

HETEROSPECIFIC MATING BEHAVIOR OF *PAPILIO PALAMEDES* IN FLORIDA (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT.— Male *Papilio palamedes* frequently approach tiger swallowtail females of *P. glaucus* and *P. canadensis* in field experiments with tethered females. We observed one male actually copulate and (we later learned) transmit a spermatophore to a *P. canadensis* female under these field conditions at Highlands Hammock State Park. This observation is rare for interspecific mating behavior, but does emphasize the lack of total prezygotic reproductive isolation in the Papilionidae.

KEY WORDS: behavior, ecology, interspecific copulation, mating preference, Nearctic, reproductive isolation, USA.

It has been estimated that at least 6% of *Papilio* species hybridize in nature, and it has been suggested that this persistent formation of interspecific hybrids in the field indicates that species are made up of populations primarily maintained by ecological selection (Sperling 1990). A large body of experimental data from laboratory hybridizations between *Papilio* species suggests that postzygotic barriers to genetic introgression are minimal (Ae, 1979; Scriber and Lederhouse, 1989; Scriber *et al.*, 1990a, 1990b, 1991, 1995). However, sex-linked differences in postzygotic genetic compatibility due to the Haldane effect (Haldane, 1922) and the X-effect have been shown to result in greater mortality with greater genetic distances among the paired species in the *P. glaucus* group of tiger swallowtail butterflies (Scriber, 1990; Hagen and Scriber, 1995). This suggests that not all barriers to gene flow among *Papilio* species are prezygotic.

OBSERVATIONS

In an attempt to assess the degree of behavioral reproductive isolation at the mate selection stage, we have tethered size-matched, virgin female pairs of *P. canadensis* Rothschild & Jordan and *P. glaucus* Linnaeus in the field (Deering, 1998). Mating preferences of free-flying natural populations of males for different females have been assessed in this fashion (Lederhouse, 1995; Lederhouse and Scriber, [in press]). In the process of determining the geographic variation in relative mating preferences for females of *P. canadensis* and *P. glaucus* by males of *P. glaucus* in natural populations in Florida (Highlands Hammock State Park; Highlands County), we observed regular interspecific activity and apparent attractiveness of these females to males of *Papilio palamedes* Drury. In addition to *P. glaucus* males, *P. palamedes* males (but not *P. troilus* Linnaeus) were also regularly observed approaching, circling, and often touching or landing upon *Papilio glaucus* females (yellow morphs) or *P. canadensis* females that were tethered out in heterospecific pairs on threads (30cm long, with alligator clips for attachment to the twig or branch). This behavior was also observed with pairs of pinned and mounted tiger swallowtail females placed out near cryptically caged live females for evaluation of potential chemical (pheromone) involvement.

The culmination of these behaviors was a male that actually approached, circled, and copulated with a female *P. canadensis* (Fig. 1; 28 March 1997). The virgin female was from brood #12154 of our lab rearing and had a forewing length of 50mm. This pair remained

in copulation for more than 40 minutes and separated naturally. The female was taken to the Archbold Biological Station for oviposition and possible hybrid rearing. While she laid 17 eggs over a 5 day period, unfortunately none were viable. Upon dissection of the female, it was noted that a spermatophore was transferred from the male *P. palamedes*.

DISCUSSION

This courtship and field copulation of *P. palamedes* with *P. canadensis* represents an unusual phylogenetic spanning of 3 species groups, including the South American *P. scamander* group which is with molecular systematics now confirmed to be intermediate between the *P. troilus* (*P. palamedes*, *P. pilumnus* Boisduval) and *P. glaucus* group (Scriber *et al.*, 1991; Scriber, 1996; Sperling and Reed, pers. comm). This mating of *P. palamedes* and *P. canadensis* spans the greatest genetic distance (and natural geographic separation) among all members of the *P. glaucus*, *P. troilus*, and *P. scamander* groups from North and South America (Hagen and Scriber, 1991; Sperling, 1991; Scriber, 1996).

Of the many interspecific hybridizations that have been summarized for *Papilio* by Sperling (1990), most (80%) are within the same species group. Moreover, we know of only one interspecific field copulation record in the Papilionidae which spans a greater phylogenetic distance than our observation: a natural mating between a female *Battus philenor* (Linnaeus) and male *Eurytides marcellus* (Cramer) in East Texas in which no spermatophore was transferred (Rauscher and Berenbaum, 1983).

The biggest difficulty in assessing the occurrence of hybridization in nature with genetic introgression beyond the F₂ or backcross generations is the identification of these hybrids. We have previously used multivariate morphometric analyses with known hybrids as one of the reference groups (Luebke *et al.*, 1988; Scriber, 1990), as well as diagnostic allozymes (Hagen and Scriber, 1991; Scriber, 1996). While some characters are intermediate between the parent species (West and Clarke, 1988; Ae, 1995; Clarke, 1995; Scriber *et al.*, 1995) others are recessive or due to sex-linked suppressors/enablers which can skip a generation (Scriber *et al.*, 1996). Furthermore, we have observed from larval color and morphological traits that sperm precedence for multiply-mated *Papilio* may not be complete. The *Papilio glaucus* group is known to have multiple matings among males and females (Lederhouse *et al.*, 1989, 1990). It remains to be determined if a female receiving a spermatophore from a distantly

