butterfly species lay their eggs in clusters rather than singly. Stamp (1980) lists records for Papilioninae (one species), Pierinae, Nymphalinae, Danainae (one species), Acraeinae and Lycaeninae. Representative genera in other subfamilies (and other Papilioninae) that lay clusters of more than ten eggs include the following: Papilioninae—*Papilio*, *Battus* (Miles Moss 1920); Parnassiinae—*Luehdorfia* (Shirôzu & Hara 1960-1962); Ithomiinae—*Mechanitis* (Fox 1967); Satyrinae—*Neope* (Shirôzu & Hara 1960-1962); Brassolinae—*Brassolis* (Bondar 1940), *Caligo* (Malo & Willis 1961); Amathusiinae—*Faunis* (Johnston & Johnston 1980) Morphinae—*Morpho* (refs. in Young 1973); Riodininae—*Euselasia* (Hoffmann 1931, Kendall 1976), *Hades* (Robbins unpublished), *Audre* (Bourquin 1953); Coeliadinae (Hesperiidae)—*Bibasis* (Johnston & Johnston 1980); Hesperiinae—*Thymelicus* (Shirôzu & Hara 1960-1962). The widespread occurrence of this life-history trait is evident. Clusters may contain the eggs of more than one female (Mallet & Jackson 1980) or be laid next to previously deposited clusters (DeVries 1977, Stamp 1981b). We include larval gregariousness in our discussion below because it is so closely correlated with cluster-laying.

In his original theoretical discourse on the evolution of distastefulness, Fisher (1930)

predicted that cluster-laying species would tend to be distasteful and conspicuously coloured. Unpalatability was unlikely to evolve by selection on individuals since 'any individual tasted would seem almost bound to perish . . .' However, in species with gregarious larvae, a tasted larva would afford protection to its siblings. (This discussion was the original formulation of the kin selection concept: Hamilton 1963.) Once evolved, distastefulness and conspicuous coloration would reinforce the gregarious habit by enhancing aposematic advertisement. Thus, aposematic insects would tend to be cluster-layers even if their unpalatability did not evolve by kin selection. In some instances gregarious behaviour would be 'lost' when its advantages were outweighed by a shortage of suitable food. (See also Ch.14.)

Evidence supports Fisher's proposed association between cluster-laying and aposematic coloration. Cluster-layers shown to be relatively unpalatable include adults or larvae of various species of Heliconiinae, *Euphydryas*, Acraeinae, Ithomiinae, *Battus*, *Mylothris*, *Delias*, and *Pieris brassicae* (references in Brower & Brower 1964, Bowers 1980, 1981). Cluster-layers whose larvae appear aposematic include the lycaenid *Eumaeus* (with bright red larvae; DeVries 1977) and the riodinine *Hades*. Stamp (1980) discusses examples of insects that lay clusters of toxic, aposematic eggs. However, many butterfly eggs, whether clustered or single, are relatively unpalatable to an array of invertebrate predators (Swynnerton 1915a,b; but see Baker 1970).

Aposematically coloured butterflies that oviposit singly indicate that other factors influence cluster-laying. Benson (1971) noted the poor correlation between cluster size and palatability of heliconiines, but later (Benson 1978) showed that cluster size is partly a response to competition for limited larval food resources. Troidines are among the most unpalatable, conspicuously coloured butterflies, but females of most genera (e.g. *Parides*, *Atrophaneura*) oviposit singly or in small clusters (Straatman & Nieuwenhuis 1961, Young 1972). Danainae are also exceptions (except *Amauris albimaculata*, a cluster-laying species, Van Son 1955).

Gregarious lycaenid and riodinid larvae are more likely to have obligate myrmecophilous relationships than solitary larvae. Ants may protect these larvae in return for nutritious 'honeydew' (Ross 1966, Pierce & Mead 1981). Groups of larvae may produce more honeydew or other chemical attractants and should be more dependably tended by ants. Further, since gregarious larvae are not cannibalistic (unlike solitary lycaenid larvae—Downey 1962a), females can oviposit near larvae, and secure protection for their eggs through the presence of ants.

Available evidence suggests that cluster-laying lycaenids are usually ant-attended. All Australian lycaenids that lay clusters of ten or more eggs are obligate myrmecophiles ( $n=11$ ) while only about a third of the species that oviposit singly ( $n=26$ ) have an obligate relationship with ants (Kitching 1981). Females of *Ogyris amaryllis* lay larger egg-clusters after tactile contact with ants (Atsatt 1981a). There is a paucity of data on riordinines, but species of *Audre* oviposit small to moderate sized clusters, and apparently are obligate myrmecophiles (Bruch 1926, Bourquin 1953, Robbins & Aiello 1982). A striking counter-example, however, is the lycaenid cluster-layer *Eumaeus atala*, which is not tended by ants (J. Weintraub, pers. comm.) but whose bright red larvae appear aposematic. DeVries (pers. comm.) reports similar findings for *E. minyas* in Costa Rica; however, the larval aggregations are attended by langurid beetles.

A female may arrange her eggs in any of a variety of designs. The simplest arrangement consists of non-contiguous eggs. (The pattern is probably statistically regular.) Examples include some heliconiines (Benson *et al.* 1976), ithomiines (Fox 1967), and the parnassiine *Luehdorfia* (Shirôzu & Hara 1960-1962).

A more complex design is a single layer of eggs touching each other. Some hesperiids, satyrids and brassolids lay a single row of eggs on blades of grass (Shirôzu & Hara 1960-1962, Malo & Willis 1961). Other species (*Audre*, *Nymphalis*) lay eggs in a compact hexagonal pattern (Bourquin 1953, Shirôzu & Hara 1960-1962) resembling the arrangement of cells in honey-comb. Still others (*Melitaea*) lay eggs partially in a compact hexagonal pattern and partly loosely arranged, but usually contiguous (Shirôzu & Hara 1960-1962).

The most complex arrangement consists of contiguous eggs more than one layer deep. Two variations differ in manner of deposition. First, some species (e.g. *Aporia*, *Aglais*, *Chlosyne*, *Papilio anchisiades*) lay masses of eggs up to three or four layers deep (Shirôzu & Hara 1960-1962, Robbins unpublished). Females of *Chlosyne* lay clusters one layer at a time. We think it likely that other species behave similarly. Second, some species (e.g. *Hamadryas amphinome*, *Polygonia*, *Araschnia*, *Papilio liomedon*) lay strands or stacks of eggs (Edwards 1870, 1882, Bell 1911, Shirôzu & Hara 1960-1962, Robbins unpublished), usually several strands to a cluster. Females of *Hamadryas* oviposit one strand at a time rather than one layer at a time (Robbins unpublished).

Available substrate space may influence egg deposition. Hexagonal arrangements and multi-layered clusters permit females to lay more eggs on a smaller surface, but falling eggs constrain the number of layers. 'String clusters' of *Hamadryas*

*amphinome* (up to 15 eggs long) break during afternoon thunderstorms (Robbins, unpublished). Females of *Chlosyne lacinia* lay up to three layers on the undersides of leaves. However, in an aberrant cluster of five layers, the outermost layers fell prematurely (Robbins unpublished).

Some egg arrangements protect eggs in the centre from parasitoids. Wasps may preferentially parasitize eggs at the edge of a single layer cluster (e.g. Van Den Berg 1971) or attack the outer layers of egg masses (Howard & Fiske 1911, Stamp 1981b). The innermost eggs in clusters of Panamanian *C. lacinia* are protected, even when an excess of wasps is experimentally placed on an egg cluster. The wasps cannot squeeze their abdomens between closely packed eggs (Robbins, unpublished). (However, in Texas populations, all eggs in a cluster of *C. lacinia* may be successfully parasitized: Drummond *et al.* 1970). As clutch size increases, the proportion of gypsy moth eggs parasitized decreases with the ratio of surface area to volume (Dowden 1961, Doane 1968).

Females of *Hypolimnas antilope* stand over their egg clusters and prediapause larvae (Rothschild 1979). Although this behaviour does not afford absolute protection for their eggs (peripheral eggs may be preyed upon or parasitized), we presume that guarded clusters have lower mortality rates than unguarded ones. This result was shown in an analogous case with a pentatomid bug (Eberhard 1975).

Gregarious larvae may suffer lower rates of parasitism in groups than as solitary individuals. *Euphydryas phaeton* larvae in groups that are larger or smaller than those occurring naturally suffer greater rates of parasitism (Stamp 1981a). Gregarious larvae may show stereotypic behavioural displays that presumably deter predators or parasitoids (see Stamp 1980).

Gregarious larvae may be better able to overcome physical plant defences, such as tough leaves and trichomes, than solitary larvae (Ghent 1960 for sawfly larvae). We know of no unequivocal evidence for butterflies. Gilbert (1971) proposed that trichomes on the leaves of *Passiflora adenopoda* pierce and kill larvae of some *Heliconius* species. Rathcke & Poole (1975) suggested that gregarious larvae of *Mechanitis polymnia isthmia* spin a web as an adaptation for crawling over trichomes without being pierced. However, larvae of some heliconiine species, which may lay single eggs, successfully feed on *P. adenopoda* in the wild (Benson *et al.* 1976, K. S. Brown, pers. comm.). Further, Panamanian larvae of *Mechanitis p. isthmia* (second or third instar) are not adversely affected by placing them individually on their solanaceous foodplants, even though the leaves have sharp recurved spines (Robbins unpublished).

