HOLARCTIC LEPIDOPTERA, 5(2): 53-62

NOTES ON SWALLOWTAIL POPULATION DYNAMICS OF THREE *PAPILIO* SPECIES IN SOUTH-CENTRAL FLORIDA (LEPIDOPTERA: PAPILIONIDAE)

J. M. SCRIBER, M. D. DEERING[1], L. N. FRANCKE[2], W. F WEHLING, AND R. C. LEDERHOUSE[3]

Dept. Entomology, Michigan State University, East Lansing, Michigan 48824, USA

ABSTRACT.– South-central Florida (Highlands County) has experienced unusually intense wetland and wooded habitat loss due to agricultural, ranching, and developmental drainage programs since the 1960's. During the last 20-30 years, general declines have been observed in the numbers of swallowtail butterflies (*Papilio*), with the exception of woodland and hammock preserves such as Highlands Hammock State Park. Here we report the last 6 years of population size estimates of *Papilio glaucus*, *P. palamedes*, and *P. troilus*, the most common swallowtail butterfly species in this county. We found that the frequency of dark (mimetic) morph *P. glaucus* has remained high (31-44%) for the last 10 years for all spring and fall broods observed unlike the low proportions before the 1960's drainage projects. In addition, we report on lizard, spider, and mantid predation on large *Papilio* adults.

KEYWORDS: Asclepiadaceae, *Battus*, behavior, biology, *Callosamia*, Compositae, conservation, habitats, Hemiptera, hostplants, Iteaceae, Labiatae, Lauraceae, Magnoliaceae, Mantidae, Miridae, Nearctic, nectar sources, predation, Saturniidae, spiders.

Two decades of observations on the eastern tiger swallowtail, *Papilio glaucus* Linnaeus, in Highlands County, Florida, have detected what appears to be an alarming decline in the suitable habitat containing the only hostplant for the species in that area (sweet bay, *Magnolia virginiana* L., Magnoliaceae) (Scriber, 1986; Bossart and Scriber, 1995). However, the most rapid decline in swallowtail populations may have occurred in 1959 and 1960 due to the draining of vast acreages of wetlands with nectar plants near the Lake Placid, Parker Islands region as a result of the East Chain of Lakes Watershed Project and the Fisheating Creek Project with an associated increase in agriculture and development (Scriber, 1986).

Lederhouse and Scriber (1987) noted a significant increase in the frequency of dark morphs (putative mimics of *Battus philenor* (Linnaeus) (Brower and Brower, 1962) subsequent to this population bottleneck. Before 1961, the frequency of dark morph females was only 3-9%, whereas studies in the 1970's and early 1980's have shown the dark morph frequency to generally average 35-40%. However, the frequency of putative model, *Battus philenor*, was extremely low in these studies in Highlands County, with only a total of 3 individuals of the model species observed while collecting 890 female *P. glaucus* (Brower and Brower, 1962; Pliske, 1971; Lederhouse and Scriber, 1987). The increase in relative frequencies of dark females was concluded to be due to genetic drift rather than decreases in the predation pressure on dark (mimetic) morphs or differential mating preferences. Our mating studies using tethered size-matched virgin females during 1989 and 1990 (Lederhouse, 1995; Lederhouse and Scriber, unpubl.) showed that males of these Florida populations preferred the more abundant yellow females (however males from Ohio populations preferred the more abundant dark females).

The swallowtail butterflies *Papilio troilus* Linnaeus and *P. palamedes* Drury are closely related species that are plant family specialists on the Lauraceae (Scriber *et al.*, 1991). Native North American hosts of *P. troilus* include sassafras (*Sassafras albidum* [Nutt.] Nees), spicebush (*Lindera benzoin* [L.] Blume), silky spicebush (*Lindera melissifolium* [Walt.] Blume), and redbay (*Persea borbonia* [L.] Spreng.), as well as camphortree (*Cinnamomum camphora* [L.] Karst.), an introduced ornamental that has become naturalized in parts of southeastern United States (Tietz, 1972; Morris, 1989). Native hosts listed for *P. palamedes* include *Sassafras albidum* and *Persea boronia* (Brooks, 1962).

