Genetic Studies Using the Orange Body Color Type of *Nezara viridula* (Hemiptera: Pentatomidae): Inheritance, Sperm Precedence, and Disassortative Mating

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ABSTRACT   *Nezara viridula* (L.) (Hemiptera: Pentatomidae), the southern green stink bug, has body color polymorphisms. *N. viridula* f. *smaragdula* is the common green morph, whereas the rare morph *N. viridula* f. *aurantiaca* is uniformly orange. Crossing studies were conducted to determine the inheritance of the orange body color trait. Mendelian genetic analysis suggested that orange body color is a simple, sex-linked recessive trait. In sperm precedence studies using orange females crossed with green and then orange males, or vice versa, the proportion of offspring attributable to the second male, *P2*, averaged 73.3% (extremes 23.5–100%). The average *P2* in the first egg mass deposited after the new pairing was 71.8%. The pattern of sperm use provided evidence for incomplete sperm mixing, sperm stratification, and sperm displacement. Green females preferred mating with orange males (88%) compared with green males (12%), suggesting that disassortative mating may operate.

KEY WORDS   southern green stink bug, inheritance, X-linked trait, color polymorphism

The southern green stink bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae) has body color polymorphisms. Nine color morphs are known that are derived from four basic types (Kiritani and Yukawa 1963, Yukawa and Kiritani 1965, Kiritani 1970, Hokkanen 1986). Although the color polymorphisms are manifested in both nymphal and adult stages, previous studies have focused only on the more obvious adult traits. The four main color forms were distinguished and given names based on the color pattern on the dorsum (Kiritani and Yukawa 1963, Yukawa and Kiritani 1965). *N. viridula* f. *smaragdula* F. (G-type) is the common green form, f. *torquata* F. (O-type) has median and lateral lobes and the anterior margin of the pronotum yellow or orange, f. *viridula* L. (R-type) has green spots on a background of yellow or orange over the entire body, and an unnamed morph (F-type) is like f. *torquata* except it also has yellow or orange along the margins of the convexium. Other morphs with combinations of these orange and green color traits exist, including an entirely orange morph called f. *aurantiaca* (Y-type). The ventral and dorsal coloring of *N. viridula* f. *aurantiaca* is uniformly orange.

The mix of *N. viridula* color polymorphisms varies with region. The greatest diversity of color polymorphisms occurs in Japan, whereas *N. viridula* populations in many parts of the world (Australia, Pacific Islands, United States, Central America, and the West Indies) seem to be only or primarily green (Yukawa and Kiritani 1965). The f. *aurantiaca* morph is very rare in Japan, occurring in ≈1 in 5,000 individuals (Yukawa and Kiritani 1965). In Brazil, the frequency of f. *aurantiaca* is higher at 0.7% (Vivan and Panizzi 2002).

The different color polymorphisms are under genetic control. Crossing studies using the main color morphs (O-, G-, and R-types) suggested the body color polymorphisms are controlled by two sets of genes on two independent loci (Ohno and Alam 1992). *N. viridula* f. *aurantiaca* was not included in the study. McLain (1981) showed that an orange color polymorphism discovered in an *N. viridula* population in Florida was sex linked and recessive.

N. viridula is a primary pest of macadamia nut in Hawaii and the focus of pest management studies (e.g., Golden et al. 2006). In June 2004, we collected two adult *N. viridula* f. *aurantiaca* in a patch of glycine, *Glycine wightii* (Wight and Arnott) Verdc., and castor bean, *Ricinus communis* L., next to a macadamia (*Macadamia* spp.) orchard in Pahala on the island of Hawaii (Golden and Follett 2007). During the next few months, we collected another 12 f. *aurantiaca* from the same site and brought them into the laboratory for rearing. This was the first discovery of the orange color morph in Hawaii since *N. viridula* was accidentally introduced in 1961 (Davis 1964). Thirteen of the 14 field-collected f. *aurantiaca* were males, suggesting this color polymorphism might be sex linked, as was determined for the orange color morph in Florida (McLain 1981).

