

CONQUERING SOLDIERS: THE SUCCESSFUL INVASION OF FLORIDA BY *DANAUS ERESIMUS* (LEPIDOPTERA: NYMPHALIDAE)

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ABSTRACT.—*Danaus eresimus* (Cramer) (Nymphalidae) was believed to be a very rare stray into Florida until the early 1970's when the first suspected populations were documented. Currently, this species is firmly established and locally common in southern Florida. In 1994, this species was found at a number of sites in central Florida. Results are presented that document the biology, ecology, behavior and distribution of *D. eresimus* in Florida. Brief descriptions of the early stages are given. Taxonomic issues and the factors influencing the dynamics of this species in Florida are also discussed.

KEY WORDS: *Agraulis*, Anacardiaceae, *Anartia*, Arizona, *Asbolis*, Asclepiadaceae, Asteraceae, Bahamas, behavior, Boraginaceae, *Calpodus*, Compositae, Danainae, distribution, early stages, ecology, *Electrostrymon*, habitat, *Heliconius*, Hispaniola, hostplants, immigration, Labiatae, Lamiaceae, Lycaenidae, Malvaceae, Mexico, mimicry, *Ministrymon*, parasites, Pieridae, phenology, *Phocides*, *Phoebis*, *Siproeta*, *Strymon*, taxonomy, USA, Verbenaceae, West Indies.

The soldier, *Danaus eresimus* (Cramer) (Nymphalidae), is a widespread Neotropical danaid, ranging throughout much of the West Indies and northern South America, northward to Florida, Arizona, New Mexico, and Texas (Ackery and Vane-Wright, 1984; Stanford and Opler, 1993) (Fig. 1, inset). It has also been recorded twice in Georgia (R. Hirzel, pers. comm.). The subspecies *D. e. tethys* Forbes is reputed to occur in the Greater Antilles (except Puerto Rico) and Florida (Ackery and Vane-Wright, 1984). Until recently, *D. eresimus* was rarely encountered in Florida where it was generally regarded as an irregular stray from the West Indies (e.g. Kimball, 1965; Pliske, 1971). During the 1970's, this species suddenly increased in abundance in Florida, becoming a firmly established resident with a rapidly expanding range. This paper presents the results of a study to determine and understand the factors influencing the distribution of *D. eresimus* in Florida and includes information on the ecology, biology, behavior, and taxonomy of this poorly understood relative of the familiar queen, *Danaus gilippus* (Cramer) (Nymphalidae).

DISTRIBUTION AND ABUNDANCE IN FLORIDA

Prior to the 1970's, records of *D. eresimus* in Florida were few. The oldest known specimen purportedly from Florida is a male from the Rev. George D. Hulst (1846-1900) collection (currently deposited in the American Museum of Natural History (AMNH), New York) labelled simply "Fla." Although complete data are lacking, there is no evidence to suggest the record is invalid. Hulst originally donated a portion of his collection, including the butterflies, to Rutgers University in 1891, after which he concentrated solely on moths (Smith, 1900) [his entire collection was

acquired by the AMNH in 1954 (Rindge, 1954)]. The specimen possibly was caught in April 1879, when Hulst collected extensively in the vicinity of Enterprise, Volusia County, Florida (Hulst, 1879). However, he complained about poor collecting during the trip and did not mention any unusual captures (unless he confused the specimen with the common *D. gilippus*). Regardless of whether Hulst personally collected the specimen, it was probably obtained between 1875 and 1890, when Florida had become popular with collectors and Hulst was enjoying the peak of his entomological pursuits.

The first published record of *D. eresimus* in Florida was of a single female collected by F. E. Church on 28 Feb 1932, on Lower Maticumbe Key, Monroe County (deposited in the AMNH) (Bates, 1934). Bates was unaware of the earlier Hulst record and reported the Church specimen as the first of the species from the United States. Clark (1941) reported *D. eresimus* from Florida on the authority of this record. Young (1955) also referred to this record when he described *D. eresimus* as "a rarity that should be looked for on the keys." Due to the paucity of records, Klots (1951) wondered if the species was merely "accidental" in Florida (Pl. 10, Fig. 3), but designated a "safe record" by R. L. Chermock "(R.L.C.)" who collected at least one specimen (probably during the 1940's) near Paradise Key ("Royal Palm State Park"), Dade County. These published reports were the only Florida records known to Kimball (1965). Surprisingly, no additional *D. eresimus* were recorded in Florida until 1970 when T. E. Pliske captured two individuals in the vicinity of Miami, Dade County (Pliske, 1971) (although he reported the first date as 6 June, his specimen, now in the Florida State Collection of Arthropods (FSCA), Gainesville, Florida, is labelled 3 June). He wrote that "if *D. eresimus* is established in Florida, it is rare", proposing that "it is more likely that individ-

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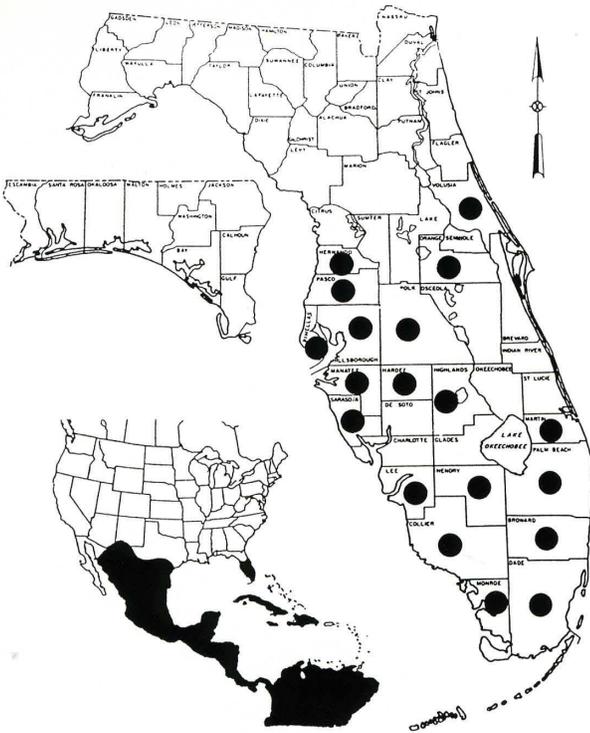


Fig. 1. Distribution of *D. eresimus* in Florida. Inset map shows the generalized range of the species.



Fig. 2. The penetration of the Florida peninsula by *D. eresimus* based on specimens and literature records.

uals stray in from the West Indies as suggested by Kimball." Pliske (1975) noted additional captures in Dade County during 1970-1973.