Larval performances by both species vary across these potential hosts. Larval survival and first instar growth rate was highest for *P. troilus* on spicebush and for *P. palamedes* on redbay (Lederhouse *et al.*, 1992). The lowest survival and first instar growth rate was exhibited by *P. troilus* on redbay and *P. palamedes* on spicebush. Survival of both swallowtails was intermediate on *Sassafras*, but larvae that survived on this host had the highest lifetime growth rates and produced the heaviest pupae (Lederhouse *et al.*, 1992). Local adaptation of *P. troilus* may be of considerable ecological importance in maintaining a poulation in southern Florida where redbay is the only common host. A population of *P. troilus* from southcentral Florida survived and developed better on redbay than did a population from outside the range of redbay (Nitao *et al*,. 1991). However, the divergence between *P. troilus* populations was small when viewed in the context of interspecific variability (Lederhouse *et al.*, 1992).

Redbay grows in wet areas in association with sweetbay (*Magnolia virginiana* L., Magnoliaceae) and loblollybay (*Gordonia lasianthus* (L.) Ellis, Theaceae) (Bell and Taylor, 1982). However, a mistake in oviposition by either *P. troilus* or *P. palamedes* on Magnolia bay is certain death of the neonate larvae (Scriber, 1986). In southern Flo-

Fig. 1 (p. 54). *Argiopes* spp. spiders with *Papilio* adult at a web in a patch of tickweed (*Verbesina virginica* L.) October 27, 1997 at the orange grove of the Highlands Hammock State Park, FL. A) with male *P. glaucus* (#93 red); B) with dark morph female and a live male at the left; C) ten spider wrapped corpses of *Papilio glaucus*, *P. palamedes*, and *P. troilus* found on the ground underneath spider "A"; D) nectaring butterflies being filmed near palmetto hammock edge; E) the spider, *Nephila clavipes*, in a *Citrus* tree 4 meters above the ground that captured and ate 3 adult *P. glaucus* in 4 days.

Fig. 2 (p. 55). Hammock habitat A) Hall Road (Highlands Co., FL) in 1984; B) in 1995; C) Sweet bay, *Magnolia virginiana* (the only host of *P. glaucus* in the area), D & E) Field crew assisting in mark-release-recapture studies.

[1]Current Address: Sophia Sachs Butterfly House and Education Center Forest Park, Chesterfield, MO 63107
[2]Current Address: 17270 Quail Creek Dr., Spring Lake, MI 49456
[3]Current Address: 6530 Bear Ridge Rd., Lockport, NY 14094


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rida, bayheads and wet woods have been greatly reduced by drainage and development for agricultural and residential use and are now limited to isolated habitat islands such as the Parker Island area to the south and the 1 km forest edge on the west side of Lake Istokpoga near Lake Placid. Highlands Hammock State Park, just west of Sebring, Florida, retains one of the largest areas (15-20 sq km) of undisturbed bay vegetation. We were interested in determining the relative population levels of *P. palamedes* and *P. troilus* where they share the only available host as well as the *P. glaucus* color morph frequency changes and its population sizes during the recent decade.

We initiated some mark-release-recapture studies in 1992 in bayhead areas of different sizes to assess the relative population sizes of *Papilio* species at different locations including the larger protected bayhead in the Highlands Hammock State Park, which is what we report in this paper. We also recorded the frequency of dark morph females of *P. glaucus* throughout the recent decade of these studies. We also report some natural adult *Papilio* mortality factors during these periods because, other than bird predation, adult *Papilio* mortality is very rarely reported in the literature.

MATERIALS AND METHODS

Butterflies were captured with a net, marked individually, and released immediately at the site of capture. Redundant marks were placed on both the right and left sides of the dorsal and ventral wing surfaces using red, blue, or green felt-tipped pens following a modification of Lederhouse (1978). The identity of a butterfly could be determined at a distance of 3m or less through observation of a perched or feeding individual. The term "recapture" is used to denote the identification of a marked butterfly either by capture or observation on any day following the date that it was marked.