Gregarious larvae feed more efficiently in groups. Long (1953, 1955) reared larvae of *Pieris brassicae* singly and in groups of 60, and found that larvae in groups developed faster; individuals apparently stimulated their neighbours to feed. Larvae of *Chlosyne lacinia* hatching under normal group conditions spin a web and then feed. Solitary larvae, however, walk until they starve (80% mortality within two days,  $n = 31$ ), or as occurred in 20% of the cases, spin a small web and then feed (Robbins, unpublished). Group feeding, however, does not facilitate feeding efficiency in *Euphydryas phaeton* (Stamp 1981a).

That normally gregarious larvae feed more efficiently in groups or have reduced rates of parasitism in groups is not surprising; it is invalid, however, to interpret these results as advantages of egg clustering (e.g. Stamp 1980). As gregarious feeding evolves, for whatever reason, behavioural adaptations for group feeding also evolve. We visualize 'normal behaviour' as an adaptive peak (Wright 1967) steepened by modifying behaviours. Comparing group feeding efficiency, for example, with abnormal solitary feeding supports the adaptive peak concept, but cannot be used to infer the general advantages of gregariousness. Even if the original factors favouring gregarious behaviour should change, the gregarious habit may well be retained because of these modifying behaviours and their secondary advantages.

Other advantages of clustering eggs have been suggested. Tutt (1899) proposed that strings of geometrid eggs resemble tendrils of their foodplant. Stamp (1980) suggested myriad other hypothetical possibilities; the reader is referred to her paper. Many of these hypotheses, and the one discussed above, could be tested by manipulating arrangements of eggs.

Systematics may be one of the most useful techniques for determining why life-history traits, such as egg-clustering, evolve. The combination of ecological methods and systematics has produced some remarkably original papers (e.g. Ehrlich & Raven 1965, Benson *et al.* 1976). We believe that systematics, particularly cladistics, may contribute much to evolutionary analysis (Mitter & Brooks 1983). Arnold (1981) presents a mostly jargon-free introduction to the methods used by cladists in reconstructing phylogenies. We present below a representative example of how cladistics might profitably be used.

The relationship between egg-clustering and type of larval foodplant (annual or perennial) is presently unclear. Stamp (1980) found that some cluster-laying Nearctic nymphalids use annual larval foodplants while others use perennials, and concluded that these factors are not related. An alternate explanation is that cluster-laying evolved

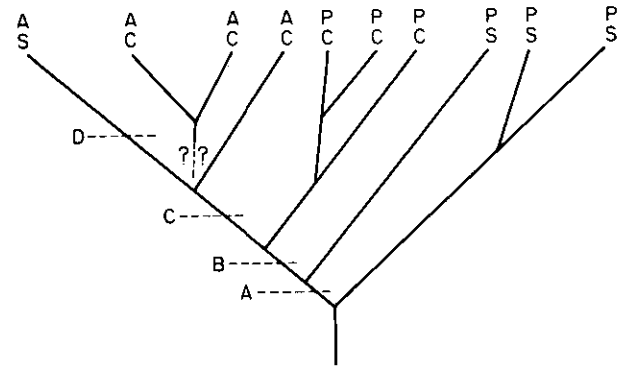


Fig. 6.1. Hypothetical cladogram of ten species with type of larval foodplant (annual [A] or perennial [P]) and manner of egg deposition (single [S] or clusters [C]) noted.

once in a species that used perennial foodplants and was ancestral to extant nymphalid cluster-layers. Further, the cluster-laying trait persisted through changes to annual foodplants because gene complexes adapted for gregariousness, such as those determining larval behaviours, presented too steep an adaptive peak for reversion to single egg-laying.

A cladogram can be used to test these hypotheses. We present an hypothetical cladogram of ten species, annotated for manner of egg deposition and type of larval foodplant (Fig. 6.1). We would infer that at point (A), the ancestral species laid single eggs on perennials, at point (B) cluster-laying evolved, at point (C) there was a change to annual foodplants, and at point (D) egg deposition reverted to single eggs. This cladogram would support the alternative hypothesis above whereas one in which cluster-laying evolved a number of times, sometimes when species were feeding on annuals and sometimes on perennials, would support Stamp's no-correlation hypothesis.

Cladistic analysis presents certain difficulties. First, cladograms are based on parsimony methods not readily amenable to statistical testing. There is no objective way to measure how well a cladogram represents phylogenetic relationships. Second, reasoning may be circular if the trait being examined is used to construct a cladogram. For instance, if manner of egg deposition had been used to construct Fig. 6.1, then the analysis would be biased against changes in egg deposition because fewer changes are more parsimonious than more changes. Despite these difficulties, cladistic analysis potentially provides a window for viewing evolutionary history that is not otherwise available.

### Evolution of Oviposition Specificity

We discuss here mechanisms promoting changes in specificity to novel foodplants, considering first

cases in which butterflies change to a related foodplant, and then instances in which they switch to unrelated foodplants. Undoubtedly most changes involve a switch to a plant that is phylogenetically and phytochemically closely related to the old foodplant, such as from one cruciferous species to another. Work on variation in oviposition preferences, conditioning of preferences and the heritability of specificity, although scanty, provides a framework for our discussion (in the first part of this section) of such changes. Theoretical cost-benefit analysis of exploiting new foodplants offers a different approach to this problem (Levins & MacArthur 1969, Jaenike 1978).

We believe that large 'jumps' in specificity are responsible, at least in part, for the wide range of plants that are used by butterflies as a group. For example, the use of gymnosperms, monocots, and a diverse group of dicot families (Loranthaceae, Ericaceae, Asteraceae, Verbenaceae, etc.) by the 'subgenera' of *Callophrys* (Howe 1975, Robbins & Aiello 1982) provides a representative example in which large changes in specificity must have occurred rapidly on an evolutionary time scale. It is unlikely that long-term association during phylogenetic branching (see Ehrlich & Raven 1965, Edgar *et al.* 1974, Benson *et al.* 1976, Edgar 1982 for proposed examples), or accumulated small changes in specificity between related plants, could account for this diversity of taxonomically unrelated larval foodplants. We propose mechanisms in the second part of this section that might account for large changes in specificity.

#### Foodplant Changes among Related Plants

Conditioning larvae to specific foodplants has been suggested as a mechanism for generating variation and for changing preferences in oviposition behaviour within population. The Hopkins Host Selection Principle (Hopkins 1917) proposed that adult female insects prefer to oviposit on those hosts that they ate as larvae. By this means, an individual larva that eats a novel foodplant could introduce that plant species to its population's resources; oviposition specificity for the plant would be induced.

We know of no unequivocal evidence that larval conditioning persists through metamorphosis to the imago. Larval preferences may be influenced by experiences as young larvae (e.g. David & Gardiner 1966, Hanson 1976 and references therein, Copp & Davenport 1978a; but see also Wiklund 1975b, Copp & Davenport 1978a, and Chew 1980 for negative results). Adult oviposition preferences may be similarly influenced by experience as adults (e.g. Traynier 1979, Rausher

1978, Stanton 1980; but see Tabashnik *et al.* 1981 for negative results). However, attempts to link larval experience with adult preference have either confused selection with conditioning effects (Hovanitz & Chang 1963) or provided negative evidence (Takata 1961a,b, Wiklund 1974b, 1975b, Copp & Davenport 1978b, Tabashnik *et al.* 1981). Claridge & Wilson (1978) and Jaenike (1982) provide negative results in Homoptera and *Drosophila* respectively, and review evidence in other insects.

Extensive behavioural observations of individuals document variation of oviposition preferences among individual females (Stanton 1979, Tabashnik *et al.* 1981, Singer 1982a); this variation is a prerequisite to changes in oviposition specificity. Some of this variation is attributable to the motivational state of females; females accept 'suboptimal' oviposition substrates when preferred ones are rare or absent (Singer 1971, Stanton 1982a, Wiklund 1981) or when they are strongly motivated to oviposit by heavy egg loads (Singer 1971, Jones 1977b). Some evidence suggests that females in a population share similar 'generalist' behaviour (each female oviposits on a similar range of plants, Chew 1977) while other evidence shows that a population may appear to contain a diversity of 'specialists' that exhibit consistent individual preferences (Tabashnik *et al.* 1981, Singer 1982a). Wiklund (1981) suggests that female *Papilio machaon* accept potential foodplant species in the same hierarchical order, but some individuals retain preference for the 'optimal' larval foodplant longer than others.

Evidence that variation in oviposition preference is heritable includes correlation of parent-offspring preferences (Tabashnik 1981) and artificial selection experiments (Hovanitz & Chang 1963; see also Wasserman & Futuyma 1981 for work on a bruchid beetle). To the extent that oviposition preferences are highly correlated with the fitness of a female, e.g. as might be the case if young larvae were very sedentary, we would expect heritabilities to be low (Falconer 1960).

Heritable variation in oviposition preference may not, however, be a particularly important factor in mediating changes in specificity. The detailed studies of Tabashnik (1981) on host shifts from native to crop plants in *Colias* suggest that although behavioural differences among females may have a genetic basis, genetic changes are not necessarily a prerequisite to foodplant shifts among related plants. If phenotypic plasticity produces sufficient ability to exploit newly encountered resources, selection may favour increased phenotypic plasticity rather than genetically fixed predisposition to exploit specific (novel) resources (Mayr 1963).

