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THE WINTER ECOLOGY OF *COLIAS EURYTHEME* BOISDUVAL (PIERIDAE) AND ITS DEPENDENCE ON EXOTIC LEGUMES IN SOUTHERN NEW JERSEY.

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ABSTRACT. *Colias eurytheme* adults were seen by 12 April in all of twelve years with observations near Delaware Bay in Cumberland County, New Jersey. Adults can occur in all months but successful reproduction is virtually impossible from mid November until very late February or March. Second through last instar larvae and pupae can survive local winters (January mean ca. +1.4°C). Pupae and most larvae overwinter without diapause. Survival outdoors for reared lots was 50% for second instars and 71% to 100% for older larvae and pupae. Larvae fed, grew, and molted over winter. Larvae deprived of food in December died in January. Nonnative legumes, especially vetches, provide essential food for larvae in autumn and winter, and the establishment of *C. eurytheme* in New Jersey apparently coincided with that of vetches. Lack of diapause allows for an earlier start in spring and an extra (sixth) annual generation combined with exceptional cold hardiness of larvae and pupae pre-adapted this species to exploit anthropogenic habitats with exotic cold season legumes where winters have some mild days and a January mean near or above freezing. The "*ariadne*" phenotype in spring is reliable evidence of local overwintering as late instars or pupae. Overwintered second instars produce summer form adults more than a month later. Southward movement was observed in two autumns and to an unknown extent *C. eurytheme* is a two way migrant.

Additional key words: *Viccia*, *Coronilla varia*, exotic foodplants, cold tolerance, *Problema bulenta*.

The orange sulphur (*Colias eurytheme* Boisduval) is often the most common butterfly in non-drought summers in Cumberland County, New Jersey, and is usually the most commonly seen butterfly from October through February. In a few decades in the mid 20th century this species became one of the most common butterflies in the eastern United States. At a time when many native Lepidoptera are declining as their habitats are being disrupted, overrun by alien weeds, eaten by out of control deer, or obliterated by development, the orange sulphur is a spectacular ecological success. It is the only native butterfly to occasionally reach pest status in eastern North America. Most authors now realize that immigrants from farther south repopulate the northern portions of its range each summer. Ferguson (1955) was perhaps the first to realize *C. eurytheme* is only a summer immigrant northward, specifically in Nova Scotia where the first worn immigrants appear in June or July. Ferguson (1991) also considered it a migrant that has reached Bermuda. Shapiro (1967, 1974) recognized this species as a late spring immigrant in central New York. However, the overwintering limits of the Orange Sulphur are poorly understood (e.g. compare maps by Scott, 1986 and Opler, 1992) and the literature is inconsistent as to whether larvae or pupae or even adults overwinter. Scott (1986) reports larval overwintering for almost every North American species of *Colias* including this one, and pupal overwintering for none. Harry (2005a,b) explicitly mentions overwintering larvae of five *Colias* species, including *C. eurytheme*, outdoors at West Jordan, Utah. However, many authors at least as far back as Klots (1951) claim *C. eurytheme* pupae overwinter. Shapiro (1967) demonstrated that pupae can withstand chilling for at least four weeks, but he was unable to overwinter larvae in a refrigerator. He suggested that pupae and possibly some mid instar larvae overwinter near Philadelphia, Pennsylvania, and reported adults as early as late March (1966, 1970). However he provided no direct evidence regarding overwintering stages outdoors and he (1967) noted a 33% incidence of cripples among adults from pupae chilled for only three or four weeks, about a third as long as a Philadelphia winter. I address overwintering ability of larvae and pupae under actual outdoor conditions less than 100 km farther south.

Winter populations of *C. eurytheme* near Delaware Bay in Cumberland County, New Jersey are almost certainly bolstered by progeny of immigrants from the north, whose southward progress may be blocked by the Bay. From 25 September to 4 November 1988 I recorded approximate flight directions for 51 *C. eurytheme* observed in sustained flight: 48 were headed south-southwest, two southeast, and one northeast. One female was observed to descend from above a several thousand hectare forest into a field, make five oviposition sequences, reascend over forest on the other side and continue on her southeast course. On 18 September, 1997 while driving I saw over 100 flying south-southwest across roads in Salem County, New Jersey, Cecil County, Maryland, and Chester County, Pennsylvania. Both sexes sometimes fly over forests, apparently to maintain direction, but will also often deviate from course to follow roads or powerlines heading generally south. Distances covered are unknown, but their flight is faster than that of a Monarch. Scott (1986) also reports a southward movement in Manitoba and speculates that movements of this species are probably large but not those of a strong migrant. Females reaching Cumberland County in September and October will find good conditions for reproduction unless drought curtails autumnal greening of alien vetches, which are now the primary foodplants locally. However, low temperatures slow growth in autumn and on 5 December the average daily maximum falls below 10ºC and remains so through 7 March.[1]