Population size was estimated using a Jolly-Seber calculation adapted for microcomputer (Ibrahim and Trpis, 1986). The Lincoln-Peterson index was used for comparison of selected samples. In this index the (Total Population ÷ Original Number Marked = Total Second Sample ÷ Total Recaptured). Of course, various assumptions underlie the method of capture-recapture (Poole, 1974; Southwood, 1978). The primary concern of immigration-emigration into or out of this population is minimized since the sweetbay hostplant and habitat is really an "island" in a great area of pasture, grasslands, or citrus groves. Natality (eclosing adults from pupae) is certainly involved as we see from the local appearance of new fresh individuals (scored as #1 of the "age" or "wear" classification system we used; Lederhouse et al 1989). The absence of mortality is another assumption of mark-recapture studies and moreover, a major ecological aspect that has not really been well-studied for natural *Papilio* adult butterfly populations (Scriber *et al.*, 1995). We report some adult mortality observed during on study. Our collecting was done carefully with nets and, wherever possible, we used the clearly visible markings to identify a recapture individual without need for netting it. The effects of red, blue, or green permanent marking are unknown, however we observed no negative effects on their behavior during the 8 years of sampling and study. The marked individuals appear to mix thoroughly with the other specimens at nectar sources and in spider webs (see following). We collected all individuals possible from approximately 0900-1700h every day. Rainy, windy, or cool days generally inhibit butterfly flight which were therefore generally not sampled. However, continuous daily sampling was always attempted by our group. This also allowed us to gather data on age class changes throughout our studies. Since we had no assurance that mortality of adults was independent of age and since new individuals eclosed throughout the periods of study, the Jolly-Seber method was used (Southwood, 1978).

RESULTS

The daily population estimates for male *Papilio glaucus* at Highlands Hammock State Park in 1992, 1993, 1995 (Table 1), range from 260 to 740 individuals, with a lower estimate for 1994 (range 81-227). The total population in 1996 was too low to accurately estimate. These estimates in the five years 1992-96 were conducted only for males, however the results with females included in 1997 suggest that similar recapture rates may have been expected for females as for males (Table 2). The 1997 sex ratio appears to be skewed toward male *P. glaucus* both in the Fall and Spring (Table 3), with approximately 35% of the females of the dark morph. This dark morph frequency appears to be the average relative proportion from year to year since 1980, ranging from 32% to 44% except for the abnormally low population sample in 1996 (Fig. 3).

The Lauraceae feeding *Papilio palamedes* and *P. troilus* both feed on the same hostplant species (redbay, *Persea borbonia*) in this Highlands Hammock preserve. Population size estimates from 1992-95 are generally slightly higher (approximately twice as large) for *P. palamedes* than *P. troilus* (Tables 4 and 5). Male populations of *P. troilus* averaged 100 or less, while male populations of *P. palamedes* averaged 150 or more. Recapture frequencies were similar for these 2 species (Chi square = 2.5, P>0.10) except for 1997 (Table 4). In 1997, *P. troilus* population size estimates were roughly equal to *P. palamedes* in March-April (Table 6) even though *P. palamedes* recaptures were less frequent.

Table 1. *Papilio glaucus* male population estimates (P) and the standard error (SE) are given for Highlands Hammock State Park (Sebring, FL) on selected dates and years[1] (Jolly-Seber calculation; Poole, 1974; Southwood, 1978).

		P	SE
1992	Mar 26	553	649
	Mar 27	408	383
	Mar 31	260	305
	Apr 1	595	679
	Apr 2	342	305
1993	Mar 24	380	331
	Mar 27	300	227
	Mar 30	639	375
	April 5	466	274
	Apr 7	458	256
	Apr 12	341	290
1994	Mar 30	140	77
	Apr 1	190	60
	Apr 4	227	74
	Apr 6	132	52
	Apr 8	81	21
	Apr 11	103	31
1995	Mar 27	657	327
	Apr 7	705	388
	Apr 14	744	291
	Apr 16	460	153
	Apr 18	377	139

[1]The sample (and population) too small to measure in 1996.
The 1997 values are listed separately in a table for Spring and Fall, as well as for both males and females (see Table 3).