The subsequent penetration of peninsular Florida by *D. eresimus* was impressive (Fig. 2). Only three years after its modest discovery near Miami, the species was reported in 1973 as "common locally at certain times of the year in south Florida" (Mather, 1974). By 1974, it had extended northward along the east coast of Florida to Lauderhill, Broward County (Mather, 1975), and had reached Palm Beach County by 1975. Along the west coast, adults were found in 1975 in southeastern Collier County and H. K. Clench collected two males on Sanibel Island, Lee County, the same year (specimens located in the Carnegie Museum of Natural History (CMNH), Pittsburgh, Pennsylvania, too late for inclusion in Fig. 2). It was reported as "abundant" in 1976 in the central Everglades, westward to near Naples, Collier County, and "abundant through the year in Dade, Broward, and Collier Counties" in 1977 (Mather, 1977, 1978). Baggett (1979) expected the species to extend its known range in Florida, where it had reached "record population peaks in 1978." Lenczewski (1980) remarked that *D. eresimus* was "particularly common in August 1979" and considered it to be a resident of Everglades National Park. During the next decade, captures continued to be reported from southern Florida (Baggett, 1980; 1981; 1982; 1983; 1988a, b, c; 1989; 1990a, b; Brewer, 1982; Calhoun, 1985; Roman and Baggett, 1985; Beck, 1989). Despite these numerous records, authors still referred to the rarity of *D. eresimus* in Florida (e.g. Howe, 1975; Pyle, 1981; Ackery and Vane-Wright, 1984), thus Florida specimens collected during the 1970's and early 1980's were still perceived as significant. Opler and Krizek (1984) and Scott (1986) were the first popular publications to treat *D. eresimus* as a locally common resident of Florida.

During the 1980's, *D. eresimus* continued to spread northward. By 1984, it had reached Hillsborough County on the west coast, finally extending its range into central Florida (Beck, 1985). Despite this expansion, *D. eresimus* was not believed to reproduce outside southern Florida until 1989 when I found what appeared to be two populations in northwestern Hillsborough County. In 1994, I unexpectedly located another apparent population of *D. eresimus* in a citrus (*Citrus* spp., Rutaceae) grove in coastal Volusia County, about 70km further north than any previous record. This discovery prompted me to conduct a more thorough survey of similar habitats throughout central Florida. As a result, adults and early stages of *D. eresimus* were found in seven counties, extending the known range of the species on the west coast northward into Hernando County and confirming the suspicion that it reproduced in central Florida. With the addition of these records, *D. eresimus* has now been found in at least nineteen counties in central and southern Florida (J. V. Calhoun, unpublished) (Fig. 1).

Although *D. eresimus* was recorded in the Florida Keys as early as 1932 (Bates, 1934), there have been few captures off the mainland. All such reports have come from the upper Keys; Elliott Key, Key Largo, Plantation Key, Upper Matecumbe Key, Lower Matecumbe Key and Long Key (P. A. Opler, 1983; Minno and Emmel, 1993). Schwartz (1987) did not list any records from the lower Keys and suggested *D. eresimus* has invaded the upper Keys from the mainland. Opler and Krizek (1984) considered the species to be a resident of the Keys, but Minno and Emmel (1993) and Smith et al. (1994) believed it to merely stray from the mainland. Nonetheless, *D. eresimus* is probably an uncommon or irregular resident of the Keys, especially since one of the hostplants is locally abundant on the islands (Minno and Emmel, 1993).

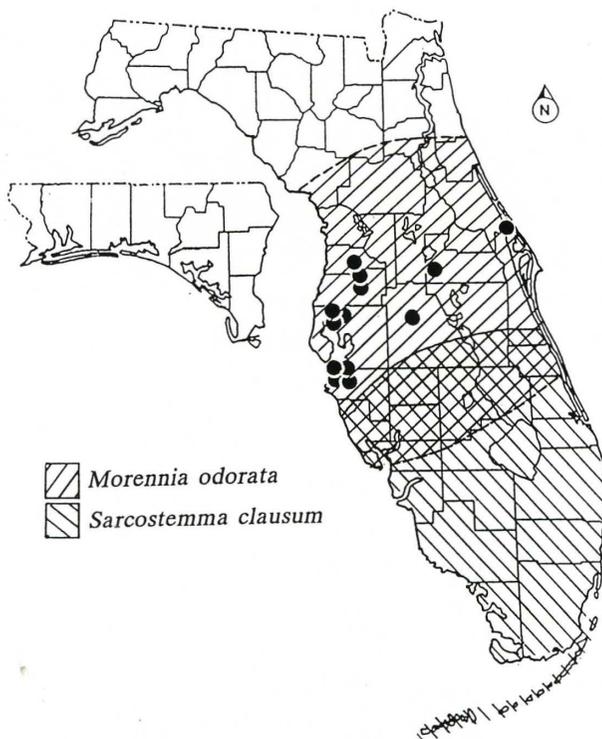


Fig. 3. Generalized distribution of *Sarcostemma clausum* and *Morrenia odorata* in Florida. Dots represent *D. eresimus* populations in central Florida.

In Florida, populations of *D. eresimus* are extremely localized, but it can be common where found. This is consistent with observations in Jamaica and Hispaniola (Brown and Heineman, 1972; Schwartz, 1989). Because they share hostplants, *D. eresimus* is usually found in the same habitats as *D. gilippus*, but typically in lower numbers.

HABITAT AND HOSTPLANTS

In southern Florida, including the Keys, *D. eresimus* is found along weedy drainage ditches, roadsides and in scrubby vacant lots and other open locations with an abundance of flowers, especially *Bidens alba* (L.) DC. In central Florida, *D. eresimus* is most closely associated with citrus groves that have not been treated with herbicides or recently mowed between the rows, and possess much *B. alba* (Fig. 4). The only reported larval hostplants of *D. eresimus* in Florida are plentiful in these disturbed habitats.

