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Andre Porter

Jack Frankel, *Howard University*



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Frequency-Dependent Mate Selection in the Guppy (*Poeciliidae: Poecilia reticulata*)

Andre N. Porter and Jack S. Frankel*

Department of Biology, Howard University, Washington, DC 20059, USA.

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Abstract

Heterogeneity within a population enhances its long-term survival. A fundamental method of maintaining population heterogeneity is the retention of rare or uncommon phenotypes by selective mating strategies. Employing two color morphs, red tuxedo and red, of the guppy (*Poecilia reticulata*, *Poeciliidae*), this study was designed to investigate whether *P. reticulata* females would preferentially seek out heterogeneous groupings of males exhibiting two color morphs. Adult female guppies were exposed simultaneously to two groups of males (n=10); one comprised of only the tuxedo color morph (n=5) and the other of both color morphs (n=5). For the latter group, the ratio of males exhibiting the two colorations was changed incrementally over multiple trials, beginning and ending with homogeneous groupings (5:0, 4:1, 3:2, 2:3, 1:4, 0:5). Experiments were conducted employing a 76 L aquarium partitioned at both ends to house the male groups. Individual females were placed into an acclimation, holding column located in the center compartment of the experimental aquarium. Subsequent to a five minute acclimation period in the holding column, each female was released. Courting behaviors and population affinities (i.e. female location relative to the male compartments) were recorded every five seconds over a five minute observation period. Females did not show a preference for male groupings exhibiting either the 4:1 or 1:4 color ratios. However, females clearly showed affinity for the male groupings of 3:2 and 2:3 ($p < 0.05$). This investigation on female mate choice in *P. reticulata* clearly reveals that a mating strategy is occurring in this species and that it is frequency-dependent.

Key Words: *Poecilia reticulata*, guppy, mate choice, frequency-dependent selection, color morphs.

Introduction

Genetic variation and phenotypic diversity are central concepts in evolutionary biology and closely linked to the complexity of organisms, ecosystem recovery, and the ability of species to respond to environmental changes (Bazin et al., 2006). Mate choice is known to be a powerful evolutionary mechanism influencing the stability and maintenance of polymorphisms within a species (Pryke and Griffith, 2007). In general, females of a species are more selective than males in discriminating among prospective mates, as they evaluate genetic quality and resource-holding potential based on secondary sexual characteristics, such as body size, coloration, ornamentation, and aggressiveness (Basolo, 1990; Clotfelter et al., 2006; Bierbach et al., 2013).

Elucidating mate choice strategies can assist in ascertaining and accessing possible cause and effect relationships in mating preference. Within non-random mating systems, selective mechanisms must be in place to maintain population heterogeneity. The retention of rare or uncommon phenotypes is a fundamental method of maintaining such heterogeneity. Thus, in species where mating is non-random, females are often found to be particularly selective when the parental male investment is low (Baldauf et al., 2009). Here, females would be expected to select and court with males that exhibit traits present in low phenotypic frequency (i.e. uncommon phenotypes), thereby ensuring that those phenotypes remain within the population. Utilizing such a frequency-dependent selection mating strategy, populations would ultimately exhibit an increase in the frequency of those rarer phenotypes, thereby insuring their genetic diversity (Gross, 1991; Pilastro et al., 1997; Punzalan et al., 2005).

Coloration has been shown to affect both species recognition and mate choice in poeciliid fishes (Endler, 1983). In fact, the maintenance and benefits of color variation in numerous species of poeciliids by selective mating strategies has been investigated in both natural and artificial populations (Borowsky and

* Corresponding author: jfrankel@Howard.edu

Kallman, 1976; Houde and Endler, 1990; Baer et al., 1994; Royle et al., 2008; Culumber and Rosenthal et al., 2013). Additional studies have illustrated the importance of coloration in mate selection by poeciliid females, where they exhibit a natural affinity towards certain colorations when shown a population of males containing phenotypically variable color morphs (Houde, 1997; Kingston et al., 2003).

The study presented here was designed to investigate the validity of frequency-dependent selection based on a body color polymorphism in the freshwater guppy *Poecilia reticulata* (Poeciliidae). The Poeciliidae include over 40 species from North, South and Central America, which occupy a wide range of habitats within these regions and exhibit both morphological and behavioral differentiation within and between species (Breden et al., 1999). As a group, they are relatively small fishes, ranging from 1.5 – 6.0 cm in length, with highly developed sexual dimorphisms.

