JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 41 1987 Number 2

Journal of the Lepidopterists' Society
41(2), 1987, 83–93

ECOLOGICAL SIGNIFICANCE OF A POSTMATING DECLINE IN EGG VIABILITY IN THE TIGER SWALLOWTAIL

ROBERT C. LEDERHOUSE AND J. MARK SCRIBER[1]
Department of Entomology, University of Wisconsin,
Madison, Wisconsin 53706

ABSTRACT. The number of times that field-collected tiger swallowtail females had mated increased significantly with age. Mean number of spermatophores per female was 1.97, and 65% of the females had mated more than once. Egg fertility and viability were independent of the number of eggs a female had oviposited. Both parameters declined significantly with time for sequential samples of eggs from both hand-paired and field-collected females. Between 10% and 25% of field-collected females that carried a spermatophore and laid over 15 eggs produced no viable eggs. Fresh singly-mated females and worn multiply-mated females did not differ in egg viability, but singly-mated worn females had significantly lower egg viabilities. Thus, an additional mating may be advantageous for females that receive inadequate spermatophores or live for more than a week.

Additional key words: Papilionidae, *Papilio glaucus*, infertility, spermatophore counts, multiple matings.

Mating histories of female tiger swallowtails, *Papilio glaucus* L. (Papilionidae), as revealed by spermatophore counts, probably are documented better than for any other species of butterfly (Drummond 1984). Although the debate about the role of sexual selection in maintaining the female color polymorphism remains unresolved (Burns 1966, Pliske 1972, Platt et al. 1984), it is clear that multiple mating is common in this species. This is in contrast to suggestions on theoretical grounds that female butterflies should prefer monogamy (Wiklund 1977a, 1977b, 1982). Levin (1973) was unable to demonstrate experimentally a selective advantage for multiple mating in *P. glaucus*.

The maintenance of the color polymorphism in female tiger swal-

---

[1] Present address of both authors: Department of Entomology, Michigan State University, East Lansing, Michigan 48824.

lowtails requires frequency-dependent selection or a balancing of selection pressures (Burns 1966, 1967, Prout 1967, Levin 1973). The loci that control it are on the sex chromosomes (Clarke & Sheppard 1962, Scriber 1985). Dark-morph females benefit as Batesian mimics of the unpalatable, aposematic pipevine swallowtail, *Battus philenor* (L.) (Brower 1958). One subspecies, *P. glaucus canadensis*, which occurs N of the range of *B. philenor*, has only monomorphic yellow females. Both yellow and dark female morphs occur in the other two subspecies, *P. g. glaucus* and *P. g. australis*, which are sympatric with the model, and the relative frequency of the dark morph is correlated positively with the abundance of the model (Brower & Brower 1962, Lederhouse & Scriber 1987).

Burns (1966) documented a greater mean number of spermatophores carried by field-collected yellow females than by dark females. He suggested that sexual selection favored yellow females by shortening the interval between emergence and mating. Yellow females would also benefit if a single spermatophore were inadequate to fertilize all eggs a female was likely to oviposit. However, subsequent spermatophore-count studies of other *P. glaucus* populations have not revealed significant differences in spermatophore number for the two color morphs (Pliske 1972, 1973, Makielski 1972, Platt et al. 1984). In addition, Levin (1973) showed that a single spermatophore was sufficient to fertilize all the eggs laid by *P. glaucus* females in the laboratory. This eliminated preferential mating with respect to color as the balancing selective pressure, but did not explain why roughly half of the females in these studies mated more than once.

However, closer examination of Levin's data revealed that his experimental females averaged only about 113 eggs during 5.4 days. Both Remington (1959) and Lederhouse (1981) observed declines with time in the viability of eggs from singly mated females of other swallowtail species. In the black swallowtail, *P. polyxenes* F., a decline in fertility was detectable only after about 10 days and was independent of the number of eggs laid (Lederhouse 1981). In the present study, our purpose was to investigate the fertility and viability of eggs laid by *P. glaucus* females with longer mating intervals than those in the study by Levin (1973). In addition, we wanted to determine under what circumstances a female would benefit from multiple matings.

