The Monarch Butterfly: A Review

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Abstract. — A novel view of the monarch butterfly's (*Danaus plexippus*) life history is presented through the synthesis of theories developed in the last few years with more traditional ecological models of the monarch. The important factors directing monarch butterfly population dynamics are now understood to be: 1) Oviposition and Range Dynamics, 2) Energetics, 3) Mating Kinetics, and 4) Predation Deterrence. An understanding of the evolutionary basics and interaction of these factors in *D. plexippus* provides a foundation for the study of other endangered species.

Danaus plexippus, the monarch butterfly, has long been of scientific interest, due to its annual cyclic appearances, spectacular aggregations, and apostatic coloration (Urquhart 1960; Ackery and Vane-Wright 1984; Malcolm and Zalucki 1992). More recently, California monarch butterfly populations have been the center of social-political activity as land development interests in California infringe upon monarch natural habitat (e. g., Schultz 1989; Associated Press 1990; Allen and Snow 1991, Brower and Malcolm 1991). However, only recently has research elucidated several of the factors which drive the unique life history of the monarch butterfly. These selective forces, though more pronounced in *D. plexippus,* present insights for understanding the life histories of a wide range of species, and should be the focus of study in conservation efforts and legal decisions involving monarch butterflies. Although this article is centered on our knowledge of the California populations of *D. plexippus,* the principles should be applicable to monarch butterfly populations worldwide; and in fact, some information utilized for this synthesis is based on non-California monarch studies.

The factors which have interacted to shape monarch life history through natural selection now appear to be: 1) Oviposition and Range Dynamics, 2) Energetics, 3) Mating Kinetics, and 4) Predation Deterrence.

I. Oviposition and Range Dynamics

Oviposition constraint was the first factor recognized as one of the fundamental forces directing the life history of *D. plexippus.* Field observations and laboratory studies indicate that monarch butterflies worldwide oviposit only on plants in select genera of the families Asclepiadaceae (milkweed) and Apocynaceae (dogbane), and that these plants are the only hosts for the larvae (Nicholson 1935; Urquhart 1960; Wise 1963; D'Abrera 1971; Brower et al. 1972; Common and Waterhouse 1972; Tietz 1972; Smithers 1973; Brower 1977; Koch et al. 1977; Ackery and Vane-Wright 1984). Although select Apocynaceae are generally con-

sidered to be monarch host plants, one controlled study claims otherwise (Borkin 1991). Reports of monarch oviposition and larval feeding on plants of additional families (Convolvulaceae, Euphorbiaceae, Malvaceae, Rutaceae) represent rare instances and in most cases are considered questionable (Ackery and Vane-Wright 1984).

Orientation to host plants is probably based initially upon olfaction. Monarch adults typically approach milkweed patches from downwind using a zig-zag behavior characteristic of anemotactic odor search by flying insects (Kennedy 1983; Carde 1984; Wenner and Wells 1990). The ability of *D. plexippus* to find very isolated milkweed patches in coniferous forests (Shapiro 1981) supports this hypothesis. Subsequent host plant recognition by adults appears to be aided by vision and confirmed by tactile chemoreceptors (Urquhart 1960). Apparently, larvae will not feed on plants of other genera even in the absence of these host plants. It is inferred (Ackery and Vane-Wright 1984), and our experience confirms, that California monarch oviposition and larval feeding are as restricted.

Oviposition of eggs invariably occurs on a suitable host plant. Eggs are ovoid, leathery, about 1 mm in length, and appear faceted due to crossing of approximately two dozen vertical with many transverse ridges (Doherty 1886, 1891; Urquhart 1960). Time from laying to egg hatching varies with ambient temperature; it averages 3 to 4 days at summer temperatures ($\simeq 30°C$), but takes 8 to 12 days at 18°C (Urquhart 1960). We observed that in Southern California milkweed populations, *D. plexippus* eggs typically hatched 5 to 6 days after oviposition. Eggs are initially cream colored, but change to gray with embryo development (Urquhart 1960).

Larvae escape the egg shell by enlarging an initial transverse slit in the membrane. Upon hatching, the larvae consume most of the egg shell (Urquhart 1960). The larvae feed on host plant tissues while progressing through five instars, each instar having distinct markings, but apparently only statistically separable by size (Urquhart 1960). *Danaus plexippus* larval stage development is temperature dependent. Progression through the five instars (hatching to pupation) requires 10 days at 35°C (Urquhart 1960), but can take as long as 38 days in a cool (7°C) climate (Zalucki 1980, 1982). Basking reduces larval stage duration by as much as 50 percent (Rawlins and Lederhouse 1981). First instar larvae are approximately 2 mm while fifth instar larvae reach up to 50 mm in length. During development of the larvae wet mass increases approximately 1000 fold (Urquhart 1960). Later instars are capable of moving from one host plant to another (personal observations). In general, feeding larvae are negatively geotactic and positively phototactic (Mayer and Soule 1906). Caterpillar markings apparently are aposematic (Ackery and Vane-Wright 1984), and cardenolides consumed from the host plant may act as a predation deterrent (see section IV). When mildly disturbed, larvae wave their tubercles, which has been inferred to be a behavior that deters parasitism (Ordish 1975). Stronger mechanical stimuli cause the larvae to curl and fall to the ground (Urquhart 1960; Ordish 1975), and can also induce oral regurgitation (Brower 1984). Larvae usually wander from the host plant to pupate (Ackery and Vane-Wright 1984).

Pupa formation is initiated by the larva spinning a pad of silk attached to a suitable site from which the pupa can hang. The larva subsequently grasps the silk stalk with its anal claspers and hangs head down, assuming a fish hook shape. Finally, the larva molts and the pupa attaches to the silk pad by means of the

Fig. 1. North American monarch butterfly winter and summer geographic ranges. Overwintering areas are primarily limited to coastal California between San Francisco and Los Angeles, and a small region in the Transvolcanic Mountain Range of central Mexico (striped). Small relicts of summer populations survive in southern Florida and the low deserts of Arizona in some years, but represent insignificant numbers in terms of the population biology of the monarch butterfly. Each spring the geographic range expands from the overwintering areas as depicted by the stippled bands. Monarch populations normally decline in the gulf states in mid summer. Range contraction occurs each fall.

cremaster (Urquhart 1960, 1970). Eclosion occurs 9 to 15 days after pupation, depending upon temperature and other environmental conditions (Urquhart 1960; Petersen 1964a). Pupae are green except for a row of gold spots, whose function remains speculative (Taylor 1964; Petersen 1964a; Urquhart 1960, 1972a, b, c, d, 1973; Ackery and Vane-Wright 1984). Imago emergence from the pupa is described in detail by Urquhart (1960).