### Foodplant Changes to Unrelated Plants

In this section, we discuss two general mechanisms which we believe account for many large 'jumps' in butterfly foodplant specificity. The first mechanism occurs when old and new foodplants chronically grow in physical proximity to each other. The second involves adults that oviposit on flowers and are chronically exposed to other flowers on which they nectar. Both mechanisms require long-term association between the butterfly and its new foodplant, thus allowing time to select for improved ability to exploit the new host. It is hard to believe that large changes in specificity to phylogenetically and phytochemically unrelated plants occur frequently without such contact.

Large changes in specificity may occur when old and new foodplants grow in physical proximity to each other. Larvae are exposed to taxonomically unrelated potential foodplants for many generations; selection favours those larvae that can advantageously supplement their diets with the new foodplant (see King 1971 and Chew 1975 for further discussion of the consequences at the population level of supplementing diet). Actual change in oviposition behaviour, which is independent of larval digestive capabilities (see previous section), might occur in various ways as outlined in the following examples.

Females of some species normally oviposit in the vicinity of their foodplant, not on it, and may thus oviposit on unrelated plants that larvae may eventually utilize. *Euptychia* species generally use grasses as larval foodplants, but frequently oviposit on plants near grasses. Singer *et al.* (1971) found a Panamanian *Euptychia* species that feeds on lycopsids growing in the vicinity of grasses. They reasoned that habitual oviposition on lycopsids, coupled with the advantages that would accrue to larvae able to complete development on lycopsids, might explain this switch in foodplant specificity.

Females of many lycaenids and riodinids preferentially oviposit in the vicinity of ants (e.g. Atsatt 1981b). Larvae are thus chronically exposed to those homopterans that ants tend, to ant brood, and to lichens and fungi that grow in 'ant runs' and ant nests. The cannibalistic tendencies of lycaenid larvae, coupled with long-term exposure to ant-tended homopterans and ant brood, has undoubtedly resulted in the repeated independent evolution of carnivorous feeding on these animals (Ehrlich & Raven 1965). Significantly, lycaenid larvae are not known to feed on insects other than those tended by ants. The switch to lichens, which frequently grow in 'ant runs', by the African liptenines (over 500 species; Ehrlich & Raven 1965, van Someren 1974) may have a similar explanation

(see Atsatt 1981b), but may also have occurred as described in the next mechanism.

Females may chronically oviposit near to or on epiphytes (or parasites) that commonly grow on a butterfly's foodplant. This behaviour may mediate large 'jumps' in specificity from ancestral foodplants to epiphytes. Additionally, epiphytes also may act as a conduit in foodplant specificity over evolutionary time if species switch from the original foodplant to the epiphyte, and thence to another unrelated plant species on which the epiphyte grows.

A possible result of oviposition near parasitic plants is the repeated changes of specificity to mistletoes (Loranthaceae) among pierids, lycaenids, and nymphalids; these changes are not easily explained by similarity of secondary compounds (Ehrlich & Raven 1965). This is a difficult hypothesis to test because in most cases the switch to Loranthaceae occurred too long ago to determine the ancestral foodplant. Further, subsequent changes in foodplant specificity from mistletoes growing on the old foodplant to those growing on other plants may have occurred. The only valid test is to examine genera whose species feed on a well-defined set of plants (i.e., the proposed ancestral foodplant) except for one or two species feeding on Loranthaceae. An example would be species of *Euthalia* (Nymphalidae). These feed on trees of the family Anacardiaceae, except for one species that feeds on mistletoes which grow on these trees (L. Young 1907). Another possible example is the Nearctic genus *Mitoura* (Lycaenidae). Most species feed on Cupressaceae, but two species switched (probably before they speciated) to mistletoes that grow only on gymnosperm trees (Howe 1975).

A second mechanism for large changes in specificity occurs when butterflies which oviposit on flowers are chronically exposed to other flowers on which they nectar. If tactile cues or absence of chemical deterrents stimulate oviposition (see above), then females may occasionally oviposit on flowers which they visit for nectar. Further, larvae may occasionally complete development on these flowers because they might be exposed to relatively low concentrations of secondary compounds (as compared to larvae which find themselves on *leaves* of a 'strange' plant). Selection would then favour those individuals that oviposit (and whose larvae can develop) on flowers of the new plant, particularly in years or seasons when the usual foodplants produce few or no flowers. This mechanism would cause an increase in polyphagy which might be followed by specialization, if favourable conditions for it arise, on either the new or the old foodplants. This mechanism may account for the taxonomic polyphagy of individual lycaenid species (e.g. *Strymon melinus*) and for the

wide range of plants used by the flower-feeding lycaenids as a group (Robbins & Aiello 1982).

This mechanism predicts the testable hypothesis that the plants which a flower-feeding species uses as larval foodplants are a subset of those that it uses as sources of nectar. Available evidence is scanty, but there is some 'anecdotal' evidence supporting this hypothesis among Neotropical eumaeine lycaenids. Males and females of *Strymon 'basilides'* are the only lycaenids in Panama that nectar on *Heliconia* (Moraceae) flowers (Robbins

unpublished); they are also the only lycaenids in Panama known to oviposit on these flowers (Robbins & Aiello 1982). *Cordia* (Boraginaceae) and *Mangifera* (Anacardiaceae) flowers attract more species of nectaring lycaenids than any other Panamanian plants; a phylogenetically wide range of lycaenid species has been reared from flowers of each of these plants (d'Araújo e Silva *et al.* 1967-68, Robbins unpublished). This evidence suggests that the mechanism is plausible and worthy of testing in the future.

#### Acknowledgements

For helping with various aspects of this paper, including providing access to unpublished data, reading early drafts and giving us benefit of stimulating discussion, we thank Annette Aiello, Deane Bowers, Phil DeVries, Paul Feeny, Ira Heller, Charles Mitter, Dennis Murphy, Jan Pechenik, Miriam Rothschild, Julian Shepherd, Robert Silberglied, Michael Singer, Maureen Stanton, and Margaret Thayer. For financial support of some of our research described in this paper, we thank the National Science Foundation (DEB 7805960 to FSC), the US Department of Agriculture (CRGO 7900435 to FSC), and the Smithsonian Institution (to RKR).

- AIELLO, A. and SILBERGLIED, R.E. 1979. Life history of *Dynastor derlius* (Lepidoptera: Nymphalidae: Brassolini) in Panama. *Psyche* 85:331-345.
- ALDRICH, J.K., SODERLAND, D.M., BOWERS, W.S., and FELDLAUER, M.F. 1981. Ovarian sequestration of [14-C]-inulin by an insect: Index of vitellogenesis. *J. Insect Physiol.* 27:379-382.
- ARNOLD, E.W. 1981. Estimating phylogenies at low taxonomic levels. *Z. Zool Syst. Evolut.-Forsch.* 19:1-35.
- ARNOLD, R.A. and FISCHER, R.L. 1977. Operational mechanisms of copulation and oviposition in *Speria* (Lepidoptera: Nymphalidae). *Ann. Entomol. Soc. Amer.* 70:455-468.
- ATSATTI, P.R. 1981a. Ant-dependent food plant selection by the mistletoe butterfly *Ogyris amarilla* (Lycenidae). *Oecologia* (Berl.) 48:60-63.
- ATSATTI, P.R. 1981b. Lycenid butterflies and ants: selection for enemy-free space. *Amer. Nat.* 118:638-654.
- BAKER, R.R. 1968. Evolution of the migratory habit in butterflies. *B Phil. Trans. R. Soc. Lond.* B 253:309-341.
- BAKER, R.R. 1970. Bird predation as a selective pressure on the immature stages of the cabbage butterflies, *Pieris rapae* and *P. brassicae*. *J. Zool.* 162:43-59.
- BANKER, J.F. and HERMAN, W.S. 1973. On the neuroendocrine control of ovarian development in the monarch butterfly. *J. Exp. Zool.* 183:1-10.
- BEHAN, M. and SCHOONHOFEN, L.M. 1978. Chemoreception of an oviposition deterrent associated with eggs of *Pieris brassicae*. *Entomol. Exp. Appl.* 24:163-179.
- BELL, T.M. 1911. The common butterflies of the plains of India. *J. Bombay Nat. Hist. Soc.* 20:1115-1136.
- BENSON, W.W. 1971. Evidence for the evolution of unpalatability through  
 min selection in the Heliconiinae (Lepidoptera). *Amer. Nat.* 105:213-226.
- BENSON, W.W. 1978. Resource partitioning in passion vine butterflies. *Evolution* 32:493-518.
- BENSON, W.W., BROWN, K.S., Jr., GILBERT, L.E. 1976. Coevolution of plants and herbivores: passion flower butterflies. *Evolution* 29:659-680.
- BERENBAUM, M. 1981. An oviposition "mistake" by *Papilio glaucus* (Papilionidae). *J. Lepid. Soc.* 35:75.
- BERUBE, D.E. 1970. Host-plant finding by odor in adult *Coryphista madi* (Geometridae). *J. Lepid. Soc.* 24:220-224.
- BERUBE, D.E. 1972. Behavioral and physiological adaptations in the evolution of foodplant specificity in a species complex of *Collis* butterflies. Ph.D. dissertation, Yale Univ., New Haven.
- BOGGS, C.L. 1981a. Nutritional and life history determinants of resource allocation in holometabolous insects. *Amer. Nat.* 117:692-709.
- BOGGS, C.L. 1981b. Selection pressures affecting male nutrient investment at mating in heliconiine butterflies. *Evolution* 35:117-124.
- BOGGS, C.L. and GILBERT, L.E. 1979. Male contribution to egg production in butterflies: evidence for transfer of nutrients at mating. *Science* 206:83-84.
- BOGGS, C.L., SMILEY, J.T. and GILBERT, L.E. 1981. Patterns of pollen exploitation by *Heliconius* butterflies. *Oecologia* (Berl.) 50:320-324.
- BOGGS, C.L. and WATT, W.B. 1981. Population structure of pierid butterflies. IV. Genetic and physiological investment in offspring by male *Collis*. *Oecologia* (Berl.) 50:320-324.
- BONDAR, G. 1940. Insetos nocivos e moléstias do coqueiro (*Cocos nucifera*) no Brasil. *Inst. Central de Fomento Econ. da Bahia* 8. 160 pp.
- BOURQUIN, F. 1953. Notas sobre la

metamorfosis de *Hamaxia susanae* Orfila, 1953 con *Oruga mirmeocofila* (Lep., Riondin.). Rev. Soc. Entomol. Argentina 16:83-87.