MATERIALS AND METHODS

Samples of females were collected from several locations. The *P. g. glaucus* used for determining number of spermatophores carried were captured in Adams and Scioto counties, Ohio. The *P. g. canadensis* were collected in several counties in north-central Wisconsin. These females were assigned to one of four categories of wing wear when they were collected (Lederhouse 1978). After they died, field-collected females and a portion of hand-paired females were dissected, and the number of spermatophores was determined.

Laboratory-reared (lab) females were hand-paired once to field-collected (field) or laboratory-reared males. All females were set up in plastic boxes (10 cm × 20 cm × 27 cm) with a sprig of black cherry, *Prunus serotina*, under saturated humidity. The boxes were placed about 70 cm from continuously lighted 100-watt incandescent bulbs. Females were fed a mixture of 1 part honey to 4 parts water at least once daily. Most females were allowed to oviposit until death.

Eggs were collected and counted at two-day intervals except on weekends. Larvae were removed as they hatched, and the remaining eggs were monitored for 10 days after the last larva hatched. Because the green eggs of *P. glaucus* become mottled and then turn black as the embryo develops, eggs could be assigned to one of three mutually exclusive categories. Eggs were classified as infertile if they showed no development, inviable if they developed but did not hatch, or viable if they hatched.

Unless otherwise indicated, values are presented as means ± standard deviations. Since the lab-reared males and females were the offspring of mothers from a variety of locations, and since numerous combinations were mated, the Friedman two-way analysis of variance was used for the analyses of fertility and viability (Siegel 1956). Sequential samples from each female were ranked for both variables. A modified Tukey test was used for multiple comparisons of ranked samples (Zar 1984). Only females that laid eggs for at least three sampling intervals, produced at least 50 eggs, and had some eggs hatch were included in these analyses. In addition, each field-collected female with at least one spermatophore and that laid 15 or more eggs was monitored for egg fertility and viability.

RESULTS

Field-collected dark-morph females averaged 1.97 ± 0.90 spermatophores (Table 1). All had mated at least once, and 65.4% had mated more than once. The females were distributed uniformly across wear classes with a mean of 2.45. Mean number of spermatophores per female increased significantly with increasing wing wear (Table 1). The correlation between spermatophore number and wear class was highly significant (Spearman Rank Correlation, $r = 0.52$, $P < 0.001$).

Although the actual percent hatching was highly variable from female to female (Table 2), the pattern of decreasing egg viability was detectable by the end of the first week of oviposition. All laboratory-

Table 1. Number of spermatophores contained by *P. glaucus* females collected in Adams Co., Ohio in relation to wing condition. z and P values are for one-tailed Mann-Whitney *U*-tests comparing the means for adjacent condition classes.

	Number of spermatophores							
Condition	n	1	2	3	4	Mean	z	P
Fresh	23	16	6	1	0	1.35	2.30	<0.02
Slightly worn	34	13	17	2	2	1.79	1.82	<0.04
Intermediate	29	7	12	9	1	2.14	2.18	<0.02
Very worn	21	1	8	8	4	2.71		
Total	107	37	43	20	7	1.97		

reared groups of females showed a significant decline for the first three samples of eggs (Friedman two-way analysis of variance, Table 3). When only females that laid eggs for four intervals were considered, again all groups of lab females had significant decreases in viability (Table 4). The reverse pattern occurred in the analysis of infertility. The only group without a significant infertility increase through three samples was the 1984 lab females paired with lab males (Table 3). All three groups of lab females had significant increases in infertility through four samples (Table 4). There was no discernible pattern for the inviable category of eggs, although one group had a significantly nonhomogeneous result. In sum, the decline in viability with sample resulted mostly from an increase in infertile eggs and was not clearly related to a change in the inviable class.