Danaus plexippus in California appear to be limited to plants of the genus *Asclepias* plus *Apocynum androsaemifolium* (taxonomy of Munz and Keck 1970). *Asclepias* are perennial herbs, which under normal west coast conditions, annually die back to their deep-seated roots. West coast milkweeds reappear each spring (primarily from underground rootstock), first in California southern coastal regions, followed by *Asclepias* populations at progressively higher elevations and more northerly latitudes (Munz and Keck 1970). Monarch butterflies are sequentially abundant at these seasonal oviposition sites (Urquhart 1966). The result is a displacement of the population annually, with the population center following a geographically cyclic pattern each year (Williams 1958; Urquhart 1960; Johnson 1969; Orr 1970; Nagano et al. 1992) as depicted in Figure 1.

A similar pattern of geographic range expansion moves annually from central Mexico towards southern Canada east of the Rocky Mountains (Urquhart 1976; Urquhart and Urquhart 1976b; Brower 1977), and in parts of Australia (Smithers 1965, 1977, 1983). Studies based upon Mexican monarchs show that butterflies

at the extremes of their summer geographic range are several generations distant from the individuals leaving the overwinter areas (Brower 1961; Herman 1988). Presumably the same is true for California based populations. Therefore, several generations annually are required to complete the geographic cycle.

Physiologically, none of the developmental stages of the monarch butterfly can survive prolonged freezing temperatures (Zalucki 1982; Ackery and Vane-Wright 1984). Range contraction to frost free zones in the winter, therefore, correlates both with survival and the region where hosts plants will first reappear. The wintering areas in California are typically frost free, support vegetation for roosting, and offer moisture sources. They are also cool throughout the night and during most hours of the day (Hill et al. 1976; Tuskes and Brower 1978; Chaplin and Wells 1982). The monarch's behavior of moving to warmer microhabitats within the overwinter areas provides further assurance of survival from occasional frosts (Calvert et al. 1983; Calvert and Cohen 1983). Suitable vegetation helps to provide a frost free environment, and is thus one important aspect of overwintering areas (Calvert and Brower 1981).

The winter geographic range of *D. plexippus* in California is, in fact, not only limited mainly to coastal regions between San Francisco and Los Angeles but is also centered in a small number of large aggregations within that coastal area (Williams et al. 1942; Urquhart 1960; Urquhart et al. 1965; Wenner and Harris 1991). These large overwinter aggregations are each composed of between 50,000 and several hundred thousand butterflies in California, to perhaps several million butterflies at some sites in Mexico. Aggregations coalesce in late fall. Butterflies roost in groups upon trees in the aggregations. Except for occasional flights to drink water there is little activity throughout winter in these large clusters (Fig. 7, 8). Without water, however, mortality due to desiccation occurs in overwintering butterflies. Thermoregulation by shivering, movement to warmer microhabitats, and basking are important, since these behaviors allow butterflies to attain body temperatures at which flight to obtain water is possible on cool days (Krammer 1970; Masters et al. 1988).

Smaller fall clusters which coalesce in the coastal region apprently are of a more transient nature, existing only until temperatures decline (Ackery and Vane-Wright 1984; Nagano et al. 1992). Members of these transient clusters may gradually join the major overwinter aggregations as winter progresses. However, it is also possible that mortality is high for butterflies in transient clusters and that most individuals do not survive winter. Additional continuously breeding winter populations in coastal California south of Los Angeles have been mentioned in mark and recapture studies focused upon the Los Angeles basin (Urquhart et al. 1970). Study of these populations over an entire winter, however, is likely to show that few butterflies actually survive. Native milkweeds of this region die back to rootstock in winter, and there is a dearth of food resources for nectivores. Only unnatural conditions created by suburb expansion would create exceptions.

Finally, a few West Coast monarchs, at least theoretically, may overwinter in the Arizona-California low deserts; e.g., Funk (1968) reported such an observation for southwestern Arizona. At present, the regularity of overwinter low desert monarch populations is doubtful, and occasional monarch butterflies in this region during winter are probably insignificant in the overall natural history of the species.

Sustained periods of flight, thought by some to be involved in range contraction, may lead to juvenile hormone inactivation (Lessman and Herman 1981), and

this in turn degresses maturity of both male and female reproductive tracts (Herman 1975a, b; Herman et al. 1981). However, low post-eclosion temperature appears to be the primary environmental factor which leads to reproductive dormancy in both sexes of monarch butterflies (Barker and Herman 1976; James 1983). Photoperiod apparently does not control reproductive tract maturity (James 1983), but it may be a factor influencing reproductive behavior (Barker and Herman 1976). Photonegative behavior of overwintering butterflies may indirectly curtail reproductive tract development by minimizing heliothermic warming (James 1983).

During overwinter aggregation, reproductive tract maturity of most monarch butterflies is not complete (Herman et al. 1989), and mating is rare (Hill et al. 1976; Tuskes and Brower 1978); however, oligopause is incomplete in California populations (Ackery and Vane-Wright 1984). A similar natural history has been described for monarchs in southeastern Australia (Smithers 1965; James 1979), including absence of a true reproductive diapause (James 1982; James and Hales 1983), and in central Mexico (Urquhart 1976; Urquhart and Urquhart 1976b; Brower et al. 1977), where oligopause (possibly true diapause: Herman 1981) can be complete and of a longer duration (Herman et al. 1989).