Color polymorphisms can be used as markers to examine sperm precedence. *N. viridula* is polyan-

drous, and because *N. viridula* females can mate with multiple males, the opportunity exists for sperm competition. Possible outcomes of multiple inseminations are first-male precedence, second-male precedence, and random mixing of sperm. Last-male sperm precedence is the most prevalent in insects (Parker 1970, Simmons 2001). Multiple strategies are used by male insects to improve the competitive outcome of their sperm, including prolonged copulation, mate guarding, multiple inseminations, stratification of sperm, and flushing of sperm from previous matings (displacement) (Thornhill and Alcock 1983, Alcock 1994, Simmons 2001). *N. viridula* mates multiple times, and exhibits male guarding via prolonged postinsemination copulation. Stratification occurs when the last male's sperm lies over or in front of the sperm of earlier males in the spermatheca and is used first to fertilize eggs (the last in/first out principle). Sperm mixing can result in the use of sperm from multiple males during fertilization. Complete sperm mixing produces an equal contribution from all males, maximizing genetic diversity within each egg batch.

The orange color morph was used in crosses with the green morph to examine the inheritance mechanism of the orange morph and sperm precedence in *N. viridula*. An experiment also was performed to test for assortative mating between the orange and green color morphs.

Materials and Methods

Inheritance. *N. viridula* adults were collected in the wild and reared in screen cages (28 by 52 by 54 cm, width by length by height) in the laboratory on a diet of green beans, peanuts, and cabbage at $25 \pm 2°C$ and a photoperiod of 14:10 (L:D) h. Voucher specimens are located in P.A.F.'s collection at the USDA–ARS laboratory in Hilo, HI. Adults were allowed to mate randomly and then copulating pairs were removed and placed in individual screen cages (27 by 27 by 27 cm). Strips of paper towels were suspended from a wire extending between two sides in the middle of the cage to serve as an oviposition substrate. The green strain was started from equal numbers of males and females collected from several locations around the island of Hawaii, and new wild *N. viridula* from around the island were added to the colony regularly. The orange strain was started from 13 males and one female collected from Pahala, HI. Males were crossed with green females. To obtain a large number of orange females for crossing studies, female offspring of several green female × orange male crosses were backcrossed to the field-collected orange males.

Reciprocal crosses were made between cohorts of orange and green males and females in screen cages. To ensure virginity, cohorts were established using newly emerged second-generation adults that were collected daily during a 5-day period. The refractory period for females is ≈7–10 d (unpublished data). Once copulation occurred, pairs were isolated in individual containers and maintained until the death of the female. Mated females typically laid multiple egg masses. Egg masses were collected daily, and hatching nymphs were raised to adults to determine phenotype and sex. The color morph can be positively determined in third, fourth, and fifth instars (Fig. 1), but sex cannot be determined until the adult stage. The progeny of over 141 mated pairs representing six different crosses were raised and counted. The crosses were (female × male): green × green, orange × orange, orange × green, green × orange, F$_1$ heterozygous green × green, and F$_1$ heterozygous green × orange (see key to presumptive genotypes in Table 1 and crosses in Table 2). Data also were taken on female longevity, the number of eggs per mass, the number of infertile eggs, the number of eggs that developed but did not hatch, and the number of nymphs that hatched but did not leave the egg case (incomplete emergence). These data were used to compare the fitness of the various crosses.

Phenotype (green or orange) frequencies of F$_1$ male and female offspring (raised to adult) were subjected to chi-square analysis to determine whether they fit expected Mendelian ratios for a simple sex-linked recessive trait. Yates' correction for continuity was used for comparisons with only two expected phenotype categories (1 df) (Sheskin 2000). Fitness data were log transformed and subjected to analysis of variance (ANOVA) and means separations using a Tukey's test (SAS Institute 2002).

Sperm Precedence. Orange females were mated with orange males and allowed to lay two to three egg masses. The orange male was subsequently removed, and the female was allowed to produce another egg mass without a male. Then, a green male was introduced to the cage and allowed to mate with the orange female. The test was repeated using orange females but introducing the green male first and the orange male second. All offspring were raised to adults to determine phenotype and sex. Sperm use can be determined because all female offspring from the orange female × orange male cross ($X^gX^g \times X^gY$) are expected to be orange, whereas all female offspring from the orange female × green male cross ($X^gX^g \times X^GY$) are expected to be green.