BOWERS, M.D. 1980. Unpalatability as a defense strategy in *Euphydryas* phaeton (Lepidoptera: Nymphalidae). Evolution 34:586-600.

BOWERS, M.D. 1981. Unpalatability as a defense strategy of western checkerspot butterflies (*Euphydryas* Scudder, Nymphalidae). Evolution 35:367-375.

BREEDLOVE, D.E. and EHRLICH, P.R. 1968. Plant-herbivore coevolution: lupines and lycaenids. Science 162: 672-673.

BREEDLOVE D.E. and EHRLICH, P.R. 1972. Coevolution: patterns of legume predation by a lycaenid butterfly. Oecologia (Berl.) 10:99-104.

BROWER, L.P., and BROWER, J.V.Z. 1964. Birds, butterflies, and plant poisons: a study in ecological chemistry. Zoologica 49:137-159.

BROWER, L.P., McEWY, P.B., WILLIAMSON, K.L., and FLANNERY, M.A. 1972. Variation in cadlao glycoside content of monarch butterflies from natural populations in eastern North America. Science 177:426-429.

BRUCH, C. 1926. *Orugas mirmeocofilas de Hamaxia epulus signatus* Stieh. Rev. Soc. Entomol. Argentina 1:1-9.

CALVERT, M.H. 1974. The external morphology of foretarsal receptors involved with host discrimination by the nymphalid butterfly *Chlosyne lacinia*. Ann. Entomol. Soc. Amer. 67:853-857.

CHADHA, G.K. and ROOME, R.E. 1980. Oviposition behaviour and the sensilla of the ovipositor of *Chilo partellus* and *Spodoptera litoralis* (Lepidoptera: Noctuidae). J. Zool. 192:169-178.

CHAPMAN, R.F. and BLANEY, W.M. 1979. How animals perceive secondary compounds. pp. 161-270 in Herbivores: Interactions with secondary plant metabolites. G.A. Rosenthal and D.H. Janzen). Academic Press, New York.

CHEW, F.S. 1975. Coevolution of pierid butterflies and their cruciferous foodplants. I. The relative quality of available resources. Oecologia (Berl.) 20:117-127.

CHEW, F.S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution 31: 568-579.

CHEW, F.S. 1980. Foodplant preferences of *Pieris caterpillars* (Lepidoptera). Oecologia (Berl.) 46:347-353.

CHEW, F.S. 1981. Coexistence and local extinction in two pierid butterflies. Amer. Nat. 118:655-672.

CHEW, F.S. and ROMAN, J.E. 1979. Plant resources for chemical defense. Pp. 271-306 in Herbivores: Their interactions with secondary plant metabolites (G.A. Rosenthal and D.H. Janzen, eds.). Academic Press, New York.

CLARIDGE, M.F., and WILSON, M.B. 1978. Oviposition behaviour as an ecological factor in woodland canopy leafhoppers. Entomol. Exp. Appl. 24:101-109.

CLARK, G.C. and DICKSON, C.G.C. 1971. Life histories of the South African lycaenid butterflies. Farnell, Cape Town. 272 pp.

COPP, M.H. and DAVENPORT, D. 1978a. *Agraulis* and *Passiflora*. I. Control of specificity. Hol. Bull. 155:98-112.

COPP, M.H. and DAVENPORT, D. 1978b. *Agraulis* and *Passiflora*. II. Behavior and sensory modalities. Biol. Bull. 155:113-124.

COURTNEY, S.P. 1980. Studies on the biology of the butterflies *Anthocharis cardamines* (L.) and *Pieris napi* (L.), in relation to speciation in Pierinae. Ph.D. dissertation, University of Durham.

COURTNEY, S.P. 1981. Coevolution of pierid butterflies and their cruciferous foodplants. III.

- Anthocharis cardamines  
(L.) survival, development and oviposition on different hostplants. *Oecologia* (Berl.) 51:91-96.
- COURTNEY, S.P. 1982. Coevolution of pierid butterflies and their cruciferous foodplants. IV. Crucifer apparency and Anthocharis cardamines oviposition. *Oecologia* 52:258-265.
- COURTNEY, S.P. and COURTNEY, S. 1982. The "edge-effect" in butterfly oviposition: causality in Anthocharis cardamines (L.) and related species. *Ecol. Entomol.* 7: in press.
- CRIPPS, C. 1947. Scent perception in some African myrmecophilous Lycaenidae (Lepidoptera: Rhopalocera). *Proc. R. Entomol. Soc. Lond. Ser. A* 22:42-43.
- CROMARTIF, W.J., JR. 1975a. Influence of habitat on colonization of collard plants by Pieris rapae. *Environ. Entomol.* 4: 783-784.
- CROMARTIF, W.J. 1975b. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *J. Appl. Ecol.* 12:517-533.
- DAVID, M.A.L. and GARDINER, B.O.C. 1962. Oviposition and hatching of the eggs of Pieris brassicae L. in a laboratory culture. *Bull. Entomol. Res.* 53:91-109.
- DAVID, M.A.L. and GARDINER, B.O.C. 1966. The effect of sinigrin on the feeding of Pieris brassicae larvae transferred from various diets. *Entomol. Exp. Appl.* 9:95-98.
- DEB, D.C. and CHAKROWORTHY, S. 1981. Effect of a juvenoid on the growth and differentiation of the ovary of Coryx cephalonica (Lepidoptera). *J. Insect Physiol.* 27:103-111.
- DE JONG, K. 1978. Functional morphology of the genitalia of Cartharodius beeticus Stammeri Rev. (Lepidoptera, Neperidae). *Neth. J. Zool.* 28:206-212.
- DEW OTTER, C.J., BEHAN, M. and MAES, F.W. 1980. Single cell responses in female Pieris brassicae (Lepidoptera: Pieridae) to plant volatiles and conspecific egg odours. *J. Insect Physiol.* 26:465-472.
- DETHIER, V.G. 1941. Chemical factors determining the choice of foodplants by Papilio larvae. *Amer. Nat.* 75:61-73.
- DETHIER, V.G. 1959. Egg-laying habits of Lepidoptera in relation to available food. *Canad. Entomol.* 91: 554-561.
- DETHIER, V.G. 1970. Chemical interactions between plants and insects. Pp. 83-102 in *Chemical Ecology* (E. Sondheimer and J.B. Simons, eds.). Academic Press, New York.
- DETHIER, V.G. 1973. Electrophysiological studies of gustation in lepidopterous larvae. II. Taste spectra in relation to food-plant discrimination. *J. Comp. Physiol.* 82:103-134.
- DETHIER, V.G. 1978. Other tastes, other worlds. *Science* 201:224-228.
- DETHIER, V.G. 1980. Evolution of receptor sensitivity to secondary plant substances with special reference to deterrents. *Amer. Nat.* 115:45-66.
- DE VRIES, P. 1977. Eumaeus minyas Hubner, an aposematic Lycaenid butterfly. *Brenesia* 12:269-270.
- DOANE, C.C. 1968. Changes in egg mass density, size, and amount of parasitism after chemical treatment of a heavy population of the gypsy moth. *J. Econ. Entomol.* 61:1288-1291.
- DOLLINGER, P.M., ENHRLICH, P.R., FITCH, W.L., and BREEDLOVE, E.E. 1973. Alkaloid and predation patterns in Colorado lupine populations. *Oecologia* (Berl.) 13: 191-204.
- DOUMES, P. 1968. Host selection and host funding in the egg-laying female Cidarja sibirica L. (Lepidoptera: Geometridae). *Opusc. Entomol.* 33: 233-279.
- DOUMES, P. 1976. Activity in Hexodes virgaurae (Lepidoptera, Lycaenidae) in relation to air temperature, solar radiation, and time of day.

