VOLTINISM AND DIURNAL EMERGENCE-FLIGHT PATTERNS OF *IPS CALLIGRAPHUS* (COLEOPTERA: SCOLYTIDAE) IN FLORIDA

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ABSTRACT

Field studies revealed that *Ips calligraphus* (Germar) may complete up to nine generations during a 1-year period in north-central peninsular Florida. Brood development took place in felled trees of slash pine, *Pinus elliottii* Engelmann var. *elliottii*, with thick phloem (2.5-3.5 mm; i.e., >adult pronotal width). Generational times ranged from 27 days in the summer to 81 days in the winter. Generally, female brood adults emerged earlier than did males of the same cohort; the male:female ratio was ca. 1:1.2. Adult emergence-flights occurred as a single peak during late afternoon in spring (mostly from 1500-1700 h EST) and fall (1400-1700 h), compared to near midday in winter (1200-1400 h), emergence-flights were bimodal during summer with activity peaking in early morning (0700-0900 h) and early evening (1700-1900 h). An average of 457°D (day-degrees) above a 10°C (822°D above 50°F) threshold were accumulated per generation using the mean-minus-threshold method of day-degree estimation. Based on weather records for Florida, the theoretical number of generations per year in slash pine trees with thick phloem was estimated to vary from as few as 7 near Pensacola to as many as 12 in the Florida Keys.

RESUMEN

Ensayos de campo revelaron que *Ips calligraphus* pudiera completar hasta nueve generaciones durante un período de un año en el centro-norte de la península de la Florida. El desarrollo de la cría se llevó a cabo en árboles caidos del pino *Pinus elliottii* Engelmann var. *ellittii*, con la parte exterior de la corteza interior que contiene los tubos llamados "de tamiz" muy gruesos (2.5-3.5 mm; ej., > anchura pro-nodal del adulto). El tiempo de una generación varió de 27 días en el verano a 81 días en el invierno. Generalmente, los adultos de la cría de hembras salieron antes que los machos del mismo cohorte; la proporción de macho:hembra fue de approx. 1:1.2. En la primavera, el apogeo de los vuelos de salida de los adultos fue sencillo y bien en la tarde (mayormente de 1500 a 1700 hrs. Hora Normal del Este), y en el otoño (1400 a 1700 hrs), comparados con cerca del medio-día en el invierno (1200 a 1400 hrs.); los vuelos de salida fueron bi-modales durante el verano, con el auge de las actividades en la mañana (0700 a 0900 hrs.) y temprano en la tarde (1700 a 1900 hrs.) Un promedio de 457°D (grados-día) sobre un umbral de 10°C (822°D sobre 50°F) fue acumulado por generación, estimando el grado-día usando el método de promedio-menos-umbral. Basado sobre el record del tiempo de la Florida, el número teorético de generaciones por año en pinos con corteza grueza, se estimó que varía de 7 cerca de Pensacola, a 12 en los Cayos de la Florida.

Slash pine, *Pinus eliottii* Engelmann var. *elliottii*, is the principal commercial forest tree species in Florida, with nearly 2 million ha of plantations under intensive management. Tree mortality due to all factors results in a loss of about 3.6 m^3/ha per 20-year

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rotation. The three southeastern *Ips* species and the black turpentine beetle, *Dendroctonus terebrans* (Olivier), are associated with much of this loss (Chellman 1980). The sixspined ips, *Ips calligraphus* (Germar), often is the most aggressive and destructive of the bark beetle species infesting the phloem (inner bark) of slash pine (Fatzinger et al. 1983).

The number of generations per year completed by *I. calligraphus* varies from four in the mountains of California (Wood and Stark 1968), to a minimum of six in the southeastern USA (Thatcher 1960), to as many as 12 in parts of Mexico (Ascencio 1979). Such a variation can be explained in terms of latitudinal and elevational temperature differences among these areas. However, within a given forest stand, average phloem thickness could influence voltinism patterns of *I. calligraphus* by affecting its developmental rate, which is faster in thick phloem (Haack et al. 1985).

Vité et al. (1964) distinguished among emergence-flight (from logs), dispersal-flight (caught in rotary nets), and response-flight (to baited traps). A bimodal pattern of response-flight was observed during July for *I. calligraphus* in Florida, with peaks of activity at 0600-0900 and 1600-2000 h (Wilkinson 1964). However, no consistent flight pattern was observed in Texas during July (Vité et al. 1964).