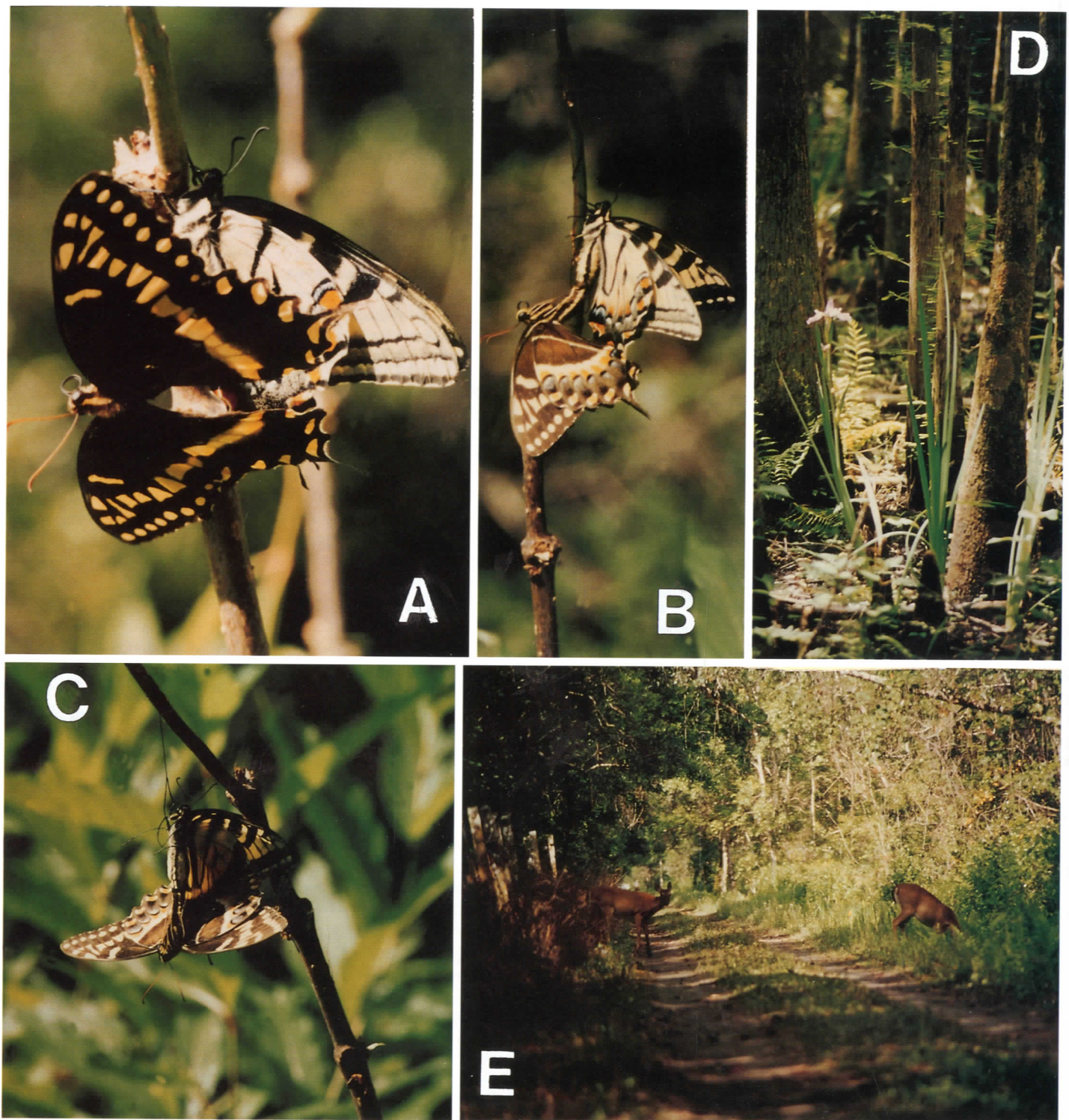


Fig. 1. A) Male *Papilio palamedes* initiating copulation with a "tethered" *P. canadensis* at the Highlands Hammock State Park, near Sebring, Florida (1997). B-C) same in copulation for 40 minutes. D-E) the south canal road and habitat in the park where our population dynamics and mate preference studies have centered.

related male species (as our *P. canadensis* female with the *P. palamedes* male) would use conspecific sperm from a previous natural mating rather than lay sterile hybrid eggs. In the future we will need to evaluate this possibility of "cryptic sexual selection" (Eberhard and Cordero, 1995; Eberhard, 1996) by multiply-mated females in their "choice" of conspecific versus heterospecific sperm.

Documenting both the effectiveness of natural behavioral constraints, as well as genetic/physiological barriers to gene flow

among (or within) species or species groups, will help clarify the patterns of distribution and the processes involved in speciation. While human-mediated hybridization and introgression from increased interspecific contact can be a serious threat to some species (Rhymmer and Simberloff, 1996), this type and frequency of interaction between *P. palamedes* and *P. canadensis* (or *P. glaucus*) is not likely to result in viable hybrids nor serious losses of genetic identity to either species.

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