In polyandrous organisms, *P2* is the statistic describing sperm use and is equal to the proportion of offspring attributable to the second of two competing males (Parker et al. 1990, Roderick et al. 2003). *P2* is often reported as a single statistic based on the overall outcome of sperm use by a group of individuals. In animals that produce multiple and distinct egg batches or clutches, as many insects do, *P2* can be calculated for each cohort. *P2* (x) is the partial *P2*, where x is the clutch number in a series of clutches (Roderick et al. 2003). Sperm precedence was summarized for each egg mass as *P2* (x). All statistical comparisons were performed on arcsine-transformed data.

Assortative Mating. A choice experiment was conducted to determine whether females distinguish between male phenotypes. Newly emerged adults were removed from the colony, transferred to cages for males or females, and held on the standard diet until testing. When sufficient adults were available, 10 fe-

Fig. 1. Green and orange body color morphs of *N. viridula* adults and five nymphal stages.

males of the green or orange phenotype were placed individually in separate empty screen cages (27 by 27 by 27 cm). One green male and one orange male were transferred to each cage and placed in proximity to the female. All cages were inspected every 15 min for a 4-h period, and pairing type was recorded. Females invariably mated only one time during the testing period, and once coupled, they remained so for the

Table 1. Genotypes for different color morphs of *N. viridula* f. *aurantiaca* assuming the orange trait is simple, sex linked, and recessive

Genotype	Sex	Phenotype
$X^G X^G$	Female	Green
$X^G Y$	Male	Green
$X^G X^g$	Female	Green
$X^g X^g$	Female	Orange
$X^g Y$	Male	Orange

G, dominant; g, recessive.

duration of the test. The experiment was replicated on four dates, which served as replicates.

Results and Discussion

Inheritance. Mendelian genetic analysis suggested that the orange body color of *N. viridula* f. *aurantiaca* is a simple sex-linked recessive trait (Table 2). Observed phenotypic ratios for male and female progeny were consistent with predicted Mendelian ratios for five of the six crosses. The cross between heterozygous green females ($X^G X^g$) and orange males ($X^g Y$) produced the correct phenotypes, but significantly more green offspring were produced than expected ($\chi^2 [1] =$ 4.4, $P < 0.05$). Also, significantly more orange males than females were produced in this cross than would be predicted by a typical 1:1 sex ratio ($\chi^2 [1] = 9.11$, $P < 0.01$). The skewed sex ratio in adults may reflect differences in survival of the sexes during development to the adult stage rather than true differences in

Table 2. Frequencies of color morph production for crosses and backcrosses between green and orange color morphs of *N. viridula* f. *aurantiaca*

Parental crosses			Expected ratio in progeny				Observed frequencies in progeny				
Assumed genotype	Female color	Male color	Green females	Green males	Orange females	Orange males	Green females	Green males	Orange females	Orange males	χ^2 value[a]
$X^GX^G \times X^GY$	Green	Green	1	1	—	—	569	569	—	—	0.0008
$X^GX^g \times X^gY$	Green	Orange	1	1	—	—	1497	1491	—	—	0.008
$X^GX^g \times X^GY$	Green	Green	2	1	—	1	32	17	—	18	0.16
$X^GX^g \times X^gY$	Green	Orange	1	1	1	1	343	300	248	321	16.41**
$X^gX^g \times X^GY$	Orange	Green	1	—	—	1	640	—	3	611	0.63
$X^gX^g \times X^gY$	Orange	Orange	—	—	1	1	—	—	404	389	0.25

[a] The χ^2 values followed by double asterisk (**) were significant at $P < 0.01$ by using a chi-square goodness-of-fit test. A significant chi-square test indicates frequencies departed from Mendelian ratios.

the sexes of progeny. The cross between orange females (X^gX^g) and green males (X^GY) produced three orange females, which was unexpected (Table 2); this result may have been caused by low-level incomplete dominance of the green trait in the heterozygous condition.

Strain Fitness. Homozygous green, homozygous orange, and heterozygous green females crossed with green or orange males did not differ in their longevity ($F_{2, 59} = 0.61; P = 0.68$) (Table 3). The average number of eggs per egg mass (data not shown) and the average net number of eggs per egg mass (subtracting infertile and incompletely emerged eggs) varied significantly among the genetic crosses ($F_{4,126} = 7.2; P < 0.001$ and $F_{4, 126} = 3.6; P < 0.01$, respectively). Wild-type green females crossed with orange males produced the highest average net eggs per egg mass, 50.6. The $X^gX^g \times X^GY$ and $X^gX^g \times X^gY$ crosses used in the sperm precedence studies produced an average of 31.7 and 28.3 net eggs per egg mass, respectively, which was not significantly different (Table 3).