The objectives of this investigation were to (1) determine the number of generations that *I. calligraphus* completed per year under optimal conditions (i.e., in thick-phloem slash pines) in north-central peninsular Florida, (2) record the diurnal pattern of emergence-flight throughout the year, and (3) analyze the above findings in relation to available weather data for Gainesville (lat. 29.4°N, long. 82.2°W), Alachua County, Florida.

Materials and Methods

Because *I. calligraphus* is active throughout the year in north Florida (R. C. Wilkinson, Department of Entomology & Nematology, University of Florida, Gainesville, Florida 32611, personal communication) it was considered acceptable to begin the study during any season of the year. Additionally, because this species has overlapping generations the following methods were necessary to monitor discrete generations.

Tree Selection and Infestaton

Apparently healthy, dominant and co-dominant, 21- to 22-year-old slash pine trees were used from a plantation (site index of 17.6 m at 25 years) near Orange Heights, Alachua County, Florida. All selected trees (see "Generation synchronization" for details) were growing within ca. 100 m of one another and had 2.5-3.5 mm thick phloem along the trunk. Such phloem was considered "thick" relative to the average pronotal width of *I. calligraphus* adults (1.7-1.8 mm) in Florida populations (Haack 1984). Thick phloem provides an optimal environment for *I. calligraphus* as evidenced by increasing adult reproductive and larval developmental rates with increasing phloem thickness (Haack et al. 1984a, 1984b, 1985).

Each tree was felled and then supported off the ground and left to undergo natural infestation by *I. calligraphus* and associate invertebrates. Felled trees were located such that they received partial shade for much of the day and thus subcortical temperatures on the upper exposed surfaces probably were not greatly elevated above ambient conditions (Graham 1925). The trees were inspected every 2-5 days for evidence of bark beetle attack by noting pitch tubes and extruded boring material. Bark was removed from a few attack sites to determine gallery development and beetle life stages. When most individuals were in the pupal stage, 50- to 90-cm long sections of trunk were cut, transported (ca. 20 km) to an open-air insectary in Gainesville and put into screened emergence cages (ca. 1 m on a side). The cages were located such that they received little direct solar radiation.

Collection of Brood Adults

Ips calligraphus adults readily flew from the logs to the screen walls throughout the day and were collected several times daily. The number of adults collected from the screen walls was considered to be an appropriate index of their natural, diurnal emergence-flight activity. Collections were usually made at 2-h intervals from early morning [0700-0900 h, Eastern Standard Time (EST)] until dusk (1700-2000 h); flight activity of pine-infesting bark beetles generally ceases between sunset and sunrise (Fares et al. 1980). Adults were put into labelled containers frozen, and later sexed according to the form of the third elytral tooth (Hopping 1963).

Generation Synchronization

The date that corresponded to mean brood emergence for a particular generation (at the Gainesville insectary) was considered the starting date for the subsequent generation (at the Orange Heights plantation). Because the exact date on which mean brood emergence would occur for a given cohort could not be predicted, several trees were felled to bracket this probable time. This was done for each generation by felling 2-6 uninfested slash pines throughout the period of brood emergence at 3-7 day intervals. These newly felled trees were inspected regularly for signs of beetle attack. The tree selected as the "brood tree" for the following generation was the one most fully colonized closest to the date of mean brood emergence of the then-current generation. Apparently, there was a difference of 2 days or less between mean brood emergence for a given generation and the estimated date of full colonization along the trunk of the tree selected for the subsequent generation.

The above procedures were begun in March 1982 and continued through May 1983. The initial generation was used primarily to develop techniques and to generate the first date of 50% emergence (28 April 1982); the study was terminated after 386 days on 19 May 1983.

Data Analyses

For each generation, the daily counts of emerged brood adults were used to calculate the average emergence times for the sexes separately and combined. Mean emergence times were compared between sexes and among generations using the t-test and Duncan's multiple-range test. Most analyses were performed using the general linear models procedures of the Statistical Analysis System, version 1982.3 (SAS Institute 1979); significance was tested at the $P<0.05$ level. Generational time was calculated as the number of days between dates of mean brood emergence for two consecutive generations. The proportion of males in each generation was compared to 0.5 for departures from a 1:1 sex ratio using a two-tailed z-test (Freund 1960). Similarly, the mean proportion of males for all generations was compared to 0.5 using the t-test (Freund 1960).