METHODS

Field observations were made in appropriate habitats in 1989 and 1995–2005, mostly about 2 km below Dividing Creek and at Port Norris, Cumberland County, New Jersey and occasionally farther inland in the same Townships. Reared larvae and pupae were observed in my yard at Port Norris, about half a km north of the Delaware Bay salt marshes, less than 10 meters above sea level at 39.2º North Latitude, where the January mean is about 1.4ºC.[2]

During the winters of 1988–1989 and 1990–1991 I overwintered reared larvae and pupae of *Colias eurytheme*. Staggered sibling lots from females collected 29 October 1988 and 31 October 1990 were started outdoors beginning about 20 November; many were moved to a cool indoor room in early December. Larvae were fed potted white clover (*Trifolium* sp.) and whether indoors or outside all were kept under strictly ambient light. Those indoors were at mostly 13–20ºC with bright indirect sun, but were placed outside two or three times per week on subfreezing nights to mimic late November conditions. A thin transparent nylon cover was usually placed on pots containing fourth or fifth instars during warm weather and on all indoor containers. Various instars were placed outside for the winter in December to as late as 1 January. Larvae that were first or second instars on 31 December 1988 had been reared entirely outdoors. Eight newly formed pupae and two prepupae were placed out in late January 1989. In 1990 I was able to obtain pupae earlier (Table 1). Larvae that year were sorted by instar and placed out on 3 December, but about five of the 41 "third" instars molted by 31 December.

Flower pots containing larvae were kept over winter in the outside corner of a large screen porch, about 3 meters from the house, for protection from birds, mammals and various winter-active invertebrates like ants and spiders. At that corner both sides were screen from floor to ceiling so larvae were fully exposed to ambient temperature, and partial mid-day sun. Since they were about a meter off the ground they probably experienced lower temperatures and perhaps more wind than they would have at the soil surface in nature. Except for one containing ten third instars in 1988–1989, all flower pots containing larvae were placed in my garden for all freezing precipitation and associated rain, and for most relatively light rain storms, but not heavy rains that might have flooded them. Most larvae were released in March since I did not have time or food resources to rear large quantities. The few that were reared to adults in the porch are now in my collection. In December 1990, 20 third instars were allowed to run out of food to determine whether winter feeding is essential. Their soil was kept moist and they were moistened with a plant mister on mild days to prevent dehydration. They were not exposed to snow and ice.

Except for the two lots previously noted, larvae were in direct contact with light snow and ice repeatedly and were snow-covered several times for up to two days in both winters. The maximum snow depth was about 6 cm. Most had moisture on or contacting them freeze overnight or longer, although none were encased in ice. Larvae were exposed to one minor ice storm each winter. The lowest temperature at Port Norris was about -15ºC in January 1989 and about -12ºC in 1991, but no periods longer than two days below freezing occurred in either winter. Periods of a week below freezing occurred in about half of the years when field observations were made. Snow cover of four weeks or more occurred starting in January 2002 and 2003, and the ground was snow covered for a week in January 1996.

For those pupae that could be safely removed, small pieces of the original substrate (usually the nylon cover) with a pupa attached were stapled on the underside of low vegetation, either in grass clumps or on the underside of *Plantago* rosettes (fairly typical pupation sites in nature), or were stapled to the underside of bamboo leaves on short stems and inserted in the soil at the edge of grass clumps. All pupae were about 2 to 4 cm above the soil and not exposed to direct sun. All pupae were moved to the screen enclosure on 5 March 1989 and 15 March 1991 and placed out of direct sun. Pupae formed on the flower pots were left in place and stored with the larvae. All pupae were outside within 12

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[1] Climate data were obtained from The Weather Channel Website visited January or February 2005. Fahrenheit temperatures were used and converted to Celsius to one decimal place.

[2] There is no weather station on the New Jersey side of lower Delaware Bay. The mean at Millville, about 20 km north of the study area, is 0.3ºC, but Port Norris minima are commonly 5º, and occasionally 10ºC, warmer than at Millville on clear, calm winter and spring nights; temperatures are otherwise similar. Wildwood, with a January mean of 1.4ºC, is probably more representative for winter, but that locality is much colder on spring afternoons.

TABLE 1. Pupation and eclosion dates for overwintered pupae of *Colias eurytheme* at Port Norris, New Jersey.

Pupation date, location	**Eclosion dates 1991**	**Sex**
on flower pots		
18 December	31 March	Male
23 December	8 April	Female
24 December	7 April	Male
2 January	9 April	Male
5 January	7 April	Female
8 January	10 April	Male
in garden		
15 December	8 April	Female
17 December	6 April	Male
19 December	3 April	Male
19 December	7 April	Male
19 December	9 April	Female
20 December	9April	Female
21 December	9 April	Male
21 December	11-15 April	Female
27 December	9 April	Male
29 December	11-15 April	Female
31 December	11-15 April	Female
3 January	10 April	Male

hours after pupation and remained there until eclosion. Pupae attached to the flower pots received substantially more direct sun in winter and the plastic surfaces warmed noticeably, causing eclosion to be a few days earlier than those kept in the garden. Therefore their eclosion dates were analyzed separately. Spearman rank correlation tests were performed by L. F. Gall, using SAS software version 6.04 (with the correction for ties). Chi square tests were done by the author on a hand calculator. Forewing measurements were taken on the left forewing from the mid-basal point to the apex using an ordinary ruler and rounded to the nearest mm.