Since field-collected females were older and probably had laid some eggs before capture, it was more difficult to get samples of eggs for sufficiently long periods for analyses. Females from neighboring populations (northern Michigan, northern Wisconsin and so on) were grouped together without regard to year because there were few differences between years for lab females. The results for field females were similar to those for lab females. Females from both *P. g. glaucus* and *P. g. canadensis* populations showed significant declines in viability after three samples (Table 3). The decline was not significant for *P. g. canadensis* females with four samples each (Table 4). This probably represents random variability between the very low viabilities of the third and fourth samples (Table 2). The increases in infertility were significant for both groups for three samples and for *P. g. glaucus* for four samples. Again, there was no pattern in inviable eggs with sample. The significantly nonhomogeneous result for *P. g. canadensis* females with four samples was a decrease in inviable eggs from sample to sample.

The significant sequential decline in egg viability could be related to either the number of eggs that had been oviposited already or the

TABLE 2. Average egg viability (percent hatching) for each of four sequential samples from *P. glaucus* females. Top values are means; lower values are SD. The first sample size (n_1) is for the first three means; the second (n_2) is for the fourth.

Group	n_1	n_2	Sample no. 1	2	3	4
1984 lab female–lab male	18	14	79.0 23.4	67.6 27.2	58.5 34.8	46.9 32.8
1984 lab female–field male	20	12	74.2 29.6	56.9 26.1	45.4 32.1	40.2 31.8
1985 lab female–field male	18	13	91.2 11.7	81.0 29.1	64.1 35.6	46.4 37.7
P. g. glaucus field females	21	11	87.8 17.7	70.1 26.8	50.9 39.6	37.0 41.1
P. g. canadensis field females	21	12	79.3 24.3	38.9 31.2	28.7 33.0	38.2 42.1

time interval since mating. To distinguish between the two possible causes, lab females were divided into those that laid fewer than 125 eggs and those that laid more than 125 in the first two samples. For lab females mated to lab males, the viability of eggs in the first two samples combined did not differ significantly for the two groups (Mann-Whitney *U*, $P > 0.50$, Table 5). In addition, viability of third-sample eggs was independent of the number of eggs previously oviposited by the females (Mann-Whitney *U*, $P > 0.50$, Table 5). For lab females mated to field males, egg viability was actually higher for females that had laid more eggs. The differences were significant for the first two samples combined and for the third samples (Mann-Whitney *U*, both P's < 0.05). Therefore, any decline in egg viability was not the result of females using up their supplies of sperm as they laid more eggs. The potential for a single insemination to fertilize a large number of eggs is illustrated by two females that laid 290 and 306 eggs within 5 days

TABLE 3. Analyses for homogeneity for each category of eggs for three sequential samples from *P. glaucus* females. Mean interval is number of days between mating or capture and oviposition of the last sample. Probabilities are for a more extreme value of the Friedman two-way analysis of variance statistic.

Group	n	Interval (no. days) Mean	SD	P Viable	Inviable	Infertile
1984 lab female–lab male	18	6.9	1.6	0.05	n.s.	n.s.
1984 lab female–field male	20	7.7	2.1	0.01	0.05	0.05
1985 lab female–field male	18	7.9	2.0	0.01	n.s.	0.01
P. g. glaucus field females	21	10.0	2.6	0.02	n.s.	0.01
P. g. canadensis field females	21	8.3	2.7	0.001	n.s.	0.001

TABLE 4. Analyses for homogeneity for each category of eggs for four sequential samples from *P. glaucus* females. Mean interval is number of days between mating or capture and the oviposition of the last sample. Probabilities are for a more extreme value of the Friedman two-way analysis of variance statistic.

		Interval (no. days)		P		
Group	n	Mean	SD	Viable	Inviable	Infertile
1984 lab female–lab male	14	10.3	2.7	0.001	n.s.	0.001
1984 lab female–field male	12	11.1	3.4	0.01	n.s.	0.05
1985 lab female–field male	13	11.8	3.0	0.01	n.s.	0.01
P. g. glaucus field males	11	12.5	2.8	0.01	n.s.	0.001
P. g. canadensis field females	12	10.9	3.4	n.s.	0.05	n.s.

after mating. The viabilities for these two clutches were 90.0% and 97.1%, respectively.

