Journal of the Lepidopterists' Society
38(3), 1984, 254–256

BOOK REVIEW

PHENETICS AND ECOLOGY OF HYBRIDIZATION IN BUCKEYE BUTTERFLIES (LEPIDOPTERA: NYMPHALIDAE). John E. Hafernik, Jr., University of California Publications in Entomology, Volume 96. 118 pp., 35 line drawings, 15 halftones, February 1983, $16.50, ISBN 0-520-09649-5.

This work analyzes the ecological and phenetic ordinant relationships of *Junonia* in North and Central America, exclusive of the Caribbean. Hafernik assesses competition in the field between *J. coenia*, *J. nigrosuffusa*, and *J. zonalis* and infers their genetic relationships. The text has 42 pages divided into five sections: Intraspecific and Interspecific Crosses; Courtship Behavior; Population Size, Vagility and Dispersion of South Texas *Junonia*; Larval Resource Partitioning; and Phenetics.

Hafernik notes that while electrophoretic assays of enzyme variability allow quantitative estimates of genetic differentiation between taxa, he prefers hybridization studies, because they illuminate hybrid fitness via egg fertilities, embryo viabilities, skews of sex ratios and progeny mortality. He investigates these relationships within *Junonia* by crossing F_1 and F_2 hybrids, and backcrossing among *J. coenia* from California and Texas, *J. nigrosuffusa* from Texas, and *J. zonalis* from Guatemala. Hybrid matings were obtained by substituting a different female in the middle of a natural courtship. Data for egg fertility, egg viability and percent of hatch were not statistically analyzed. Data on sex ratios were analyzed using chi-square to compare both individual broods and pooled values of like broods with an expected 1:1 ratio. Noncontrolled rearing environments precluded quantitative comparisons of generation times, but these data, as well as mortality estimates, emergence synchronies of the sexes, and incidences of aberrations were compared qualitatively.

Hafernik's hybridization data suggest that North and Central American *Junonia* are one polytypic species rather than a circle of races, since interpopulation genetic compatibility is high regardless of geographic distances. These findings are in contrast with other studies of papilionoids; Hafernik reviews many similar studies.

Hafernik states that *Junonia* lack complicated courtship rituals. Males rest on a bare spot on the ground and pursue suspect females pugnaciously. Visual stimuli, especially background color of the dorsal wing surfaces, appear to trigger male responses. Hafernik tested male response to females using various wing marking and obscuring techniques and also tested models and wing transplant females. Color differences limiting *coenia* and *nigrosuffusa* courtship interactions are considered unrelated to either thermoregulation or crypsis. Aposematicity was not tested (*Junonia* and *Euphydryas* share similar hosts in the Scrophulariaceae with iridoid glycosides). There is no evidence of pheromone involvement in *Junonia*, although no experimentation was carried out in this vein.

Hafernik's estimates of population dynamics and vagility for *Junonia* are based on populations at Brazos Island, Texas. Mark/recapture studies followed Ehrlich and Davidson (1960, J. Lepid. Soc. 14:227–230), with vagility analyzed between two sectors over distances of ca. 2 km using Scott's (1972, Ph.D. thesis, U. of Calif., Berkeley) technique. Jolly's (1965, Biometrika 52:225–247) method was used for estimates of population. Dispersion was analyzed using the variance mean ratio and Morisitas indices (Southwood, 1966, Ecological Methods, Methuen, London). Hafernik concludes that *coenia* and *nigrosuffusa* have similar vagility patterns with males markedly more aggregated due to mating and females more dispersive for host selection. The micro-distribution of females in the environment is different for these species, with *nigrosuffusa* using and spending more time at clumped host plants, while *coenia* spend more time in transit between unclumped hosts. Males showed similar highly contagious distributions but had little spatial overlap. Male *coenia* chose short vegetation for loitering, while *nigrosuffusa* chose taller vegetation, chiefly stands of sedges. Hafernik postulates that *coenia* males may have a competitive advantage in short vegetation, based upon sympatric interaction with male *nigrosuffusa* and upon the latter's behavior and mating area choice, in Arizona under allopatric conditions.