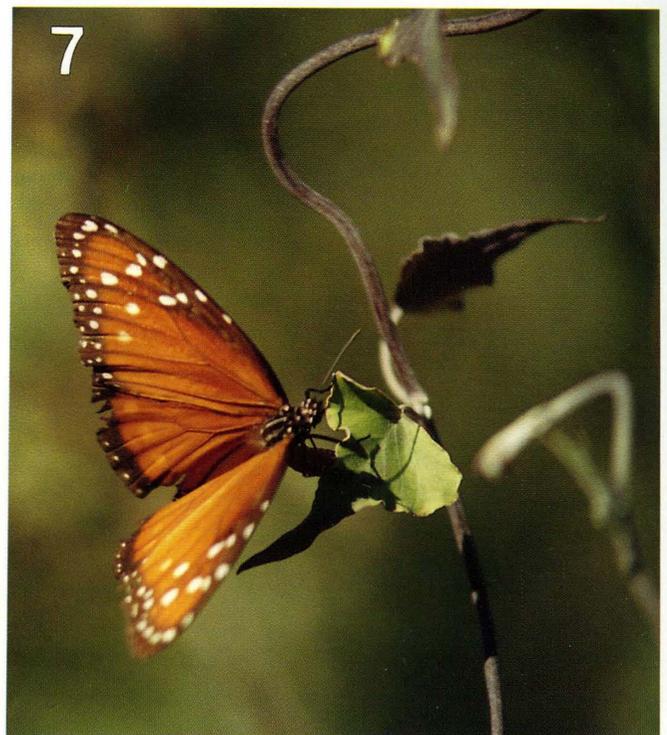
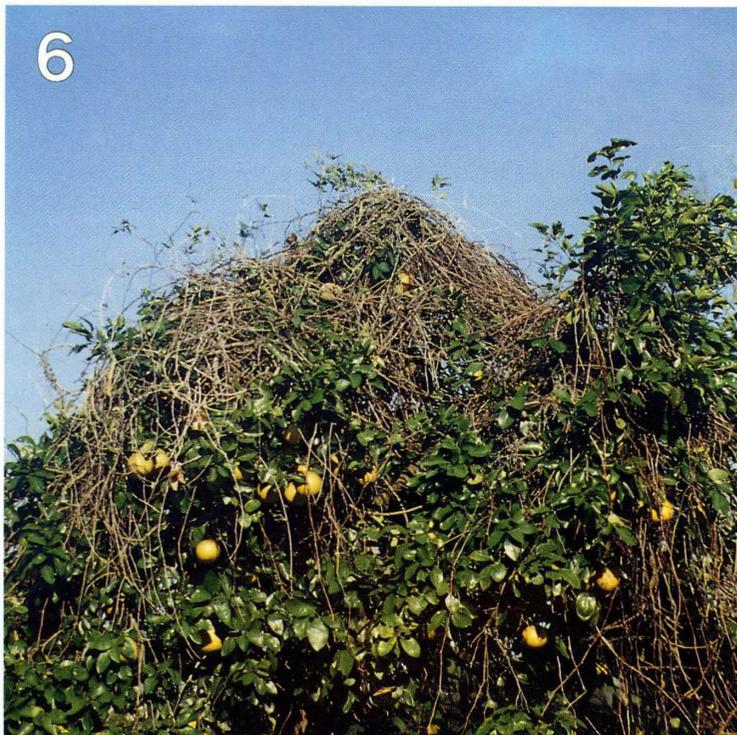
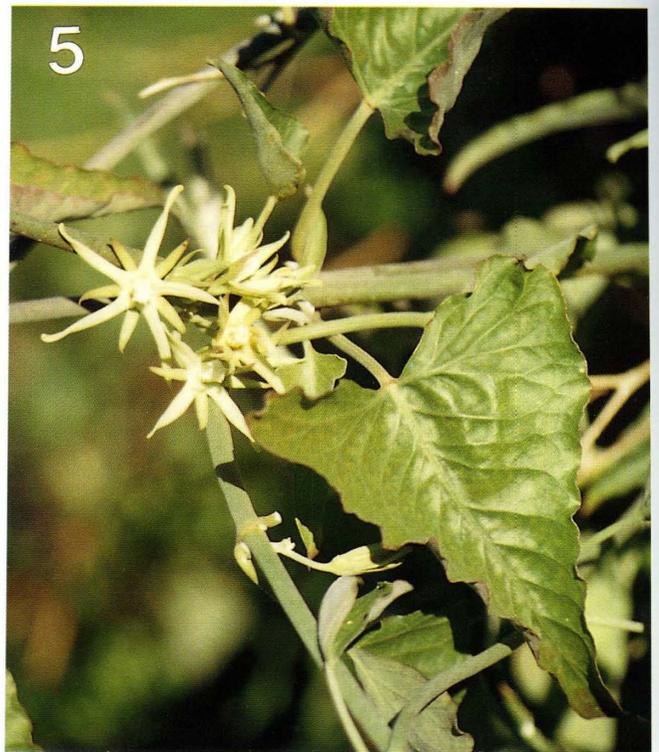
As with most members of the Danainae, all confirmed hostplants of *D. eresimus* belong to the Asclepiadaceae (milkweeds). Compared to the closely related *D. gilippus*, hostplant utilization by *D. eresimus* is poorly known. Ackery and Vane-Wright (1984) listed only *Asclepias curassavica* L., *Calotropis procera* (Ait.) Ait. f., *Cynanchum undulatum* K. Sch., and *Cynanchum unifarium* (Scheele) Woods. Also given was *Spigelia anthermia* L., a very toxic member of the Loganiaceae, but this is based on Kaye (1931) who noted that a *D. eresimus* larva had been found on the plant in Trinidad. Brown and Heineman (1972) doubted the validity of this record and questioned whether the larva was "feeding on the plant or just resting there." All these plants are native to the Neotropics except *C. procera* which is generally considered to have Old World origins (Willis, 1973).

Although *D. eresimus* had become widespread in southern Florida by the mid-1970's, no hostplant was known until 1980 when a female was observed ovipositing on *Sarcostemma clausum* (Jacq.) Roemer and Schult. (Asclepiadaceae) in Dade County (Adair and Roman, 1980; Baggett, 1981). Eggs and larvae have subsequently been found and reared on this vine, which also is the suspected hostplant of *D. eresimus* on Hispaniola (Schwartz, 1989). Eggs and larvae of *D. gilippus* and *Danaus plexippus* (L.) also have been found on *S. clausum* in southern Florida (Pliske, 1971; Baggett, 1981; Minno and Emmel, 1993). In Texas, *D. eresimus* has been found and reared on *Sarcostemma cynanchoides* Dcne. (R. O. Kendall, pers. comm.). *Sarcostemma* is a newly reported host genus for *D. eresimus* and *D. plexippus*, but not *D. gilippus* (Ackery and Vane-Wright, 1984).

Sarcostemma clausum is locally common throughout southern Florida, including the Keys, northward to Polk County (Long and Lakela, 1971; Minno and Emmel, 1993; R. P. Wunderlin, pers. comm.) (Fig. 3). Its status in Florida is somewhat controversial. Wunderlin (1982) and Hall (1993) treated the plant as a native, but most botanists consider it to be an exotic (e.g., Austin, 1978; Black and Black, 1980; Bell and Taylor, 1982; Johnson and Barbour, 1990). Long and Lakela (1971) consider *Sarcostemma* to be an Old World genus.

