

Dimensionality of mate choice, sexual isolation, and speciation

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Multiple cues, across multiple sensory modalities, are involved in mate choice in a wide range of animal taxa. This multiplicity leads to the prediction that, in adaptive radiations, sexual isolation results from divergence in multiple dimensions. However, difficulties in directly measuring preferences and detecting multiple effects limit our ability to empirically assess the number of independent traits contributing to mate choice and sexual isolation. We present an approach to estimate the dimensionality of sexual isolation using mating trials across groups of related populations. We analyze nine radiations: seven in fruit flies (*Drosophila*) and one each in salamanders (*Desmognathus*) and cichlid fishes (*Pseudotropheus*). We find strong evidence that multiple latent traits—linear combinations of phenotypic traits and preferences—are responsible for the patterns of sexual isolation in all nine radiations but that dimensionality has a strong upper limit. Just two latent traits are implicated in the majority of cases. Mapping along latent trait axes tests predictions of sexual-selection models and allows correlation with specific phenotypic traits and functional components of mate choice. We find support for the role of stabilizing natural selection on the sexually selected (male) traits. In the cichlids, latent-trait axes incorporate male-coloration patterns and exhibit convergence as well as divergence among populations. In the salamanders, temporal patterning in sensory modalities and male vs. female preferences are reflected in different latent-trait axes.

behavioral isolation | female preference | multidimensional scaling | prezygotic isolation | sexual selection

Sexual isolation arising from disruptions in sexual communication is central to the process of speciation (1, 2), and such disruptions may arise from trait divergence driven by sexual selection (3, 4). Mate choice can involve a wide range of sensory modalities (chemical, auditory, visual, tactile, etc.), and multitrait, multimodal sexual communication is apparent across many animal taxa (5–8). Even within a single sensory modality (e.g., acoustic signaling in anurans), temporal patterning of signals is often complex and multivariate (7, 9). A few direct measurements of sexual selection have shown multivariate mate choice (10–16).

Unfortunately, most studies of mate choice focus on just one or two traits because of difficulties in detecting multivariate effects and directly measuring mate preference (7, 17). Furthermore, we lack a way to estimate the total number of functionally independent traits involved—the dimensionality of mate choice. This issue is analogous to the dimensionality of genetic variation for phenotypic traits; whereas genetic variation may be observed in many single traits, the prevalence of genetic correlation constrains the response to selection and phenotypic divergence (14, 18–21). We do not know to what extent the dimensionality of mate choice constrains the evolution of sexual isolation and speciation by sexual selection.

Here, we describe a method for determining the dimensionality of mate choice and sexual isolation. We use data from surveys of sexual isolation rather than direct examination of candidate traits. Sexual (behavioral) isolation is the degree to which the incidence of mating between populations is less than that within populations, which is assessed in mating trials (22). Ideally, multiple

populations are surveyed so that sexual isolation is measured in all or most of the possible pair-wise combinations.

Our analysis builds on quantitative genetic models that describe the joint evolution of male traits and female preference, typically assuming both to be polygenic and normally distributed (23). Previous work extended such models to assess the effect of a single linear combination of traits on sexual isolation among populations (24, 25). We refer to such a combination as a latent trait. Here, we allow any number of independent latent traits (Fig. 1). Mating probability between males and females is a function of the distance between male traits and female preferences along all of the latent-trait axes (or equivalently, female traits and male preferences, some combination of both, or any set of quantitative traits for which similarity between males and females determines probability of mating). We use information-criterion statistics to determine the number of latent traits that best explains the observed pattern of sexual isolation and mate choice within and among populations in nine radiations across three taxa (24, 26–31).

