PNAS RESEARCH ARTICLE | EVOLUTION

Phenotypic polymorphism via mate copying

Srishti Patil[a,b], Sabine Nöbel[c], and Chaitanya S. Gokhale[d,1]

Affiliations are included on p. 8.

Edited by Marcus Feldman, Stanford University, Stanford, CA; received April 30, 2025; accepted January 20, 2026

Classical mate choice theories assume independent decision-making, yet mounting evidence shows that individuals often use social information and copy conspecifics' mate choices, a behavior termed mate copying. While this nonindependent mate choice has been documented across vertebrates and notably in *Drosophila melanogaster*, theoretical and experimental frameworks have been mainly restricted to binary choice scenarios, limiting our understanding of its evolutionary implications in natural populations. Here, we develop a theoretical model of mate copying applicable to populations with multiple morphs, incorporating both private (inherent) and public (cultural) information in mate choice decisions. The population dynamics of the different male morphs are driven by the differing intensities of conformist and anticonformist mate copying. We demonstrate that mate copying can lead to the fixation of low-quality morphs and identify the conditions necessary for the existence of a polymorphism consisting of all male morphs in the population. Furthermore, we identify a plausible mechanism that could maintain a stable polymorphism in the case of conformist mate copying with two morphs. Our findings provide a theoretical framework for understanding how social learning in mate choice can influence evolutionary trajectories and contribute to maintaining phenotypic diversity in populations, with potential implications for sexual selection and speciation.

conformity | culture | mate choice | social learning | multiple morphs

A foundational assumption of classical mate choice theories is that individuals select high-quality mates independently of conspecifics based on private information, i.e., personal information that is not available to others and gained through direct interactions with other individuals or resources (1). However, signals and cues associated with chosen mates can serve as public information, i.e., social information indirectly gained by observing the performance of other individuals (1), which influences the decisions of others. This phenomenon, known as nonindependent mate choice, is supported by growing evidence across taxa (1–4). In this context, individuals rely on a combination of private and public information to make mate choice decisions.

A prominent form of nonindependent mate choice is mate copying, where individuals copy the mate choice of conspecifics. This behavior has been experimentally demonstrated across many vertebrates, including birds (5–7), mammals (8, 9), and fish (10, 11). In invertebrates, mate copying was first observed in the common fruit fly, *Drosophila melanogaster* (2). Although numerous studies have demonstrated the prevalence of mate copying in diverse taxa across vertebrates and invertebrates, the costs and benefits, as well as their long-term effects on populations are challenging to quantify.

Theoretical studies show that mate copying can both promote and hinder adaptation. It facilitates the spread of fitter novel traits (12) even if the copying allele itself could be mildly deleterious (13). Social information use via mate copying may also lead to maladaptive outcomes, such as preferring lower-quality mates (14) or following suboptimal social cues (15, 16). The costs and benefits of using social information for copying vs. choosing based on private information (17), depend on many ecological factors like operational sex ratio, population density, and spatial distribution (18, 19). This ultimately determines whether there is an opportunity to observe the mate choice of conspecifics (and how many).

Building on previous theoretical frameworks (13, 20–24), our study incorporates two key types of information: private and public. Private information reflects inherent preferences independent of conspecific behavior, while public information stems from social learning and cultural preferences (3). The interaction between these information types determines whether mate copying induces directional or frequency-dependent selection. The availability of public information does not guarantee that it will be processed in the same fashion by all individuals. Mechanisms of processing public

Significance

Social learning is a fundamental learning mechanism shared by both humans and nonhumans. An intriguing example of such learning includes the influence on mate choice, leading to mate copying. We study the evolutionary outcomes of mate copying by developing a theoretical framework incorporating both private and public information. Dropping the assumptions of previous models, we study the behavior of mate copying in multiple male morphs. This approach enables us to investigate the conditions under which phenotypic diversity can be maintained and identify potential evolutionary trajectories. Beyond the studies in *Drosophila melanogaster*, our findings contribute to understanding the dynamics of sexual selection in systems with social learning, offering a theoretical framework that generates testable predictions for empirical observations across systems.

Author contributions: S.P., S.N., and C.S.G. designed research; performed research; analyzed data; and wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

[1] To whom correspondence may be addressed. Email: chaitanya.gokhale@uni-wuerzburg.de.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2510849123/-/DCSupplemental.

information can link mate copying and conformity in *D. melanogaster* (25). Conformity is the exaggerated tendency to copy the majority (26), and mate copying in *D. melanogaster* exhibits this behavior as long as the majority is small enough (25). This behavior in fruit flies stabilizes traditions but depends on the number and quality of observations and environmental stability (20, 25). This result makes it possible to apply many insights from studies on conformity to mating in *D. melanogaster*. For instance, different ways to evaluate "majority" may lead to varying outcomes in conformist decision-making (27) (although see refs. 28 and 29). A wide range of results on conformist biases in cultural transmission and how they interact with other evolutionary forces, such as natural selection (30), can be applied.