The guppy, *P. reticulata*, one of the more common poeciliids, is distributed world-wide. This species ranges in size from 1.5 to 3.5 cm for adult males and from 3.0 to 6.0 cm for adult females. While native to Antigua, Barbados, Jamaica, Trinidad, Tobago, Brazil, Venezuela, and the U.S. Virgin Islands, populations of *P. reticulata* have been introduced to many other habitats and have readily occupied bodies of freshwater made accessible to them. The guppy is extremely popular in the aquarium trade, due to ease of upkeep and the colorfully ornamented caudal and dorsal fin morphs found in males through artificial selection. This species is not only sexual dimorphic with regard to both coloration and color intensity, but exhibits a wide array of shape and fin morphology polymorphisms as well.

As with other poeciliids, *P. reticulata* serves as an excellent model organism to employ in a study on frequency-dependent mate selection, since it exhibits both distinct and uniform color morphs. Utilizing red and red tuxedo color morphs, this study investigated whether *P. reticulata* females would preferentially seek out heterogeneous groupings of males as opposed to homogeneous ones. It is hypothesized that phenotypic heterogeneity amongst potential male mates is more attractive to females than a homogeneous grouping, as determined by observing the courting behaviors of females when confronted with these diverse male groupings.

Materials and Methods

To investigate female preference for male groups based on the phenotypic frequencies of two color morphs, a series of experimental trials were conducted employing similar constructs as those described for examining female color preference in the pygmy swordtail, *Xiphophorus pygmaeus* (Baer et al., 1994). In the work presented here, two phenotypes were chosen; a red tuxedo color morph exhibiting a red trunk with a dark blue caudal peduncle, red dorsal and caudal fins with dark blue margins, and a red color morph which displays a red trunk with red dorsal and caudal fins. These phenotypes were selected for their uniformity in overall coloration and color pattern from individual to individual within these two color morphs.

Adult guppies were obtained from G & G Aquatics Inc., Lor-

ton, VA., USA. Male and female guppies were housed in 76 L capacity, high configuration (61cm x 32cm x 42cm) holding aquaria during the course of this investigation. Females were chosen at random from an all-female stock population (n = 120) maintained in a dedicated aquarium. Males of each color morph were selected from initial stock populations (n = 80) for uniformity in total body length, dorsal and caudal fin lengths, and coloration. Males selected from the stock populations were maintained with individuals of like phenotypic coloration, i.e. red males with red males, tuxedo males with tuxedo males. Water temperature was maintained at 23 ± 2 °C by the laboratory HVAC system. Fish were fed TetraMin flakes twice daily. Water quality (ammonia, nitrite and nitrate) was assessed weekly. The pH level in all aquaria was maintained between 6.8 and 7.2.

Experimental trials were conducted in a 76 L capacity, long configuration (74cm x 20cm x 30cm) aquarium (Fig. 1). Groups consisting of five males (all-tuxedo, all-red, or tuxedo/red combinations) were held on either side of the experimental aquarium in 11cm x 20cm x 30cm male compartments, designated as Sections A and B. Male compartments were constructed with solid Plexiglas sheets secured to the aquarium with a continuous strip of aquarium silicon to physically separate males from females during the trials. Lighting consisted of fluorescent lights directly above the experimental aquarium. Additionally, three sides of the experimental aquarium were covered with white paper, leaving only the front and top uncovered to allow for observation of female location and courting behavior while eliminating distractions from the sides and back.

To begin each trial, two groups of five males were collected and placed in each of the male compartments. Initially, one section was selected for placement of all-tuxedo males and the other for all-tuxedo males, combinations of tuxedo and red males, or all-red males. Male groups were then subsequently designated as A or B; correlating with the corresponding partitioned side as seen in Figure 1. One female was then randomly chosen and placed in a Plexiglas acclimation column (11cm x 11cm x 50cm) located in the center of the experimental aquarium, designated as “no preference” Section D. Once a female was placed in the acclimation column, she was given a five minute acclimation period. When the acclimation period expired, the column was removed, releasing a female within section D and allowing her five minutes to move freely within that section and into areas A and B which are juxtaposed to the male compartments. The relative position of each female was designated by her location in A, B, or D and was recorded at five second intervals throughout the duration of each five minute trial period. Time intervals spent in section D was interpreted as “no preference,” while time intervals spent in preference areas A or B as “preferentially courting” males in sections A or B. After each trial, females were captured and placed in a separate holding aquarium to prevent reuse for a given trial set. To avoid side bias, all trial sets were repeated with male groupings switched from section A to B.