Results

Dimensionality of Sexual Isolation. We estimated the dimensionality of sexual isolation in nine radiations—seven from *Drosophila* and one each from species complexes in the salamander genus *Desmognathus* and the cichlid fish genus *Pseudotropheus*. All nine radiations exhibit divergence along multiple latent-trait dimensions (Table 1). However, there is strong evidence for an upper limit to dimensionality. In all cases, the best-fit number of dimensions [i.e., with the lowest Akaike Information Criterion (AIC) score] is much less than the maximum; all but two of the datasets require just two latent-trait dimensions. The remaining datasets require three and four latent-trait dimensions, respectively, and in the latter case (*D. prosaltans*), the AIC scores are nearly indistinguishable between three and four dimensions. In addition, both the log-likelihood values and the effective number of dimensions n_D (19) reach a plateau at a dimensionality d well below the maximum (Table 1). Thus, as the points are placed in higher-dimensional spaces with d approaching the number of populations, the best-fit arrangement still occupies a subspace of dimensionality less than d . In fact, n_D does not exceed three for any radiation and shows no correlation with the number of populations sampled (Spearman $\rho = 0.085$, $P = 0.83$) (32).

Models of Sexual Selection. Patterns of divergence along latent-trait axes (Fig. 2) test some predictions of sexual-selection models. Important factors are natural selection on the male trait(s), typically modeled as a Gaussian fitness function with width ω^2 ,

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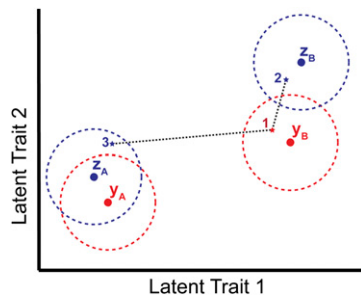


Fig. 1. Schematic diagram of the mate-choice model for two populations (A and B) in two latent-trait dimensions, with population means (solid circles) and within-population variation (dashed circles) for male traits (blue; z) and female preferences (red; y). The probability of mating between, for example, a female chosen randomly from population B (star 1) and a male chosen from either the same population (star 2) or population A (star 3) is a function of the distance between them (black dotted lines) in this phenotypic space.

and strength of female mating preference, a Gaussian function with width v^2 (23, 33). In seven of nine datasets, female latent-trait means exhibit greater divergence across populations than male means [measured as the trace of the within-sex, among-population (co)variance matrix] (Fig. 2 C and G). The model by Lande (33) predicts greater divergence among female means (equation 20 in ref. 33), and this effect is more pronounced if stabilizing natural selection on the male trait is strong relative to female preference (i.e., ω^2 is small relative to v^2). Thus, our results suggest that natural selection generally constrains the male traits.

The datasets differ in relative amounts of among-population versus within-population (between-sex) divergence; redundancy indices report the proportion of variance in each sex that is explained by the other sex (Fig. 2). The model by Lande (33) predicts (equation 10 in ref. 33) that, at equilibrium, the expected distance between the male and female mean should be roughly proportional to v^2/ω^2 and the deviation of the male mean from its optimum. This result suggests that, in some taxa (Fig. 2H), in which the means are close together, female preferences are strong (small v^2), and/or stabilizing natural selection on the male traits is weak (large ω^2). In other groups (Fig. 2C), female preferences are apparently weak (large v^2), and/or natural selection on the male traits is strong (small ω^2).

Some models of sexual selection predict an equilibrium deviation between male and female values within populations (24, 25, 33, 34). Across related species lying along an equilibrium line or plane, consistent directional natural selection on the male trait(s) would produce a consistent direction of deviation between males and females, maintained by a tension between sexual selection and natural selection on the male trait. We found scant evidence for this prediction; the mean within-population male to female vector differed significantly from zero in only one of nine radiations (Fig. 2H) (Hotelling's $t^2 = 113.8$, $P = 0.03$).

Testing Other Hypotheses. Divergence along latent-trait axes mirrors taxonomic assignment of populations in some cases. The largest redundancy indices occur in a dataset with multiple species (Fig. 2H), illustrating among-species divergence. In the *Desmognathus* group, which was split into three species (35) after mating trials were conducted, the latent-trait values cluster the populations concordant with taxonomic revision (Fig. 2A). In contrast, in *Pseudotropheus*, our results support previous inferences of parallel evolution and a lack of phylogenetic signal in traits involved in mate choice; phylogenetic analysis places the Chisumulu (CH) population outside a clade containing the other four pop-