In central Florida, *S. clausum* is replaced as the hostplant of *D. eresimus* by *Morrenia odorata* (Hook. and Arn.) Lindl. (Asclepiadaceae) (Fig. 5). This was first realized in October, 1994, when I discovered larvae of *D. eresimus* on *M. odorata* in a citrus grove in coastal Manatee County, Florida. I subsequently surveyed citrus groves throughout central Florida for the presence of *D. eresimus* populations. As a result, twelve populations were found in association with *M. odorata* (Fig. 3) and ten individuals were reared from eggs and larvae found on the plants. Although no hostplant was identified in Volusia County, *M. odorata* is probably utilized there as well. Eggs and larvae of *D. gilippus* and *D. plexippus* were also found and reared on *M. odorata*. *Morrenia* apparently represents a new host genus for all three *Danaus* species (Ackery and Vane-Wright, 1984). South American in origin, *M. odorata* was first discovered in west-central Florida in 1939 and became a major pest of citrus groves throughout central Florida by 1970 (Tucker and Phillips, 1974; Ziegler and Wolfe, 1975). It is now a widespread perennial in the citrus growing region of Florida, from Alachua County southward to Highlands County (Tucker and Phillips, 1974; R. P. Wunderlin, pers. comm.) (Fig. 3). This vine grows rapidly and damages the trees by shading and girdling the limbs as it climbs. Trees that are heavily infested with *M. odorata* become laden with the vines across their canopies (Fig. 6). This vine also spreads over fence rows and herbaceous growth in the vicinity of the groves and is very difficult to eradicate (Tucker and Phillips, 1974). Kimball's (1965) unlikely hostplant report of *Citrus* for *D. plexippus* is probably referable to *M. odorata* which was growing among the branches of the fruit trees. Unfortunately, the use of *Danaus* as a biological control would not be effective as these insects would not reach high enough densities to negatively impact populations of *Morrenia*.

Other species of Asclepiadaceae undoubtedly serve as hostplants of *D. eresimus*, including many utilized by *D. gilippus*.



Figs. 4-7. Habitat and hostplant of *D. eresimus* in central Florida (Hillsborough Co.). 4. Typical citrus grove habitat; 5. *Morrenia odorata* leaves and flowers; 6. *Morrenia odorata* covering crown of citrus tree; 7. Female *D. eresimus* ovipositing on *M. odorata*.

Ackery and Vane-Wright (1984) listed ten genera of *D. gilippus* hostplants. In Florida, *D. gilippus* is known to feed upon at least nine species of milkweeds; *Asclepias curassavica* L., *A. curtissii* A. Gray, *A. humistrata* Walt., *A. incarnata* L., *A. tomentosa* Ell., *A. tuberosa rolfsii* (Britt.) Woods, *Cynanchum angustifolium* Pers., *S. clausum*, and *M. odorata* (Matteson, 1930; Brower, 1961; Pliske, 1971; Brown and Heineman, 1972; Malcolm and

Brower, 1986; Minno, 1992). Eighteen species of Asclepiadaceae occur in southern Florida alone (Long and Lakela, 1971), thus additional hosts probably await discovery. Surprisingly, the only species of *Asclepias* reported to be utilized by *D. eresimus* in nature is the tropical American *A. curassavica*, which is a widespread exotic throughout much of central and southern Florida. However, larvae of *D. eresimus* will apparently accept

other species of *Asclepias*, at least under artificial conditions. R. W. Boscoe (pers. comm.) has reared both *D. eresimus* and *D. gilippus* on *Asclepias syriaca* L. from eggs obtained by confining Floridian females in bags filled with cuttings of *S. clausum*. *Asclepias syriaca* does not occur in Florida and would not normally be encountered by *D. eresimus*. It is of interest that all the adults of *D. eresimus* reared on *A. syriaca* possess enlarged black pattern elements and a richer orange-brown ground color (specimens in FSCA).

EARLY STAGES

The early stages of *D. eresimus* have not been published in detail. Most descriptions have concerned only the larva, but even these are largely ambiguous or inaccurate. Although a thorough investigation of the early stages was not undertaken, the information below is based primarily on observations of *D. eresimus*, *D. gilippus*, and *D. plexippus* that were found and reared on *M. odorata* in central Florida during 1994.

Eggs.— The eggs of *D. eresimus* are deposited singly on the dorsal or ventral surfaces of the host leaves. Females prefer to oviposit on younger leaves, but eggs have also been found on larger, older leaves. The eggs are barrel-shaped, wider and flattened basally, tapering toward the apex. They are white or yellowish in color, and somewhat translucent. This agrees with other observations in Florida by Minno and Emmel (1993) and R. W. Boscoe (pers. comm.), as well as those of T. W. Turner (pers. comm.) in Jamaica. However, this contradicts several published reports (e.g. Opler and Krizek, 1984; Scott, 1986; Smith et al., 1994) based on data from the same source that the eggs of Floridian *D. eresimus* are bright orange and resemble aphids (Aphididae) commonly found on *S. clausum*. They are slightly more elongated than those of *D. gilippus*, and smaller and less rotund than those of *D. plexippus*. The eggs turn grey prior to hatching and the egg shells are consumed by the young larvae.

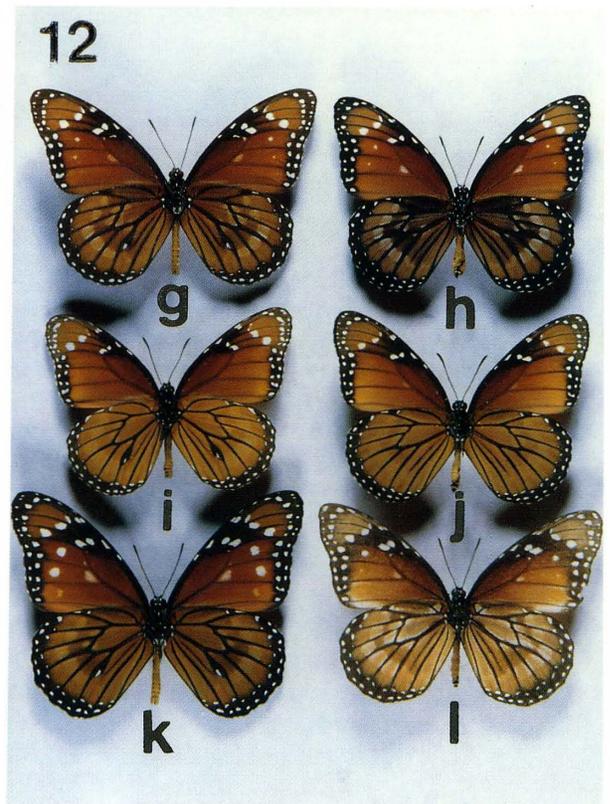
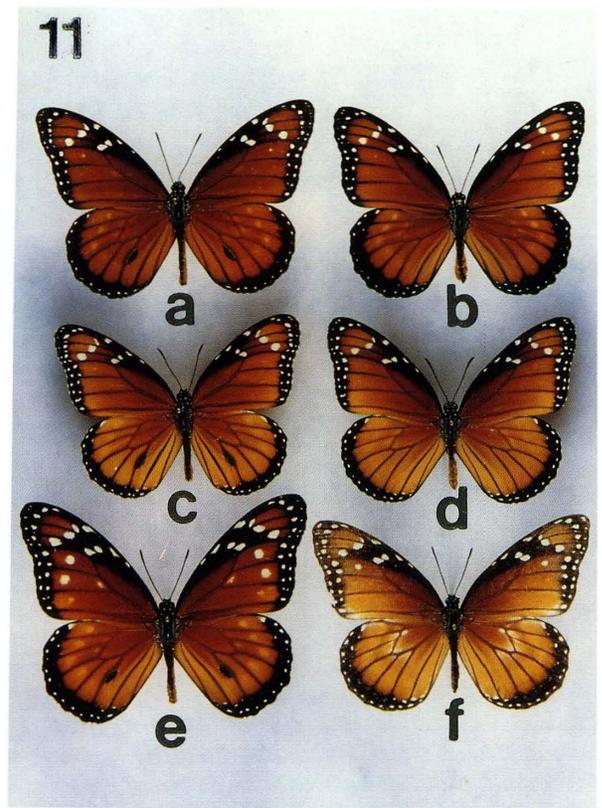
LARVAE.— Young larvae of *D. eresimus* are very similar in general appearance to those of *D. gilippus*, but slightly lighter in color. Descriptions of the mature larva by Riley (1975), Scott (1986), Opler and Malikul (1992), and Minno and Emmel (1993) are not very helpful in differentiating *D. eresimus* from *D. gilippus*. DeVries (1987) based his larval description on a color drawing of a mature *D. eresimus eresimus* larva from French Guiana figured in Fontaine (1980). Smith et al. (1994) provided the most detailed and precise verbal description. Ackery and Vane-Wright (1984) figured what they believed to represent a mature larva of *D. eresimus montezuma* Talbot from El Salvador (Pl. V, Fig. 41). However, this larva does not resemble the drawing of larval *D. e. eresimus* in Fontaine (1980) or any of the larvae of *D. eresimus tethys* I reared in 1994. Rather, it appears to be identical to a dark form of larval *D. gilippus berenice* Cramer that I also reared in 1994 (Fig. 10). In this form, the large yellow dorsal spots normally found on the larva of *D. gilippus* are replaced by small and indistinct yellowish-red spots, giving the caterpillar a much darker overall appearance. This could represent an extreme example of the sex-linked (female) form of *D. gilippus* larva discussed by Hopf (1954) in which several dorsal spots are obscured. P. R. Ackery (pers. comm.) did not personally photograph the larva used for his figure and could not confirm its identity. He admitted that the