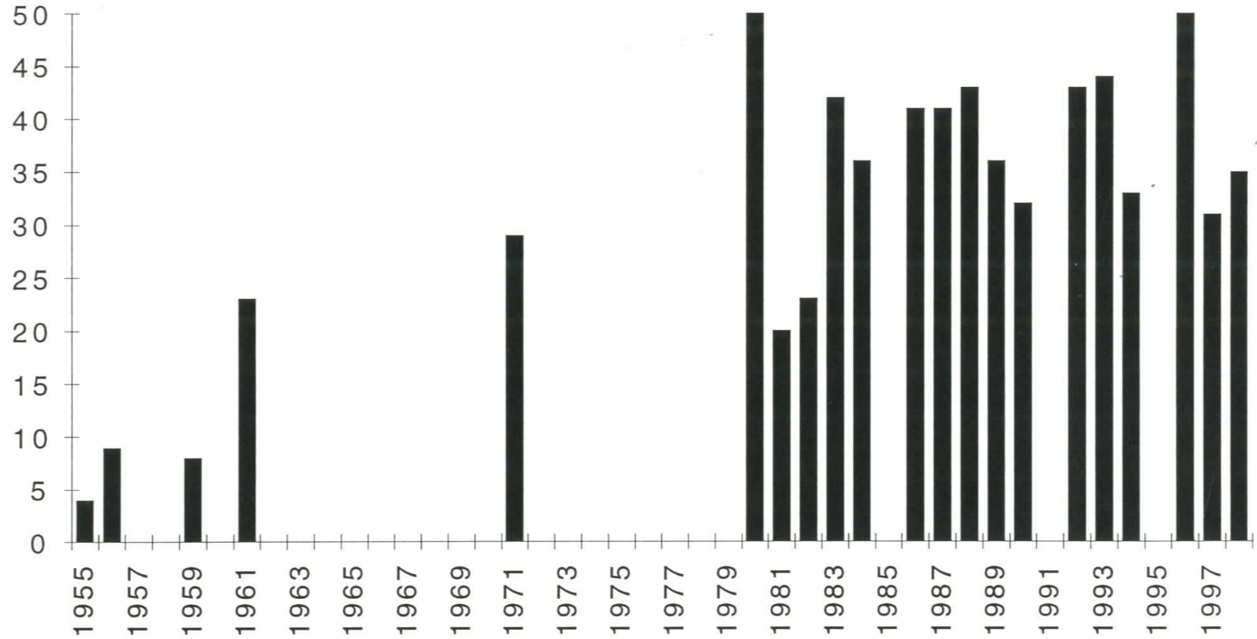

Fig. 3. The percentage of Highlands County *Papilio glaucus* females that are dark morph. Remington (1958) reports 3-5% dark in years prior to 1956, Brower and Brower (1962) report less than 9% dark (n = 501 females) in 1956 and 8% dark (n=517) in 1959. Pliske (1973) reports 23% dark for 1961 (n = 150 females) and 29% dark for 1971 (n = 155; Pilske, 1972). Our studies from 1980-1997 are reported from mid-March through mid-April samples with the following total sample sizes: 14, 1980; 10, 1981; 40, 1982; 12, 1983; 45, 1984; 29, 1986-87; 35, 1988; 311, 1989; 94, 1990; 109, 1992; 156, 1993; 115, 1994; 353, 1995; 6, 1996; 130, 1997 Spring; 187, 1997 Fall (37%).

Table 2. The number of *Papilio glaucus* males (and females 1997) that could be recaptured more than once (N) with the percent actually recaptured once (%R1) or more than once (%R2+), at Highlands Hammock State Park, Florida.

Year	Date	N	%RI	%R2+	# Marked (male/female)
1992	22 Mar-9 Apr	164	0.12	0.02	222 males
1993	22 Mar-18 Apr	318	0.12	0.01	240/128
1994	27 May-17 Apr	217	0.35	0.16	234/115
1995	19 Mar-21 Apr	601	0.20	0.06	652/353
1996	3 Apr-12 Apr	20*	0.15	0.00	25/7
1997	24 Mar-9 Apr				
	males	264	0.43	0.21	341
	females	97	0.32	0.12	130
1997	21 Oct-28 Oct				
	males	183	0.26	0.05	205
	females	155	0.22	0.05	187
1998	28 Mar-17 Apr	179	0.05	0.00	196

*March 20-25, 1996 was abnormally cold (38-44°F at night, daily highs in low 60's or high 50's).

DISCUSSION

The populations at Parker Island and Lake Istokpoga (near Lake Placid, FL) (where the populations collected in the 1950s-1970s were relatively abundant) have now nearly disappeared (fewer than 10 individuals of *P. glaucus* at the former and 40 individuals at the latter were observed in 1996 and 1997). Another site along Hall Road has been completely extirpated for *Papilio* and the sweet bay silkmoth (*Callosamia securifera* (Maassen), Saturniidae) (Johnson, 1993). Unlike these populations near Lake Placid, the populations of *P. glaucus*, *P. troilus*, and *P. palamedes* near Sebring, Florida have remained quite high and stable in the Highlands Hammock State Park preserve. This park has protected one of the largest remaining bayhead woodland habitats in Highlands County or any of Florida. Except for 1994 and 1996, the population estimates of *P. glaucus* have annually averaged 500-800 males (Table 1). In 1995, we actually marked 652 males and 353 females of *P. glaucus* over a 33 day period (Table 2). The sex ratio of our tiger swallowtail captures was approximately 2 males: 1 female (Tables 2 and 3). We also observed significant variation in age classes as indicated by wing wear (Lederhouse 1978). This may indicate that some individuals overwinter as adults through February into March, since the older wear class individuals represent a majority of the captures before the mid-March brood peaks (with a large number of perfectly fresh males and females).