Table 1. Dimensionality of sexual isolation for nine datasets

d	c or p	$\ln L$	par	cAIC	n_D
<i>D. ochrophaeus</i> complex (nine populations) (24)					
1	0.59	-214.22	18	464.43	1.00
2	0.71	-139.28	34	346.57	1.47
3*	1.00*	-119.62*	49*	338.24*	1.65*
4	1.00	-113.48	63	354.96	1.76
5	1.00	-111.86	76	378.72	2.00
6	1.00	-111.13	88	402.26	2.06
7	1.00	-111.02	99	425.04	2.04
8	1.00	-111.02	109	446.03	2.03
<i>D. paulistorum</i> (Amazonian race; four populations) (26)					
1	1.00	-45.54	8	107.07	1.00
2*	0.82*	-36.16*	14*	100.32*	1.56*
3	0.93	-35.41	19	108.83	1.76
<i>D. paulistorum</i> (Andean-South Brazilian race; eight populations) (26)					
1	0.82	-121.43	16	274.86	1.00
2*	1.00*	-89.16*	30*	238.32*	1.60*
3	1.00	-86.70	43	260.41	1.94
4	1.00	-86.70	55	285.40	2.00
5	1.00	-86.70	66	307.39	2.00
6	1.00	-86.70	76	328.39	2.07
7	1.00	-86.70	85	347.39	2.07
<i>D. paulistorum</i> (multiple races; seven populations) (26)					
1	0.82	-145.44	14	318.89	1.00
2*	1.00*	-57.88*	26*	167.76*	1.22*
3	1.00	-53.98	37	182.96	1.37
4	1.00	-53.94	47	202.87	1.39
5	1.00	-53.94	56	221.87	1.39
6	1.00	-53.94	64	238.87	1.39
<i>D. sturtevantii</i> (five populations) (27)					
1	0.53	-112.10	10	244.20	1.00
2*	0.60*	-71.42*	18*	178.84*	1.80*
3	0.64	-66.72	25	183.45	2.38
4	0.62	-66.70	31	195.39	2.38
<i>D. willistoni</i> (five populations) (28)					
1	0.69	-66.99	10	153.98	1.00
2*	0.75*	-51.57*	18*	139.15*	1.62*
3	0.77	-51.15	25	152.29	2.01
4	0.78	-51.15	31	164.29	2.17
<i>D. prosaltans</i> (seven populations) (29)					
1	1.00	-232.73	14	493.47	1.00
2	1.00	-156.99	26	365.98	1.50
3	1.00	-130.75	37	335.50	2.05
4*	1.00*	-120.40*	47*	334.81*	2.46*
5	1.00	-118.87	56	349.74	2.41
6	1.00	-118.67	64	366.33	2.36
<i>D. auraria</i> complex (four species) (31)					
1	0.89	-279.09	8	574.19	1.00
2*	1.00*	-53.68*	14*	135.36*	1.75*
3	1.00	-53.60	19	145.20	1.77
<i>P. zebra</i> complex (five populations) (30)					
1	81.28	-52.98	10	127.95	1.00
2*	59.19*	-35.70*	18*	114.41*	1.34*
3	77.52	-32.12	25	128.24	2.03
4	74.11	-31.68	31	148.35	2.25

The constant p is estimated under the Poisson model (*Pseudotropheus*), and c is estimated under the binomial model (all others). $\ln L$, log likelihood of the full model; par, number of parameters; cAIC, corrected Akaike Information Criterion; n_D , effective number of dimensions.

*For each dataset, the best-fit number of dimensions d .

ulations (36), contrary to the clustering along latent-trait axes (Fig. 2I). The datasets differ widely in the distribution of divergence among latent-trait axes, such that the primary axis accounts for anywhere from 41.6% to 81.6% of the total variance