original photographic slide could have been mislabelled. The larvae of *D. eresimus* I reared in 1994 were virtually identical to the larva figured in Fontaine (1980), suggesting that the species exhibits the same distinctive pattern throughout its range. Thus, the larva identified as *D. eresimus montezuma* by Ackery and Vane-Wright (1984) is probably referable to *D. gilippus thersippus* Bates from El Salvador.

The striped color patterns of mature *D. eresimus* and *D. gilippus* larvae are basically variations on a theme (Figs. 8 and 9). In both species, the head is concentrically banded with white or yellowish stripes and they possess a number of transverse white and yellow pattern elements on each body segment. In *D. eresimus*, the most obvious pattern element is a broad white band across the anterior portion of each segment. This band is followed by two conjoined pale yellow elongated spots. In *D. gilippus*, the anterior white band is narrow and the yellow spots are enlarged, rounded, and more richly colored. Due to the broad white band on each segment, *D. eresimus* larvae appear lighter in color than those of *D. gilippus*. Unlike *D. plexippus* (subgenus *Danaus*) which has only two pairs of fleshy tubercles, both *D. eresimus* and *D. gilippus* (subgenus *Anosia*) have three pairs (on the second thoracic, second abdominal and eighth abdominal segments).

Larval behavior in *D. eresimus* is also similar to *D. gilippus*. When actively feeding or crawling, both species hold the anterior and posterior tubercles erect and perpendicular to the body. When resting, the body is held in a linear position, with the anterior tubercles positioned downward and forward over the head, while the posterior tubercles are held downward and backward. This is also the posture employed prior to molting. When disturbed, larvae of both species curl up and drop from the hostplant onto the ground. These behaviors have been noted in other danaid larvae as well (Urquhart, 1960; Ackery and Vane-Wright, 1984). During the warmest period of the day, larvae tend to rest on the shaded stems and ventral leaf surfaces of the host plant. Larvae feeding on *M. odorata* have been found primarily on vines growing within the shaded interiors of the citrus trees. Larval cannibalism was not noted in *D. eresimus* or *D. gilippus*.

PUPAE.— Few references to the pupae of *D. eresimus* are found in the literature. Only Smith et al. (1994) offered characteristics to differentiate *D. eresimus* and *D. gilippus*. Both species possess chrysalids typical of the genus *Danaus*: stout, light green in color, and adorned with a gold bordered ridge on the third abdominal segment and a number of gold spots on the head, mesothorax, and forewing encasements (Fig. 13a-d). I found that the number and size of the gold spots was the most reliable method of differentiating *D. eresimus* from *D. gilippus*. In *D. eresimus*, only two gold spots (medial notal spots) are located on the mesothorax, while four such spots (medial and lateral notal spots) are found on *D. gilippus*. In addition, the gold spot on the discal region of the forewing (alar spot) is smaller (sometimes nearly absent) in *D. eresimus* [spot terminology follows Urquhart (1960)]. The head region of *D. eresimus* also tends to be narrower than that of *D. gilippus*. Although Smith et al. (1994) noted that the chrysalid of *D. eresimus* is slightly larger than that of *D. gilippus*, the reverse was true among most individuals I reared in 1994. The chrysalid of *D. plexippus* is much larger and more robust than both *D. eresimus* and *D. gilippus* and pos-



Figs 8-12. Larvae and adults of *Danaus* species. 8. mature larva of *D. eresimus* (Manatee Co., FL); 9. mature larva of *D. gilippus* (Manatee Co., FL); 10. dark form of mature *D. gilippus* larva reared in 1994 (Manatee Co., FL); 11-12. dorsal and ventral individual variation of *D. eresimus* in Florida.

sesses a dorsal black spot on the last abdominal segment (Fig. 13e,f).

The pupal development period for individuals of *D. eresimus* reared in 1994 varied from nine to 14 days.

PARASITES.— Two species of parasitic flies emerged from pupae

of *D. eresimus* and *D. gilippus* reared from larvae found in Manatee County, Florida in 1994. Several individuals of a *Lespesia* sp. (Tachinidae) emerged from a *D. eresimus* chrysalid and a single *Hyphantrophaga* sp. (Tachinidae) emerged from a chrysalid of *D. gilippus*.