Table 3. *Papilio glaucus* population estimates for Highlands Hammock State Park (Sebring, FL) for Spring and Fall 1997 (Lincoln index; Poole, 1974; Southwood, 1978).

DATES	MALES	FEMALES	
		Dark	Yellow
Spring:			
Mar 25	279	-	138
Mar 26	217	70	92
Mar 27	275	32	107
Mar 28	245	18	135
Mar 29	324	-	228
Mar 30	389	27	135
Mar 31	529	48	195
Apr 5	464	51	389
Apr 6	605	208	433
Apr 9	626	110	364
Fall:			
Oct 22	720	-	-
Oct 23	381	140	101
Oct 25	277	-	171
Oct 26	406	162	131
Oct 27	471	140	304
Oct 28	660	192	-

A dash (-) indicates no recaptures on that date.

Table 4. Recapture comparisons for *P. palamedes* and *P. troilus* males. N is the number potentially available to be recaptured more than once. Percent recaptured once or more than once are given.

Year	N	%R1	%R2+
1992			
P. palamedes	112	0.31	0.15
P. troilus	48	0.33	0.13
1993			
P. palamedes	267	0.43	0.19
P. troilus	111	0.36	0.12
1994			
P. palamedes	118	0.38	0.14
P. troilus	48	0.44	0.10
1995			
P. palamedes	202	0.33	0.13
P. troilus	124	0.30	0.10
1996			
P. palamedes	22	0.18	0.13
P. troilus	14	0.11	0.00
1997 Spring			
P. palamedes	90	0.23	0.04
P. troilus	100	0.39	0.12
1997 Fall			
P. palamedes	31	0.03	0.00
P. troilus	24	0.21	0.00
1998 Spring			
P. palamedes	72	0.17	0.01
P. troilus	34	0.03	0.00

This possibility led us to conduct a Fall sample (21-28 Oct 1997), where we observed that the *P. glaucus* is as large as the Spring brood. This seems not to be the case for *P. troilus* and *P. palamedes* (Table 6), where the late Fall populations seemed low for these 2 species. It is possible that these Lauraceae-feeders were between broods, perhaps with an early November peak in emergences and a long slow development of larvae on redbay during November-January/February, or else a 2 month pupal diapause until the March peak (Table 4). Florida populations (27-29° N latitude) of both *Papilio troilus* and *P. glaucus* appear to have a critical threshold for pupal diapause induction at around 11.5-12h of photophase which is reached in the fall in late September (Tidwell, 1995). The induction of diapause for Michigan populations of *P. troilus* is around 15-15.5h and *P. glaucus* is between 16-18h of photophase (Valella *et al.*, 1998). By mid-March the photophase increases from a winter low of about 10h, to reach 12h in mid-March. We have observed short-day lab-reared *P. troilus* pupae from Ohio that were held in diapause for several months inside a growth-chamber set for a simulated winter of 2-4°C with total darkness, emerged as adults at all temperatures (18, 22, and 26°) under the 18:6 photoperiod, as well as 12:12 at any temperature (Deering *et al.*, 1998). Photoperiod seems less important than temperature for breaking diapause in the spring.

In 1997, 43% of the 264 potential males marked were recaptured at least once in the State Park in the spring flight, and 26% of those 183 potential males in the fall flight of late October were recaptured at least once. Recaptures of marked females were almost as high (Table 2) with 32% of 97 and 22% of 155 recaptured at least once. Such high recapture rates are not unexpected in well-defined habitats such as this woodland island preserve in central Florida. In contrast, only 2 male *P. canadensis* were recaptured of more than 400 marked in the contiguous boreal forest during the 2 weeks in June 1993 at Thumb Lake, in Charlevoix County, northern Michigan, one of which was recaptured 12 days later at the same spot (Scriber, unpubl.).

In the spring generation at Highlands Hammock, *Papilio palamedes* was about twice as abundant as *P. troilus* for 1992, 1993, and 1994. This is consistent with the lower survival and first instar growth rate of *P. troilus* on redbay (Nitao *et al.*, 1991; Lederhouse *et al.*, 1992). The smaller neonate larvae *P. troilus* have difficulty in initiating feeding on tough redbay leaves. Although many other factors could produce the measured difference in population levels, many life history aspects of these closely related swallowtails are similar. Predators and parasitoids appear to be generalized enough to attack any *Papilio* caterpillar. Our data on field survival indicate little difference between the two species. The 5 day survival for paired *troilus* and *palamedes* neonate was 31% and 38%, respectively on red bay trees. Of more than 100 starting eggs or young larvae found naturally on red bay from 19 March to 4 April 1996, 25 survived to 13 April and appeared to be equally *P. troilus* and *P. palamedes*.