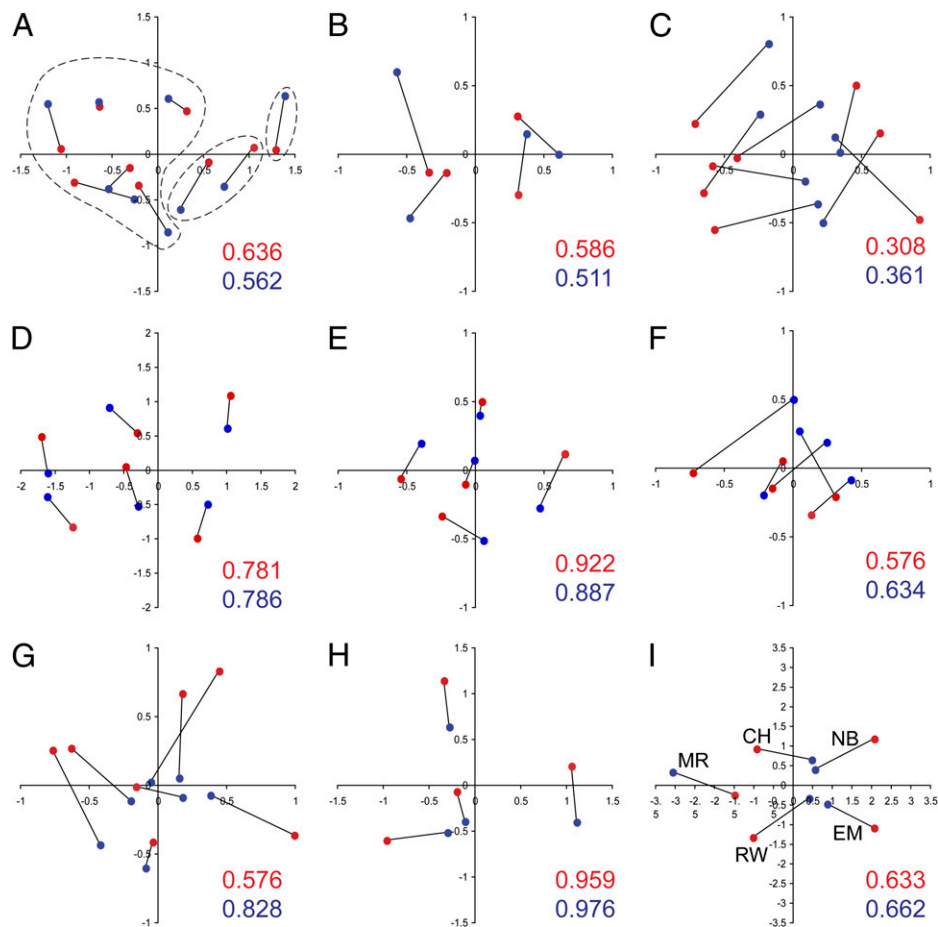


Fig. 2. Best-fit male (blue) and female (red) population means for latent traits underlying sexual isolation in nine radiations. Black lines link male and female means for each population. For all but A and G, these two axes represent the best-fit number of dimensions; for A and G, these are the first two of three or four axes, respectively. Canonical correlation-redundancy indices (bottom right of each plot) show the proportion of female variance explained by males of the same population (red) and male variance explained by females (blue). (A) *Desmognathus* (24); dashed lines enclose populations in three currently recognized species. (B) *D. paulistorum*, Amazonian race (26). (C) *D. paulistorum*, Andean–South Brazilian race (26). (D) *D. paulistorum*, multiple races (26). (E) *D. sturtevantii* (27). (F) *D. willistoni* (28). (G) *D. prosaltans* (29). (H) *D. auraria* complex (31). (I) *Pseudotropheus* (30); labels indicate populations.

across traits (Fig. S1). They also differ substantially in the degree to which males and females diverge along separate axes (Fig. 2H versus 2C and Fig. S1).

Linking Latent Traits to Phenotypes. Latent-trait mapping in *Pseudotropheus* indicates some correlates with male nuptial coloration (Fig. 2I). Our results support a hypothesis (30) that two populations, Nkhata Bay (NB) and CH, show a low level of sexual isolation because of similar coloration in the males, evidenced by the males’ similar latent-trait values, despite phylogenetic distance. Two discrete male coloration traits vary conspicuously among these five populations (36). Yellow chest occurs only in Mara Rocks (MR), and this difference explains 98.8% of the variance among males along latent-trait axis 1. In contrast, the orange dorsal phenotype occurs only in Mphanga Rocks *emmilotos* (EM), accounting for minimal proportions of variance in either latent trait.