Sperm Precedence. In sperm precedence studies using orange females crossed with green then orange males, or vice versa, the last male on average accounted for a greater proportion of offspring (Table 4). In the first test using green males in the second pairing, *P2* was 65% ($n = 12$). In the second test using the orange male in the second pairing, *P2* was 87.5% ($n = 7$). The average *P2* values were not significantly different between the two male reversal tests ($F_{1, 17} = 3.1; P = 0.10$), suggesting that sperm from orange males is not at a selective advantage over sperm from green males. Overall, the *P2* values for individual dams varied

from 23.5 to 100%, and the mean *P2* was $73.3 \pm 6.1\%$ (mean $\pm$ SEM). Regression analysis showed there was a slight trend toward an increase in *P2* with an increase in the number of egg masses laid [*P2* (x) = $66.9 + 4.7x$, $R^2 = 0.04$; egg masses 1–5 only], but the slope was not significantly different from 0 ($F_{1, 41} = 1.8; P = 0.18$). The data provide evidence for the sperm mixing, sperm stratification, and sperm displacement hypotheses. McLain (1981) reported low *P2* values in *N. viridula* (mean = 14–15%) in the first egg mass after remating. In our study, the average *P2* in the first egg mass laid after the new pairing was 71.8% ($n = 14$). In nine of the 14 dams, *P2* values were 85–100% in the first egg mass after remating, and values remained high in subsequent egg masses (Table 4). This pattern sug-

Table 4. Percentage of *N. viridula* offspring attributable to the second male (*P2*) for orange females mated to the two male phenotypes

Dams	Egg mass after introduction of second male						Total *P2*
	1	2	3	4	5	6	
Orange female $X^gX^g \times$ orange male (X^gY, first mating) $\times$ green male (X^GY, second mating)							
G28	—	29	—	18			23.5
G5	30						30.0
G27	38						38.0
G7	0	—	0	100	100		50.0
G26	—	0	100				50.0
G20	—	75	25	57			52.3
G6	71	—	—				71.0
G14	100	0	100	100			75.0
G41	88	89	100				92.3
G11	100	100	100	100	88	100	98.0
G4	100	100	100	100	100		100.0
G38	100	100	100	100	100	100	100.0
Orange female (X^gX^g) $\times$ green male (X^GY, first mating) $\times$ orange male (X^gY, second mating)							
O8	8	—	57	—	87		50.6
O1	85	—	—	83			84.0
O9	—	—	86				86.0
O13	85	100					92.5
O14	100	97	100	100			99.3
O10	—	100					100.0
O20	100						100.0

Orange or green sires were expected to produce 100% females of the same color. *P2* values are the percent F_1 adult females showing the same color as the second male. Families from each cross were sorted by total *P2* values. Egg masses producing no survivors to the F_1 adult stage are denoted by a dash.

Table 3. Fitness of the green, orange, and hybrid color morphs of *N. viridula* f. *aurantiaca*

Parental cross	n	Female longevity (d)	n	Avg. net eggs hatching/egg mass[a]
$X^GX^G \times X^GY$	3	44.0 (9.9)a	29	38.6 (3.9)ab
$X^GX^G \times X^gY$	22	45.5 (4.7)a	25	50.6 (3.6)a
$X^GX^g \times X^gY$	19	36.6 (6.1)a	38	34.6 (3.2)b
$X^gX^g \times X^GY$	11	41.8 (7.8)a	18	31.7 (6.7)b
$X^gX^g \times X^gY$	8	31.5 (10.8)a	21	28.3 (5.5)b

Information from the $X^GX^g \times X^GY$ cross omitted due to low numbers of females ($n = 3$).