- Oecologia (Berl.) 22:287-298.
- DOWNEN, P.B. 1961. The Gypsy moth egg parasite *Oncocryptus kumagai*, in southern Connecticut in 1960. J. Econ. Entomol. 54:876-878.
- DOWNY, J.C. 1962. Host-plant relations as data for butterfly classification. Syst. Zool. 11:150-159.
- DOWNY, J.C. and ALLYN, A.C. 1980. Eggs of *Hodiniidae*. J. Lepid. Soc. 34:133-145.
- DOWNY, J.C. and ALLYN, A.C. 1981. Chorionic sculpturing of eggs of *Lycenidae*. Part 1. Bull. Allyn Mus. 61. 29 pp.
- DRUMMOND, B.A. III, BUSH, G.L., and EHRLICH, T.C. 1970. The biology and laboratory culture of *Chlosyne lacinia* Geyer (Nymphalidae). J. Lepid. Soc. 24:135-142.
- DUNLAP-PIANKA, H.L. 1979. Ovarian dynamics in *Heliconius* butterflies: correlations among daily oviposition rates, egg weights, and quantitative aspects of oogenesis. J. Insect Physiol. 25:741-749.
- DUNLAP-PIANKA, H., BOGGS, C.L., and GILBERT, L.E. 1977. Ovarian dynamics in *Heliconius* butterflies: programmed senescence versus eternal youth. Science 197: 487-490.
- DYAR, H.G. 1890. The number of moults of Lepidopterous larvae. Psyche 5:420-422.
- EBERHARD, W.G. 1975. The ecology and behavior of a subsocial pentatomid bug and two scoliid wasps: strategy and counterstrategy in a host and its parasites. Smithsonian Contrib. Zool. 205. 39pp.
- EDGAR, J.A. 1982. Pyrrolizidine alkaloids sequestered by Solomon Island Danaine butterflies: the feeding preferences of the *Danaidae* and *Ithomiinae*. J. Zool., in press.
- EDGAR, J.A., CULVENOR, C.C.J., and PLISKE, T.E. 1974. Coevolution of danaid butterflies with their host plants. Nature 250:646-648.
- EDWARDS, E.D. 1973. Delayed ovarian development and aestivation in adult females of *Heteronympha seropa seropa* (Lepidoptera: Satyriinae). J. Aust. Entomol. Soc. 12:92-98.
- EDWARDS, W.H. 1870. Notes of *Graptas c-aurea* and *interrogator*. Trans. Amer. Entomol. Soc. 3:1-9.
- EDWARDS, W.H. 1882. Description of the preparatory stages of *Graptas interrogator*. Fab. Canad. Entomol. 14:201-207.
- EHRLICH, A.H. and EHRLICH, P.R. 1978. Reproductive strategies in the butterflies: I. Mating frequency, plugging, and egg number. J. Kansas Entomol. Soc. 51:666-697.
- EHRLICH, P.R. 1958. The comparative morphology, phylogeny and high classification of the butterflies (Lepidoptera: Papilionoidea). Univ. Kans. Sci. Bull. 39:305-370.
- EHRLICH, P.R. and RAVEN, P.H. 1965. Butterflies and plants: a study in coevolution. Evolution 18:586-608.
- EHMEL, T.C., and EHMEL, J.F. 1969. Selection and host plant overlap in two desert Papilio butterfly species. Ecology 50:158-159.
- ENGELHANN, F. 1979. Insect vitellogenin: identification, biosynthesis, and role in vitellogenesis. Adv. Insect Physiol. 14:49-108.
- ERICKSON, J.M. and FEENEY, P. 1974. Sinigrin: a chemical barrier to the black swallowtail butterfly, *Papilio polyxenes*. Ecology 55:103-111.
- ESAU, K. 1965. Plant anatomy. second ed. Wiley, New York.
- FALCONER, D.S. 1960. Introduction to quantitative genetics. New York, Ronald Press.
- FEENEY, P.F. 1975. Biochemical coevolution between plants and their insect herbivores. pp. 3-19 in *Coevolution of Animals and Plants* (ed. L.E. Gilbert and P.H. Raven), Univ. Texas.
- FEENEY, P., ROSEBERRY, L., and CARTER, M. 1982. Chemical aspects of oviposition behaviour in butterflies. In *Herbivore insects:*

- Host-seeking behavior and mechanisms (ed. S. Ahmad), Academic, New York.
- FISHER, R.A. 1930. The genetical theory of natural selection. Clarendon, Oxford. 272 pp.
- FOX, R.H. 1966. Foreles of butterflies. I. Introduction: chemoreception. *J. Res. Lepid.* 5:1-12.
- FOX, R.H. 1967. A monograph of the Ithomiidae (Lepidoptera). Part III. The tribe Mechanitini. *For. Mem. Amer. Entomol. Soc.* 22. 190 pp.
- FRAENKEL, G.S. 1959. The raison d'être of secondary plant substances. *Science* 129:1466-1470.
- FRIEDLANDER, M. 1975. Nucleated and anucleated, two types of concomitant spermatzoa in inseminated female moths. Pp. 75-82 in *Gamele competition in plants and animals* (D.H. Mulcahy, ed.), North-Holland, Amsterdam.
- FRIEDLANDER, M. and GILBY, H. 1972. The fate in the normal-anucleated spermatozoa in inseminated females of the silkworm, *Bombyx mori*. *J. Morphol.* 138:121-130.
- FRIEDLANDER, M., JAMS, P. and BENZ, G. 1981. Precocious reprogramming of epyrene-apyrene spermatogenesis commitment induced by allatectomy of the penultimate larval instar of the moth *Actias selene*. *J. Insect Physiol.* 27:267-269.
- FRINGS, H. and FRINGS, M. 1949. The loci of chemoreceptors in insects. *Amer. Midl. Nat.* 41:602-658.
- GHENT, A. 1960. A study of the group-feeding behavior of larvae of the Jack pine sawfly, *Neodiprion pratti baikalanae* Nob. *Behaviour* 16:110-148.
- GILBERT, L.E. 1971. Butterfly-plant coevolution: has Fuzzi flora adenopoda won the selectional race with heliconine butterflies? *Science* 172: 595-86.
- GILBERT, L.E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. Pp. 210-240 in *Coevolution of Animals and Plants* (ed. L.E. Gilbert and P. H. Raven), Austin, Univ. Texas Pr.
- GILBERT, L.E. and SINGER, M.C. 1973. Dispersal and gene flow in a butterfly species. *Amer. Nat.* 107:58-72.
- GILBERT, L.E. and SINGER, M.C. 1975. Butterfly ecology. *Minu. Rev. Ecol Syst.* 6:365-397.
- GOSSARD, T.W. and JONES, R.E. 1977. The effects of age and weather on egg-laying in Pieris rapae L. *J. Appl. Ecol.* 14:65-71.
- GOULD, S.J. and LEVONTIN, R.C. 1979. The spandrels of San Marco and the adaptationist programme. *Proc. R. Soc Lond B* 205:581-598.
- HAMILTON, W.D. 1963. The evolution of altruistic behavior. *Amer. Nat.* 97:354-356.
- HANSON, F.E. 1976. Comparative studies on induction of food choice preferences in lepidopterous larvae. *Symp. Biol. Hung.* 16:71-77.
- HARCOURT, D.G. 1961. Spatial pattern of the imported cabbageworm, Pieris rapae (L.) (Lepidoptera: Pieridae), on cultivated Cruciferae. *Canad. Entomol.* 93:945-952.
- HEFLEY, H.M. 1937. The relations of some native insects to introduced plants. *J. Anim. Ecol.* 6: 138-144.
- HERMAN, W.S. 1975. Endocrine regulation of post-eclosion enlargement of the male and female reproductive glands in monarch butterflies. *Gen. Comp. Endoor.* 26:534-540.
- HERMAN, W.S. 1981. Studies on the adult reproductive diapause of the monarch butterfly, Danaus plexippus. *Biol. Bull.* 160:89-106.
- HERMAN, W.S. and BAKER, J.F. 1977. Effect of mating on monarch butterfly oogenesis. *Experientia* 33:688-689.
- HERMAN, W.S. and DALLMAN, S.H. 1981. Endocrine biology of the Painted Lady butterfly Vanessa cardui. *J. Insect Physiol.* 27:103-108.

- HIGGINS, L.B. 1975. A classification of European butterflies. Collins, London.
- HINTON, H.E. 1981. The Biology of Insect Eggs. 3 vols. Pergamon, Oxford.
- HOFFMAN, F. 1931. *Euschasia eucerus* Hew. (Erycinidae). Entomol. Rundschau 48:55-56.
- HOLT, G.G. and NORTH, D.T. 1970. Effects of gamma irradiation on the mechanisms of sperm transfer in *Trichoplusia ni*. J. Insect Physiol. 16:2211-2222.
- HOPKINS, H.D. 1917. A discussion of C.G. Hewett's paper on insect behavior. J. Econ. Entomol. 10:92-93.
- HOVANITZ, W. 1969. Inherited and/or conditioned changes in host plant preference in *Pieris*. Entomol. Exp. Appl. 12: 729-735.
- HOVANITZ, W. and CHANG, V.C.S. 1963. Ovipositional preference tests with *Pieris*. J. Res. Lepid. 2:185-200.
- HOVANITZ, W. and CHANG, V.C.S. 1964. Adult oviposition responses in *Pieris rapae*. J. Res. Lepid. 3: 159-172.
- HOWARD, L.O., and FISKE, M.F. 1911. The Importation into the United States of the parasites of the gypsy moth and the brown-tail moth. U.S.D.A. Bur. Entomol. Bull. 91. 344 pp.
- HOWE, W.H., ed. 1975. The butterflies of North America. Doubleday, Garden City.
- ILSE, D. 1937. New observations on responses to colors in egg-laying butterflies. Nature 140:544-545.
- ILSE, D. 1956. Behavior of butterflies before ovipositing. J. Bombay Nat. Hist. Soc. 53:486-488.
- IRIKI, S. 1941. The two sperm types in the silkworm and their functions. Zool. Mag., Tokyo. 53:123-124.
- IVES, P.M. 1978. How discriminating are cabbage butterflies? Aust. J. Ecol. 3: 261-276.
- JAENIKE, J. 1978. On optimal oviposition behavior in