In *Desmognathus*, courtship is a multiphase process, and termination at different phases may reflect the contribution of different sensory modalities or functional components of mate choice to overall sexual isolation. We assessed the contribution of these factors to the three latent traits using correlation analysis on male–female distances along each axis and four behavioral measures of sexual isolation (37): the proportions of mating trials ending with no sexual activity, ending after the persuasion phase, and ending after the persuasion phase, and the time taken

to reach the persuasion phase in pairs that reached it (Table 2). One correlation remained highly significant after correction for false discovery rate (FDR) (38)—that between latent trait 1 and termination after the pursuit phase (Spearman $\rho = 0.569$, $P = 0.0008$). The correlation between latent trait 2 and time to persuasion was elevated but not significant after FDR correction because of a smaller sample size ($\rho = 0.496$, $P = 0.028$).

Discussion

Dimensionality of Mate Choice and Sexual Isolation. We found consistent support for the view that multiple cues are used in mate choice, but we also found that only a small number of independent latent traits are actually responsible for sexual isolation among populations in a radiation. Each latent trait may be a linear combination of many actual phenotypic traits, which are strongly correlated with each other across populations in their contribution to sexual isolation.

A central assumption in this analysis is that the linear combinations of traits and preferences that make up the latent traits remain constant across the radiation. A few lines of evidence support this assumption and the conclusion that divergence may proceed repeatedly along a limited number of latent-trait axes. Radiation among similar environments may lead to parallel evolution in mate-choice traits, either as a byproduct of divergent selection on other traits or because of direct environmental correlates with

Table 2. Correlation of latent traits with phases of courtship in *Desmognathus*

Latent trait	No activity	Pursuit	Persuasion	Time to persuasion
1	0.307 (0.093)	0.569 (0.0008)*	0.403 (0.025)	−0.066 (0.782)
2	0.302 (0.099)	0.410 (0.022)	0.190 (0.306)	0.496 (0.028)
3	−0.088 (0.637)	0.089 (0.634)	0.099 (0.595)	−0.081 (0.734)

Shown are Spearman rank correlation coefficients (P values) between pair-wise male–female distances along latent-trait axes in the best-fit model and measures of the behavioral basis of sexual isolation from ref. 37. The first three measures are proportions of mating trials that terminate at the listed phase, given that they progressed through the previous phase (calculated from table 3 in ref. 37). Time to persuasion is mean time before the persuasion phase, given that a pair progressed to this phase (table 4 in ref. 37). For time to persuasion, $n = 20$; for all others, $n = 31$.

*Correlation is significant at the $\alpha = 0.05$ level after correction for FDR (38).

mate-choice factors (39–42). Male nuptial coloration patterns have evolved repeatedly in Lake Malawi cichlids, including the populations analyzed here (36). Hypotheses for constraints on divergence in nuptial coloration include the physical aspects of color vision in the lake and feeding ecology (36). Correlation among mate-choice traits may also arise, because multiple cues are indicators of a smaller number of underlying axes, such as body condition of prospective mates (43–47). Finally, strong genetic correlations among traits may constrain divergence by both sexual selection and genetic drift by limiting the dimensionality of the G matrix of additive genetic variation. In *Drosophila* species, such strong correlations have been observed among both cuticular hydrocarbon (CHC) traits in males and female preferences for those traits (16, 48).

Implicit in the analysis is that the phenotypic covariance structure among traits and preferences within males and females, as well as the covariance structure of the multivariate preference functions, is constant across populations within a radiation (*Methods*). Comparative empirical data are limited, although similarity in the genetic covariance structure of CHCs has been observed across populations in *Drosophila* (49, 50). We conducted numerical simulations to test the effect of this assumption of constant covariance structure on estimates of dimensionality. Variable covariance structure creates variation in, but does not systematically bias, the estimated dimensionality of sexual isolation. Thus, the upper limit to dimensionality of sexual isolation among populations is robust to relaxation of this assumption (*SI Text* and *Fig. S2*).

Finally, our analysis assumed unimodal preference functions (*Methods*). The functional form of individual preferences is difficult to estimate (7), but a few studies suggest that unimodal preference functions are common in nature (9, 23, 51–53). Also observed are open-ended preference functions (7, 54). Further analysis is needed to test whether open-ended preferences result in substantially different estimates of dimensionality. Better still, a comprehensive analysis would allow multiple functional forms of preference to co-occur for different traits (13, 55).

