

GENERAL NOTES

NOTES ON THE NATURAL HISTORY OF *PAPILIO POLYXENES* *STABILIS* (PAPILIONIDAE) IN COSTA RICA

The black swallowtail butterfly *Papilio polyxenes* Fabr. occurs from southern Canada and the United States east of the Rocky Mountains through Mexico and Central America and into northern South America. Although the natural history of temperate populations has been well documented (e.g. Scudder 1889, *The Butterflies of the Eastern United States and Canada with Special Reference to New England*. Cambridge, Mass.; Clark, 1932, *The Butterflies of the District of Columbia and Vicinity*. U.S. Natl. Mus., Bull. 157; Rawlins & Lederhouse, 1978, *J. Lepid. Soc.* 32: 145-159), next to nothing is known about the species within its tropical range. As part of a comparative evolutionary study of temperate and tropical populations of the black swallowtail (Blau, 1978, *A comparative study of the ecology, life histories, and resource utilization of temperate and tropical populations of the black swallowtail butterfly, Papilio polyxenes* Fabr. Ph.D. diss., Cornell University; Blau, 1980, *Ecology*: in press), I spent ten months during 1976 near Turrialba, Costa Rica conducting experiments on the ecology of local populations. During these experiments, I noted many aspects of the natural history of the species, and those observations are summarized here.

The town of Turrialba is located on the Atlantic slope of the Cordillera Central of Costa Rica where the subspecies *P. polyxenes stabilis* Rothschild and Jordan is found. I studied localized colonies on the grounds of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), at about 600 m above sea level. Most of the land in this region is either cultivated for coffee and sugarcane or is used for pasture. The mean monthly temperature is nearly constant throughout the year at 22°C. The daily extremes average 5°C above and below the mean. The annual rainfall is approximately 2.6 m, with a dry season from January through April. (Meteorological data are from the weather station at CATIE.)

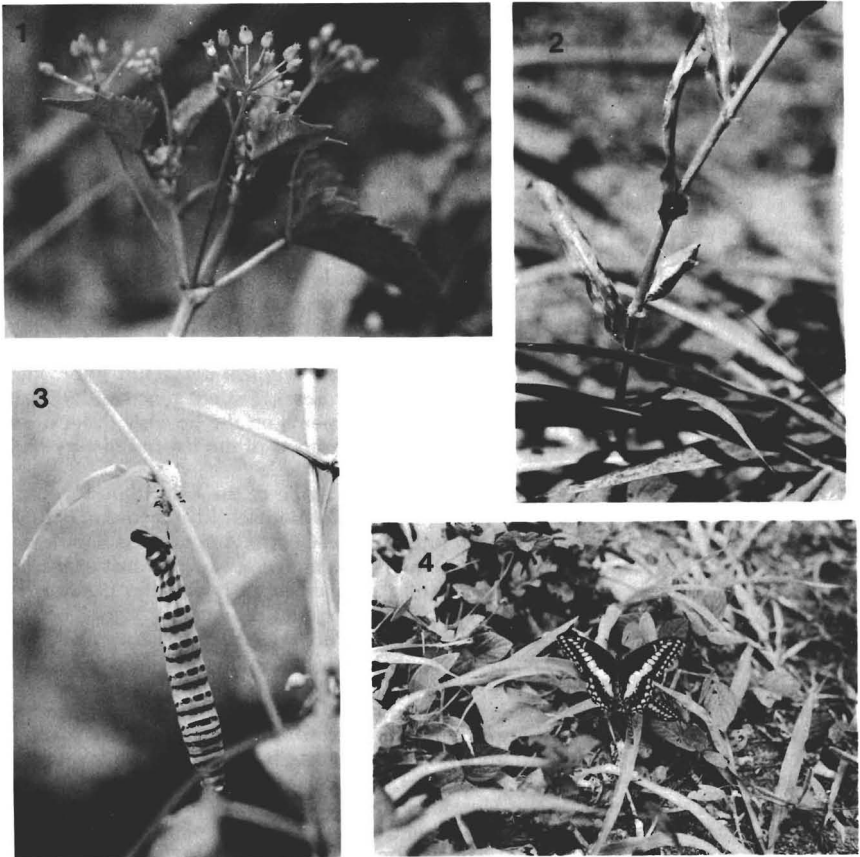
The black swallowtail probably occurs throughout Costa Rica wherever appropriate host plants are available. It has never been reported from the lowlands, but has been found at higher elevations up to about 1500 m. It has been sighted as far north as Monteverde (P. DeVries, D. Janzen, pers. comm.), as far south as San Vito (pers. obs.), and at many locations both on the Meseta Central and near Turrialba.