RESULTS AND OTHER OBSERVATIONS

Field observations. From 1995 through 2005 I collected adults, nearly always fresh and often teneral near their pupal shell, on warm (usually >16ºC) days in January (17 in five different years with 12 in 2000), February (18 in four different years), and March (25 in seven different years) at Dividing Creek or Port Norris, New Jersey. I saw a few dozen others from 28 February to 31 March, especially in 1998. The fact that I rarely encountered worn adults in January and February probably reflects avian predation. They are so conspicuous while basking that I can sometimes spot them at >30 m and surely birds can do better. Winter adults are very cold hardy and a night in the freezer (ca. -15ºC) does not reliably kill them. Shapiro (1967) found that most unfed adults could survive more than a month at 3ºC. Although slightly subfreezing nights are harmless to all stages, a single frigid period and perhaps prolonged cold probably can kill pupae that are close to eclosion. Usually after a night below about -12ºC several warm (>15ºC) days must occur before adults are seen again. An extreme case occurred in late 2004. Adults were seen flying on mild days into mid December but on 20 December 2004 the afternoon high reached only -8ºC with strong winds and two mornings were about -12ºC. Most winters do not have any days that cold. Several days exceeded 10ºC later that month, and 31 December through 14 January were completely frost free at Port Norris (two days reaching 18ºC). Maxima were 15º-16ºC on 8 and 16 February 2005. No observers saw any sulphurs locally after 20 December 2004 until 30 March 2005 (Damon Noe), although I visited reliable fields on the four warmest winter days. Since 1989, the start of major spring flights (several patrolling males per hectare in good habitats) has varied from 26 February in 1998 to 12 April in 2003 at Dividing Creek. I also found a wandering last instar larva there on 22 February 1998, which I fed clover. It attached on 5–6 March, yielding an "*ariadne*" form male on 17 April. These field observations indicate that both larvae and pupae overwinter locally.

Field collected males were 90% "*ariadne*" (="*vernalis*") phenotypes in January (n=10), 100% in February (n=12), and 94.4% in March (n=18). This form occurs into mid April. Although placement of some females is difficult, I would consider all of 12 February and March and six of seven January females to be spring phenotypes. The "*ariadne*" phenotype is small with reduced orange, often as little as on the Texas male illustrated by Opler (1992). The black border is pale, usually narrower than in Klots' (1951) illustration or even fragmented on males, and in February and especially March (22%) the forewing black border may be nearly limited to the apical region. A few have the discal spot reduced to a ring on the forewing. Some males show a row of weak dark postmedian spots on the forewing above, as is discernable on Hoffman's (1973) Fig. 1C. A heavy basal black shading dorsally sometimes expands to infuse most of the hindwing on females. Ventral hindwings are always infuscated. While summer form males rarely have forewing lengths below 25 mm, 40 males field collected from January to March range from 17 to 24 mm, with the means 21.0 mm for January, and 20.2 mm for both February and March. Much smaller specimens are known (e.g. Shapiro, 1996, Anthony McBride, pers. comm., 2005). Forewing length of nine of my 30 February and March males are under 20 mm as is one of ten collected in January. A newly eclosed non-"*ariadne*", dorsally nearly summer form, male collected 20 January 2005 is also small (forewing length 22 mm). Klots (1951), Ae (1957), Hoffman (1973), Scott (1986, Plate 12, fig. 37), Iftner et al., (1992, p. 190 bottom center), and Opler (1992) illustrate "*ariadne*" males, but I suspect the Iftner et al. spring female is a hybrid. These forms overwhelmingly predominate from January into April whether or not *Colias philodice* Godart was present the previous fall. Ae's and Hoffman's stocks came in part from places where *C. philodice* is quite rare. Thus, old suggestions that these forms are hybrids are untenable.

Adults were seen and sometimes collected in December in all years from 1994 to 2004, but not in 2005. Most November and December adults are summer phenotypes except for more black dusting ventrally (consistent with Hoffman, 1973, Fig.3) and usually at least basally above. I have also collected "*ariadne*" forms in late November and December (especially in 1998), although these are usually larger than those collected from February to April. Whether they mate and oviposit or not, adults in mid or late November through most of February obviously do not produce surviving offspring. Eggs laid 1–10 November require at least 20 days to hatch based on observations in three different years. Larvae from eggs laid later would usually have inadequate time to reach the second instar in cool December conditions.[3] Eggs laid in December almost never hatch, based on observations in 1988, 1990, and even the extremely warm December of 1998. Emigration of adults in mid November through December is virtually precluded by low sun angle and temperature[4], such that conditions for sustained flight occur infrequently and for less than four hours per day, and usually with a substantial southwest wind.