Eleven trials were conducted per paired male groupings. Adult female guppies were exposed simultaneously to two groups of males (n = 10); one comprised of only the tuxedo color morph (n = 5) and the other of the two color morphs (n = 5). For the latter group, the ratio of males exhibiting the two

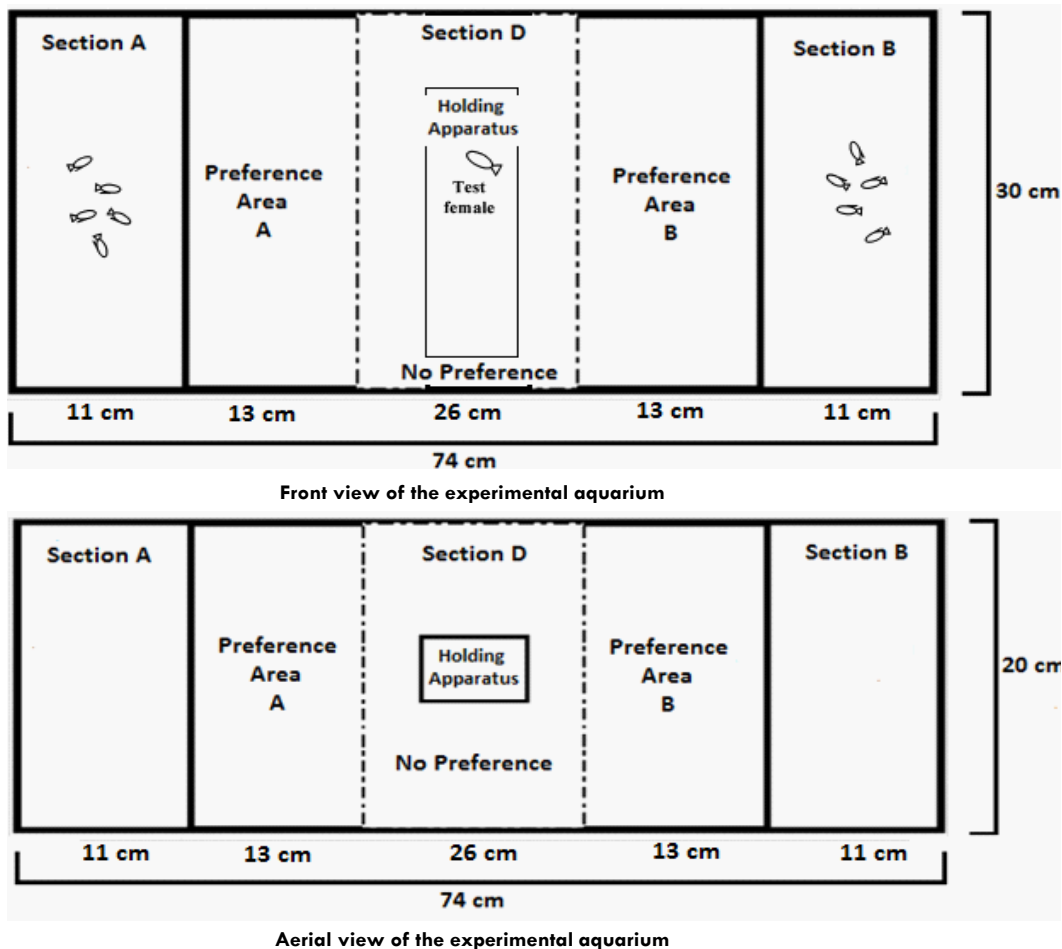


Figure 1. Front and top aerial views of the experimental aquarium. Overall dimensions were 74 cm long x 20 cm wide x 30 cm tall. Male compartments are labeled Sections A and B. The female preference areas, A and B, are juxtaposed to the male compartments. The female no preference area, labeled Section D, is in the center of the aquarium and contains the holding column.

colorations was changed incrementally over multiple trials, beginning and ending with homogeneous groupings (5:0, 4:1, 3:2, 2:3, 1:4, 0:5).

For this study, two complete trial sets were undertaken. For each individual trial (e.g. 1, 2a, 2b, 3a, 3b, etc.), 11 observations were recorded for 11 different females. Designations "a" and "b" indicate replicate trial observations. A total of 60 observations were recorded (one every five seconds for five minutes) per trial female, giving a total of 660 observations for each group of 11 females/trial. At the completion of all trial sets, a total of 12,540 data points were recorded. The data was then subjected to chi-square analysis for the probability of females deviating from the expected time interval allocation of 1:1 for movement into preference areas A or B due to chance alone. All trials were conducted under an approved Howard University IACUC protocol (IACUC-GSAS-11-03).