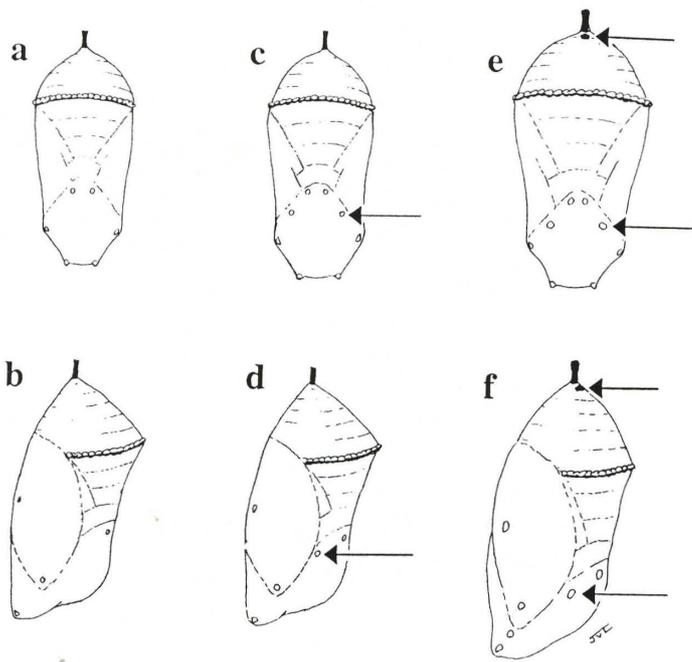


Fig. 13. Pupae of *Danaus* species. a, b. *D. eresimus*; c, d. *D. gilippus*; e, f. *D. plexippus*. Arrows indicate gold or black spots used to differentiate species.

ADULT BEHAVIOR AND PHENOLOGY

Little information is available on the behavior of *D. eresimus*. Opler and Krizek (1984) speculated that it is "believed to be similar to that of the queen" (*D. gilippus*). With few exceptions, this is indeed the case. The flight of *D. eresimus* resembles that of *D. gilippus*: wandering, but not as slow and gliding as *D. plexippus*. Adults of *D. eresimus* are wary and more likely than *D. gilippus* to be disturbed when approached. When disturbed, *D. gilippus* tends to flutter for only a short distance before settling, while *D. eresimus* often flies rapidly to a more distant location, occasionally soaring over low trees in the process. The flight of *D. eresimus* appears to be stronger than *D. gilippus*. Brown and Heineman (1972) and DeVries (1987) noted similar flight behavior.

Males of *D. eresimus* appear to search more actively for females than do males of *D. gilippus* which encounter females more haphazardly during the course of feeding activities. Males of both species quickly recognize females of the other species and no lengthy interspecific courtships have been observed. I have observed pre-courtship encounters between these species and the similarly marked *Basilarchia archippus floridensis* (Strecker) (Nymphalidae) in central Florida. L. C. Koehn also has witnessed males of *B. a. floridensis* pursuing *D. eresimus* and *D. gilippus* in southern Florida (Baggett, 1988b). Such activities are probably the result of mistaken visual identity during mate location.

Copulation of *D. eresimus* has been observed in the early afternoon (1300h and 1321h). The male is the carrier, which is consistent with *D. gilippus* in Florida (Miller and Clench, 1968). Oviposition has been noted at 1430h. Females of *D. gilippus* seem to prefer to oviposit on more isolated, low-growing vines of *M. odorata*, while *D. eresimus* females are usually observed frequenting and ovipositing on vines at higher levels, including

those growing among the canopies of citrus trees (Fig. 7). Both sexes dorsal bask on leaves at a height of about 1.0-3.5m. On several occasions in Florida, *D. eresimus* has been observed roosting in groups, sometimes in the company of *D. gilippus* (Mather, 1978; Brewer, 1982; Baggett, 1988c).

Danaus eresimus and *D. gilippus* are usually found visiting nectar sources together in close proximity to areas containing the host plants. When the weather is warm and sunny, adults of both species visit flowers during much of the morning and afternoon hours. They prefer nectar sources that are at least 0.3m in height and are most attracted to *B. alba*, but *Lantana camera* L. (Verbenaceae) serves as a secondary source, or a primary source if *B. alba* is scant or unavailable. Ackery and Vane-Wright (1984) found that the Asteraceae and Verbenaceae are the most common nectar sources for the Danainae as a whole. In central Florida, I also have seen *D. eresimus* visit *Fumaria officianalis* L. (Fumariaceae), *Sida* sp. (Malvaceae), and *Brassica juncea* (L.)Coss. (Brassicaceae). Additional nectar sources in southern Florida are *A. curassavica*, *Eupatorium serotinum* Michx. (Asteraceae) (Pliske, 1970), *Piloblephis rigida* (Bartr. ex. Benth.)Raf. (Lamiaceae) (Calhoun, 1985), and *Ageratum houstonianum* Mill. (Asteraceae) (specimen in FSCA). Nectar sources elsewhere in the United States include *Eupatorium havanense* H. B. K. (Asteraceae), *Chromolaena odorata* (L.)King and Robins (Asteraceae) (southern Texas: R. O. Kendall, pers. comm.), *Baccharis* spp., including *B. sarothroides* Gray (Asteraceae), and *Tithonia* sp. (Asteraceae) (southern Arizona: R. A. Bailowitz, pers. comm.). There are no known records of *D. eresimus* visiting the flowers of the hostplants in Florida, although Schwartz (1989) reported the species is attracted to *S. clausum* on Hispaniola and R. A. Bailowitz (pers. comm.) has noted visitation at a *Sarcostemma* species in southern Arizona.

Pliske (1975) reported *D. eresimus* and *D. gilippus* in southern Florida visiting uprooted *Heliotropium curassavicum* L. (Boraginaceae) and cut shoots and branches of *Argusia gnaphalodes* (L.) Heine. (Boraginaceae). These plants contain pyrrolizidine alkaloids which are necessary to produce some sex pheromones in Lepidoptera. Adults congregate on the dead stems, seeds, and foliage to feed. I observed adults of *D. eresimus* and *D. gilippus* gathering in this fashion around the cut stem of an unidentified plant in Volusia County, Florida.

Adults of *D. eresimus* have been reported during every month of the year on the southern Florida mainland. On the offshore keys of Monroe county, *D. eresimus* has been found only during February, May, June, and November (Bates, 1934; Minno and Emmel, 1993), but it certainly has the potential to occur there throughout the year. In central Florida, the species has thus far been recorded only during the months of August through January. Although most Florida records are from August through December, this may be more a reflection of the activity of vacationing collectors, rather than the actual seasonal abundance of *D. eresimus*. Schwartz (1989) recorded the species on Hispaniola during every month but September and November.

TAXONOMIC CONSIDERATIONS

Danaus eresimus is most readily distinguished from *D. gilippus* by the presence of a series of pale post-discal spots across the

ventral surface of the hindwing. These spots vary from faint (sometimes nearly absent) to well defined. Only the South American *Danaus plexaure* (Godart) (Nymphalidae) exhibits similar spots, strengthening the notion that these taxa may be conspecific (Ackery and Vane-Wright, 1984). Clark (1941) inexplicably identified and figured an obvious example of *D. eresimus* from Texas as the very different Antillian *Danaus gilippus cleothera* (Godart).