To determine if broad seasonal shifts occurred in the diurnal pattern of emergence-flight the data from the various collection times were pooled into three daily collection periods: 0700-1000, 1100-1400, and 1500-2000 h EST. Means were compared among generations and collection periods using Duncan's multiple-range test; analyses were based on data from those days on which at least five males or females were collected and when collections were made at ca. 2-h intervals throughout the day. This lower limit was chosen in order to have confidence in the emergence-flight pattern for days when few beetles emerged.

The day-degree (°D) accumulation for each generation was summed over all days within a generational time as defined above. The mean-minus-threshold method of day-degree estimation (Pruess 1983) using 10°C as the threshold temperature was used because it gave the lowest coefficients of variation (Arnold 1959) for the methods and temperatures tested (Haack 1984). Daily maximim, minimum, and 70-year average air temperatures were obtained from the Official Weather Data for Gainesville 3 WSW, Florida (Department of Agronomy, University of Florida, Gainesville, in cooperation with NOAA).

Results and Discussion

Voltinism, Adult Emergence and Day-Degree Summation

Ips calligraphus completed nine generations during a 371-d period (28 April 1982-4 May 1983) in north-central peninsular Florida (Fig. 1; Table 1). The period from first to last brood emergence for a single generation (G) ranged from 68 days during winter (G1) to 11 days in late summer (G7). Similarly, generational times were long (81 days) during the cooler months (G1,2), and short (27-28 days) during the warm summer months (G4-7).

A total of 4112°D above 10°C (7399°D above 50°F) was accumulated during the 371-d period. The average heat unit requirement per generation was 457°D above 10°C and ranged form 340 to 569°D (Table 1).

Because the day-degree accumulation during the course of this study was similar to that predicted by Gainesville's 70-yr mean annual temperature of 21.2°C [i.e., 4122 (actual) vs 4155°D (predicted)], the completion of nine generations in ca. 1 yr by *I. calligraphus* may be representative of the Gainesville area. However, this value is probably the maximal number of generations attainable near Gainesville under average conditions because optimal conditions for *I. calligraphus* colonization, reproduction, and development were provided throughout the study; i.e., felled trees with thick phloem were perpetually made available.

One would expect that the day-degree accumulation required for physiological development of a generation would remain about the same since developmental time would vary with temperature. In the present study, the day-degree figures for seven of the nine generations were remarkably close. However, the relatively large day-degree accumulation for G2 (569°D) may reflect the slow rate at which host colonization occurred during the winter months (ca. 5 wk) and possible protracted development as a result of freezing temperatures and host-tissue desiccation. A likely explanation for the relatively small day-degree accumulation for G9 (340°D) is that *I. calligraphus* development in the tree selected for G9 was probably too advanced relative to the date of mean emergence time for G8.

The maximal number of generations per year that *I. calligraphus* could likely complete in various parts of Florida may be estimated using 457°D above 10°C as the average heat unit requirement per generation and the 40-year average temperature data for selected Florida cities (U.S. Department of Commerce 1964). Using these data, from as few as seven generations would occur annually at Niceville (near Pensacola) in northwestern Florida, to as many as 12 at Sugarloaf Key (near Key West) (Fig. 2). Such statewide variation may explain, in part, why *Ips* infestations tend to be larger in central and southern Florida compared with northern and panhandle Florida. However, it should be noted that this method (1) oversimplifies how temperature affects insect developmental rates and (2) assumes a linear relationship for developmental rate versus temperature and thus accumulates too few day-degrees during the cool times of the year and too many during the hot times.