One difference between *P. palamedes* and *P. troilus* is how their caterpillars spend their inactive periods. Although *P. palamedes* caterpillars frequently rest on a silk pad on a host leaf in typical tree-feeding swallowtail fashion (Brower, 1958), *P. troilus* caterpillars usually rest inside a rolled leaf (Lederhouse, 1990). Whatever additional protection this affords *P. troilus*, it would only decrease the population differential between the two species.

While various causes of larval mortality for all 3 species have been observed during field studies over the years (Feeny *et al.*, 1985; Lederhouse, 1990; Takagi *et al.*, 1995), little has been documented regarding the natural enemy losses of adults, despite the prevalent assumptions about bird predation and benefits of mimicry (Brower, 1958; J. V. Z. Brower, 1958; Brower and Brower, 1962; Burns, 1966, Pliske, 1972, 1973; Lederhouse and Scriber, 1987; Codella and Lederhouse, 1990; Uesugi, 1996). We have observed mantids, var-

Table 5. *Papilio palamedes* and *P. troilus* male population estimates (P) for Highlands Hammock State Park, FL. Dates are for March and April. Estimated standard error (SE) is given (Jolly-Seber, for 1992-1995[1]).

		P. palamedes		*P. troilus*	
Date		**P**	**SE**	**P**	**SE**
1992					
	27	92	52	56	41
	1	122	48	51	32
	4	99	40	16	4
	5	69	25	60	36
	7	99	76	36	19
1993					
	23	159	67	54	31
	27	258	96	89	50
	29	277	54	149	67
	7	192	47	105	38
	9	167	53	98	64
1994					
	28	105	86	30	28
	31	143	72	77	62
	2	66	18	27	11
	4	51	15	13	5
	8	50	21	8	4
1995					
	28	93	44	84	48
	2	173	72	245	192
	4	212	104	220	157
	8	357	185	85	47
	14	143	55	43	18

[1]1996 and 1997 are listed separately (see Table 7).

Table 6. *Papilio troilus* and *P. palamedes* population estimates for Highlands Hammock State Park (Sebring, FL) for Spring and Fall 1997 (Lincoln index; Poole, 1974; Southwood, 1978).

	P. troilus		*P. palamedes*	
	Males	**Females**	**Males**	**Females**
SPRING:[1]				
Mar 25	230	-	193	15
26	113	12	184	19
27	192	21	143	25
28	142	11	177	34
29	183	17	-	-
30	209	12	208	21
31	221	12	245	19
Apr 5	310	13	224	-
6	130	84	200	40
9	149	-	567	-
FALL:				
Oct 22	13	-	-	-
23	77	-	-	-
25	-	-	-	40
26	-	-	75	-
27	-	-	-	-
28	24	14	-	-

A dash (-) indicates no recaptures for that date.

[1]Spring samples in 1996 were very low due to exeptionally cold weather; daily population estimates of *P. troilus* ranged from 6 to 103 while *P. palamedes* ranged from 15 to 27 during the period 25 March to 7 April 1996.

ious spiders, and anoles to eat *P. glaucus* adults. We have also observed *P. troilus* and *P. palamedes* adults eaten by spiders.

Mantid predation

While making field collections of *Papilio glaucus* south of Lake Placid, in Highlands County, Florida (4 Aug 1983), predation was observed of a large (forewing length 66mm) yellow morph female of *Papilio glaucus* by a last instar nymph of a mantid (presumably *Mantis religiosa* Linnaeus, Mantidae) on a bloodroot flower head (*Lachnanthes* spp., Haemodoraceae). This species of plant was found flowering along the edges of muck farms and was used frequently by male and female butterflies during this August (2nd-4th) collecting period. The green mantid, was extremely cryptic and was difficult to visually discern even as the butterfly was being dismantled and consumed. It is interesting that such a large butterfly could have been captured at all, as the butterfly was approximately twice the dry weight of the mantid. This capture may be partially explained by the fact that the morning temperatures had apparently only just reached those which allow butterfly flight. The first adult tiger swallowtail observed in flight was moving very slowly, barely gliding, at 0940h. The mantid with partially consumed prey was discovered at 0945h. Differential predation of mimetic and non-mimetic butterflies by birds at these times of low activity has been suggested by Rawlins and Lederhouse (1978) as a major source of roost mortality in *Papilio*.