Two putative subspecies of *D. eresimus* are generally recognized in the northern portion of the species' range. *Danaus eresimus montezuma* (type locality; "Misantha, Veragua" [prob. Misantha, Veracruz], Mexico) is distributed from northern Panama, northward into Mexico and the southwestern United States. *Danaus eresimus tethys* (type locality; Fond Parisien, Haiti) is attributed to Hispaniola, Cuba (including the Isle of Pines), the Cayman Islands, Jamaica, the Bahamas, and Florida. At least four additional subspecies are recognized in South America (Ackery and Vane-Wright, 1984; Smith et al, 1994). Forbes (1943) remarked that the blend zone between *D. e. eresimus* (type locality; "Surinam"), *D. e. montezuma*, and *D. e. tethys* is "embarrassingly large." To further complicate matters, Forbes (1943) cast doubt on the propriety of his own decision to differentiate West Indian populations. Urquhart (1960) lamented that "it is most difficult to separate the subspecies of *Danaus eresimus*. I have been unable to find any clear demarcation between any of these populations; any color differences appear to be of degree rather than of kind, nor do there seem to be any well-defined geographical limitations." Brown and Heineman (1972) and Schwartz (1989) discussed at length the confusing subspecific status of West Indian material and questioned the validity of applying the name *tethys* to these populations. Brown and Heineman (1972) ultimately chose to disregard *tethys* and refer Jamaican material to the nominate subspecies.

Northward, darker specimens of *D. eresimus* are generally associated with *D. e. montezuma*, lighter specimens with *D. e. tethys*. Forbes (1943) further separated these "subspecies" on the basis of the pale ventral hindwing spots ("even-colored" in *tethys*; "scaled conspicuously with white along the veins, sometimes reduced to their white edges" in *montezuma*) and the white dorsal post-median forewing spots (present in cells M_3 , Cu_1 , and sometimes Cu_2 in *tethys*; lacking below cell M_3 in *montezuma*). However, these distinctions are weak and a series of specimens from Florida can possess any combination of these features (Fig. 11-12).

In Florida, as elsewhere, *D. eresimus* displays extensive individual variation. Although Smith et al. (1994) called *D. eresimus* in Florida "abundantly distinct" from *D. gilippus berenice*, some individuals can be nearly indistinguishable in the field. Darker individuals of *D. eresimus* (Fig. 11a, b) closely resemble typical *D. g. berenice*, while lighter individuals (Fig. 11c, d, f) can be tawny enough to even be confused at a distance with females of *Agraulis vanillae* (L.) (Nymphalidae). The ventral hindwing spots of *D. eresimus* may be indistinct or quite vivid (Fig. 12h, j). The dorsal forewing spots are also extremely variable, both in size and number (Fig. 11c, e). Occasionally, white scales are present in the discal region of the dorsal hindwings, similar to the figure of *D. eresimus montezuma* in Klots (1951; plate 10, fig. 3) (Fig. 11f). Bates (1935) and

Forbes (1943) discussed such variation in Cuba. Alayo and Hernández (1987) also noted subspecific contradictions in specimens from Cuba, and went as far as to consider *montezuma* a form of *D. e. tethys*. In a preliminary examination of numerous specimens of *D. eresimus* from Florida, Texas, Arizona and Mexico, I could find no reliably consistent differences. In fact, based on the morphological characteristics summarized by Forbes (1943), both *D. e. tethys* and *D. e. montezuma* occur in Florida (!). In a note contained in the CMNH collection, G. Lamas concluded that two specimens from Sanibel Island, Lee County, Florida "ought to be considered as *eresimus montezuma*, in spite that they have some weak characteristics of *e. tethys*; nevertheless, they are closer to *montezuma* than to *tethys*." Indeed, a large series of specimens I have examined from Florida, the Bahamas, western Cuba and the Cayman Islands clearly trend toward Mexican *D. e. montezuma* rather than material (including the types) of *D. e. tethys* from Jamaica and Hispaniola, alluding to continuing mainland influences via the Yucatan peninsula into Cuba. In order to avoid additional confusion, no trinomials should be used for populations in Florida and the Greater Antilles until the relationship between these taxa is clarified.

DISCUSSION

The flora and fauna of southern Florida has many affinities to the West Indies which makes it more difficult to ascertain whether the few early records of *D. eresimus* represented strays or the species was actually a rare resident. It is easier to understand the historical status of several other Neotropical butterfly species currently established in Florida because they have developed distinctive subspecific characteristics, verifying their long-term residency [e.g. *Strymon acis bartrami* (W. P. Comstock) (Lycaenidae), and *Phocides pigmalion okeechobee* Worthington (Hesperiidae)]. This is further complicated by the fact that *D. eresimus* is not significantly differentiated on any of the islands of the Greater Antilles where it is thought to be a long-term resident. Although no organized migrations have been reported for *D. eresimus* in the West Indies, inter-island (including the Florida Keys) movements are probably of regular occurrence and may account for the isolated early captures of the species in Florida. Any such movements into Florida undoubtedly originate in Cuba; thus all current Floridian populations probably are derived from Cuban stock.

Bates (1934) believed that the initial rarity of *D. eresimus* in Florida was possibly due to its resemblance to the abundant *D. gilippus*; the less common *D. eresimus* was simply overlooked. Until recently, the species was also considered rare in Cuba (e.g. Bates, 1935), but the former paucity of records may be a result of limited field work (L. R. Hernández, pers. comm.). This does not appear to be the case in southern Florida where a number of resident collectors were active from the turn of the century through the 1960's, including M. S. Forsyth (Florida City), F. M. Grimshawe (Miami), J. H. Matteson (Miami), J. M. Plomley (Hollywood), and A. T. Slosson (winter home near Miami). Although these individuals recorded many unusual Neotropical species, *D. eresimus* was not among them, suggesting the species was truly a rarity in Florida. This further supports the idea that *D. eresimus* was not established in southern Florida until about

1970. Due to a lack of evidence in support of long-term residency in Florida, *D. eresimus* must be considered a recently established immigrant arthropod as broadly defined by Whitehead and Wheeler (1990): a resident or probable resident species of known or suspected alien origin. An intriguing question remains: why did *D. eresimus* suddenly become successfully established and locally common in Florida following nearly a century of recorded rarity?

Over 900 immigrant species of insects have been documented in Florida, at least 271 during the last twenty years (Frank and McCoy, 1992, 1995). The early to mid-1970's appears to have been especially favorable for the immigration of Neotropical butterfly species into southern Florida (see Anderson, 1974; Bennett and Knudson, 1976). This may, in part, be due to the widespread elimination of coastal vegetation in Cuba during this period (L. R. Hernández, pers. comm.). Unusual climatic conditions, such as tropical storms, may also have aided or elicited these movements. At least eight tropical storms passed over or very near Florida between 1969 and 1975 (Neumann et al., 1978). The modified ecological conditions in southern Florida have probably facilitated the establishment of exotic insect species.