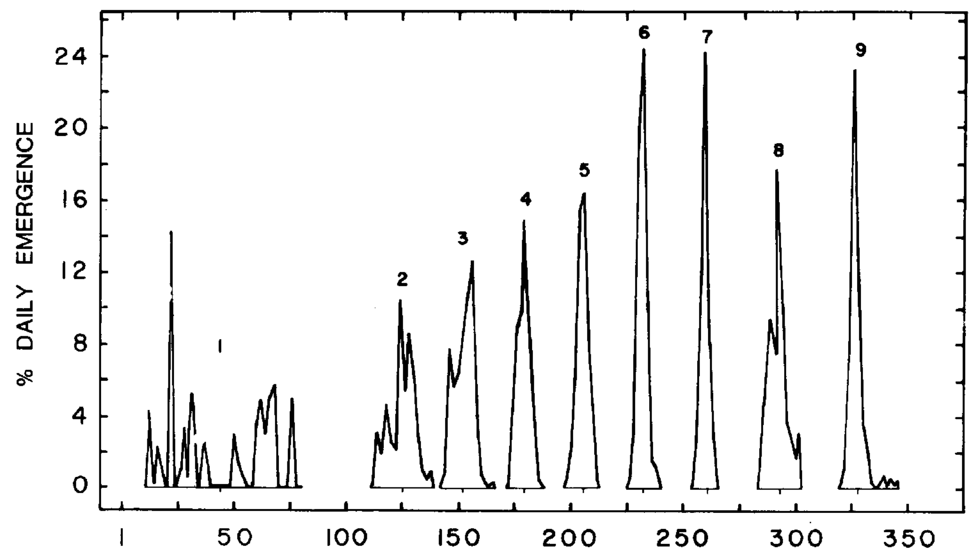

Fig. 1. Percent daily emergence by brood adult *Ips calligraphus* for each of the nine generations completed during a 1-year period near Gainesville, Florida (1982-83).

Given that only trees with relatively thick phloem were used and that larval development occurs faster in thicker phloem (Haack et al. 1985), fewer generations per year would be expected for slash pine stands consisting of mostly thin-phloem trees. If *I. calligraphus* developmental time for each generation were extended by 3-5 days (Haack et al. 1985) then 7-8 generations would probably occur annually in thin-phloem slash pines near Gainesville, Florida.

For each generation, females tended to emerge before males (Table 1). Differences between mean emergence times for females and males ranged from 8 days for the cohort that developed and emerged during the cooler months (G1), to 1-2 days for those that developed during the warmer months (G4-9).

The fact that *I. calligraphus* brood females emerge sooner (see also Dale 1967) and have smaller average body size (Dale 1967, Haack et al. 1985) than males of the same cohort suggests that females develop over a shorter period of time than males. Since *I. calligraphus* males initiate attack, earlier female emergence would probably reduce the number of matings among siblings. Similarly, the smaller size of *I. calligraphus* females would facilitate their entry into the male-constructed nuptial chambers and allow greater movement during mating and initial gallery construction (see Gouger et al. 1975). In other bark beetle species, the sex that initiates attack tends to emerge later (Cameron and Borden 1967, Billings and Gara 1975) and be larger in body size (Hedden and Billings 1977).

SEX RATIO

The sex ratio was approximately 1:1 for five generations (G2,3,5,6,8), but in the other four (G1,4,7,9) it was significantly female-biased (Table 1). The overall male proportion (0.45) was significantly different from 0.5 ($t=3.4$; $df=8$).

The sex ratio of *I. calligraphus* brood adults usually is 1:1 (Dale 1967; Cook et al. 1983). If developmental times were longer for males, they could suffer greater mortality rates due to parasitism, predation, and interspecific competition with cerambycids (Coulson et al. 1976). Additionally, lower male survival may be positively correlated

TABLE 1. VOLTINISM STUDY SUMMARY DATA OF *Ips calligraphus*, GAINESVILLE, FLORIDA (1982-83).

G[a]	Brood tree felling date	N[b]	Brood Emergence							G[d]		
			Dates			Total days	Mean time[c] ± SE (days)			Time	%♂[e]	°D
			First	Last	Mean		♂♂	♀♀	♂♂±♀♀			
1	17NOV82	427	11JAN	19MAR	12FEB	68	38±1.6a1	30±1.2a2	33±1.0a	81	40*	446
2	9JAN83	381	21APR	19MAY	4MAY	29	15±0.4b1	13±0.4b2	14±0.3b	81	45	569
3	23APR82	2170	22MAY	13JUN	31MAY	23	10±0.1c1	10±1c2	10±0.1c	33	48	446
4	22MAY82	1720	20JUN	6JUL	27JUN	17	9±0.1de1	7±0.1d2	8±0.1de	27	42*	446
5	23JUN82	750	17JUL	3AUG	24JUL	16	9±0.1de1	8±0.1d2	8±0.1d	27	47	471
6	21JUL82	591	14AUG	28AUG	20AUG	15	8±0.1e1	7±0.1d2	7±0.1e	27	49	464
7	18AUG82	551	11SEP	21SEP	17SEP	11	8±0.1e1	7±0.1d2	7±0.1e	28	41*	483
8	13SEP82	258	11OCT	28OCT	19OCT	18	10±0.3cd1	8±0.4d2	9±0.3d	32	52	447
9	14OCT82	520	16NOV	11DEC	23NOV	26	9±0.2de1	8±0.2d2	8±0.1de	35	39*	340