Lifetime oviposition was high for females in this study. Lab *P. g. glaucus* females laid an average of 181.2 eggs ± 77.2 ($n = 36$). Yellow- and dark-morph individuals did not differ significantly in number of eggs laid. Field-collected *P. g. glaucus* laid 141.1 ± 61.4 eggs ($n = 21$), and *P. g. canadensis* laid 130.0 ± 44.0 eggs ($n = 23$). These values did not differ significantly (*t*-test, $P > 0.20$), but both were significantly less than the value for lab females (*t*-test, $P < 0.05$ and 0.01, respectively).

Since the decline in viability was significant using the Friedman two-way analysis of variance, a multiple comparison analysis was applied to the ranked samples to determine which were significantly different from the others. Using a modified Tukey procedure (Zar 1984), a general pattern emerged. Females mated to lab males had fourth samples that were significantly lower in viability than the first two. In both groups of females hand-paired to field males, the first sample was significantly

TABLE 5. Viability (percent hatching) related to number of eggs laid by *P. glaucus*. Females were grouped by oviposition during the first two sample intervals. Means for oviposition and viability are given for the first two samples combined and for viability for the third sample.

				Viability (percent hatching)			
		No. of eggs		Two combined		Third	
Female group	n	Mean	SD	Mean	SD	Mean	SD
Lab female–lab male							
Less than 125 eggs	8	80.6	29.5	77.8	15.7	62.6	28.1
More than 125 eggs	10	176.4	19.7	69.6	29.5	55.2	40.5
Lab female–field male							
Less than 125 eggs	24	74.2	20.9	69.6	22.4	44.2	34.8
More than 125 eggs	14	173.5	59.1	84.6	13.3	71.4	27.7

higher than the fourth sample. This suggests that the declines occurred sooner in females that had mated with males that may have mated before. For field-collected *P. g. glaucus* females, the first sample was significantly higher than the last two for both three- and four-sample analyses. For *P. g. canadensis*, the first sample was significantly higher than the last two for three samples per female. Since field-collected females had mated some time before capture, this reflects the longer intervals between mating and completion of oviposition for these females (Tables 3, 4).

Not all matings produced high levels of fertility and hatching. A proportion of the field-collected females that contained at least one spermatophore and laid 15 or more eggs laid no viable eggs. In 1985, 21.4% of 28 Ohio *P. g. glaucus* females produced clutches with total hatching failure. In 1986, 21.3% of 89 Ohio females also produced no viable eggs. A similar sample of 28 *P. g. canadensis* females had a 10.7% total failure rate. Comparable results are illustrated by 57 hand-pairings using males collected in Adams Co., Ohio. In 5 cases (8.8%), no spermatophore was transferred. An additional 12 females (21.0%) with spermatophores laid fewer than 5 eggs. Nine pairings (15.8%) resulted in entirely infertile eggs even though a spermatophore had been transferred. The remaining 31 pairings averaged 62.4% ± 23.3% larval hatch. Thus, for hand-paired females that had a spermatophore and laid eggs, 22.5% produced clutches with total hatching failure.

An additional mating often had a substantial effect on the viability of eggs laid subsequently. The effect of additional matings on hatching rate was investigated by comparing the first samples of eggs from field-collected Ohio females that mated once and that mated more than once. Females that had total hatching failure were excluded. Fresh singly-mated females had a mean hatching rate of 64.2% ± 29.8% ($n = 26$) which was significantly higher than the 35.5% ± 28.1% of 5 worn singly-mated females (Mann-Whitney *U*, $P < 0.05$). Worn multiply-mated females had a mean hatching rate of 69.4% ± 27.0% ($n = 14$). This was not different from that of fresh singly-mated females but was significantly higher than worn singly-mated females (Mann-Whitney *U*, $P > 0.30$ and <0.05, respectively).