Since this morning observation indicates that mantid predation of tiger swallowtail adults does occur it would be interesting to determine whether such instances of predation also occur throughout the warmer portions of the day. It would also be interesting to assess whether differential selection of the female butterfly color morphs exist for mantids. The presumed model, *Battus philenor* (Linnaeus), is basically absent from this area of Florida (Brower and Brower, 1962). While bird migration carries "learned avoidance" behavior into areas where the model species may not exist (Waldbauer and Sternberg, pers. comm.), it seems less likely that mantid dispersal (although variable in different species; Bartley, 1982) with mimetic-avoidance behavior could account for the increasing proportion of dark morph females in this Florida (Highlands Co.) *P. glaucus* population over the last 30 years (Table 4). Nonetheless, the frequency and significance of differential yellow/dark morph predation by mantids throughout the areas with high populations of the presumed model species deserves consideration, and additional study.

Mantid habits are diverse and have been the subject of several ecological studies designed to assess food limitation in natural populations (Mook and Davies, 1966; Eisenberg *et al*., 1981), and coexistence via preference for feeding sites in vegetation (Rathet and Hurd, 1983). Mantids have been shown to be effective in prey capture over a relatively narrow range of prey sizes (Holling, 1964) with larger insects sometimes evoking a "startle" response rather than attack (Kramer, 1960). Prey recognition is of ecological, as well as, behavioral significance (Rilling *et al*., 1959). In addition, it has been shown that mantids can be trained with the use of electric shock to avoid certain insect prey (Gelperin, 1968). Moreover, Berenbaum and Miliczky (1984) have demonstrated that individuals of the mantid, *Tenodera ardifolia sinensis* show evidence of poisoning when fed milkweed bugs, *Oncopeltis fasciatus* (Miridae) raised on seeds of milkweed, *Ascelpias syriaca* (Asclepiadaceae). After several encounters these mantids refuse milkweed bugs altogether. This phenomenon suggests that invertebrate predators may possess significant powers of discrimination and could represent a major selective force in mimicry associations, which to date has generally attributed exclusively to vertebrate predators (Berenbaum and Miliczky, 1984).

Lizard Predation

As with the mantid-induced vulnerability of *Papilio* nectaring during cool morning temperatures, so too lizards were observed to be very active adult butterfly predators early in the day at the Highlands Hammock State Park. As part of another study, interspecific pairs of virgin, size-matched females of *P. glaucus* and *P. canadensis* were tethered on a fine thread with about 1-2 feet of mobility while anchored to the bush branch or twig by small metal alligator clips. During these studies, 4 different anoles (*Anolis carolinensis*) simultaneously stalked the 4 different tethered females as they gently settled on a resting spot. One anole attacked and killed one individual by trying to drag it off down the branch. The predator pressure was pervasive and intense enough at these locations that the original mate-preference study had to be postponed and moved.

Elsewhere, lizards have been shown to be major causes of mortality for butterflies (e.g., iguanid lizards, *Propidurus torquatas* in Brazil, Ehrlich and Ehrlich, 1982; anoles, *Anolis* (Reptilia) in Texas, Odendaal *et al.*, 1987).

Spider predation

The large size and strong flight abilities of *Papilio glaucus* and *P. troilus* and *P. palamedes* was not sufficient to avoid being caught in spider webs or caught by spiders at flowers. We observed several live butterflies caught in webs of the garden spider, *Argiope* spp. (Argiopidae), as well as *Nephila clavipes*, and a round orb-weaver spider in a web. In addition we observed a salticid crab spider (Salticidae) at a deer-tongue flower (*Carphephorus odoratissimus* (J. F. Gmel), Compositae), eating a *P. palamedes*. In two cases we observed both a dark morph and a yellow morph *P. glaucus* caught in single webs. After wrapping the butterfly, the spiders generally ate the head and thorax dropped the wings with the shell of a thorax to the ground. Five males or yellow morph females, two dark morph females of *P. glaucus*, and two *P. troilus* were found under one individual *Argiope* (Fig. 2). One large *Argiope* in an orange tree captured one of our specimens marked the day before on October 23rd (red male #72). It was gone and a new marked individual was observed in the web the next day October 25th. This was gone and a third *P. glaucus* was caught in the web on October 27, 1997 (red #188, male).