[a]G = Generation.
[b]N = Number of brood adults collected for each generation.
[c]Mean emergence times were based on all brood adults collected for a given generation, starting from the day of first emergence for that generation. Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).
[d]G time = Generational time; G time for generation 3 was calculated from 28 April 1982 (the date corresponding to mean adult emergence for the cohort that developed in the initial tree used in this study) to 31 May 1982.
[e]Proportions followed by an * are significantly different from 0.5 when tested as a proportion (z-test).

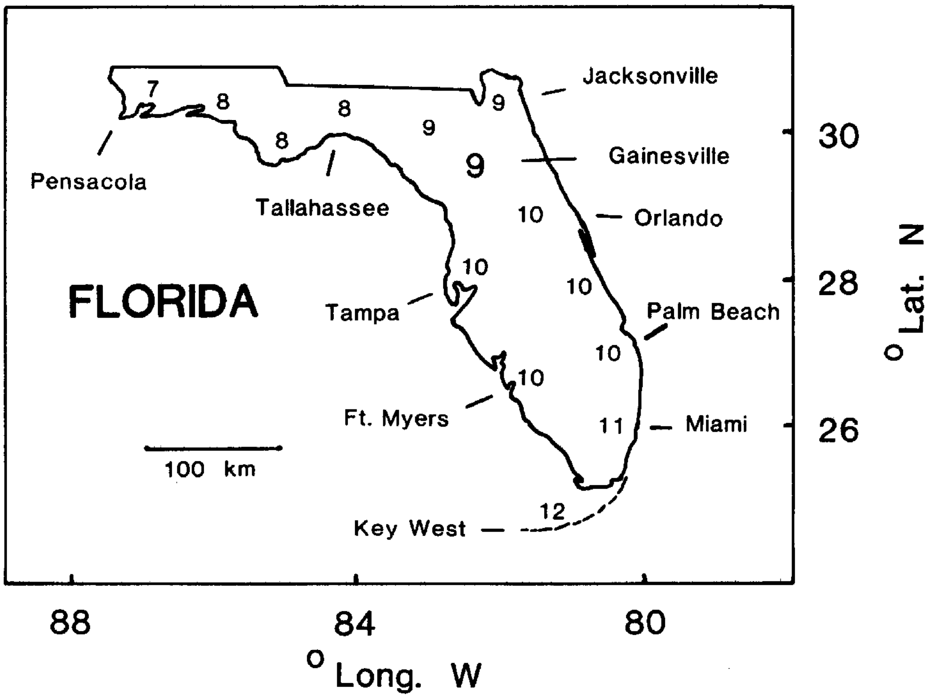

Fig. 2. Observed (Gainesville) and estimated number of generations per year completed by *Ips calligraphus* at selected locations in Florida. Based on 40-year mean temperatures (U.S. Department of Commerce 1964), and the assumption that the average day-degree requirement for completion of a single generation is 457°D above 10°C as given in the text.

with exposure time to cold (Safranyik 1976) and degree of host-drying (Amman and Cole 1983).

DIURNAL EMERGENCE-FLIGHT PATTERNS

The emergence-fight patterns of males and females were similar within each generation, therefore the data were pooled with respect to sex. Similarly, the emergence-flight pattern did not differ significantly among generations 4-7; therefore these data were pooled for the seasonal comparisons. Data from G3 and G9 were omitted from analyses because daily collection times were not consistent.

The diurnal pattern of emergence-flight shifted from season to season (Table 2). In the spring (G2), 64% of the adults were collected from late afternoon to mid-evening (peak activity was 1500-1700 h). As days became warmer during spring, beetles were collected progressively earlier during the day; in G2, beetles were collected first at 1000 h on 8 May and at 0800 h on 16 May. During the summer (G4-7), 51% of the adults were collected in the early evening (1700-1900 h), with an additional active period in the morning (0700-0900 h); no beetles were collected between 1100-1300 h on several cloudless days. Few adults were collected on windy days or during heavy summer rains. Adult activity began earlier in the afternoon on overcast than on sunny days. In the fall (G8), beetles were most active during late afternoon and early evening (1400-1700 h). During the winter (G1), 76% of the adults were recovered at midday (1200-1400 h). During the 68-day emergence period for G1, five or more beetles were collected on 24

TABLE 2. SEASONAL EMERGENCE-FLIGHT OF *Ips calligraphus* BROOD ADULTS DURING THREE DAILY PERIODS, GAINESVILLE, FLORIDA (1982-83).