DISCUSSION

Analysis of spermatophore counts for the Ohio *P. g. glaucus* documents the highest mean value for any population of this species studied to date. Not only is the mean nearly 2 spermatophores per female, but the proportion (65.4%) of the females that had mated more than once is also higher than any other reports for this species (Drummond 1984). Burns (1968) reported a mean of 1.75 spermatophores per female for one population and a multiple-mating percent of 63% for another population of *P. g. glaucus.* Number of spermatophores carried by Ohio females increased significantly with wing wear (age). This agrees with results of Platt et al. (1984) and helps to explain the only low mean spermatophore values reported for this species. Pliske (1972, 1973) reported means of about 1.15 spermatophores per female, but his samples of females were considerably less worn.

As Levin (1973) demonstrated, a single normal insemination is sufficient to fertilize all the eggs a *P. glaucus* female is likely to lay. Our study confirms this even for females that oviposited over 50% more eggs on average than those in Levin's study as long as they were laid within a week of mating. In addition, our experiments document the potential for the sperm of one mating to produce fertilities of over 95% for females laying 300 or more eggs. That one normal insemination is sufficient also generally agrees with reports for *Papilio zelicaon* Lucas (Sims 1979), *P. polyxenes* (Lederhouse 1981), and *Pieris rapae crucivora* Bsd. (Suzuki 1979).

In contrast to Levin (1973), however, we document two situations in which an additional mating would be selectively advantageous for a *Papilio glaucus* female. First, a particular mating by a female is not always effective in fertilizing eggs. Second, even for a highly effective mating, the viability of the eggs of singly-mated females declines considerably with time regardless of oviposition rate.

In *P. zelicaon,* a newly emerged male or one that has mated frequently produces an abnormally small spermatophore often with a low sperm count (Sims 1979). In our study, 22.5% of hand-paired females that had spermatophores and laid eggs had total hatching failure. Another 15% of hand-pairings with some eggs hatching resulted in viabilities of less than 50% for the first two samples of eggs. Between 10% and 20% of field-collected females carrying at least one spermatophore laid no viable eggs. Although the complete hatching failure of some field-collected females may have resulted from a decline in viability with the time interval between mating and oviposition in the laboratory, our results suggest that the failure rate for natural matings is considerable (Drummond 1984).

The potential for long-term sperm storage is present in butterflies. Females of several species of *Heliconius* are capable of laying fertile eggs over 4–6 month lifespans (Dunlap-Pianka et al. 1977) although they usually mated only once (Ehrlich & Ehrlich 1978). However, in relatively short-lived species such as various swallowtails the sperm supply does deteriorate fairly quickly. Remington (1959) noted that later samples of eggs from hand-paired *Papilio* females had low fertility. In *P. polyxenes,* this decline was time-related but independent of the number of eggs that had been laid (Lederhouse 1981). In *Euphydryas editha* Bsd., a single mating was effective for only 7 to 10 days (Labine 1966).

Egg viabilities and fertilities of singly-mated tiger swallowtails decreased over time. Our results for *P. glaucus* appear at odds with those of Levin (1973). However, this is likely the result of the average lifespan of 5.4 days for the females in his study. There was a decline in fertility for this period in Levin's study, but it was not significant. Both male and female *P. glaucus* live up to two weeks in the field (Berger 1986, Lederhouse 1982, unpubl. data). The 7- to 13-day average lifespans of the females in our study are more representative of a proportion of the females in the field. Females of short-lived butterfly species in thermally limiting environments may not benefit from mating more than once (Wiklund 1977a, 1982).

Egg viability decreased more gradually throughout the first week for females mated to virgin males. Only the fourth sample was significantly lower than the first for these females. These values declined sooner and more if the males were field-collected. This suggests that these males provided smaller spermatophores, possibly as a result of depletion of fluids from a previous mating, as is the case for multiply-mating *P. zelicaon* males (Sims 1979). Since spermatophores much smaller than average do not produce a mating refractory period (Sugawara 1979), females in the field could correct deficiencies by mating an additional time. Indeed, 50% of the Ohio females in the two freshest wear classes that had mated more than once had a first spermatophore that was considerably smaller than average (R. Lederhouse unpubl. data).