Alternative theories have been proposed to account for fall contraction of the range of *D. plexippus*. The long distance directed (LDD) migration hypothesis infers that California overwintering populations are the product of a fall adult monarch flight from southwestern Canada, Washington, Oregon, and northern California (Urquhart and Urquhart 1977) down the coast, and from the western slopes of the Rocky Mountains and Sierra Nevada Mountains though the Sacramento and San Joaquin Valleys to coastal regions of California (Urquhart and Urquhart 1977). The summer range of *D. plexippus,* under the LDD migration hypothesis, is geographically density skewed, such that the highest densities of monarch butterflies occur in regions farthest from the overwinter areas (Urquhart 1966). Eastern monarch populations, originating from Mexican overwinter sites, do in fact decline (are often absent) in mid-summer throughout the Gulf Coast states and are largest in states bordering Canada (Brower 1961, 1962; Neck 1976; Urquhart and Urquhart 1976a), due perhaps to monarch intolerance of high temperatures (Malcolm et al. 1987). According to the LDD migration hypothesis, individuals leaving the summer range are the same individuals as those that arrive at the overwinter sites; the seasonal movement is thought to resemble that of migratory birds (Urquhart 1960).

Alternatively, the California overwinter population of monarch butterflies has been hypothesized to reflect a relatively local range contraction; most individuals of the more extreme summer range simply die as winter weather comes to the areas they inhabit (Smithers 1977; Wenner and Harris 1992). Overwintering California aggregations have been predicted under this theory to be primarily the result of autumn upwind flight by butterflies produced in summer populations (Wenner and Harris 1991) of the Sacramento and San Joaquin Valleys, adjacent lower and mid-elevation Sierra Nevada and coastal mountains (Ackery and Vane-Wright 1984), as well as the coastal plain and river drainages (Wenner and Harris 1991).

Thus, the large overwinter aggregations are thought by some to be the direct result of long distance directional migration to avoid harsh northern winters (Urquhart 1960). Others believe these aggregations are the result of seasonal

contraction of the environmentally suitable monarch butterfly range, thus representing relatively local surviving individuals (Wenner and Harris 1992). Note, however, that neither the migration nor the seasonal range contraction hypothesis explains winter monarch aggregation; dispersed roosting in the overwintering regions would be as beneficial under either of these theories.

Lipid content of monarch butterflies arriving at the overwinter range is high, as would be expected under the local range constriction hypothesis (Chaplin and Wells 1982). However, a version of the LDD migration theory suggests that feeding during migration might produce similar results (Brown and Chippendale 1974), especially given the speculation that flight-work may be minimized by soaring flight behavior (Gibo and Pallet 1979; Gibo 1981). Future determination of summer range geographic density distribution may help to resolve the debate. That is, data may show any LDD migratory individuals to be an unimportant percentage of the California overwinter population, particularly if probability of death due to random misfortune is related to distance traveled. On the other hand, density distribution may indicate that there is not locally a large enough population to represent an important fraction of the overwinter aggregations, although this argument seems untenable for Santa Barbara County (Wenner and Harris 1992).

Aggregations also have been theorized to be sanctuaries where, *en masse,* individuals are protected by metabolic heat and thermal insulation from winter cold. However, studies designed to test this hypothesis did not find a temperature gradient between the outside and center of overwintering groups of butterflies (Chaplin and Wells 1982), as found in some communal bees, and isopods (Simpson 1961; Friedlander 1965; Wilson 1971).

Three additional lines of evidence also suggest that aggregations are not the result of selection by this environmental factor. First, aggregations in California have remained coastal, and Mexican populations inland. Selection would be expected to have either caused Californian overwintering aggregations to move to cooler elevations, where metabolic rates would be lower, or Mexican overwintering clusters to move to lower elevations where the likelihood of death due to freezing would be minimized.

Second, new aggregation site formation can occur, as evidenced by monarch clusters in *Eucalyptus* forests in California (e.g., Urquhart et al. 1965; Hill et al. 1976). *Eucalyptus* species were introduced, the *Eucalyptus* forests subsequently planted, and their use as roosting sites established within the last 150 years (Chaplin and Wells 1982). Thus, locations of Californian and Mexican aggregation sites cannot be ascribed to innate behavior which inhibits selection for new cluster localities.

Finally, if clustering were simply the result of a selection which would protect butterflies from occasional freeze periods, California coastal populations would be largely exempt from selective pressure to aggregate. Aggregation within the winter range of the monarch is thus not explained simply by distribution of oviposition sites or geographic areas which are equable throughout winter.

II. Energetics

The second major factor shaping the life history of the monarch butterfly is energetics. Energetics, the dynamics of metabolism and the processes whereby energy is stored chemically is, of course, basic to all life. Just how energetics has
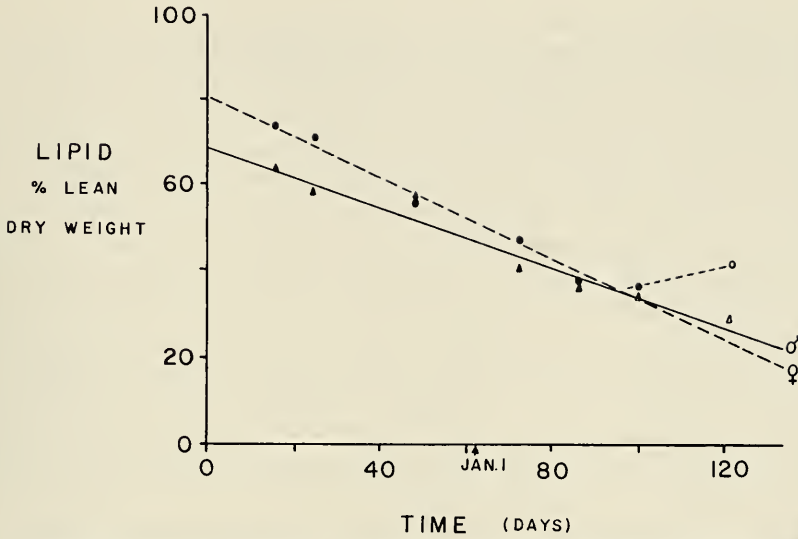
Fig. 2. Least squares linear regression performed separately on male and female data. Each point represents 25 pooled individuals (all male or all female). Regression analyses were performed on pre-mating samples (solid points). Male and female regressions are signficantly different. Only the female post-mating sample (o, male △) was significantly different than predicted by the 95% prediction limits based on the regression analyses (from Wells et al. 1992).

shaped the life history of *D. plexippus,* however, has only gradually become apparent over the past ten years.