- phytophagous insects. Theor. Pop. Biol. 14:350-356.
- JAENIKE, J. 1980. A relativistic measure of variation in preference. Ecology 61:990-991.
- JAENIKE, J. 1982. Environmental modification of oviposition behavior in *Drosophila*. Amer. Nat. 784-802.
- JOHANSSON, A.S. 1951. The food plant preference of the larvae of *Pieris brassicae* L. (Lepid., Pieridae). Norsk. Entomol. Tidsk. 8:18-195.
- JOHNSTON, G. and JOHNSTON, B. 1980. This is Hong Kong: butterflies. Hong Kong Govt. Publ. 224 pp.
- JONES, R.E. 1977. Movement patterns and egg distributions in cabbage butterflies. J. Anim. Ecol. 46: 195-212.
- JONES, R.E., HART, J.R., and BULL, G.D. 1982. Temperature, size, and egg production in the cabbage butterfly *Pieris rapae* L. Aust. J. Zool. in press.
- JONES, R.E. and IVES, P.M. 1979. The adaptiveness of searching and host selection behaviour in *Pieris rapae* (L.). Aust. J. Ecol. 4:75-86.
- JONES, R.L., BURTON, R.L., BOWMAN, M.C., and BEROZA, M. 1970. Chemical inducers of oviposition for the corn earworm, *Heliothis zea* (Boddie). Science 168:856-857.
- JORDAN, C.T. 1981. Population biology and host plant ecology of caper-feeding pierid butterflies in northeastern Mexico. Ph.D. dissertation, University of Texas, Austin. 165 pp.
- KAFATOS, F.C. 1981. Structure, evolution and developmental expression of the silkworm chorion multigene families. Amer. Zool. 21:707-714.
- KATSUNO, S. 1977. Studies on eupyrene and apyrene spermatozoa in the silkworm *Bombyx mori* (Lepidoptera, Bombycidae). IV. The behavior of the spermatozoa in the internal reproductive organs of female moths. Appl. Entomol. Zool. 12:352-359.
- KENDALL, R.O. 1976. Larval

LUNDGREN, L. 1975. Natural plant chemicals acting as oviposition deterrents on cabbage butterflies (*Pieris brassicae* (L.)) P. Rapae (L.) and P. napi (L.). Zool. Ser. 4: 253-258

MA, W.C. and SCHOONHOVEN, L.M. 1973. Tarsal chemosensory hairs of the large white butterfly Pieris brassicae and their possible role in oviposition behavior. Entomol. Exp. Appl. 16: 343-357.

MACKAY, D.A. and SINGER, M.C. The basis of an apparent preference for isolated hostplants by ovipositing Euptychia libys butterflies. Manuscript.

MALLEY, J.L.B. and JACKSON, D.A. 1980. The ecology and social behaviour of the Neotropical butterfly Heliconius xanthoolus Bates in Colombia. Zool. J. Linn. Soc. 70:1-13.

HALO, R. and WILLIS, E.A. 1961. Life history and biological control of Caligo eurilochus, a pest of banana. J. Econ. Entomol. 54:530-536.

MATILE, P. 1976. Vacuoles. pp. 189-224 in Plant Biochemistry, 3rd ed. (ed. J. Bonner and J.E. Varner). Academic Press.

MATTSON, W.J. 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Syst. 11:119-161.

MAYR, E. 1963. Animal species and evolution. Harvard, Cambridge.

McNEILL, S. and SOUTHWOOD, T.H.E. 1978. The role of nitrogen in the development of insect/plant relationships. pp. 77-98 in Biochemical aspects of plant and animal coevolution (ed. J.B. Harborne). Academic, London.

MEVES, F. 1963. Ueber oligopyrene und apyrene Spermaten und über ihre Entstehung, nach Beobachtungen an Peludina und Pygaera. Arch. Mikrosk. Anat. Entwicklungsmech. 61:1-62.

HILLER, J.R., STRICKLER, K.V. 1982. Plant-herbivore relationships: locating and identifying the host. in press in Chemical Ecology of

foodplants and life history notes for some metalmarks (Lepidoptera: Rhodnidae) from Mexico and Texas. Bull. Allyn Mus. 32. 12 pp.

KING, C.E. 1971 Resource specialization and equilibrium population size in patchy environments. P.M.A.S. (USA) 68:2634-2637.

KITCHING, R.L. 1981. Egg clustering and the southern hemisphere lycaenids: comments on a paper by M.E. Stamp. Amer. Nat. in press.

1982. Perceps-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.

KOBAYASHI, S. 1966. Process generating the distribution pattern of the common cabbage butterfly Pieris rapae crucivora. Res. Popul. Ecol. 8: 51-61.

LABINE, P.A. 1964. Population biology of the butterfly, Euphydryas editha. I. Barriers to multiple insensations. Evolution 18:335-3356.

LABINE, P.A. 1968. The population biology of the butterfly Euphydryas editha. VIII. Oviposition and its relation to patterns of oviposition in other butterflies. Evolution 22: 799-805.

LEVIN, D.A. and BERUBE, D.E. 1972. Phlox and Colias: the efficiency of a pollination system. Evolution 26:242-250.

LEVINS, R. and MACARTHUR, R.H. 1969. An hypothesis to explain the incidence of monophagy. Ecology 50: 910-911.

LONG, D.B. 1953. Effects of population density on larvae of lepidoptera. Trans. R. Entomol. Soc. Lond. 104:543-565.

LONG, D.B. 1955. Observations on subsocial behavior in two species of lepidopterous larvae, Pieris brassicae L., and Phaia gamma L. Trans. R. Entomol. Soc. Lond. 106:421-437.

Klijnsma, J.W.  
 1982. Perceps-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.  
 KOBAYASHI, S. 1966. Process generating the distribution pattern of the common cabbage butterfly Pieris rapae crucivora. Res. Popul. Ecol. 8: 51-61.  
 LABINE, P.A. 1964. Population biology of the butterfly, Euphydryas editha. I. Barriers to multiple insensations. Evolution 18:335-3356.  
 LABINE, P.A. 1968. The population biology of the butterfly Euphydryas editha. VIII. Oviposition and its relation to patterns of oviposition in other butterflies. Evolution 22: 799-805.  
 LEVIN, D.A. and BERUBE, D.E. 1972. Phlox and Colias: the efficiency of a pollination system. Evolution 26:242-250.  
 LEVINS, R. and MACARTHUR, R.H. 1969. An hypothesis to explain the incidence of monophagy. Ecology 50: 910-911.  
 LONG, D.B. 1953. Effects of population density on larvae of lepidoptera. Trans. R. Entomol. Soc. Lond. 104:543-565.  
 LONG, D.B. 1955. Observations on subsocial behavior in two species of lepidopterous larvae, Pieris brassicae L., and Phaia gamma L. Trans. R. Entomol. Soc. Lond. 106:421-437.

- Insects (ed. M. Bull and R. Cardé).
- MINNICH, D.E. 1924. The olfactory sense of the cabbage butterfly, *Pieris rapae* L., an experimental study. *J. Exp. Zool.* 39:339-359.
- MITCHELL, M.D. 1978. Differential host selection by *Pieris brassicae* (the large white) on *Brassica oleracea* ssp. *oleracea* (the wild cabbage). *Entomol. Exp. Appl.* 22:208-219.
- HITTER, C. and BROOKS, D.R. 1982. Phylogenetic aspects of coevolution. In *Coevolution* (ed. D.J. Futuyma and M. Slatkin). Sinauer, Sunderland, Mass.
- MOSS, A.H. 1919. The Papillos of *Para. Novit. Zool.* 26:295-319.
- MURPHY, D.E. 1981. The role of adult resources in the population biology of *Euphydryas editha* butterflies. Ph.D. dissertation, Stanford University.
- MYERS, J. 1969. Distribution of foodplant chemoreceptors in the female Florida Queen Butterfly, *Danaus gilippus berenice* (Nymphalidae). *J. Lepid. Soc.* 23:196-198.
- MYERS, J.H. 1978. Selecting a measure of dispersion. *Environ. Entomol.* 7:619-621.
- NAKAMURA, I. 1976. Female anal hair tuft in *Normanna dylalis* (Lycaenidae): 488-Osmouffaging function and taxonomic significance. *J. Lepid. Soc.* 30:305-309.
- NECK, R.W. 1977. Foodplant ecology of the butterfly *Chlosyne laonia* (Geyer) (Nymphalidae). *J. Lepid. Soc.* 23: II. Additional larval foodplant data. *J. Res. Lepid.* 16:69-74.
- NICEVILLE, L. De. 1890. The butterflies of India, Burma, and Ceylon, vol. III. Calcutta Central Press, Calcutta. 503 pp.
- NICHOLSON, S.W. 1976. Hormonal control of diuresis in the cabbage white butterfly, *Pieris brassicae*. *J. Exp. Biol.* 65:565-575.
- OHSAKI, N. 1979. Comparative