Declines in egg viability were substantial for all groups of females amounting to a reduction to half the initial viability level by 10 days after pairing. Although an additional mating does not guarantee higher viability, multiply-mated worn females had significantly higher viabilities of their eggs than singly-mated worn individuals. The average viability values for multiply-mated worn females did not differ from those of singly-mated fresh females. For females that live more than a week, an additional mating could be very advantageous since it is likely to restore viability levels to average values. Females of *Pieris brassicae* L. and *P. rapae crucivora* typically mate a second time a week after the first mating (David & Gardiner 1961, Suzuki 1979).

The rate of mating failure in natural copulations (10–20%) and the decline over time in the viability of eggs fertilized by a single male combine to make the probability of remating important in the tiger swallowtail. Sexual selection by males for yellow females could provide a differential favoring this morph. The dark morph females should on average live longer because of their mimetic advantage. However, if the additional eggs they might lay during this period are largely infertile resulting from lower or slower remating rates, the advantage of their greater longevity would be reduced. The importance of sexual selection in maintaining the color polymorphism in the tiger swallowtail will not be resolved using spermatophore count data alone because of the limitations of this technique. However, mating frequency clearly affects lifetime reproductive success in *P. glaucus*. Suggestions that female butterflies should mate only once (Wiklund 1977b) must be limited to short-lived species. In longer-lived species, selection should favor regular mating intervals or more effective sperm storage. Such factors warrant further investigation in long-lived species.

ACKNOWLEDGMENTS

We thank S. G. Codella, B. A. Drummond, R. H. Hagen, D. D. Murphy, and S. J. Rockey for helpful comments on drafts of this paper. We are grateful to M. Evans, Y. Allen, J. Johnson, C. Plzak, E. Schuh, J. Sibenhorn, J. Thorne, V. Viegut, and D. Ware for their assistance. Support for this research was provided in part by NSF grants DEB 79-21749 and BSR 8306060; USDA grant 85CRCR-1-1598 and the Graduate School and the College of Agriculture and Life Sciences (Hatch 5134) of the University of Wisconsin, Madison.

LITERATURE CITED

BERGER, T. A. 1986. Habitat use and reproductive ecology of the eastern tiger swallowtail, *Papilio glaucus* L. Dissertation, Rutgers University, Newark, New Jersey, USA. 109 pp. Diss. Abstr. Int. microfilm order No. 8616563.

BROWER, J. vZ. 1958. Experimental studies of mimicry in some North American butterflies. Part II. *Battus philenor* and *Papilio troilus*, *P. polyxenes* and *P. glaucus*. Evolution 12:123–136.

BROWER, L. P. & J. vZ. BROWER. 1962. The relative abundance of model and mimic butterflies in natural populations of the *Battus philenor* mimicry complex. Ecology 43:154–158.

BURNS, J. M. 1966. Preferential mating versus mimicry: Disruptive selection and sex-limited dimorphism in *Papilio glaucus*. Science 153:551–553.

——— 1967. Reply to: Selective forces in *Papilio glaucus*. Science 156:534.

——— 1968. Mating frequency in natural populations of skippers and butterflies as determined by spermatophore counts. Proc. Nat. Acad. Sci. 61:852–859.

CLARKE, C. A. & P. M. SHEPPARD. 1962. The genetics of the mimetic butterfly *Papilio glaucus*. Ecology 43:159–161.

DAVID, W. A. L. & B. O. C. GARDINER. 1961. The mating behaviour of *Pieris brassicae* (L.) in a laboratory culture. Bull. Entomol. Res. 52:263–280.

DRUMMOND, B. A. 1984. Multiple mating and sperm competition in the Lepidoptera, pp. 291–370. *In* Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press.