Survival and other observations of larvae and pupae. Survival to 15 March 1989 was 50% for larvae placed out as second instars (n=20), 71% for third instars (n=17, excluding one I crushed and two escapees) including four of seven protected from snow and ice and eight of ten exposed larvae, 100% for fourths (n=10). All 8 pupae eclosed 11–16 April. Both prepupae died in February. All surviving larvae had molted by 15 March. None of about 20 that were first instars in mid December survived through January although a few died as early second instars. As of 5 March 1991, survival was 98% for thirds (n=41), 100% for fourth and fifth instars (n=5), and 86% of pupae (n=21). These pupae eclosed from 31 March to 15 April (Table 1). Most larvae molted in February and all third and fourth instars except the two discussed below had molted or were in molt by 5 March. Some of these had also molted in December. Harry (2005b) states that his larvae resumed feeding 24 February in Utah. None of the 20 third instars that ran out of food in December or 29 first instars survived through January 1991. None of approximately 20 unhatched eggs survived past early January in either year. One last instar larva was dislodged in a storm and submerged in about 2 cm of near freezing water for five to twelve hours, but recovered and produced an adult. All three pupae that died had become partially dislodged and imbedded in the soil. The immediate cause of death appeared to be bacterial sepsis, with two deaths in March. Survival of second and third instars in 1989 does not differ significantly (χ^2=1.6), nor do fourth instars and thirds (Fisher's exact p=.124). However, seconds and thirds pooled do differ from fourths (χ^2=5.95, p<.025), suggesting that in some winters older larvae may fare better. All mortality of third instar larvae in both years was associated with interruptions of molts by cold spells

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[3] The mean for 1 December is 5.0ºC dropping to 1.1ºC by the 31st at Millville, New Jersey.

[4] Given low wind and full sun the minimum for sustained patrolling by males is about 17ºC in December-January falling with increased insolation to about 4ºC in mid April in Cumberland County, New Jersey at 39.2ºN.

which extended some mid-winter molting periods to nearly a month. Four died in pre-molt and two died while being unable to feed after molting.

Larvae fed on days that reached 9ºC, and on sunny days as cold as 6-7ºC.[5] First to third instar larvae remained on the upper surface of the clover leaves most of the time, and these leaves probably act as miniature parabolic reflectors on sunny days. Third instars often left the foliage when the air temperature fell to 4ºC, especially if this happened in the daytime. Older larvae rested on stems or on the soil. In both years most larvae overwintered without diapause and were observed to feed and molt. However, two third instars in 1990–1991 were much less active than the others but occasionally moved a few cm. They apparently did not feed in January or February, and appeared to be in diapause. Both were actively feeding, but still third instars, on 5 March and were not tracked separately after that date.

Spring 1991 eclosion dates (Table 1) were significantly coupled with pupation dates: r=.882, p=.02 for garden males, r=.929, p=.008 for garden females (but note ties), and r=1, p<.05 for males in flower pots. Coupling of pupation and eclosion dates indicates that pupae developed during warm periods in winter and were not in diapause. Exposure to warmth, and therefore eclosion dates, varied as a function of pupation dates. Maximum daily temperatures were 16–18ºC on 18, 21 (the median pupation date), 22, 23 December 1990 and 20ºC on the 30th but then remained below 10º C through 14 January 1991. Wild adults were observed six and three days before my first eclosions in 1989 and 1991, again verifying pupal overwintering in the field, presumably from pupae formed before December.

Adults from overwintering pupae were 96% vernal form "*ariadne*", as were those from overwintered last instars. A few overwintered third instars were reared to adults. Eclosions started 30 April 1991 and 6 May 1989. Adults were nearly as large as wild summer adults, and the three males were close to summer forms, while the four females had reduced orange. Such intermediate phenotypes would be expected based on Hoffman (1973, Figs. 3, 4), since they were at about 11 hour days as late third instars[6] , and about 12 hours as late 4ths. Transitional phenotypes usually appear in late April, with the males close to summer phenotypes dorsally. Two larvae that were second instars on 1 January produced slightly small summer form males on 16 and 20 May 1989, 35 and 39 days after their first sibling eclosed from an overwintered pupa. Wild adults of similar phenotypes were seen 20 May.