Winter presents the monarch butterfly with acute energetics problems not normally faced by most species. Specifically, energy resources for both monarch adults (nectar) and larvae (milkweed) are scarce or absent during winter throughout the West Coast geographic range of *D. plexippus* (Tuskes and Brower 1978; Chaplin and Wells 1982). The scant nectar resources that may be present (Brower 1977) are insignificant in terms of monarch energetics (Ackery and Vane-Wright 1984). Similar conditions exist seasonally for Mexican and Australian aggregating monarchs (James 1984; Masters et al. 1988). Monarch butterflies must overwinter on stored lipid reserves (Chaplin and Wells 1982; James 1984; Masters et al. 1988).

Particularly important in this light is the fact that metabolic rates of ectotherms are dependent upon temperature of the environment; ectotherm metabolism exponentally increases as temperature is raised (Gordon 1968). This correlation dictates that the overwinter range of the monarch butterfly must be consistently cool. Otherwise, death from starvation would occur prior to the availability of spring oviposition sites (Chaplin and Wells 1982).

Even though North American *D. plexippus* is very widely distributed throughout summer, the physiological limits requiring above freezing temperatures and the energetics requirement of a continuously cool climate severely constrict the winter range of the monarch butterfly (Calvert and Brower 1985). California south coastal areas are the only predictably cool frost-free winter regions with moisture sources west of the Sierra Nevada. Under these conditions lipid reserves of inactive butterflies within the winter cluster should not be rapidly depleted by basal metabolic processes (Chaplin and Wells 1982). In fact, a slow and linear decline in

butterfly lipid content is observed in natural aggregations (Fig. 2), although lipid utilization rates in male and female butterflies differ (Wells et al. 1992). Thus, energy reserves of overwintering monarch butterflies are predictable using a linear model, based upon an initial measurement of the fall butterfly lipid reserve. Again, as with the previously discussed factors, adaptive as these features of the environment may be to monarch survival, they are independent of aggregation *per se* within the wintering areas. Dispersed roosting would serve as well.

Female adult monarch butterflies have a potential energy source in addition to nectar. Energy transfer from male to female monarch butterflies occurs during mating (Boggs and Gilbert 1979; Wells et al. 1991). Monarch external and internal anatomy, including male and female reproductive tracts, have been described (Erhlich 1958; Erhlich and Davidson 1961). The male monarch transfers sperm and nutrients, encased in a proteinaceous spermatophore, to the females. Monarch butterfly spermatophores can reach 10% of the male's wet weight (Oberhauser 1988). Spermatophores are deposited in the female butterfly's bursa copulatrix, a sack-like organ surrounded by transverse muscles and lined internally by four lateral rows of chitinous teeth. Spermatophores are mechanically disrupted open by the bursa copulatrix (Rogers and Wells 1984) and released nutrients are very quickly incorporated into both reproductive and non-reproductive female tissues; incorporation of labeled spermatophore carbon is detectable within four hours (Boggs and Gilbert 1979; Wells et al. 1992). Rapid assimilation suggests that a specialized mechanism for material absorption may have evolved in the female reproductive tract. However, details of the nutrient absorptive process and the molecule or molecules absorbed are still not well defined.

Just prior to and during dispersal of aggregations a "frenzied" period of mating occurs for approximately two weeks. Photoperiod and temperature act together through the neuro-endocrine system, and regulate reproductive activity (Herman 1973). Temperature appears to be the dominant factor determining the rate of egg maturation (Barker and Herman 1976; James 1983). This intense mating period probably is the first coincidence of warm weather and longer days. Individual monarch butterflies mate repeatedly during this mating period (Hill et al. 1976; Tuskes and Brower 1978). However, monarch butterflies mate at most once per day, due to an extensive copulation time (average 10 hrs, Shields and Emmel 1973; Hill et al. 1976; Ackery and Vane-Wright 1984; Oberhauser 1988; 6 to 18 hrs, personal observations). Energy transfer from male to female butterflies through multiple mating has been demonstrated to significantly increase lipid reserves of overwintering female butterflies in natural California aggregations at the time of aggregation dispersal (Wells et al. 1992). In fact, average female lipid content increases approximately 60% during this mating period. Multiple mating is thus critical for significant energy gain by females at this time of year.

Due to the intensive mating period whereby both male and female butterflies mate repeatedly at the time of aggregation dispersal, female energy reserves increase markedly. After the period of intensive mating, female energetics suddenly are no longer represented solely by depletion of fall lipid reserves. Female butterfly energy reserves after aggregation dispersal must include nutrients gained through mating. These two models have been the key to evaluating the effect of multiple mating on fecundity, generating testable expectations, and contributing to our current concept of monarch butterfly life history.

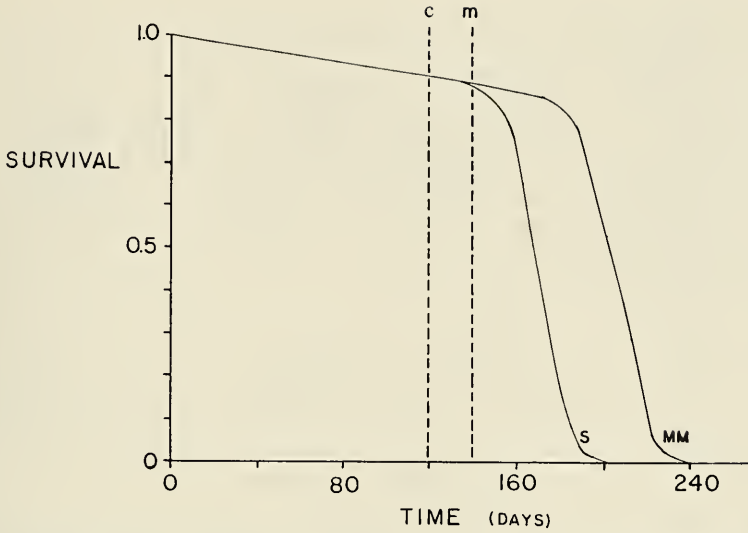Nectar resources are, in fact, few and not abundant even at the time of aggre-

Fig. 3.   Mathematical model of female butterfly survival versus time with and without the multiple mating resulting from February mating frenzy. Survival is based on chance death and upon lipid energy reserves which are depleted while overwintering (death due to starvation). Lipid depletion rates and fat content used were those observed (Fig. 1). MM = multiple mating, S = single mating, c = mean time of cluster dispersal, m = mean time of milkweed first appearance (from Wells et al. 1992).

gation dispersal (Tuskes and Brower 1978). The continued energy impoverishment of males during this period confirms that nectar foraging is not a primary source of increased female energy reserves. Successful reproduction requires that females disperse to the locations of species of plants suitable for oviposition. Increased life expectancy at this time relates directly to female oviposition success. Overwintering female fecundity is thus a function of life expectancy after aggregation dispersal (Wells et al. 1992).