DUNLAP-PIANKA, H., C. L. BOGGS & L. E. GILBERT. 1977. Ovarian dynamics in heliconiine butterflies: Programmed senescence versus eternal youth. Science 197:487–490.

EHRLICH, A. H. & P. R. EHRLICH. 1978. Reproductive strategies in the butterflies: I. Mating frequency, plugging, and egg number. J. Kansas Entomol. Soc. 51:666–697.

LABINE, P. A. 1966. The population biology of the butterfly, *Euphydryas editha*. IV. Sperm precedence—A preliminary report. Evolution 20:580–586.

LEDERHOUSE, R. C. 1978. Territorial behavior and reproductive ecology of the black swallowtail butterfly, *Papilio polyxenes asterius* Stoll. Dissertation, Cornell University, Ithaca, New York. 155 pp. Diss. Abstr. Int. order No. 7902342.

——— 1981. The effect of female mating frequency on egg fertility in the black swallowtail, *Papilio polyxenes asterius* (Papilionidae). J. Lepid. Soc. 35:266–277.

——— 1982. Factors affecting equal catchability in two swallowtail butterflies, *Papilio polyxenes* and *P. glaucus*. Ecol. Entomol. 7:379–383.

LEDERHOUSE, R. C. & J. M. SCRIBER. 1987. Increased relative frequency of dark morph females in the tiger swallowtail, *Papilio glaucus* (Lepidoptera: Papilionidae) in S-central Florida. Am. Midl. Nat. in press.

LEVIN, M. P. 1973. Preferential mating and the maintenance of the sex-limited dimorphism in *Papilio glaucus*: Evidence from laboratory matings. Evolution 27:257–264.

MAKIELSKI, S. K. 1972. Polymorphism in *Papilio glaucus* L. (Papilionidae): Maintenance of the female ancestral form. J. Lepid. Sco. 26:109–111.

PLATT, A. P., S. J. HARRISON & T. F. WILLIAMS. 1984. Absence of differential mate selection in the North American tiger swallowtail, *Papilio glaucus*, pp. 245–250. *In* Vane-Wright, R. I. and P. R. Ackery (eds.), The biology of butterflies. Sympos. 11. Academic Press, London.

PLISKE, T. E. 1972. Sexual selection and dimorphism in female tiger swallowtails, *Papilio glaucus* L. (Lepidoptera: Papilionidae): A reappraisal. Ann. Entomol. Soc. Am. 65: 1267–1270.

——— 1973. Factors determining mating frequencies in some New World butterflies and skippers. Ann. Entomol. Soc. Am. 66:164–169.

PROUT, T. 1967. Selective forces in *Papilio glaucus*. Science 156:534.

REMINGTON, C. L. 1959. Wide experimental crosses between *Papilio xuthus* and other species. J. Lepid. Soc. 13:151–164.

SCRIBER, J. M. 1985. The ecological and genetic factors determining geographic limits to the dark morph polymorphism in *Papilio glaucus*. Bull. Ecol. Soc. Am. 66:267.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 pp.

SIMS, S. R. 1979. Aspects of mating frequency and reproductive maturity in *Papilio zelicaon*. Am. Midl. Nat. 102:36–50.

SUGAWARA, T. 1979. Stretch reception in the bursa copulatrix of the butterfly, *Pieris rapae crucivora*, and its role in behaviour. J. Comp. Physiol. A. 130:191–199.

SUZUKI, Y. 1979. Mating frequency in females of the small cabbage white, *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae). Kontyû 47:335–339.

WIKLUND, C. 1977a. Oviposition, feeding, and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). Oikos 28:56–68.

——— 1977b. Courtship behaviour in relation to female monogamy in *Leptidea sinapis* (Lepidoptera). Oikos 29:275–283.

——— 1982. Behavioural shift from courtship solicitation to mate avoidance in female ringlet butterflies (*Aphantopus hyperanthus*) after copulation. Anim. Behv. 30:790–793.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.

Received for publication 15 August 1986; accepted 14 January 1987.