Approximately 22 species of Umbelliferae (the principal host plant family) occur in Costa Rica (Standley, 1938, *Flora of Costa Rica*. Field Mus. Nat. Hist., Chicago, Botanical Series, Publication 420; R. Rodriguez, pers. comm.), and perhaps 6 are potential hosts. Only 2 are known with certainty—*Apium leptophyllum* (Pers.) F. Muell (pers. obs.), and *Spananthe paniculata* Jacq. (obs. by D. Janzen, L. Gilbert; confirmed by P. Feeny). Both grow on the Meseta Central and are eaten by *P. polyxenes*, but the latter is the only common host plant in the Turrialba region. It is a broad-leaved forb which grows throughout the year from about 500-1500 m elevation. Occurring in moderate to severely disturbed sites, it is frequently a weed in sugarcane, coffee, and recently abandoned fields.

Favorable habitat for *P. polyxenes* is defined by the presence of the host plant. Because *S. paniculata* occurs early in succession, it is locally transient and grows in patches that vary greatly in size, condition and proximity to one another. The seeds germinate two weeks after a disturbance. About six weeks later, when the first small flowers are produced, the first ovipositions by *P. polyxenes* occur. The plants grow rapidly, flourish, and begin to senesce five or six months after germination.

The eggs of *P. polyxenes* are spherical, about 1 mm in diameter. They are laid singly on the flower or seed umbels (Fig. 1) and occasionally on the undersides of leaf edges of *S. paniculata*. They pass through a series of color changes—first all yellow, then yellow with a brown ring, turning completely brown, and then black—before hatching in 5-6 days.

The larvae are similar in appearance to those described from North America, with the exception that the dorsolateral rows of spots tend to be orange rather than lemon-



FIGS. 1-4. 1, *P. polyxenes* egg (arrow) on a developing seed of *S. paniculata*; 2, green pupa of *P. polyxenes* on a blade of grass; 3, fifth instar larva being attacked by an adult pentatomid bug; 4, naturally mating pair of adults, female with wings spread.

colored (cf. Scudder, loc. cit.). During the first instar, larvae feed predominantly on flowers and young seeds. Later they feed on leaves as well, and by the end of the fifth (final) larval instar, they have grown to a length of 35-40 mm. Larval development is usually completed on a single plant, over 15-20 days. The larvae become quiescent for a short period before voiding the gut contents. They then wander in search of an appropriate pupation site which is usually within 2 m of the host plant (mean = 1.5 m, N = 5). After one-half to over two hours, a larva chooses a spot 10-50 cm (mean = 25 cm, N = 17) above the ground on a stem or other nearly vertical surface, and spins a silken pad to support the pupa. About a day later the final molt occurs, producing a pupa that may be green or brown depending on the characteristics of the substrate (Fig. 2) (West et al., 1972, J. N.Y. Entomol. Soc. 80: 205-211).

Most adults eclose after about two weeks, although some laboratory reared individuals have remained in the pupal stage for several months before eclosing. Prolonged pupal duration may be the result of gene exchange with populations of the Meseta

Central. There the dry season is more severe and appears to be passed in pupal diapause.

The larvae of *P. polyxenes* are attacked by several predators, including spiders, the wasp *Polistes canadensis costaricensis* Bequaert, bugs in the families Reduviidae and Pentatomidae (Fig. 3), and probably ants. Members of the latter two groups also feed on pupae. Birds and lizards (genus *Ameiva*) are potential vertebrate predators. One parasitoid has been observed—a tachinid fly which attacks larvae and emerges as a prepupa during the host pupal stage. The rate of attack appears to be very low, however. Of 73 swallowtail pupae that were collected or followed in the field, only one produced tachinid prepupae. First and second instar larvae are also subject to drowning in water that accumulates on plant surfaces during prolonged periods of rain. The natural enemies of the adult stages are not known.

The adults of *P. polyxenes stabilis* possess a broader postmedian yellow band than the North American *P. polyxenes asterius*, and there is no sexual dimorphism in wing pattern (Fig. 4). Evidence from laboratory cultures and from the rate of wear of marked individuals in the field indicates that they survive for only three to four weeks. They commonly begin to fly by 0800, or when ambient temperatures reach about 23°C. Above this temperature flight occurs even under overcast conditions. Nectar feeding occurs on a variety of flowers, including *Emilia sonchifolia* (L.) DC. ex Wight, *Melanthera aspera* Jacq., and *Lantana* sp. A sample of 32 caged pupae yielded 18 adult males and 14 females. Although this ratio is not significantly different from unity ($P = .49$), new males were encountered three times more frequently than females over a two month period within one colony ($N = 103$), and seven times more frequently over a one month period within another ($N = 23$).