Female life expectancy has been modeled by Wells et al. (1991) based upon the probability of escaping death due to random misfortune, and the probability of avoiding death from starvation. Using the linear models described, and the assumptions that both lipid reserves of individual females entering overwinter aggregations and individual female energy gain through mating are normally distributed and independent, evidence exists that time of death due to starvation in the female population is normally distributed. Normal cumulative distribution functions thus describe life expectancy based on energetics with or without multiple mating, given that nectar resources are not available. The only difference is that the mean and variance in life expectancy are increased with multiple mating.

Lipid reserves at the time of aggregation degeneration determine female ability to disperse into the environment (Ackery and Vane-Wright 1984). Female monarch life expectancy based on overwinter metabolic rate is displayed in Fig. 3, with and without energy gained by females through multiple mating. Energy gain through multiple mating is predicted to significantly increase female longevity, and as a result, increase fecundity (Wells et al. 1992). Altered estimates of net lipid metabolic rate in dispersing females would not change the basic conclusion; longevity of females in the two groups would be changed equally. Thus, multiple mating would increase overwinter female butterfly fitness, and would be favored
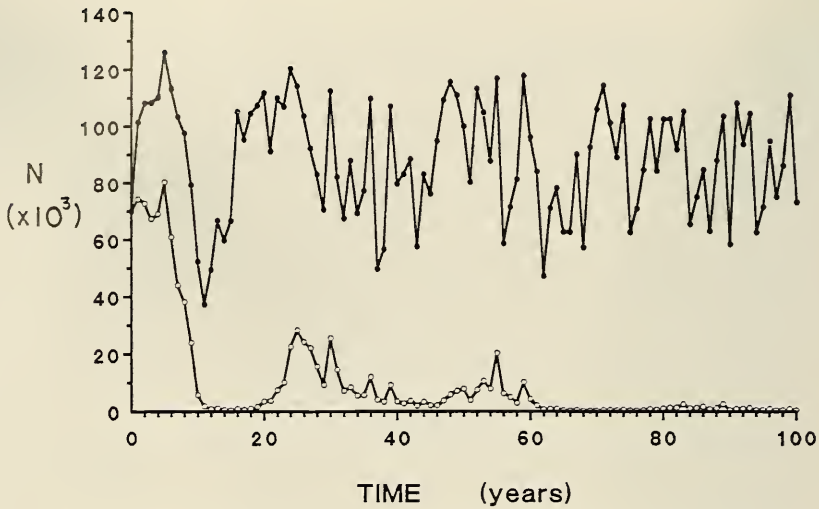
Fig. 4.   Monte Carlo simulations of monarch aggregation population size. Number of individuals (N) in an aggregation verses time with multiple mating (●) and without multiple mating (o) are presented. Life expectancies of overwintering monarchs are based on Figure 3. First appearance of milkweed each year (u = 140 σ = 10) and summer population fitness as it relates to population growth rate (e^{mt}, u_m = 1, σ_m = 0.1) were variables, normally distributed and independent. Summer population growth was based on the Pearl-Verhulst logistic model (Pielou 1977) with carrying capacity 100,000,000 and 5 generations per summer. The probability of last summer generation butterflies reaching the overwinter aggregation is 0.0015. Without multiple mating monarch populations decline to the point where extinction is likely.

by selection in the female population. Under conditions where food is abundant for nectivores, energy transfer from males to females is not an important factor for female survival (Svard and Wiklund 1988); correspondingly, monarchs need not aggregate under these conditions (e.g., Hawaii: Etchegaray and Nishida 1975; N.E. Australia: Smithers 1977).

Studies based on Australian monarch butterflies show that females move from milkweed patch to milkweed patch after dispersal from overwinter aggregations, rather than remaining at a single patch (Zalucki and Kitching 1982, 1984). This behavior leads to discovery of oviposition sites by a female as a linear function of time; thus oviposition rate is a constant. Expected total eggs oviposited by an overwintering female throughout its life is then predictable, based upon milkweed first appearance. When variable time of spring milkweed first appearance is also considered, Monte Carlo simulations using this model of population dynamics have demonstrated (Wells et al. 1992) that, without multiple mating, monarch populations would decline to the point where extinction would be inevitable in poor years (Fig. 4). Energetics are thus a central factor driving the life history of *D. plexippus*.

III. Mating Kinetics

The concept that a third central factor is important in determining the life history of the monarch is only now being realized. This third factor involves the reproduction dynamics of the monarch and may explain why overwintering monarchs are densely aggregated.

Monarch butterflies become active daily in large numbers just prior to aggregation dispersal. Thousands of butterflies are flying simultaneously at that time in the aggregation sites, resulting in a mating frenzy. Male monarch butterflies can be distinguished from females by the presence of a small black spot (alar organ) on each hind wing but that dimorphism is inconspicuous in flight. Females do not appear to actively seek male monarchs. Nor do males expose hairpencils and perform courtship maneuvers (Hill et al. 1976) as has been reported for other danaine butterflies (Ackery and Vane-Wright 1984). Rather, mating occurs through male chase and in-flight capture of females. A male only chases females which by chance come relatively close to it through crossing of flight paths. A male captures a female in-flight by pouncing on her (Hill et al. 1976). The pair tumble to the ground, where the male physically overpowers the female and initiates copulation (Fig. 9, 10, 11). The male subsequently flies, carrying the female to a roosting site where copulation (Fig. 9, 10, 11) continues for several hours (Hill et al. 1976). Similar behavior has been observed in the laboratory (Rothschild 1978) and in summer populations (Zalucki and Kitching 1982; Oberhauser 1988). Rarely, males have been reported to "nudge" a female toward the ground rather than overpower her (Pliske 1975).