DISCUSSION

The results directly demonstrate that not only pupae but also second instar and older larvae of *Colias eurytheme* can survive winters in southernmost New Jersey without diapause. Results from 1989 suggest later instar larvae probably fare better on average than second and perhaps third instars. Shapiro's (1967) larvae could not survive the winter when refrigerated at 3ºC, yet I report 50% survival of second instars and 71-100% survival of older larvae and pupae under seemingly much harsher winter conditions (roughly -15ºC to + 18ºC). Wild larvae and pupae in many years encounter periods of a week or more of continuous freezing. Since no diapause is involved, I doubt survival differences are related to rearing conditions prior to chilling. My larvae were reared at natural late autumn photoperiods mostly below 20ºC with frequent freezing nights. Many of my last instars in December showed the dark patches characteristic of short-day larvae. Shapiro's refrigerated larvae were continuously below the threshold for feeding. My outdoor larvae were able to feed several times in January and often enough to grow during February when many went into successful molts. Some larvae molted twice outdoors between 7 December 1990 and 5 March 1991. The failure of my larvae to survive outdoors without food suggests Shapiro's refrigerated larvae also died of starvation. Furthermore, adults from four of 12 pupae in various stages of development that Shapiro chilled for 21 or 28 days were at least slightly crippled. Out of my 26 adults from overwintered pupae, one failed to recover and expand after a fall, but none of the other 25 were defective. Probably expressing the small, less pigmented "*ariadne*" phenotype effectively reallocated resources among my pupae.

Colias eurytheme overwintered annually in all years with observations, specifically 1989 and 1995–2005, near Delaware Bay in New Jersey, where the January mean is about +1.4ºC. This included one very cold winter and two with persistent snow packs. Substantial numbers were flying by mid March in three of twelve years and by 12 April in all years. Occasional adults eclosed in mid winter in some years, especially in January 2000. Shapiro (1966, 1967) considered overwintering to be reliable about 100 km to the north in and immediately adjacent to Philadelphia, Pennsylvania (January mean 0ºC). Shapiro (1974) reported adults as rare in mid April, which I would interpret as pupal survival, and more regular after 5 May, which indicates larval overwintering, slightly to the northeast on Staten Island, New York City (January

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[5] The mean maximum for January at nearby Millville is 5ºC.

[6] At 39º North day length reaches 11.0 hours about 21 February.

mean between -0.3 and +0.3ºC). The January mean at Harry's (2005b) Utah site is also about -0.3ºC. Overwintering of pure *C. eurytheme* is rare (and usually as larvae) or does not occur at all in places where the January mean is below about -1ºC such as west central Illinois (Sedman and Hess, 1985), Ohio (histogram in Iftner et al., 1992), central and northeastern Pennsylvania (Thomas Manley, pers. comm., March 2003, David Wright, pers. comm., February 2005), central New York (Shapiro, 1974), Massachusetts (personal observations: none seen before June in 1973, 1974, 1984-1988), and Connecticut, (personal observations 1975-1983 and Connecticut Butterfly Atlas Project data). Shapiro (1974) states early spring (May) orange sulphurs in central New York are almost always male hybrids, as were two of five orange spring sulphurs I collected 30 April to 17 May in milder southern New England. Apparently at least one (the female illustrated by Iftner et al., 1992) of about 13 records through 15 May in Ohio is a hybrid. *C. eurytheme* populations in and north of those regions appear to depend on annual immigration. While the first pure *C. eurytheme* adults seen in these colder regions are usually summer phenotypes in late May or June, the first adults along Delaware Bay in New Jersey are "*ariadne*" phenotypes in or before early April.

An apparently reliable indicator of successful overwintering of *C. eurytheme* as pupae or late instars is the occurrence of the small early spring phenotype. Transitional phenotypes, especially relatively large females with reduced orange, are probably reliable indicators of third or fourth instars overwintering. The "*ariadne*" phenotype is known to be induced by short photoperiods during the third and fourth instar (e.g., Ae, 1957[7], Hoffman, 1973). Larvae overwintering as third instars would mostly be late fourths or fifths at the vernal equinox in southern New Jersey and produce adults in late April with more normal borders in males, but reduced orange in females, and some dark frosting beneath. Larvae that overwinter as second instars would be third or fourth instars at the time of the vernal equinox, and produce essentially summer phenotypes. Virtually all more western regions, including Utah, where *C. eurytheme* overwinters, warm up earlier than southern New Jersey. Farther north if the few diapausing third instars were to survive the winter (which is purely hypothetical) they would probably resume development near the vernal equinox meaning that for much of the third instar and all of the fourth they would experience long and increasing photoperiod resulting in essentially summer phenotypes. Since they do not occur that late farther south, rare "*ariadne*" forms in May northward probably come from locally overwintered last instars or pupae such as produce this phenotype in New Jersey. Furthermore, small early adults from local colonies, seldom disperse from their natal field, and certainly do not migrate. Larger transitional phenotypes with reduced orange in females and relatively normal borders in males (such as those I reared from overwintered third instars) often occur into early, but not late, May in southern New Jersey and commonly disperse along roadsides. While the possibility of immigrants of these transitional phenotypes appearing northward during warm weather cannot be ruled out, Shapiro (1974) and Sedman and Hess (1985) are certainly right that the first immigrants northward are usually summer forms in or after late May.