- population studies of three *Pieris* butterflies, *P. rapae*, *P. melale*, and *P. napi*, living in the same area. I. Ecological requirements for habitat resources in the adults. *Res. Popul. Ecol. (Kyoto)*. 20:278-296.
- OWEN, D.F. 1959. Ecological segregation in butterflies in Britain. *Entomol. Gaz.* 10:27-38.
- PAN, H.L. and WYATT, G.R. 1971. Juvenile hormone induced vitellogenin synthesis in the monarch butterfly. *Science* 174:503-505.
- PAN, H.L. and WYATT, G.R. 1976. Control of vitellogenin synthesis in the monarch butterfly by juvenile hormone. *Dev. Biol.* 54:127-134.
- PETERSEN, B. 1954. Egg-laying and habitat selection in some *Pieris* species. *Entomol. Tidskr.* 75:194-203.
- PIELOU, E.C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York.
- PIENCE, M.E. and HEAD, P.S. 1981. Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science* 211:1185-1187.
- PYKE, G.H., PULLIAM, H.R., and CHARNOV, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.* 52:137-154.
- PLATT, A.P. 1979. Oviposition site selection and behavior in *Limnitis* spp. *Maryland Entomol.* 1:9-10.
- POWELL, J.A. 1980. Evolution of larval food preferences in Microlepidoptera. *Ann. Rev. Entomol.* 25:133-159.
- RATNKE, B.J. and POOLE, R.W. 1975. Coevolutionary race continues: butterfly larval adaptation to plant trichomes. *Science* 187:175-176.
- RAUSHER, M.D. 1978. Search image for leaf shape in a butterfly. *Science* 200:1071-1073.
- RAUSHER, M.D. 1979. Larval habitat suitability and oviposition preference in three related

- butterflies. Ecology 60:503-511.
- RAUSHER, M.D. 1979. Egg recognition: its advantages to a butterfly. Anim. Behav. 27: 1034-1040.
- RAUSHER, M.D. 1980. Host abundance, juvenile survival, and oviposition preference in *Battus philenor*. Evolution 34:342-355.
- RAUSHER, M.D. 1981. Host plant selection by *Battus philenor* butterflies: The roles of predation, nutrition, and plant chemistry. Ecol. Monogr. 51:1-20.
- RAUSHER, M.D. 1982. The ecology of host selection behavior in phytophagous insects. In Impact of Variable Host Quality on Herbivorous Insects, (R.F. Denno and M.S. McClure, eds.), Academic Press.
- RAUSHER, M.D., MACKAY, D.A. and SINGER, M.C. 1982. Pre- and post-alighting host discrimination by *Euphydryas editha* butterflies: the behavioral mechanisms causing clumped distributions of egg clusters. Anim. Behav. in press.
- RAY, T.S. and ANDREWS, C.C. 1980. Antbutterflies: butterflies that follow army ants to feed on antbird droppings. Science 210:1147-1148.
- HENWICK, J.J.A. and RADKE, C.D. 1980. An oviposition deterrent associated with frass from feeding larvae of the cabbage looper, *Trichoplusia ni* (Lepidoptera: Noctuidae). Environ. Entomol. 9:318-320.
- HENWICK, J.J.A. and RADKE, C.D. 1981. Host plant constituents as oviposition deterrents for the cabbage looper, *Trichoplusia ni*. Entomol. Exp. Appl. 30:201-204.
- RICHARDS, O.W. 1949. The relation between measurements of the successive instars of insects. Proc. R. Entomol. Soc. Lond. A 24:1-272.
- RICHARDS, O.W. and DAVIES, R.G. 1977. Insects' general textbook of entomology, tenth ed. 2 vols. Chapman and Hall, London.
- RIEHN, J.G., GASSNER, G. III. 1973. Ultrastructure of lepidopteran sperm within spermathecae. Ann. Entomol. Soc. Amer. 66:154-159.
- HOBBINS, R.K. and AIELLO A. 1982. Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. J. Lepid. Soc., in press.
- ROBINSON, T. 1979. The evolutionary ecology of alkaloids. pp. 413-448 in Herbivores: interactions with secondary plant metabolites (ed. G.A. Rosenthal and D.H. Janzen). Academic Press, New York.
- RODMAN, J.E. and CHEN, F.S. 1980. Phytochemical correlates of herbivory in a community of native and naturalized Cruciferae. Biochem. Syst. Ecol. 8:43-50.
- ROSS, G.W. 1966. Life-history studies on Mexican butterflies. IV. The ecology and ethology of *Anatoli rossi*, a myrmecophilous metalmark (Lepidoptera: Riodinidae). Ann. Entomol. Soc. Amer. 59:985-1004.
- ROTHSCHILD, M. 1979. Female butterfly guarding eggs. Antenna 3:94.
- ROTHSCHILD, M. and FAIRBAIN, J.W. 1980. Ovipositing butterfly (*Pieris brassicae*) distinguishes between aqueous extracts of two strains of *Cannabis sativa* L. and THC and CBD. Nature 286:56-59.
- VALADIN, G., MUMFERY, R. 1975. The large white butterfly: oviposition cues, carotenoids, and changes of colour. Proc. R. Entomol. Soc. 40:201.
- ROTHSCHILD, M. and SCHOONHOVEN, L.M. 1977. Assessment of egg load by *Pieris brassicae* (Lepidoptera: Pieridae). Nature 266: 352-355.
- SAXENA, K.N. GOYAL, S. 1978. Host-plant relations of the citrus butterfly *Papilio demoleus* L.: orientational and ovipositional responses. Entomol. Exp. Appl. 24:1-10.
- SCHOONHOVEN, L.M. 1977. On the individuality of insect feeding behavior. Proc. K. Ned. Akad. Wet. C 80:341-350.
- SCHOONHOVEN, L.M., SPANHAAR, T., VAN WISSER, V., HEERHAN, J. 1981. Seven-week persistence of an

- oviposition-deterrent pheromone. *J. Chem. Ecol.* 7:583-588.
- SCRIBER, J.M. and SLANSKY, F. Jr. 1981. The nutritional ecology of immature insects. *Annu. Rev. Entomol.* 26:183-211.
- SCUDDER, S.H. 1889. The butterflies of the eastern United States and Canada. Vol 1. Author. Cambridge, Massachusetts.
- SEVASTOPULO, D.G. 1964. Lepidoptera ovipositing on plants toxic to their larvae. *J. Lepid. Soc.* 18: 104.
- SHAPIRO, A.M. 1980. Egg-load assessment and carryover diapause in *Anthocharis* (Pieridae). *J. Lepid. Soc.* 34: 307-315.
- SHAPIRO, A.M. 1981a. The pierid red-eye syndrome. *Amer. Nat.* 117:276-294.
- SHAPIRO, A.M. 1981b. Egg-mimics of *Streptanthus* (Cruceferae) determined by oviposition by *Pieris silybri* (Lepidoptera:Pieridae). *Oecologia* (Berl.) 48:142-143.
- SHAPIRO, A.M. and CARDE, R.T. 1970. Habitat selection and competition among sibling species of satyrid butterflies. *Evolution* 24:48-54.
- SHEPHERD, J.G. 1974a. Activation of saturniid moth sperm by a secretion of the male reproductive tract. *J. Insect Physiol.* 20:2107-2122.
- SHEPHERD, J.G. 1974b. Sperm activation in saturniid moths: some aspects of the mechanisms of activation. *J. Insect Physiol.* 20:2321-2328.
- SHINOHU, T., and HARA A. 1960-1962. Early stages of Japanese butterflies. Hoikusha, Osaka. Vol. 1, 142 pp.; Vol. II, 139 pp.
- SILVA, A.G. d'A. e, CONCALVES, C.M., GALVAO, D.H., CONCALVES, A.J.L., GOMES, J., SILVA, M. do N., SIMONI, L. de. 1967-1968. Quarto catalogo dos insetos que vivem nas plantas do Brasil, suas parasitas e predadores. parte I. (2 vol., 906 pp.) & parte II (2 vol., 887 pp.). Ministerio da Agricultura. Rio de Janeiro, Gb, Brasil.
- SINGER, M.C. 1971. Evolution of foodplant preferences in the butterfly *Euphydryas editha*. *Evolution* 25: 383-389.
- SINGER, M.C. 1982. Quantification of host specificity by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. *Decologia* 52:224-229.
- SINGER, M.C., EHRLICH, P.R. and GILBERT, L.E. 1971. Butterfly feeding on lycopsid. *Science* 172:1341-1342.
- SINGER, M.C. and MANDRACCIA, J. 1982. On the failure of two butterfly species to respond to the presence of conspecific eggs prior to oviposition. Manuscript.
- SHILEY, J. 1978. Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science* 201:745-747.
- STAMP, W.E. 1980. Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly? *Amer. Nat.* 115:367-380.
- STAMP, W.E. 1981a. Effect of group size on parasitism in a natural population of the Baltimore Checkerspot *Euphydryas phaeton*. *Oecologia* 49:201-206.
- STAMP, W.E. 1981b. Parasitism of single and multiple egg clusters of *Euphydryas phaeton* (Nymphalidae). *J. New York Entomol. Soc.* 89:89-97.
- STANTON, M.L. 1979. The role of chemotactile stimuli in the oviposition preferences of *Collas* butterflies. *Oecologia* (Berl.) 39:79-91.
- STANTON, M.L. 1980. The dynamics of search: foodplant selection by *Collas* butterflies. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts.
- STANTON, M.L. 1982a. Searching in a patchy environment: foodplant selection of *Collas philodice eriphyle* butterflies. *Ecology* in press.
- STANTON, M.L. 1982b. Spatial patterns in the plant community and their effects upon insect search. In *Herbivore Insects: Host-seeking Behavior and Mechanisms* (S. Ahmad,

certain foodplants and its effect on the oviposition preference of the adult. Japanese J. Ecol. 11: 147-154.