gests sperm stratification, sperm displacement, or sperm depletion. Sperm in the spermatheca may have been somewhat depleted because females were allowed to lay an egg mass after removal of the first male and before remating. The sperm stratification hypothesis predicts $P2$ (x) would decrease over time as recently deposited sperm is depleted through use, removing the obstruction for previously deposited sperm to the aperture of the spermatheca. In many dams, $P2$ started and remained high and in a number of other dams $P2$ (x) increased over time, contrary to the sperm stratification model. Two of the dams produced five to six egg masses fertilized only by the second male ($P2 = 100\%$), suggesting sperm displacement. In six of the 17 dams, $P2$ never reached 100%, and most egg masses had fertilization from both pairings, indicating sperm mixing (Table 4). Last-male advantage operates in *N. viridula*, but variation is high; therefore, no one mechanism of sperm competition completely explains the observed data. Variation among dams in sperm precedence may be due partly to variation in male size, because large males were shown to fertilize more eggs than small males if the females remated (McLain 1985). The relatively high degree of sperm precedence is consistent with theoretical considerations for male guarding via prolonged postinsemination copulation (Alcock 1994). Prolonged postinsemination copulation prevents another male from mating and ensures the female will deposit an egg mass with eggs fertilized predominantly by the attending male.

Assortative Mating. In mating choice tests, green females choose orange males 79.6% of the time ($n = 29$), which was a significant departure from the expected 50% for random mating (χ^2 [1] = 8.8; $P < 0.01$) and suggested disassortative mating was operating. Orange females choose orange males 60.8% of the time ($n = 25$), which was not significantly different from the expected 50% (χ^2 [1] = 0.62; N.S.). Green females choose orange males more often than orange females choose orange males, but the difference was not significant ($F = 2.3$; df = 1, 6; $P < 0.18$). Females are known to choose larger males (McLain 1985). We did not measure male body size before each pairing in our study, but the average humeral width of orange males (mean = 7.1 mm, extremes 6.3–7.5 mm) was significantly larger than green males (mean = 6.8 mm, 6.3–7.2 mm, extremes 6.0–7.6 mm) ($F_{1,\ 38} = 4.7$; $P = 0.03$), which may have resulted in a bias toward choosing orange males.

Rarely are traits with assortative mating determined by alleles at a single locus, as seems to be the case with *N. viridula.* Disassortative mating will generally increase the frequency of heterozygous genotypes and decrease phenotypic variance (Hartl 1980). In *N. viridula*, preference of orange males by green females will tend to increase the frequency of the orange trait by increasing the number of heterozygous females above that expected by random mating. This is a possible mechanism for maintaining the alleles for the orange body trait in natural populations. Assortative mating

studies with heterozygous females were not attempted.

Frequency of the Orange Trait in the Field. The sex of *N. viridula* f. *aurantiaca* specimens collected in the field typically is not reported in the literature. Rare sex-linked traits are much more common in males than females because q^2 (q is allele frequency of the recessive trait) is much smaller than q when q is small. The frequency of *N. viridula* color morphs in populations across its range can be highly variable (Hokkanen 1986). The frequency of *N. viridula* f. *aurantiaca* in Japan was estimated from field collections as 0.0002, which in a randomly mating population would be approximately two in 10,000 males and four in 100 million females. In collections of *N. viridula* f. *aurantiaca* from the field in Brazil, 85% of the collected individuals were males ($n = 80$) (A. Panizzi, personal communication). For a simple sex-linked recessive trait in Hardy–Weinberg equilibrium, the allele frequency of the trait can be estimated from the percentage of males and females in a random sample of the population by using Mendelian ratios such that males/females = q/q^2. The orange males in the Brazilian collection are 5.67 times more common than females (85%/15%), indicating the gene frequency of the trait is ≈0.18 (q = 0.18 in males, q2 = 0.032 in females, q/q2 = 5.63). In our collections of *N. viridula* f. *aurantiaca* from one site in Hawaii, 92.9% were males. Repeating the same method as described above to calculate q from the observed sex ratio, the frequency of the orange allele in this population is estimated as 0.076. Repeated sampling of numerous macadamia orchards and other sites with wild hosts during 3 yr has produced no additional *N. viridula* f. *aurantiaca* on the island of Hawaii. The actual frequency of the orange trait in populations may be difficult to determine because a large random sample of the stink bugs often is not taken, and orange bugs may be easier to find on green host plants than green bugs, resulting in sampling bias.

The presence of the orange trait at low frequencies may allow *N. viridula* to adapt to changing environmental conditions (Vivan and Panizzi 2005, 2006). The use of color as camouflage has not been studied carefully in *N. viridula.* In Japan, where many color polymorphisms occur, birds and other visual searching vertebrates do not commonly feed on *N. viridula* (Kiritani 1970). Whether the orange polymorphisms provide defense against parasitoids or predaceous insects has not been reported but would be an interesting topic for future study.

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