A different *Argiope*, in a stand of frostweeds or tickweed flowers (*Verbesina virginia* L., Compositae) (see photos), was observed to have a live male *P. glaucus* (red #96) on 24 October. The corpse was cut out and on the ground the next day, where one other dark and two yellow corpses were observed. A single *P. palamedes* was found 24 October in an *Argiope* web on tickweed off south canal road of the Park, and several additional webs contained one or more wrapped corpses.

In summary, spider predation of large insects such as adult *Papilio* may have been historically underestimated as a major mortality factor (Uetz, 1992). These deaths of marked individuals reflect rapid prey turnover and rather formidable appetites of individual spiders. The large webs and special silk-protein capture potential are required for such large prey (Craig, 1992).

Maximum lifespan

Nectar is a key resource for these adult butterflies. Thistles (*Cirsium* spp., Compositae), pickerel-weed (*Pontedera cordata* L., Pontedariaceae), lyreleaf sage (*Salvia lyrata* L., Labiatae), and sweet spires (*Itea* spp., Iteaceae), were the primary nectar sources in the spring. A roadside purple deer-tongue (*Carphephorus odoratissimus*), small white flowers of tickweed (*Verbesina virginiana* L.), and thistles were the primary nectar sources in the Fall.

The length of adult lifespan of these 3 species is at least 4 weeks for some individuals. We don't know how long they actually live, however the physiological potential in the field is perhaps two months. In 1995, the longest interval between capture and last recapture of males was 28 days for *P. troilus*, 29 days for *P. palamedes*, and 32 days for *P. glaucus*. Based on wing wear (age class), the maximum lifespans may have even been 1-2 weeks longer but we did not stay in Florida long enough to observe this.

We conclude that populations of *Papilio* butterflies in small residual habitat "islands" are vulnerable to loss of either larval host plants or adult nectar plants. The recent decline in woodland hammock habitats and wetland nectar plants near Lake Placid (Parker Island, Hall Road, and Lake Istokpoga) in south central Florida is clearly a major reason for decline of the 3 *Papilio* species in that once rich contiguous refuge that apparently acted as a "metapopulation sinks" (Hanski and Gilpin, 1997). Stable populations of *Papilio* species at Highlands Hammock State Park have persisted during this 3 decade period.

While the adaptations of *P glaucus* to local hostplants are genetically based, and the evolution of preference for Florida sweet bay seems to be relatively recent for the species (Bossart and Scriber, 1995b), the scale of ecological hostplant and habitat adaptation is not likely to be localized as in sedentary deme-forming populations (Mopper *et al.*, 1995; Singer and Thomas, 1996). Nonetheless, the loss of small islands or island-like patches of hammock with either nectar or hostplant, has likely resulted in local extinctions, and metapopulation-like movement of individuals spreading genes across patches of different size and type (Bossart and Scriber, 1995b; Hanski and Gilpin, 1997). If with some conservation efforts, these isolated bayheads are able to partially recover and regain some lost nectar plants or expand residual host trees, they could provide a "pseudo-sink" equivalent of a small, but stable, seed population of butterflies or invite natural recolonization from larger source populations (New *et al.*, 1995; Thomas *et al.*, 1996). Human disturbances leaving small residual populations do not necessarily result in unstable populations or extinction (Singer *et al.*, 1996; Thomas *et al.*, 1996). South central Florida, with only a single host plant species for *P. glaucus* (sweet bay) still continues to exhibit a continuing metapopulation-like stability for this and other butterfly species across diverse habitats and habitat islands.

ACKNOWLEDGMENTS

Thanks go to all of our lab crew members that traveled to Florida to help with Spring research on *Papilio*: Matt Ayres, Dave Biddinger, Janice Bossart, Reneé Brenner, Molly Brown, Tara Darcy, Jessica Deering, Jason Edwards, Chip Francke, Cheryl Frankfater, Bruce Giebink, Piera Giroux, Goeffry Hoffa, Kelly Johnson, Lisa Long, James Nitao, Ahyna Redman, Doozie Snider, Aram Stump, Patti Valella, Donna Wehling and Madison Wehling.

Partial research support was provided by the Michigan Agricultural Experiment Station (Project MICL01644) and NSF Ecology Program (DEB#9220122). We also thank the Highlands Hammock Park Administration and Rangers and the Florida Department of Environmental Protection as well as the Archbold Biological Station near Lake Placid (in particular Mark Deyrup) for their assistance throughout our studies.

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