Results and Discussion

Table 1 presents the total five-second time allotments for 11 female guppies/trial occupying preference areas A and B when exposed to (i) all-tuxedo groupings in both male compart-

ments (Trial 1), (ii) all-tuxedo groupings opposed to tuxedo/red combinations (Trials 2a – 9b), and (iii) all-tuxedo groupings opposed to all-red groupings (Trials 10a and 10b). When confronted with paired homogeneous tuxedo groupings (Trial 1), females clearly showed no preference towards males in either compartment ($p = 0.491$). Further, females did not favor either all-tuxedo or all-red male groupings (Trials 10a and 10b), nor did they show an affinity towards 4 tuxedo: 1 red or 1 tuxedo: 4 red combinations (Trials 2a, 2b, 3a, 3b, 8a, 8b, 9a and 9b). In fact, females preferentially exhibited courting behaviors directed toward the homogeneous, all-tuxedo groupings when the 1 tuxedo: 4 red combination occupied the opposing compartment (Trials 8b and 9a). Females clearly exhibited a particular preference for male grouping of both 3 tuxedo: 2 red and 2 tuxedo: 3 red ($p < 0.001$; Trials 4b, 5b, 6a, 6b, 7a and 7b).

Total five-second time allotments for female guppies in preference areas A and B, when confronted with groupings of five tuxedo males and combinations of tuxedo and red males (Trials 3 – 8), are presented in Table 2. With the exception of trial sets 8b and 9a (1 tuxedo: 4 red occupying A and 5 tuxedo occupying B; 5 tuxedo occupying A and 1 tuxedo: 4 red occupying B, respectively), where females exhibited an affinity towards the

Table 1. Total time allocations per trial (in 5 second intervals) by females (n = 11) courting male groupings of red tuxedo and/or red color morphs, expected ratios, degrees of freedom (df), chi-square values, and probabilities.

| Compartment Trial | A/B | Time | | Expected | | Chi-square Value | Probability |
|----------------------|--------|----------------|----------------|----------|----|---------------------|-------------|
| | | Allocated in A | Allocated in B | Ratio | df | | |
| 1 | 5/5 | 230 | 245 | 1:1 | 1 | 0.474 | 0.491 |
| 2a. | 5/4:1 | 227 | 237 | 1:1 | 1 | 0.216 | 0.643 |
| 2b. | 5/4:1 | 185 | 205 | 1:1 | 1 | 1.026 | 0.311 |
| 3a. | 4:1/5 | 184 | 222 | 1:1 | 1 | 3.557 | 0.059 |
| 3b. | 4:1/5 | 170 | 190 | 1:1 | 1 | 1.111 | 0.292 |
| 4a. | 5/3:2 | 258 | 224 | 1:1 | 1 | 2.938 | 0.122 |
| 4b. | 5/3:2* | 145 | 225 | 1:1 | 1 | 17.297 | <0.001 |
| 5a. | 3:2/5 | 204 | 224 | 1:1 | 1 | 0.935 | 0.334 |
| 5b. | 3:2/5* | 270 | 110 | 1:1 | 1 | 67.368 | <0.001 |
| 6a. | 5/2:3* | 88 | 262 | 1:1 | 1 | 86.503 | <0.001 |
| 6b. | 5/2:3* | 95 | 200 | 1:1 | 1 | 37.373 | <0.001 |
| 7a. | 2:3/5* | 299 | 199 | 1:1 | 1 | 20.080 | <0.001 |
| 7b. | 2:3/5* | 305 | 220 | 1:1 | 1 | 13.762 | <0.001 |
| 8a. | 5/1:4 | 191 | 193 | 1:1 | 1 | 0.010 | 0.919 |
| 8b. | 5/1:4 | 255 | 205 | 1:1 | 1 | 5.435 | 0.020 |
| 9a. | 1:4/5 | 153 | 215 | 1:1 | 1 | 10.446 | 0.001 |
| 9b. | 1:4/5 | 160 | 195 | 1:1 | 1 | 3.451 | 0.063 |
| 10a. | 5/5 | 246 | 253 | 1:1 | 1 | 0.098 | 0.754 |
| 10b. | 5/5 | 210 | 205 | 1:1 | 1 | 0.060 | 0.806 |

*Females preferentially courting male groups of 3 red: 2 red tuxedo or 2 red: 3 red tuxedo over all-red tuxedo groupings. Numbers in red and blue denote the number of red and red tuxedo morphs used within the compartment.