Expression of the "*ariadne*" phenotype may be exaggerated directly by environmental factors, but since neither Hoffman (1973) nor Ae (1957) examined phenotypes produced by larvae or pupae below 15ºC, further modification of genetic expression by cold cannot be ruled out, and might be expected if functions of this phenotype include reallocation of resources under harsh conditions. Size as measured by wing length, width of male forewing border, and ventral reflectance are photoperiod controlled with the last gradually reduced by decreasing day length below 14 hours. Ae (1957) found no difference related to photoperiod in the intensity of orange but did in its extent. Overall my February and March adults have less orange than those from any other months. Wild adults then are smaller than Hoffman's or Ae's laboratory adults or my December "*ariadne*" specimens. Cold during pupal development might directly affect extent of orange pigment, black pigment in borders, and discal spots, producing the extreme phenotypes in February and March. Nutritional stress and cold acting on last instar larvae in November and December probably result directly in additional dwarfing beyond reduced size induced by photoperiod, and dwarfing is possibly exacerbated by resource depletion of pupae over winter. Between necessary cryoprotectants and respiration, metabolic costs of overwintering in insects are substantial, and resource depletion is a real possibility (e.g. Leather *et al.*, 1993, Chapter 5) and might be especially high for developing (as opposed to diapausing) pupae. Wild adults in winter and early spring also often have slightly malformed wings including one of fifteen January, four of seventeen

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[7] Ae has no statistical analyses, but for broods P-78-4 through P-78-8 five paired comparisons of 14 hour vs.10 hour photoperiod treatments show no overlap in the average forewing lengths or "black-border index" among males so U=0, n1=5, n2=5, p=.004. Similarly reduction of orange seems obviously different by inspection at least for males.

February, and three of 25 March specimens in my collection. This is consistent with Shapiro's observations with pupae chilled for 21 or 28 days. My 25 adults that eclosed from 31 March to 16 April had no such defects, perhaps reflecting relatively mild artificial conditions as last instar larvae or warmer temperatures late in the pupal stage than experienced by wild adults eclosing earlier.

Two larvae reared in natural photoperiod and placed outside in December as third instars apparently diapaused, and winter larval diapause is widespread in this genus. This begs the question of why a higher incidence of winter diapause is not selected for in *C. eurytheme*. Diapause would eliminate wasting of adults from late autumn and winter eclosion, as well as winter mortality of eggs, first instars, and prepupae. Probably diapause would improve survival of larvae in northern winters, but diapause may be disadvantageous southward and immigrants would swamp progeny of northern survivors by June. In southern New Jersey for larvae in the third instar at the onset of winter, the chance of survival is probably better with diapause if the food supply fails, but most years survival is probably not much different with or without diapause and survival prospects are probably improved by reaching the fourth or fifth instar by December rather than diapausing. Along Delaware Bay not diapausing essentially allows an extra generation for those that reach last instars or pupae by December. From about early June into mid September[8], a generation can be completed in about a month (Scott, 1986, Gochfeld and Burger, 1997). Second brood offspring of early adults eclose in late May or early June, so there is time for a partial sixth brood by mid October. This last brood is protracted by cool weather, bolstered by immigrants from the north, and probably depleted by south-bound emigrants. In non-drought seasons each brood usually outnumbers the last, so an extra brood should cancel moderate losses of ill-timed stages in late autumn and winter. Regardless of when prolonged cold sets in, most individuals should be in stages with the potential to overwinter. Winter losses are probably lower farther south. In the Carolina and Georgia piedmont, adults can probably successfully reproduce through November in years without early extreme cold and successful reproduction should be possible for adults eclosing in late February in most years[9]. Coastal plain portions of these states have average daily maxima of 11–15ºC even in January so, despite some periods of cold weather, *C. eurytheme* could potentially breed nearly year round if suitable winter foodplants were available.

The phenology of *C. eurytheme* has apparently changed very little in Connecticut, just north of the reliable overwintering zone, during the 70 years since it became common. The first known spring *C. eurytheme* adult was collected 16 May 1939, and as I interpret the Connecticut Butterfly Atlas data, there are apparently only three subsequent early collections or observations of more than one individual, four specimens collected 1 May 1954 (at Yale University), three on 30 April 1983 (my collection), two seen on 10 May 1994, and only about 16 singletons. These spring records include some hybrids. Likewise, adults were occasionally found in early December in both the 1930s and the 1990s.

I have no well-documented information on the local winter ecology of the allegedly native *Colias philodice*[10], so it is impossible to conclude whether or not introgression has affected the winter ecology of either sulphur. Since 1990, *C. philodice* has varied from zero to about 15% of summer *Colias* observed in southern New Jersey. This species is also apparently somewhat migratory (Ferguson, 1991; Gochfeld and Burger, 1997) but is considered to overwinter in almost all of its range (e.g. Scott, 1986, Opler, 1992, Ferguson, 1955) and its shorter flight season suggests a diapause. I have seen only one adult in November, and I know of no credible observations (including 114 specimen dates, some of which refer to more than one specimen, compiled by David Iftner) of *C. philodice* from 12 November through 26 March in New Jersey. The spring brood peaks and declines rapidly in April (see also Iftner et al., 1992) suggesting a single overwintering stage, probably the fourth or fifth instar larva.