From Latent Traits to Specific Phenotypes. Our method does not identify traits responsible for sexual isolation; however, it suggests testable hypotheses about specific phenotypes. After populations are mapped onto latent-trait space, correlation with traits, preferences, and functional components of the mate-choice process can be assessed. In many organisms, observational and experimental studies provide lists of candidate traits. Because of the difficulties in assessing preferences directly (7), this correlational exercise may be most fruitful using more easily measured (usually male) phenotypic traits.

In plethodontid salamanders such as the *Desmognathus* species, courtship consists of several distinct phases: male identification and pursuit of the female, a persuasion phase during which the male delivers pheromones to the female, and spermatophore deposition and sperm transfer (34, 56). Different sensory modalities are used: vision during the pursuit phase, chemical communication during

pursuit and persuasion, and tactual communication during sperm transfer (57). Breakdown in sexual communication at different phases implicates different traits and preferences as well as different sensory modalities in sexual isolation. For instance, breakdown of mating after the pursuit phase suggests incompatibility between male pheromones and their perception by females. This aspect of isolation correlated strongly with latent trait 1. Thus, latent trait 1 may primarily reflect the role of chemical communication in sexual isolation. We also found a weak relationship between divergence along latent trait 2 and time to reach the persuasion phase. During this period, the male uses visual and chemical cues to evaluate a female as a potential mate. Latent trait 2 may incorporate female traits assessed during this period (e.g., size and pheromones) and male perception of them. These relationships suggest that mate choice and sexual isolation may be somewhat modular—that evolution of different functional clusters of traits and preferences, grouped both by sensory modality and temporal phase during courtship, may occur independently.

Male coloration plays an important role in courtship and sexual isolation in the Lake Malawi cichlid fishes (36, 58). Our analysis is consistent with the role of male coloration patterns. We also confirmed that populations can diverge as well as converge along trait axes (36). Despite the myriad of visual, behavioral, auditory, and olfactory traits apparently involved in sexual selection in these taxa (59–61), divergence among populations is limited to just a few combinations of traits. In our analysis, this limit is manifest as a relatively small dimensionality; in a phylogenetic approach (36), it is apparent that replicate populations converge on similar phenotypes, and the number of male coloration patterns is surprisingly limited.

Limits to Dimensionality of Sexual Isolation. In all nine radiations, we observed an apparent upper bound to the dimensionality of sexual isolation. These populations likely diverge across a large number of phenotypic traits or preferences, and these traits together form a high-dimensional space. Within this space, however, the populations occupy a much smaller-dimensional subspace. This result may find an explanation in sexual-selection models. A general prediction is that the dimensionality of the equilibrium equals the number of genetically independent traits minus the number of selective constraints (62, 63). For example, when two traits (e.g., a male trait and female preference for that trait) evolve but only one is under selection, the expected equilibrium is a one-dimensional line (33). At any point on the equilibrium, the forces of natural and sexual selection balance, and the population drifts freely (25, 33). The dispersion of populations (*Fig. 2*) may reflect stochastic differentiation on a two-, three-, or four-dimensional equilibrium. Under this interpretation, the latent traits that we identified represent combinations of multiple traits and preferences, and the correlations among these traits are maintained by the forces of natural and sexual selection leading to equilibrium. Alternatively, if all traits and preferences are subject to direct natural selection, the equilibrium reduces to a point (64). In this

case, divergence among populations could be the result of movement of the natural-selective optima for the traits. The pattern of movement of these optima would determine the dimensionality of sexual isolation. Comparative analysis of natural selection on key traits may be able to distinguish these scenarios.

Our finding that multiple traits are involved in sexual isolation but that the number of functionally independent traits is limited carries several implications for understanding speciation driven by sexual selection. First, it reinforces the empirical strategy of testing multiple traits in studies of mate choice, sexual selection, and speciation. Second, because quantitative genetic models of sexual selection have almost always focused on a single male trait and a single female preference (23, 65, 66), these models have likely underestimated the rates at which ornamental traits and sexual isolation can evolve. We need theoretical models that explore the consequences of multivariate sexual isolation to test this supposition. Third, claiming that particular traits are important to speciation simply because trait differentiation coincides with species boundaries leaves much to be desired. Surveys of sexual isolation, combined with a multivariate study of candidate traits, could determine which traits actually confer sexual isolation and facilitate speciation.