Table 2. Total time allocations per trial (in 5 second intervals) by females (n = 11) courting heterogeneous male groupings of red tuxedo and red color morphs and all-red tuxedo groupings, expected ratios, degrees of freedom (df), chi-square values, and probabilities.

| Trial | A/B | Time Allocations | | Expected | | Chi-square Value | Probability |
|----------------------|--------|-----------------------------|----------------------------|----------|----|---------------------|-------------|
| | | Courting Red Tuxedo/ Red | Courting All-Red Tuxedo | Ratio | df | | |
| 3a. | 4:1/5 | 184 | 222 | 1:1 | 1 | 3.557 | 0.059 |
| 3b. | 4:1/5 | 170 | 190 | 1:1 | 1 | 1.111 | 0.292 |
| 5a. | 3:2/5 | 204 | 224 | 1:1 | 1 | 0.935 | 0.334 |
| 5b. | 3:2/5* | 270 | 110 | 1:1 | 1 | 67.368 | <0.001 |
| 7a. | 2:3/5* | 299 | 199 | 1:1 | 1 | 20.080 | <0.001 |
| 7b. | 2:3/5* | 305 | 220 | 1:1 | 1 | 13.762 | <0.001 |
| 9a. | 1:4/5* | 153 | 215 | 1:1 | 1 | 10.446 | 0.001 |
| 9b. | 1:4/5 | 160 | 195 | 1:1 | 1 | 3.451 | 0.063 |
| 2a. | 4:1/5 | 237 | 227 | 1:1 | 1 | 0.216 | 0.643 |
| 2b. | 4:1/5 | 205 | 185 | 1:1 | 1 | 1.026 | 0.311 |
| 4a. | 3:2/5* | 224 | 258 | 1:1 | 1 | 2.938 | 0.123 |
| 4b. | 3:2/5* | 225 | 145 | 1:1 | 1 | 17.297 | <0.001 |
| 6a. | 2:3/5* | 262 | 88 | 1:1 | 1 | 86.503 | <0.001 |
| 6b. | 2:3/5* | 200 | 95 | 1:1 | 1 | 37.373 | <0.001 |
| 8a. | 1:4/5 | 193 | 191 | 1:1 | 1 | 0.010 | 0.919 |
| 8b. | 1:4/5* | 205 | 255 | 1:1 | 1 | 5.435 | 0.002 |
| Total | | | | | 16 | 270.508 | <0.001 |
| Pooled | | 3496 | 3019 | 1:1 | 1 | 34.924 | <0.001 |
| Heterogeneity | | | | | 15 | 235.584 | <0.001 |

*Trials with significant chi-square values (p < 0.05). Numbers in red and blue denote the number of red and red tuxedo morphs used within the compartment.

all-tuxedo grouping, they did not show a preference for either all-tuxedo or 1:4 or 4:1 groupings. Further, while females were clearly attracted towards those male groupings with combinations of 3:2 and 2:3, they overwhelmingly selected heterogeneous groupings in general, regardless of compartment location ($p < 0.001$). Table 3 illustrates the comparison of total five second allotments spent within preference areas A or B as compared to those observed for females in the no-preference area D. Here, clear indications of choice were apparent, with females spending significantly more time outside of the no preference section D in 16 of 19 trial sets.

There are many potential explanations for the coexistence of color polymorphisms within populations. In practice, however, it has proven difficult to determine which mechanisms explain the presence of multiple color variants within any particular population (Munday et al., 2003). Female mate choice has been proposed as a means of increasing diversity where a strong preference for rare or novel color patterns is indicated. However, this "rare male" advantage will be detectable only when phenotype frequencies are perturbed from their equilibrium values (Hughes et al., 2013).

The results obtained from this investigation of mate choice in *P. reticulata* provide strong evidence towards female mating preference for groupings of males exhibiting multiple phenotypes. Data compiled from this study clearly indicates that when female guppies are presented with a choice between males that exhibit a single phenotype or multiple phenotypes, they exhibit some preference towards the latter. Further, in 16 of the 19 com-

plete trials, female time allocations towards preference groups (i.e. making a courting decision) exceeded the time spent for making no courting choice (i.e. remaining in section D) and is consistent with findings in other mate selection studies (Kodric-Brown, 1985; Baer et al., 1994; MacLaren and Fontaine, 2012).