Male butterflies appear to patrol mating territories atop hills in a manner similar to New York males (Lederhouse, 1978, Territorial behavior and reproductive ecology of the black swallowtail butterfly, *Papilio polyxenes asterius* Stoll. Ph.D. diss., Cornell University). Under conditions of locally high population density, however, they exhibit a less aggressive "exploratory" flight away from hilltops. This flight is similar to that of an ovipositing female and may be an active search for newly eclosed, virgin females. Shapiro (1975, *Am. Midl. Nat.* 93: 424–433) notes a similar switch in the mate-locating behavior of pierid butterflies at high densities. In either case, males tend to remain in an area longer than females. Fifty-three percent of the individual males marked at one colony were later resighted at the same area ($N = 75$) compared with 21% of the females ($N = 28$). Among resighted individuals, the average male was last seen eight days after its first sighting (range 1–21 days) and the average female was last seen after three days (range 1–8 days). Females are likely to disperse in search of new host plant patches or to be chased away by aggressive and persistent males. This would account for their apparent paucity in the field.

Of nine field-caught females that were subsequently dissected, one contained two spermatophores, indicating that some females mate twice. Laboratory experiments indicate that the average female has the capacity to lay 436 ± 100 ($\bar{x} \pm s$) eggs (Blau, 1978, loc. cit.). The fertility of eggs laid in the field is about 90% ($N = 50$). Breeding populations were found throughout the ten months of this study, including the dry season, and almost certainly occur all year.

The natural history of *P. polyxenes* in Costa Rica differs in several ways from that of the north temperate subspecies, *P. polyxenes asterius*. The significance of differences in growth, reproduction, and host plant relationships have been studied and will be published elsewhere. Other questions merit further investigation. For example, what is the adaptive basis for variability in mate locating behavior in Costa Rica? What geographic patterns in diapause occur for *P. polyxenes* within the tropics, and what environmental cues, if any, are involved? How do geographic patterns in sexual dimorphism in *P. polyxenes* relate to the distribution of *Battus philenor* (L.), the model for the dark-form female?

Adult specimens of *P. polyxenes stabilis* from the population discussed here are located in the Cornell University Insect Collection, Lot 1023, Sublot 12 C.

The field studies in Turrialba would not have been possible without the cooperation

of the Department of Crops and Soils at the Centro Agronómico Tropical de Investigación y Enseñanza. I am especially grateful to Dr. and Mrs. Saunders at that institution for their technical and moral support, to Patricia Blau for the same and for editing and typing the manuscript, and to Paul Feeny for advice and encouragement. This work was supported by NSF grants DEB 76-20114 and BMS 75-15282 to Paul Feeny, and was performed while the author was a graduate student at Cornell University.

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Journal of the Lepidopterists' Society
34(3), 1980, 324

REPEATED INTERGENERIC ATTRACTION BETWEEN INDIGENOUS AND EUROPEAN SILKMOTHS (SATURNIIDAE)

Attraction of one species of saturniid by another in the same genus is well-known, particularly with regard to the various members of *Hyalophora*, *Callosamia*, and *Samia*. Kershaw (1953, Ent. Rec. J. Var. 65: 219-220) reports an intergeneric attraction of *Phragmatobia fuliginosa* L. males to a *Panaxia dominula* L. female, both British arctiids. Dominick (1974, J. Lepid. Soc. 28: 176) even records an interfamilial attraction involving *Amphion nessus* (Cramer) (Sphingidae) males and an *Anisota virginiensis pellucida* (J. E. Smith) (Citheroniidae) female. However, the purpose of this note is to record an intergeneric attraction between two saturniids which do not normally meet in nature.

For several years I have been rearing *Saturnia pyri* Denis & Schiffermuller, from France, for study purposes. Since these moths normally emerge during the first half of May in this area, a time when most of our native saturniids are still in hibernation, I was quite surprised to discover several large moths trying to gain entrance to our screened porch on 8 May 1976, at 0130 EST. Upon allowing one to enter and discovering that it was a male *Antheraea polyphemus* Cramer, I felt certain it would seek out a female of the same species, which I had somehow failed to notice. Instead, it flew directly to a transmitting female *pyri* and tried unsuccessfully to effect copulation. Since that first experience, I have had numerous wild *polyphemus* males attracted to other transmitting *pyri* females each year. The males are determined in their efforts to mate and the females quietly submit to the incessant scratching and poking of the males for as long as 20 min before one or the other breaks off contact. None of these encounters has produced a successful union since the male *polyphemus* seems unable to clasp the abdomen of the female *pyri*.

As the male *polyphemus* attempts copulation, the female *pyri* retracts her ovipositor, making the end of her abdomen smooth with no protrusions on which to get a grip. The male's abdomen repeatedly slides from side to side without being able to "lock on." Visually, male *pyri* claspers appear to be larger than male *polyphemus* claspers. It's possible that a male *pyri* may be able to clasp the last segment of the female's abdomen and by applying pressure, force the female to extrude her ovipositor. The male *polyphemus*, on the other hand, with smaller claspers and inability to grip the female's abdomen, cannot apply pressure and mating attempts must necessarily fail.

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