Studies on larval resource partitioning involved eight localities in Texas over three years and one location in Arizona. While larvae of *coenia* and *nigrosuffusa* could not be distinguished, reared adults were identified using Discriminant Function Analysis (DFA) (see below). Host palatability was tested by presentation of hosts to allopatric populations of larvae of *coenia*, *nigrosuffusa* and *zonalis*. Adult female oviposition preferences in cages were also noted. Hafernik's data indicate considerable host overlap in south Texas with *coenia* chiefly using *Agalinis maritima*, and *nigrosuffusa* using *Stemodia tomentosa* in the presence of *coenia* but also *A. maritima* in allopatry. *J. nigrosuffusa* shows better larval development on the latter, whereas, *coenia* is limited by the leaf pubescence of *Stemodia*. Hafernik postulates that the perennial and annual habits of *Stemodia* and *Agalinis*, respectively, may account for falling numbers of adult *coenia* in winter, while adult *nigrosuffusa* populations remain high. He speculates on the implications of this regarding hybrid introgression. *J. zonalis* from Guatemala showed more restricted host preferences than *coenia* or *nigrosuffusa*, and ovipositing females rejected the favored hosts of the latter two.

In the Phenetics section, Discriminant Function Analysis (DFA) and Principal Component Analysis (PCA) were used to demonstrate the relationships between known parental and hybrid reference groups and between reference groups versus unknowns from Mexico and Central America. Hafernik chose 25 wing characters (7 continuous, 17 coded [discrete]) for his analyses. While he states that the coded characters violate the parametric assumptions of the DFA's and PCA's, he notes: (1) a statement by Blacklith and Reyment (1971, Multivariate Morphometrics, Academic Press, New York) that DFA and PCA are "robust" enough to handle [minor] violations of normality, and (2) that the derived DFA classifications of F_1 hybrids were empirically correct (his figure 18). Traditionally, however, inclusions of nonparametric data in such analyses account for less than 20 percent of characters. In Hafernik's work, they equal 68 percent and dominate the vectors. Thus, the discriminators chosen by the DFA are specifically antagonistic to the assumptions of the analyses. This bothers me, though the DFA scatter-plots are undoubtedly plausible. Interestingly, Hafernik (p. 39) states that principal component 1 of the PCA ("unlike DF1") shows moderate to high loadings for all coded characters; this demonstrates the sensitivity of the analyses to variation differences between the continuous versus coded characters used. The use of only continuous characters for the DFA would have avoided this philosophical conflict, as would have the use of Principal Coordinate Analysis or Nonmetric Multi-dimensional Scaling instead of PCA, if coded characters were retained.

Hafernik infers genetic relationships based upon DFA and PCA results, citing empirical evidence for this conclusion *via* multivariate analysis examples of Rohwer (1972, Syst. Zool. 21:313–338), Rohwer and Kilgore (1973, Syst. Zool. 22:157–165), Jackson (1973, Evolution 27:58–68) and Thaeler (1968, Evolution 22:543–555). These authors, however, followed traditional constraints in using nonparametric data in DFA and PCA. Hafernik's apparent major deviation contracts the logical consistency employed by those he cites. Not that I doubt the probability of biological (genetic) correctness of Hafernik's results (it is hard to argue against "proven" empiricism), but rather I find the results an analytical curiosity and testament to the "robustness" of multivariate analyses. One could argue, however, that in the transparent guise of "robustness" of statistical methods, the philosophy that "the end justifies the means" is a bit too visible.

In essence, I found Hafernik's work excellent biology and very interesting reading. The text is lucid and Hafernik reviews his subjects well during discussion. Seldom is this much information produced on a subject such as hybridization unless team efforts are involved. The work leaves a hunger for the answers to those inevitable questions one can ask only when well into research. I only hope Hafernik or another population ecologist will explore the other side of this coin—the electrophoretics.

On the negative side, some of the graphics could have been improved, especially labeling on histograms and scattergrams, and as stated above, parametric variables should have been used in the phenetic analyses.

Interestingly, the text of this volume is typeset, unlike some previous University of

California Publications in Entomology serials, which were typewritten. I hope this unpredictable luck continues, since appearance alone does have implications for the quality of any series (are you listening U.C. Press?).

At $16.50, Hafernik's work is well worth its price and will be necessary for any "lep'er" who claims to be a biologist or biologist who researches leps.

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