Finally, a longstanding question in evolution is how genetic variation is maintained in the presence of strong selection. One resolution to this issue lies in a multivariate perspective: genetic correlation and correlational selection mean that genetic variance can persist in many single traits, even while genetic variation is limited and evolution is constrained in the multivariate direction in which selection acts (18, 21). This view led Walsh and Blows (21) to conclude that “trait-by-trait explanations of the natural world are doomed to fail” (21). Analogously, we found that, while mate choice may involve a large number of traits, sexual isolation is constrained to just a few dimensions. The clarion call of Walsh and Blows (21) for a multivariate view of genetic variation applies equally to understanding mate choice and speciation by sexual selection.

Methods

Mating Trial Datasets. We used published data on mating trials in three taxa: salamanders, fruit flies, and cichlid fishes. We modeled mating probability as a function of distance between male and female trait values in a multidimensional space (Fig. 1). Fitting points to male and female population means relies on a matrix of pair-wise isolation estimates. Our method is most robust when this matrix is complete or nearly so (i.e., when females of each population are tested against males of each population, including their own, and vice versa). In some cases, we analyzed only a subset of published data to provide a dense matrix (extracted datasets in Tables S1–S9). Experimental design differs among mating studies, described below, and is implicit in the mating-probability functions. Conclusions about sexual isolation may be sensitive to experimental design (no-choice, male-choice, etc.); however, we found no indication of bias among the three experimental designs represented here, and mating trial results seem broadly comparable across designs (22). Differences in experimental design did necessitate alternative statistical models: binomial and Poisson.

Arnold et al. (24) used a no-choice design in the *D. ochrophaeus* complex in the southeastern United States. A single male and single female were paired for a standard period, and mating (insemination) was scored as present or absent. We used data on nine populations, now grouped as three species: *D. carolinensis*, *D. ocoee*, and *D. orestes* (35).

Several researchers have assessed sexual isolation in *Drosophila* species using a male-choice design, pairing males of one population with females from their own and another population. Mating is assessed as presence or absence of insemination in dissected females. From a massive dataset (26) on populations of *D. paulistorum*, we extracted three subsets: four populations in the Amazonian race, eight populations in the Andean–South Brazilian race, and seven populations from across six races. We used data on three other New World species: five populations of *D. sturtevantii* (27), five populations of *D. willistoni* (28), and seven populations of *D. prosaltans* (29). Finally, we analyzed data on four species in the Asian *D. auraria* complex (31).

Knight and Turner (30) used a multiple-choice experimental design among five populations of cichlid fish in the *P. zebra* species complex (tax-

onomy of these populations remains in flux) (30, 60). Males and females of all five populations were placed together in replicate enclosures, and the total number of matings of each pair-wise combination was recorded over a standardized period. Population labels are from ref. 30: CH, MR, NB, EM, and RW (Ruarwe).

Model. We begin with a univariate model of sexual isolation (24). Let z be a latent male trait (linear combination of traits with invariant coefficients) and y be a latent female preference. Assume that y and z are normally distributed within each population with means \bar{y}_i and \bar{z}_i and variances τ_i^2 and σ_i^2 , respectively. Following an absolute-preference model (or equivalently, a relative-preference model where the female trait is $y^* = y - \bar{z}$) (33), probability of mating between a female y and a male z is proportional to a Gaussian function with deviation parameter $(z - y)$ and width parameter ν_i^2 . Thus, the probability of mating between a female randomly chosen from population i and a male from population j is $\pi_{ij} = c_{ij} \exp(-(\bar{z}_j - \bar{y}_i)^2 / 2(\tau_i^2 + \nu_i^2 + \sigma_j^2))$ (24).