Johnson (1995) concludes that none of the ten southern migrant moths and Homoptera (nine apparently with no diapause) that he reviewed overwinter as far north as the 0ºC January isotherm and only three do so above the 4ºC isotherm. This is consistent with maps by Opler (1992) for a number of southern migrant butterflies and skippers. Similarly, *Pseudaletia separata* (Walker) (Noctuidae) larvae and

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[8] This is the period when the mean temperature is 20 to 25ºC at Millville, New Jersey.

[9] The daily mean falls below 10ºC on 29 November at Atlanta, Georgia and 23 November at Raleigh, North Carolina compared to 6 November at Millville, New Jersey. However -10ºC or lower has been recorded as early as 23-25 November at all three locations, but such cold is rare before late December. The daily mean reaches 10ºC on 26 February at Atlanta, 13 March at Raleigh, and 8 April at Millville. The latest recorded dates for -10ºC or lower are 5 March at Atlanta, 14 March at Raleigh, and 22 March at Millville.

[10] If some stage can reliably reach diapause by October or survive six months with no food, native *Baptisia*, *Lupinus*, and *Tephrosia* might have supported this butterfly, although *Tephrosia* is not a known foodplant for any *Colias*, and *Lupinus* (now rare) often senesces in July or August. *C. philodice* has been established at nearby Philadelphia since at least 1833 (specimens in Titian Peale collection, Academy of Natural Sciences, Philadelphia).

pupae can overwinter, apparently without diapause, in portions of China where the January mean is at least 0º to 4ºC (Hirai, 1995, Johnson, 1995) and the moths migrate into a much larger summer range. Orange sulphur larvae and pupae are obviously more cold tolerant than these other non-diapausing migrants, except perhaps *P. separata*, and apparently of very similar hardiness to diapausing adults of the migratory noctuid *Plathypena scabra* (Fabricius), which also overwinter abundantly in southern New Jersey (my observations). While places with a higher January mean often have extreme minima comparable to southern New Jersey[11], there are more warm days for feeding during winter, which may be essential for these species. Places with a January mean near 0ºC typically have an average daily maximum of 10ºC, which is warm enough for larval feeding, into early December and again by late February or early March. A few warm (10–15ºC) days usually occur each month even in mid-winter, which is adequate for *C. eurytheme* larval feeding. With increased insolation and slightly higher temperatures some larval feeding is possible for *C. eurytheme* even on near average afternoons by mid February in southern New Jersey. Several Noctuinae such as *Abagrotis, Agnorisma, Xestia* and *Eucoptocnemis* species also overwinter as larvae near the ground in southern New Jersey and feed, grow, and molt as weather permits during the winter. The geometrid, *Nemoria lixaria* (Guenee), overwinters locally as intermittently active larvae feeding on red maple (*Acer rubrum* Linnaeus) buds and flowers, based on two late winter field collections and several reared broods. None of these moths are considered migratory and the noctuids range into much colder climates but, like *C. eurytheme*, *N. lixaria* is near its limit for winter survival and apparently became established in Cumberland County recently (1980s).

Importance of exotic legumes to *Colias eurytheme*. Non-diapausing *Colias eurytheme* larvae require food during the autumn, winter, and early spring. Even my two apparently diapausing larvae fed into December and again by early March. Successful overwintering as pupae and eclosion when successful reproduction is possible in spring probably requires pupation in November or December in southern New Jersey[12]. No native legumes in southern New Jersey provide reliable larval food from mid October through early March, or any food at all in winter. The only evidence I have for *C. eurytheme* utilizing any native foodplants in southern New Jersey is a few ovipositions observed on *Baptisia tinctoria* (Linnaeus) R. Brown *ex* Aiton during May and June and this is also the only native foodplant noted by Shapiro (1966). Foliage of this plant is unreliable by the end of September.

Exotic cool season legumes apparently facilitated the relatively recent establishment of the orange sulphur eastward and both vetches and this butterfly seem to have arrived around the same time in southern New Jersey. Overwintering populations of *C. eurytheme* in southern New Jersey are usually associated with Eurasian vetches (*Vicia* spp.) although autumn females also oviposit on non-native white clovers (*Trifolium* spp.), which normally retain some leaves all winter. While clovers and sweet clovers (*Melilotus*), have been present in southern New Jersey for much longer, vetches were virtually absent in the early 20th century. Stone's (1911) exhaustive regional flora mentions only *Vicia tetrasperma* (Linnaeus) Schreber, describing it in a footnote as an "occasional weed". *Colias eurytheme* was still a rare stray (Smith, 1910). Moore (1989) lists five *Vicia* spp. as occasional to common in Cumberland County. *V. grandiflora* Scopoli increased dramatically in the 1990s (pers. obs.) and may now be the most common host for ovipositing spring *C. eurytheme*. According to Moore (pers. com.) a few additional vetches, including *V. tetrasperma*, are now established. Female *C. eurytheme* oviposit on at least *V. villosa* Roth and *V. grandiflora* locally. While the other five local *Vicia* species are spring annuals, *V. villosa* (=winter vetch) can grow as an annual, biennial, or perennial with growth from autumn through spring including winter (USDA, 2004). It dies back in dry summers. *V. villosa* often retains some old foliage until the first severe cold in December or January and in mild years bedraggled, but living, older leaves persist all winter. Seedlings commonly germinate in autumn under old plants, whether living or dead, and larvae could presumably transfer to these. Eggs are laid on seedlings, and established plants may put up basal growth as well. *V. villosa* presumably accounts for most or all of the abundant low vetch foliage in winter. *V. cracca* Linnaeus, a perennial, has not yet been verified locally but is widely established in eastern North America. Many successional fields have vetch foliage from late September or October into July, and all year in wet summers, and vetches are among the dominant late