As trials extended beyond the initial all-tuxedo groupings, females showed no preference for male phenotypic combinations of 4:1 (Trials 2a, 2b, 3a, 3b) or 1:4 (Trials 8a, 8b, 9a, 9b). In fact, females exhibited an affinity towards the all-tuxedo male grouping when confronted with that homogeneous grouping and the 1 tuxedo: 4 red combination (Trials 9a and 8b; $p < 0.05$) and occurred whether the all-tuxedo grouping occupied section A or B. In effect, for trials where male groupings had a phenotypic frequency of 0.20 for the "rare" color morph, females showed no statistically significant preference for those groups. As the phenotypic frequency of the initially rare color morph increased to 0.40, the affinity of female guppies for those male groupings became evident. Of the eight trial sets comprised of color ratios of 2:3 or 3:2, six resulted in statistical significance of female mate choice for these combinations. This clear affinity of females towards male groupings exhibiting 40 % rarity for either tuxedo or red color morphs may, in part, be due to a phenotypic threshold for frequency-dependent selection for this trait. Roff (1998) has provided evidence that certain levels of phenotypic variation may be maintained in a population at some "threshold level" and suggests that frequency-dependent selection can give rise to, and maintain, polymorphisms in a population. This may speak to an equilibrium state where male groups

Table 3. Time allocations per trial (in 5 second intervals) by females ($n = 11$) courting males in preference areas A or B, or making no decision and remaining in no preference section D, expected ratios, degrees of freedom (df), chi-square values, and probabilities.

| Compartment | Time | Time | Expected | Chi-square | Probability | | |
|-------------|-------|--------------|-----------|------------|-------------|---------|--------|
| Trial | A/B | Allocated To | Allocated | Ratio | df | Value | |
| | | A or B | To D | | | | |
| 1. | 5/5 | 475 | 185 | 1:1 | 1 | 127.424 | <0.001 |
| 2a. | 5/4:1 | 464 | 196 | 1:1 | 1 | 108.824 | <0.001 |
| 2b. | 5/4:1 | 390 | 275 | 1:1 | 1 | 21.818 | <0.001 |
| 3a. | 4:1/5 | 406 | 254 | 1:1 | 1 | 35.006 | <0.001 |
| 3b. | 4:1/5 | 360 | 300 | 1:1 | 1 | 5.455 | 0.020 |
| 4a. | 5/3:2 | 482 | 178 | 1:1 | 1 | 140.024 | <0.001 |
| 4b. | 5/3:2 | 370 | 290 | 1:1 | 1 | 9.697 | 0.002 |
| 5a. | 3:2/5 | 428 | 232 | 1:1 | 1 | 58.206 | <0.001 |
| 5b. | 3:2/5 | 380 | 280 | 1:1 | 1 | 15.152 | <0.001 |
| 6a. | 5/2:3 | 350 | 310 | 1:1 | 1 | 2.424 | 0.120 |
| 6b. | 5/2:3 | 295 | 365 | 1:1 | 1 | 7.424 | 0.006 |
| 7a. | 2:3/5 | 498 | 162 | 1:1 | 1 | 171.055 | <0.001 |
| 7b. | 2:3/5 | 525 | 135 | 1:1 | 1 | 230.455 | <0.001 |
| 8a. | 5/1:4 | 384 | 276 | 1:1 | 1 | 17.673 | <0.001 |
| 8b. | 5/1:4 | 460 | 200 | 1:1 | 1 | 102.424 | <0.001 |
| 9a. | 1:4/5 | 368 | 292 | 1:1 | 1 | 8.752 | 0.003 |
| 9b. | 1:4/5 | 355 | 305 | 1:1 | 1 | 3.788 | 0.052 |
| 10a. | 5/5 | 499 | 161 | 1:1 | 1 | 173.097 | <0.001 |
| 10b. | 5/5 | 415 | 245 | 1:1 | 1 | 43.788 | <0.001 |

Numbers in red and blue denote the number of red and red tuxedo morphs used within the compartment.

of ~20% for a novel phenotype represent a threshold level with the common phenotype (Hughes et al., 2013). Therefore, evidence exists that traits being maintained through frequency-dependent mating strategies may be not only driven by these disruptive mating strategies, but also maintained by them. In the research presented here, the affinity of females towards 2:3 and 3:2 heterogeneous male groupings when the color morphs reach frequencies between 0.40 and 0.60 may flag a threshold for female mate choice for these particular color morphs in *P. reticulata*.

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