We extend this model to d traits so that π_{ij} is now a multivariate Gaussian function of the Euclidean distance between trait values. We assume that the within-population covariance among male traits and among female preferences, as well as the covariance structure of the multivariate preference function, is constant across populations (mathematical details and a test of this assumption in *SI Text*). This assumption allows us to scale and rotate the axes of trait space by the combined (co)variance structure so that z and y are column vectors of independent traits and preferences, respectively. We assume that c_{ij} , the probability of mating when $z_j = y_i$, takes a constant value c . Then, the probability of mating between a female and a male randomly chosen from populations i and j , respectively, is $\pi_{ij} = c \exp(-(\bar{z}_j - \bar{y}_i)^T (\bar{z}_j - \bar{y}_i))$, where T represents the vector transpose. For the salamander and fruit fly datasets, we assume that mating trials are independent and use a binomial model. The probability of observing k_{ij} matings in n_{ij} trials is a binomial function of π_{ij} . The log likelihood of the complete set of population mean-trait values \bar{y}_i and \bar{z}_j is (Eq. 1):

$$\ln L(\mathbf{Z}, \mathbf{Y}) = \sum_{ij} \left[\ln \binom{n_{ij}}{k_{ij}} + k_{ij} \ln \pi_{ij} + (n_{ij} - k_{ij}) \ln(1 - \pi_{ij}) \right]. \quad [1]$$

For the cichlids, we use a Poisson model for the total number of matings k_{ij} over the experimental period. The probability distribution of k_{ij} is Poisson with parameter $\lambda_{ij} = \rho \exp(-(\bar{z}_j - \bar{y}_i)^T (\bar{z}_j - \bar{y}_i))$, where ρ is the expected number of matings when $z_j = y_i$, again assumed constant across population pairs. The log likelihood of the complete set of trait values is (Eq. 2)

$$\ln L(\mathbf{Z}, \mathbf{Y}) = \sum_{ij} [k_{ij} \ln \lambda_{ij} - \lambda_{ij} - \ln(k_{ij}!)]. \quad [2]$$

Determining Dimensionality. Given a number of dimensions d and mating-trial results, finding the maximum-likelihood values of \mathbf{Z} and \mathbf{Y} is analogous to metric multidimensional unfolding (67) but with a cost function given by Eqs. 1 or 2. Because the likelihood surfaces are relatively rugged (more so at lower dimensions), we alternated a multivariate Newton–Raphson algorithm and gradient hill climbing with systematic swapping of points to find the global best fit. For each dataset at each dimension, we also estimated the maximum-likelihood value of c (by iterative hill climbing) or ρ (with an explicit solution) for the binomial or Poisson models, respectively. The best-fit points at dimension d provided the seed for the dimension $d + 1$ (computer code to conduct this analysis is available from P.A.H.).

We determined the optimal d for each dataset using the corrected AIC (cAIC) (68). For d dimensions and m populations, \mathbf{Z} and \mathbf{Y} represent a total of $2dm$ coordinates. However, the likelihood of a set of points depends only on the pair-wise distances between them (Eqs. 1 and 2), and therefore, there are $2dm - d(d + 1)/2$ free parameters, plus one for either c or ρ . This value is given in Table 1. For m populations, in principle, a maximum of $d = 2m - 1$ dimensions may be required to fit all $2m$ points in \mathbf{Z} and \mathbf{Y} . However, the lowest AIC score was always achieved at fewer than m dimensions, and above this number, the best-fit configuration of points did not change substantially. Thus, we present results only up to dimension $m - 1$ for each dataset. At each d , we calculated the effective number of dimensions $n_D = \sum \lambda_i / \lambda_1$, where λ_i is the i th eigenvalue of the (co)variance matrix of all male and female population means (19).

For each best-fit set of points \mathbf{Z} and \mathbf{Y} , we centered and rotated the axes analogous to a principal components analysis so that the first latent-trait axis represents the maximum variance among all trait values. Plots and all further analyses were done in this rotated space. We used canonical correlation-redundancy analysis (32) between \mathbf{Z} and \mathbf{Y} to assess within- vs. among-population

divergence. To test for consistent deviation between males and females of each population, we calculated Hotelling's t^2 statistic for the m deviation vectors ($\mathbf{y}_i - \mathbf{z}_i$) in each dataset. Significance was assessed by evaluating $(m - d)t^2/d(m - 1)$ against an $F_{(d, m - d)}$ distribution.

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