Season	G[a]	N[b]	Mean percent ± SE (range)		
			0700-1000 h	1100-1400 h	1500-2000 h
Winter	1	14, 277	2 ± 2 c3[c] (0-22)	76 ± 5 a1 (43-100)	22 ± 5 c2 (0-57)
Spring	2	15, 321	6 ± 3 bc3 (0-36)	30 ± 5 bc2 (0-83)	64 ± 5 a1 (17-87)
Summer	4-7	26, 2819	36 ± 1 a2 (14-62)	14 ± 2 c3 (0-47)	51 ±3 b1 (14-80)
Fall	8	7, 145	14 ± 6 b2 (0-44)	36 ± 5 b1 (19-59)	50 ± 3 b1 (38-58)

[a]G = Generation.
[b]Number of days (left) on which both five males or females were collected and the collections were made at 2-hr intervals throughout the daylight hours, and total number (right) of adults collected on those days.
[c]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

of the days when temperatures exceeded 20°C, whereas no adults were collected on the 25 days when daily high temperatures were 17°C or less; these fluctuations in daily high temperatures are responsible in large part for the sporadic pattern of G1 emergence observed in Fig. 1.

The bimodal emergence-flight pattern of adult *I. calligraphus* noted during the summer is similar to response-flights reported by Wilkinson (1964). The major peak of late-afternoon activity for *I. calligraphus* during spring and fall, and the midday peak during winter, are reported here for the first time.

In Texas, *I. calligraphus* flew little when temperatures exceeded 30°C (Vité et al. 1964). In Florida, summer temperatures at midday usually exceed 30°C, which may explain, in part, the midday decline in adult activity. Chapman (1967) explains bimodal flight on warm sunny days in terms of "odour meteorology," i.e., in early morning and late afternoon the air is relatively stable and thus pheromone plumes can form and extend horizontally, whereas air at midday moves upward in strong convective currents. Similarly, because convective currents are reduced on overcast days, pheromone concentration can increase in the beetles' flight zone within the forest canopy (Fares et al. 1980), and thus lead to earlier beetle flight (relative to cloudless days) as noted in this study and that of Vité et al. (1964). Apparently, bark beetles have evolved to avoid flight when it is unlikely that successful orientation to pheromones could occur.

In the winter, however, adult activity appears to be more temperture-dependent, with the midday peak of *I. calligraphus* activity corresponding to the warmest part of the day. Vité et al. (1964) did not observe dispersal-flight of *I. calligraphus* when temperatures were below 20°C in Texas.

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TEMPERATURE INDUCED SEASONAL MELANISM IN THE WINGS OF *COPAEODES MINIMA* (LEPIDOPTERA: HESPERIIDAE)

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ABSTRACT

The effects of photoperiod and temperature on wing coloration in the skipper *Copaeodes minima* (Hesperiidae) was studied in the laboratory. Individuals reared in incubators at 20°C had a higher proportion of darkened scales along a transect on the dorsal surface of the secondary wings than individuals reared at 30°C. Photoperiod (10h vs. 16h light) did not affect patterns of scale coloration.

RESUMEN

Los efectos de temperatura y de fotoperíodo en la coloración de alas de la mariposa *Copaeodes minima* (Hesperiidae) fueron estudiados bajo condiciones de laboratorio. Los individuos criados en incubadoras a 20°C, mostraron una mayor proporción de escamas ennegrecidas a lo largo de un transecto en la superficie dorsal de las alas secundarias, que los individuos criados a 30°C. El fotoperíodo (10h vs. 16h de luz) no modificó los patrones de coloracion de las escamas.

Lepidopteran seasonal melanism is the occurrence of light-colored adults during the summer and of darker adults during cooler times of the year. It arises in response to variations in environmental conditions during larval and pupal development. For a review of seasonal melanism and other polyphenisms see Shapiro (1976).