Male butterflies do not always chase females when flight paths cross, or always capture chased females. In fact, males do not only chase female monarchs. A male butterfly will sometimes chase another male when they cross flight paths. If a male captures a male, however, the pair separate soon after falling to the ground (Hill et al. 1976). Flying males will sometimes even chase objects, such as falling leaves or tossed sticks, if they come relatively close, and even an occasional "amorous advance" toward a passing bird has been reported (e.g., Slansky 1971; Smith 1984; Winter 1985). Aberrant mating attempts become more prevalent toward the end of the period of intense mating which precedes dispersal, as the ratio of females to males in the aggregation declines (Hill et al. 1976).

Butterflies appear to mate at most once per day, a limit imposed by the extended period of copulation. However, monarchs can only potentially mate if two come physically close enough to detect each others presence; in terms of kinetic theory: "collide." A "collison" between monarchs may be defined as two butterflies coming into close proximity, although no physical contact is implied or need occur (Wells et al. 1990). The collision rate of butterflies is analogous to the collison rate of randomly moving gas molecules in a container because: 1) A male appears to interact with a female monarch butterfly only when they come into relatively close proximity, and both are in-flight; and 2) Butterflies coming into close proximity (a collision) while flying seems to result by chance crossing of flight paths. The rate constant for butterfly collision has therefore been shown to be a function of the squared density of butterflies (Wells et al. 1990).

Monarch butterfly mating frequency thus obeys second order kinetic laws, rather than Malthusian first order kinetics (Malthus 1798). Furthermore, unlike the Pearl-Verhulst or Lotka-Volterra type models (Verhulst 1838; Pearl and Reed 1928; Lotka 1925; Volterra 1931; Pielou 1977), increased density increases rather than slows the rate of increase in the population of mated individuals.

The rate of change of in-flight non-mated males on any specified day has been shown to be equal to that of females. The fraction of the in-flight female, q_t, and male, p_t, butterflies which have not mated by time t on a specified day may thus be predicted by equation (1) when h = 0, and by equation (2) when h ≠ 0; where

$h = X_o - Y_o$, Y_t equals female density (X_t male) at time t on the specified day (Y_o is Y_t at time zero), and "a" is a constant based on rate of mating success of collisions (Wells et al. 1990).

$$q_t = Y_t/Y_o = p_t = X_t/X_o = 1/(aY_ot + 1) \tag{1}$$

$$q_t = Y_t/Y_o = h/[(Y_o + h) e^{aht} - Y_o]$$

$$p_t = X_t/X_o = h/[(Y_o + h) - Y_o e^{aht}] \tag{2}$$

Increased density of butterflies, due to second order reproduction kinetics, increases the probability each day that each individual will mate (Fig. 5). Furthermore, high population densities result in most mating occurring in the first few hours of butterfly activity each day regardless of the length of time during which the environment is conducive to activity (Wells et al. 1990). This phenomenon may be crucial to the monarch butterfly's successful reproduction in California overwinter clusters where cool early spring temperatures may allow only a few hours of activity per day. Thus, the length of time during each day in which environmental conditions are conducive to in-flight butterfly activity affects the population densities required for monarch butterfly populations to increase in number, because multiple matings are necessary for successful reproduction. In essence, second order reproduction kinetics interacting with energetics of lipid reserve depletion and energy gain through mating, a variable time for the appearance of oviposition sites, and an environmentally constrained period of daily activity, make very dense aggregations advantageous compared to dispersed or semi-aggregated overwinter roosting.

The cumulative number of matings per individual increases linearly with each day of the spring mating frenzy as long as the daily probabilities of mating for male and female butterflies remain relatively constant. A linear relation exists between frequency of mated females per day and the cumulative number of matings per female (Wells et al. 1990). As percent mated females each day increases, cumulative number of matings per individual increases.

However, since probability of a female mating on a specified day is not linearly related to density, the cumulative number of matings asymptotically approaches the number of days mating could have occurred as cluster density increases (Fig. 6). The number of times an individual has mated thus becomes essentially density independent at high population densities. The same relation exists for male probability of mating each day (Wells et al. 1990). Under these conditions only high density aggregations cause mating success to approach first order kinetics. Therefore, high densities of butterflies are critical for widespread multiple mating in overwinter populations and, in turn, maximum fecundity. This transition in monarch mating dynamics from second to first order kinetics is predicted on theoretical grounds, using data from California monarchs, to become significant in overwintering aggregations of about 50,000 individuals and essentially complete when aggregations reach 200,000 individuals (Wells et al. 1990).

Decreasing density decreases the mating frequency of both males and females each day if the sex ratio remains unchanged. However, since the rate of female emigration exceeds that of males, sex ratio in the aggregation does change (Hill et al. 1976); the net result is an increase in the mating frequency of remaining females even though the population density declines (Wells et al. 1990).

Males are energetically capable of mating 11 or 12 times during the spring mating frenzy (based upon the Wells et al. 1991 model for an average year and
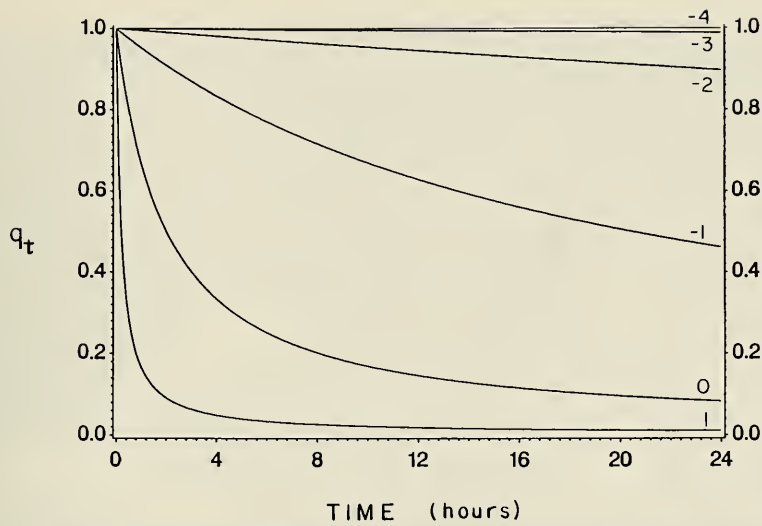
Fig. 5.   Effect of functional day length and population density on mating frequency, when frequency of males equals frequency of females in the population (h = 0). Frequency of unmated individuals (q_t = p_t) versus time during any specified day is depicted (unmated male frequency equals unmated female frequency). Results are given for values of aN_o from 10^1 to 10^{-4} (curves 1 to −4). Percent unmated individuals asymptotically approaches zero. Higher densities accelerate decline in frequency of un-mated individuals (from Wells et al. 1990).

on cumulative mating frequencies observed by Zalucki and Sasuki 1987). Statis-tically, less than 00.20% (using 11 matings), or 00.01% (using 12 matings), of the males would exceed those limits if it were energetically possible. Thus, male mating behavior in overwinter aggregations does not appear to be significantly influenced by energy limitations.