Opler and Krizek (1984) and Brown and Opler (1990) observed that several Antillean species of butterflies, including *D. eresimus*, have recently become established in southern Florida following the introduction of plants that are acceptable as hosts. Other such butterfly species include *Ministrymon azia* (Hewitson) (Lycaenidae), *Chlorostrymon simaethis* (Drury) (Lycaenidae), *Electrostrymon angelia* (Hewitson) (Lycaenidae) and *Siproeta stelenes* (L.) (Nymphalidae). Although these species are known only to feed upon exotic plants in Florida, they are probably capable of exploiting native plants. *Danaus eresimus* is almost certainly able to utilize native asclepiads that are acceptable to the closely related *D. gilippus*. Nonetheless, exotic plants are often more abundant than native relatives. For example, Brewer (1982) observed that *S. clausum* is the most common milkweed on Sanibel and Captiva islands of Lee County, Florida. Moreover, exotic plants may be more attractive than native ones to ovipositing females, regardless of whether these plants serve as natural hosts outside Florida. Such an increase in hostplant availability also can benefit native butterflies (e.g. *Erynnis baptisiae* (Forbes) (Hesperiidae) has become much more common following the widespread planting of exotic *Coronilla varia* L. in the northeastern United States). The recent increase of *D. eresimus* records in Cuba may partially be due to a greater abundance of its suspected exotic host, *C. procera*.

Extensive cultivation of exotic plants in Florida for ornamental purposes, as well as ecological changes due to agriculture and urban sprawl have resulted in a profusion of attractive potential hosts for Neotropical butterflies. The areas in which these plants occur usually support a plethora of native and/or cultivated flowers which serve as important adult nectar resources throughout the year. Perhaps in a similar manner, *Phoebis philea* (Johansson) (Pieridae) and *Asbolis capucinus* (Lucas) (Hesperiidae) became established in Florida during the first half of this century following the widespread ornamental cultivation of various *Cassia* spp. (Fabaceae) and Palms (Palmaceae) in flower-filled, urban residential environments. *Calpodus ethlius* (Stoll)

(Hesperiidae) may similarly have become established after tropical *Canna* spp. (Cannaceae) were widely planted in southern Florida. However, this species colonized Florida much earlier since larvae were pests on *Canna* planted around Miami hotels as long ago as 1899 (Slosson, 1899). An analogous relationship between the exotic flora and fauna of Florida is the reliance of introduced parrots (*Aratinga* spp. and *Amazona* spp.) on cultivated fruit trees, especially figs (*Ficus* spp.) (Myers and Ewel, 1990).

Once *D. eresimus* had become firmly established in extreme southern Florida, the species was able to spread northward at a dramatic pace (Fig. 2). When the northern limits of the range of *S. clausum* were reached, *D. eresimus* was able to replace it as its primary hostplant with *Morrenia odorata*, another exotic vine milkweed. The northward penetration of the Florida peninsula by *D. eresimus* would probably not be as successful if *M. odorata* was not widespread in the central portion of the state. *Electrostrymon angelia* has similarly been successful in expanding its range of temporary establishment into central Florida by exploiting the widespread and prolific exotic *Schinus terebinthifolius* Raddi. (Anacardiaceae). This plant was introduced into Florida for cultivation in 1898 and remained rare in the wild as late as 1959. Since that time, birds have effectively distributed the seeds throughout much of Florida, causing it to become one of the most problematic weeds in the state (Austin, 1978). Although *E. angelia* may have been a rare or irregular resident of Florida in the past (Miller, 1978), it was not known to reproduce in the state until the early 1970's (Anderson, 1974; Fisher, 1974). By 1992, it was recorded as far north as Manatee and Pinellas Counties (Baggett, 1992).

The dynamics of *D. eresimus* in central Florida is comparable to that of Neotropical butterfly species in southern Texas which occur in the region only when climatic conditions are favorable. These incursions are apparently terminated by severe winter temperatures (Neck, 1976; 1981[83]). Brown and Opler (1990) noted that the northern range limits of tropical butterfly species in Florida are likewise determined by low temperature thresholds. Kendall and McGuire (1984) proposed that freezes which defoliate the hostplants are the most detrimental to such species, killing the larvae through starvation, regardless if the temperatures are directly lethal to the insects. These species may reintroduce into formerly inhabited areas, but only after the hostplants recover. The frequency of low or freezing temperatures rapidly increases northward through peninsular Florida. Several Neotropical species, including *P. philea*, *Heliconius charitonius* (L.) (Nymphalidae) and *Anartia jatrophae* (Johansson) (Nymphalidae), annually advance northward through peninsular Florida during the wet season when weather conditions are most favorable and hostplant availability is at its peak. By autumn, temporary populations of these species may be established as far north as Georgia and South Carolina (Harris, 1972; Gatrell, 1985). At the onset of cold winter temperatures, the ranges of these species contract southward and the process begins again. An extralimital population of *Anthanassa frisia* (Poey) (Nymphalidae) was recently located in Volusia County, Florida, over 300km north of the species' normal breeding range in the state (Calhoun, 1995). This population will likely be eliminated by intolerably low winter temperatures as well. *Danaus eresimus* is undoubtedly not a permanent resident of central Florida and its northern range

limit also fluctuates depending on the severity of winter weather. It could experience lengthy absences from much of the region following particularly harsh winters, especially if populations of *M. odorata* were severely impacted. Although *D. eresimus* was not found in Florida as far north as Hernando and Volusia Counties until 1994, it has the ability to wander (and possibly establish temporary colonies) much further north, as illustrated by the capture of two females near Columbus, Muscogee, Georgia, on 27 June 1993 and 18 April 1994 (R. Hirzel, pers. comm.). In southern Texas, the range of *D. eresimus* likewise expands and contracts, possibly extending nearly 500km beyond the Mexican border before cold temperatures interrupt this northward advance (R. O. Kendall, pers. comm.). In contrast, the species is a rare, irregular vagrant into southern Arizona where it arrives from Mexico, primarily during late autumn, and is not known to reproduce (Bailowitz and Brock, 1991; R. A. Bailowitz, pers. comm.).

The increased presence of *D. eresimus* in Florida may affect relationships between other resident species of butterflies. Brower (1962) concluded that *D. gilippus* and *D. plexippus* compete ecologically in south-central Florida. It was found that hostplant preferences vary in relation to the abundance of each species. This competition could become more complicated with the arrival of *D. eresimus*. However, because *D. eresimus* appears to prefer exotic milkweeds and populations are very localized, its overall impact on native danaids remains limited. Ritland and Brower (1991) have shown that the mimicry complex involving *B. archippus*, *D. gilippus* and *D. plexippus* is Müllerian in nature, rather than Batesian as historically believed. *Danaus eresimus* has now entered into this complex in Florida, perhaps benefiting from its resemblance to all three potential co-mimics. Continued observations of *D. eresimus* in Florida will hopefully reveal more about the dynamics of this and other Neotropical butterfly species at the northern periphery of their ranges.

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