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[11] The lowest temperatures recorded for Atlanta, Georgia (January mean 5.8ºC), Raleigh, North Carolina (mean, 4.2ºC) and Millville, New Jersey (mean 0.3ºC), are very similar at -22.2ºC, -21.1ºC, and -23.3ºC respectively, but the average daily maxima for 15 January are 10.6ºC, 8.9ºC and 5.0ºC.

[12] Based on an 8 day pupal period (Shapiro, 1967 and Gochfeld and Burger, 1997) at 24-25ºC which is about the summer mean in New Jersey, at 14.5ºC (the mean for 10 October) this should approximately double to 16 days and increase to approximately 25 days at 9ºC (the mean for 9 November).

spring flora in these habitats. Vetches persist indefinitely in game management fields that are plowed every few years. Planted *Coronilla varia* Linnaeus patches on highway embankments usually have some tiny leaflets near ground level in mid winter (photographs in Pennsylvania from David Wright) which older larvae could probably find. There may be a period in autumn when no foliage is available but, unlike *Vicia* species, *C. varia* is a reliable foodplant all summer. Clovers are usually available from at least October to May in lawns and roadsides but die back in summer dry spells. *Melilotus officinalis* (Linnaeus) basal foliage probably is a minor winter foodplant. Shapiro (1966) and others have implicated increased cultivation of alfalfa (*Medicago sativa* Linnaeus) in the spread of the orange sulphur eastward. While post-harvest regrowth on this crop would probably be a suitable winter food, fields are usually plowed under before adults could eclose. Stone (1911) noted occasional escapes, but I have not seen alfalfa outside of cultivation locally.

The Orange Sulphur is far from unique in using alien foodplants. At least 24 (21%) of the regularly breeding butterflies and skippers in New Jersey utilize alien larval foodplants, often congenerics to native hosts (mostly personal observations). Besides both *Colias*, *Poanes viator zizaniae* Shapiro, and *Lycaena phlaea americana* Harris probably owe their current presence in this state to exotics. The now abundant *Poanes v. zizaniae* uses extremely invasive alien *Phragmites* strains, probably exclusively,[13] and last instars of the Rare Skipper (*Problema bulenta* Boisduval and LeConte) were recently found on this reed (pers. obs. with W.J. Cromartie and Marc Minno) where it was growing with the native foodplant (Cromartie and Schweitzer, 1993) in Atlantic County. An isolated population of *Hesperia attalus slossonae* Skinner in Cumberland County appears to be completely dependent on *Centaurea maculosa* (Lam.) and other exotic weeds for nectar, based on hundreds of observations by the author and Joseph Patt. Besides *Colias*, butterflies and skippers in the genera *Strymon, Cupido, Epargyreus, Thorybes*, and *Erynnis* have benefited from extensive use of non-native legumes in New Jersey. Across the continent, Graves and Shapiro (2003) report that about 34% of the butterfly and skipper species in California oviposit or feed as larvae on alien plants, although sometimes with lethal results.

Postscript. The fact that *Colias eurytheme* has within 75 years become one of the most abundant butterflies in eastern North America, suggests that interpretations of its life history being ill adapted to its new range (e.g. Scott, 1986) should be rethought. Rather I suggest a combination of lack of diapause with exceptional cold tolerance, presumably due to supercooling ability and hemolytic antifreezes (Leather et al., 1993), of larvae and pupae superbly pre-adapted this species to exploit anthropogenic habitats with cool season legumes in regions with moderately cold winters but with some warm winter days. Furthermore *C. eurytheme* has some success as a two way migrant exploiting climatically unsuitable regions to the north in the summer and returning south in autumn, though the extent of migratory ability is poorly documented. Finally, I suggest lepidopterists not ignore common species. The life history features contributing to their success might not be what one expects.

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[13] *P. viator* was reported by Smith (1910) and possibly originally maintained populations on then uncommon, now nearly extirpated, native *Phragmites*, but "at the edge of salt meadow" suggests the then recently established exotic. *P. viator* is scarce in the extensive wild rice marshes of the Maurice River system except near *Phragmites* patches.

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