The model predicts that, at least in overwintering butterflies, egg fertilization dependency on mating order (e.g., first, last, each) would not select for altered male behavior. Prior to the spring mating frenzy, environmental conditions are generally too cool for in-flight activity and mating, although oligopause is not complete. Occasional warm winter days would be too short to substantially in-crease the rate of gamete maturation, and days would still have a short photo-period; both would inhibit mating.

After aggregation dispersal, the probability of mating is very low because but-terfly density is low and mating success is a second order kinetic function. This is true even if females are still receptive. Finally, during the spring mating frenzy males energetically are capable of mating every day that they can catch a female. Thus, by mating every day a male would maximize its fecundity during the spring mating period (Wells et al. 1990).

In fact, some data now exist which suggest that, in addition to oviposition sites, both energetics and second order reproduction kinetics may even be limiting factors for non-overwintering monarch butterflies. That is, empirical evidence implies that multiple mating is also important energetically to non-overwintering female butterflies (Suzuki and Zalucki 1986; Zalucki and Suzuki 1987; Oberhauser 1988; Zalucki 1992). Furthermore, individual male behavior during location and capture of female monarchs for mating appears to be mechanistically similar in non-overwintering individuals (Zalucki and Kitching 1982; Oberhauser 1988) and
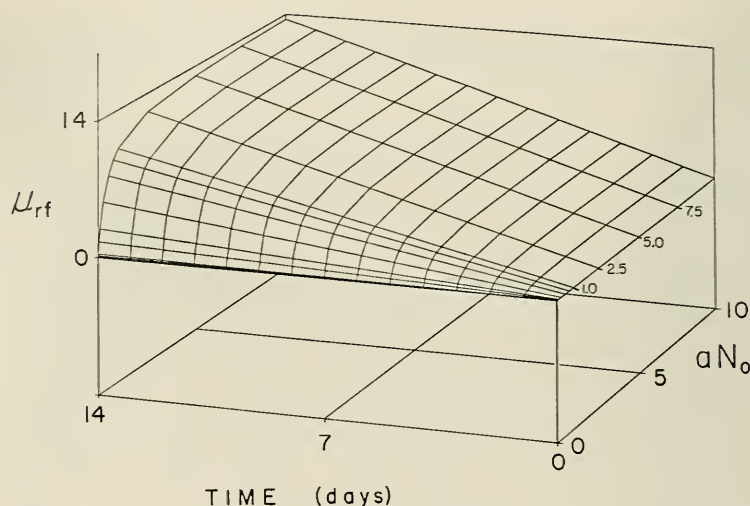
Fig. 6. Mean number of matings per individual (u_{rf}) versus number of days mating frenzy has occurred versus relative population density (aN_0) for $h = 0$. A transition occurs, after which increasing aggregation density has little additional effect on mean number of matings per individual. Essentially, reproduction kinetics change from second order to first order when considering reproduction on a population basis (from Wells et al. 1990).

in laboratory colonies (Rothschild 1978). A conclusion which necessarily follows is that mating frequency in non-overwintering populations should also obey second order kinetics. Population density should be no less a factor in monarch butterfly reproduction dynamics during summer than it is for overwintering populations.

The densities at which reproduction approaches first order kinetics in non-overwintering populations, however, should be reduced from densities required in overwinter aggregations, due to extended daily flight activity, greater food availability, and partially restored lipid reserves. Aggregation, although of a less dense nature, should still be important for efficient reproduction in non-overwintering populations (Wells et al. 1990).

In this light, observations of monarch butterfly clustering about oviposition sites (Zalucki and Kitching 1982, 1984; Bull et al. 1985; Suzuki and Zalucki 1986; Zalucki and Suzuki 1987; Zalucki 1992) are very interesting, since these summer concentrations are predicted theoretically. Male monarchs tend to remain at a milkweed patch, while females move from patch to patch. This behavior maximizes butterfly density at specific localities in the environment, maximizes multiple mating of females, minimizes male energy expenditure, and maximizes distribution of larvae among food resources.

IV. Predation Deterrence

High population densities necessitated by second order kinetics, and the monarch butterfly's relatively large physical size, would be expected to have fostered acute predation problems for *D. plexippus*. Instead, second order reproduction kinetics has led to strong selection for a predation deterrent; one predation deterrent that meets this prediction is cardenolide-based toxicity (Parsons 1965),

Fig. 7. Monarchs drinking water from dew. Although overwintering *D. plexippus* do not require a food source, they need a source of water to survive winter.

combined with apostatic coloration (Brower et al. 1967, 1968; Brower 1969, 1984). The effectiveness of that deterrent, and the importance of predation under some conditions, is attested to by a mimicry complex which includes the resemblance of *Limenitis archippus* to *D. plexippus* (Brower 1958, 1960; Brower et al. 1964; Platt et al. 1971, Ritland and Brower 1991).

The prediction that toxicity, coupled with apostatic coloration, has evolved in concert with the winter aggregation required for successful reproduction is also supported by modeling studies of avian predation on monarch butterflies (Pough et al. 1973). Non-palatability is only an effective predation deterrent when butterflies are densely aggregated (Pough et al. 1973). This prediction has, in fact, been confirmed by predation studies of summer butterfly populations (Petersen 1964b; Waldbauer and Sternburg 1987).

Apostatic coloration combined with monarch toxicity would not be expected to have evolved until monarchs overwintered in aggregations, since evolution of a trait prior to, or independent of, natural selection does not generally occur. Furthermore, while predation models do not predict a maximum density of monarch butterflies in overwinter aggregations, and in fact predict ever greater numbers of individuals in clusters (Calvert et al. 1979), second order kinetics does predict aggregation densities at which ever larger aggregations have no beneficial effect (Wells et al. 1990).