TELFER, W.H. 1965. The mechanism and control of yolk formation. Annu. Rev. Entomol. 10:161-184.

TELFER, W.H. and NUTBERG, L.D. 1960. The effects of blood protein depletion on the growth of the oocytes in the oecroia moth. Biol. Bull. 118:352-366.

THORSTEINSON, A.J. 1953. The chemotactic responses that determine host specificity in an oligophagous insect (Plutella maculipennis (Curt.) Lepidoptera). Canad. J. Zool. 31:52-72.

THORSTEINSON, A.J. 1960. Host selection in phytophagous insects. Annu. Rev. Entomol. 5:193-218.

TOJO, S., MUGUCHI, K. and KINURA, S. 1981. Hormonal control of storage protein synthesis and uptake by the fat body in the silkworm, Bombyx mori. J. Insect Physiol. 27:491-497.

TRAYNIER, R.M.M. 1979. Long-term changes in the oviposition behavior of the cabbage butterfly, Pieris rapae, induced by contact with plants. Physiol. Entomol. 4: 87-96.

TUTT, J.W. 1899. A natural history of the British Lepidoptera. Vol. 1. Swan Sonnenschein, London. 580 pp.

UNQUHART, F.A. 1960. The Hensarich Butterfly. Toronto, Univ. Toronto Pr.

VAIDYA, V.G. 1969a. Form perception in Papilio demoleus L. (Lepidoptera, Papilionidae). Behaviour 33:212-221.

VAIDYA, V.G. 1969b. Investigations of egg-laying and resting behavior of Papilio demoleus L. (Papilionidae, Lepidoptera). Anim. Behav. 17:350-355.

VAN DEN BERG, M.A. 1971. Studies on the egg parasites of the Mopani emperor moth Madurelia belina (Westw.) (Lepidoptera: Saturniidae). Phytophylactica 3:333-36.

ed.), Academic Press, New York.

STENPFER, H. 1967. The genera of the African Lycaenidae (Lepidoptera: Rhopalocera). Bull. Brit. Mus. Nat. Hist. (Ent.) Suppl. 10. 322 pp.

STERN, V.M. and SMITH, R.F. 1960. Factors affecting egg production and oviposition in populations of Collias eurythems. Boisduval (Lepidoptera: Pieridae). Hilgardia 29: 411-454.

STRAATHAN, R. 1962. Notes on certain Lepidoptera ovipositing on plants which are toxic to their larvae. J. Lepid. Soc. 16: 99-103.

STRAATHAN, R. and MIEUJENHUIS, E.J. 1961. Biology of certain Sumatran species of Atrophaneura (Trogonoptera, and Troilidae) (Lepidoptera, Papilionidae). Tijdschr. Entomol. 104:31-43.

SWYNNERTON, C.F.M. 1915a. Experiments on some carnivorous insects, especially the driver ant Dorylus and with butterflies' eggs as prey. Trans. Entomol. Soc. Lond 1915:317-350.

SWYNNERTON, C.F.M. 1915b. Further notes on the eggs of butterflies. Trans. Entomol. Soc. Lond. 1915:428-430.

TABASHNIK, B.E. 1981. Evolution into a pest niche: Collias butterfly and alfalfa. Ph.D. dissertation. Stanford University, Stanford, Calif.

TABASHNIK, B.E., WHEELLOCK, H., HAINBOLT, J.D. and WATT, W.B. 1981. Individual variation in the oviposition preference in the butterfly, Collias eurythems. Oecologia 50:225-230.

TAKATA, N. 1961. Studies on the host preference of the common cabbage butterfly Pieris rapae crucivora (Buv.). XI. Continued studies on the oviposition preference of adult butterflies. Japanese J. Ecol. 11: 124-133.

TAKATA, N. 1961. Studies on the host preference of the common cabbage butterfly Pieris rapae crucivora (Buv.). XII. Successive rearing of the cabbage butterfly with

- VAN ENDEN, H.F. 1978. Insects and secondary plant substances -- an alternative viewpoint with special reference to aphids. *Phytochem. Soc. Eur. Symp.* 15:309-323.
- VAN LENTEREN, J.C., BAKKE, K. and VAN ALPHEN, J.M. 1977. How to analyse host discrimination. *Ecol. Entomol.* 3:71-75.
- VAN SOMEREN, V.G.L. 1974. List of foodplants of some East African Rhopalocera, with notes on the early stages of some Lycopidae. *J. Lepid. Soc.* 28:315-331.
- VAN SON, G. 1955. The butterflies of southern Africa, Part II. Nymphalidae: Danaidae and Satyrinae. *Transvaal Mus. Mem No.* 8. 166 pp.
- VENSCHIAFFELT, E. 1911. The cause determining the selection of food in some herbivorous insects. *Proc. Sol. K. Acad. Wet. Amsterdam* 13:536-542.
- WALDBAUER, G.P. 1968. The consumption and utilization of food by insects. *Adv. Insect Physiol.* 3:229-282.
- WASSERMAN, S.S. and FUYUWA, D.J. 1981. Evolution of host plant utilization in laboratory populations of the southern cornear weevil *Callosobruchus maculatus* Fabricius (Coleoptera:Bruchidae). *Evolution* 35:605-617.
- WATT, W.B., HOCH, P. and MILLS, S.G. 1974. Nectar resources use by *Colias* butterflies: chemical and visual aspects. *Oecologia* 14:353-374.
- WHITE, R.B. 1974. Foodplant defoliation and larval starvation of *Euphydryas editha*. *Oecologia* (Berl.) 14:307-315.
- WHITE, H.K. and SINGER, M.C. 1974. Geographical distribution of hostplant choice in *Euphydryas editha* (Nymphalidae). *J. Lepid. Soc.* 28: 103-107.
- WIKLUND, C. 1974. Oviposition preferences in *Papilio machaon* in relation to the hostplants of the larvae. *Entomol. Exp. Appl.* 17: 189-198.
- WIKLUND, C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* (Berl.) 18: 185-197.
- WIKLUND, C. 1977a. Observationer over agglagning, fodosok och vills hos *Donzels* blävinge, *Ariola nicta* scandius Wahlgr. (Lep., Tidskr. Lycopidae). *Entomol. Tidskr.* 98:1-4.
- WIKLUND, C. 1977b. Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinopis* (Lepidoptera). *Oikos* 28:56-68.
- WIKLUND, C. 1981. Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. *Oikos* 36:163-170.
- WIKLUND, C. and AHRBENG, C. 1978. Host plants, nectar source plants, and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). *Oikos* 31:169-183.
- WIKLUND, C. and PERSSON, A. 1982. Fecundity and the relation between egg weight variation and offspring fitness in the speckled wood butterfly *Pararge aegeria*, or why don't butterfly females lay more eggs? *Oikos*, in press.
- WILLIAMS, E.H. 1981. Thermal influences on oviposition in the montane butterfly *Euphydryas gillettii*. *Oecologia* 50:342-346.
- WILLIAMS, K.S. and GILBERT, L.E. 1981. Insects as agents of natural selection on plant vegetative morphology: egg mimics of *Pasiflora* reduce egg-laying by *Heliconius* butterflies. *Science* 212:467-469.
- WOLFSON, J.I. 1980. Oviposition response of *Pieris rapae* to environmentally induced variation in *Brassica nigra*. *Entomol. Exp. Appl.* 27:223-232.
- WRIGHT, S. 1967. "Surfaces" of selective value. *Proc. Nat. Acad. Sci. (U.S.A.)* 58:165-172.
- WRIGHT, S. and CLARKE, K.U. 1981. Photoperiod and larval body size: integrated factors controlling onset of the moulting cycle in

- Heliconius melponeme (Lepidoptera).  
J. Zool. 194:143-163.
- YAMAHOTO, H. and OHTANI, T. 1979.  
Number of eggs laid by Pieris rapae  
crucivora, compared with P. napi  
nezia in Sapporo  
(Lepidoptera:Pieridae). Kontyu  
47:530-539.
- YAMANAKA, M., SUZUKI, Y. and TAKAGI,  
M. 1978. Estimation of egg number  
oviposited per day by a female of  
Papilio xuthus Linne (Lepidoptera,  
Papilionidae). Kontyu 46:329-334.
- YOUNG, L.C.H. 1907. Common  
butterflies of the plains of India.  
J. Bombay Nat. Hist. Soc.  
17:921-927.
- YOUNG, A.M. 1972. Breeding success  
and survivorship in some tropical  
butterflies. Oikos 23:318-326.
- YOUNG, A.M. 1973. Studies on  
comparative ecology and ethology in  
adult populations of several  
species of Morpho butterflies  
(Lepidoptera:Morphidae). Stud.  
Neotrop. fauna 8:17-50.