Since toxicity of individual butterflies can vary widely, automimicry is some-

Fig. 8. *Danaus plexippus* overwinter aggregation in California. Monarch aggregations are always in forests, usually around a small clearing and close to a water source. Throughout winter butterflies hang from branches in the aggregation area except for trips to drink water.

times an important aspect of the predation deterrent (Brower and Moffit 1974). Some avian insectivores have learned to taste butterflies for cardiac glycoside content (Brower and Glazier 1975) and have learned in some areas of Mexico to eat only less toxic tissues of functionally less-toxic individuals (Calvert et al. 1979). Predation under these conditions can be substantial (accounting for 75% of butterfly mortality), and is inversely related to aggregation size (Calvert et al. 1979). This type of avian behavior only appears to result in substantial monarch mortality when *D. plexippus* populations contain a relatively high percentage of palatable individuals (Calvert et al. 1979). Predation by mice also appears to be significant under these conditions (Glendinning et al. 1988).

Cardenolide sequestration by monarchs to saturation levels when feeding on *Asclepias* with widely variant cardiac glycoside contents appears to be evolutionarily important (Martin and Lynch 1988; Malcolm and Brower 1989; Malcolm et al. 1989). The fact that highest concentrations of cardenolides are in the wings (Calvert et al. 1979), by which predators capture monarchs (Smith 1979), may also be adaptive. However, cardenolide sequestration to saturation in and by itself does not protect monarch butterflies from predation, as illustrated by Mexican *D. plexippus* which apparently feed largely on species of *Asclepias* with low potency cardenolides (Fink and Brower 1981). Palatability is not only a function of cardiac glycoside concentration, but also the type of cardenolide fed upon by larvae, and the species of avian predator (Fink and Brower 1981).

While occasional beak marks in monarch wings are observed, significant avian

Fig. 9. Male monarch butterfly attempting to mate with a female. The male monarch chases the female, and upon capturing her, the two tumble to the ground where the male attempts to mate with the female. If successful, the male will fly to a branch carrying the female, where copulation will continue for several hours.

and mouse predation on monarch butterflies is not characteristic of California overwintering populations (Brower and Moffit 1974; Calvert et al. 1979). California monarch variability in cardenolide concentration is similar to that observed in Mexican populations. However, the cardenolides found in some California overwintering monarchs are more emetic (Brower and Moffitt 1974; Fink and Brower 1981).

California *Asclepias* species differ in their toxic glycoside contents and there are clonal variations within the species. The narrow leafed *A. fascicularis* is relatively nontoxic, as are approximately 47% of *D. plexippus* in the winter aggregations. Toxicities of *A. californica* and *A. speciosa* are higher, on the order of 0.15 mg cardenolide/g dried plant tissue, while glycoside contents of *A. eriocarpa*, *A. erosa* and *A. vestita* often exceed 1.0 mg/g dried plant tissue (Roeske et al. 1976). Chromatographic profiles of sequestered cardenolides in monarch butterflies raised on specific California milkweeds have also been determined (e.g., Brower et al. 1982, 1984a, b).

Larval densities also pose mortality problems for the monarch butterfly. While predation by vertebrates may be deterred by the chemical defense obtained from the host plant, parasitism by dipterans apparently is not. Tachinid fly parasitism of monarch larvae can kill up to 100 percent of the larvae in a milkweed patch, but parasitism frequencies appear to vary widely between patches (Hill 1973; Etchegaray and Nishida 1975; Zalucki 1981; pers. obs.). Monarch females, by

Fig. 10. Monarch butterflies mating. During an extended copulation time a source of energy is transferred to the female as well as sperm. The energy gained is thought to increase the female butterfly's life expectancy, and hence fecundity.

ovipositing in many milkweed patches, would maximize the frequency of having at least some offspring survive.

V. Perspective

The monarch, *Danaus plexippus,* is an immensely popular butterfly; size, color, distribution, abundance, and conspicuous winter aggregations give the monarch "celebrity status." Biology students are introduced to mimicry theory by the classical monarch-viceroy example (e.g., Curtis and Barnes 1989; Villee et al. 1989; Campbell 1990). Winter roosting, summer breeding, and land use issues involving monarchs are given media coverage (*op. cit.*). The monarch has even been nominated as the United States National Insect (H.J. Res. 411, introduced by Congressman Leon Panetta of Santa Cruz)! This high profile of the monarch butterfly cultivates appreciation of nature, sensitizes the public to ecological issues, and creates a positive image of science.

On the negative side, familiarity may foster complacency, a sense that our knowledge of the monarch butterfly is complete and correct. Familiarity also may encourage concept-centered biology (Wenner 1989) which quashes controversy and narrowly interprets natural history in support of a single popular hypothesis. Either of these simplifications retards scientific progress.

A more complex and interesting monarch butterfly life history emerges from consideration of all "factors" that have influenced its evolution and stability. These selective factors may interact, and often encompass many interrelated forc-

Fig. 11. Male *D. plexippus* in flight with female (hanging) soon after mating has been initiated. Copulation will continue for 6 to 18 hours once a suitable resting site has been located by the male.

es. For example, summer food plant distributions, restricted wintering areas, and endocrine physiology combine to define range, limit oviposition, and cyclically shift geographic population centers. Ecological chemistry, predation deterrence, and mimicry relate not only to the aspects of the life history just mentioned but also influence predator types and potential mimics (Batesian, Mullarian, or Auto-; Ritland and Brower 1991). Aggregate overwintering reflects energetics, multiple mating, and second order breeding dynamics, as well as climatic and physiographic considerations.

The picture of monarch butterfly biology presented here is neither definitive nor complete. It can be improved by continued research effort, most rapidly if that picture is never so certain that falsification and strong inference approaches are considered out of order (Wenner and Wells 1990).

California provides a natural laboratory for the study and management of the monarch butterfly; winter aggregation, spring multiple mating, and summer oviposition all occur locally. Most of California's winter monarch aggregations occur in man-made groves of trees. Thus, a well-informed management could include successful planting of new forests, and deterioration of existing sites could be controlled. Supply side management should involve deliberate nurturing of milkweed patches in parklands and rural areas, with wider use of ornamental *Asclepias* in urban-suburban landscaping.

Californians can live in harmony with the magnificent monarch through continued research, management based on the knowledge gained through scientific study, and public awareness. Finally, the lessons learned in California will be

applicable, perhaps critical, in the battle to preserve the world's other monarch butterfly populations.

Acknowledgments

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