Mate copying has the potential to influence key evolutionary processes, including sexual selection, speciation, and hybridization (21, 25, 31, 32). Previous theoretical and empirical studies have primarily studied mate copying in binary choice scenarios, where females choose between two male morphs. When the two choices have different fitness or "qualities," we expect to see rich population dynamics. In this study, we investigate whether and how mate copying maintains polymorphism in populations with multiple morphs, thereby mimicking more natural situations. We integrate insights from cultural transmission studies (26, 30, 33) to better understand how social learning interacts with evolutionary forces, such as natural selection, to maintain a phenotypic polymorphism in males.

Experimentally disentangling the effects of mate copying on evolutionary timescales remains a challenging task. Thus, theoretical studies are vital for predicting how mate copying influences the evolutionary fate of polymorphic populations. With a focus beyond binary-choice scenarios to populations with multiple male morphs, we discuss how varying copying intensities influence population dynamics and determine conditions under which mate copying can give rise to polymorphism. Finally, we discuss the implications of our work in relation to the complexities of intermingling timescales when learning theory and ecoevolutionary dynamics are concurrent. In the following sections, we start by detailing our model, analyzing its implications, and discussing how mate copying shapes evolutionary outcomes.

Model

Population Dynamics with Preferences. We track the population dynamics of the male morphs, assuming two kinds of mating preferences of the females. i) Inherent preference uses private information and is an evolutionarily determined preference depending on the quality of the male morphs. Here, "quality" refers to the classical concept of fitness, i.e. the average number of offspring. It is denoted by q_i for male morph i. ii) Cultural preference is driven by public information and constitutes mate copying. To represent the combined effect of these two kinds of preferences, we introduce a "preference factor" (P_i for morph i) that is multiplied by the quality of a male morph. This gives us an effective fitness or quality depending on the total preference level for a given morph. These modified qualities $P_i q_i$ allow us to account for female preferences in the population dynamics of the male population. The product $P_i q_i$ represents the realized fitness of male morph i, incorporating both mating success (determined by female preference P_i) and intrinsic viability or quality (q_i). This formulation follows standard sexual selection theory, where male traits can affect fitness through both their attractiveness to females and their direct effects on survival or reproductive success (39). Thus, quality appears twice in the fitness calculation: within the preference factor P_i (influencing which males females choose to mate with) and as a direct multiplier (affecting the reproductive value of those matings). Therefore, male morph quality is independent of female preference, but modified quality is not.

To predict the population dynamics of the male population under the influence of the two kinds of preferences, we assume simple growth dynamics with modified quality as the growth rate. For a male morph i with frequency $y_i(t)$ at time t and quality q_i, we have,

$$\dot{y_i}(t) = y_i(t)\Big(P_i(\gamma, \mathbf{y})q_i - \sum_{j=1}^{m} P_j(\gamma, \mathbf{y})q_j y_j(t)\Big) \qquad [1]$$

$$P_i(\gamma, \mathbf{y}) = (1-\gamma)\frac{q_i}{\sum_j q_j} + \alpha\gamma C_i(\mathbf{y}), \qquad [2]$$

where P_i, the preference factor for morph i is a function of the probability of mate copying γ and the frequencies $\mathbf{y} = (y_1, y_2, \ldots, y_m)$. The qualities of the m different male morphs are denoted by $q_1, q_2, \ldots, q_m$. The first term in the preference factor represents inherent preference, which is proportional to the relative quality. The second term accounts for mate copying by considering the probability of switching preference to male morph i. Given that mate copying occurs, $C_i(\mathbf{y})$ is the probability of switching preference to morph i from any other male morph. We multiply a factor of asymmetry α because the numerical values given to inherent and cultural preferences may not be comparable. The form of the preference factor given in Eq. **2** assumes an infinite, well-mixed population.

In addition to the differential equation model presented in Eq. **1**, we conducted stochastic simulations to validate our analytical results. Each simulation run consists of a population of size N over T generations, with individuals mating under a specified probability of mate copying γ. The switching probabilities given by $C_i(\mathbf{y})$ remain the same. For a given set of parameters and initial conditions, we recorded the equilibrium frequencies of each male morph, averaged across 50 independent simulation runs. The only parameter that does not appear in the simulations is α, since it is a fitting parameter that modulates the maximum value of $C_i(\mathbf{y})$, effectively assigning different weights to different kinds of preferences. Since the copying function $C_i(\mathbf{y})$ and normalized quality $q_i/\sum_j q_j$ are numerical values representing the effect of that kind of preference on male morph dynamics, we do not know the relative effect of copying vs. inherent preference. Therefore, the parameter α has to be inferred via fitting. We describe the simulation algorithm in *SI Appendix, Simulations*, and all model parameters with their default values are listed in *SI Appendix*, Table S2.

The copying function $C_i(\mathbf{y})$ provides a general framework to incorporate a wide range of mate copying behaviors. It allows for the implementation of diverse empirical and theoretical possibilities. These include frequency-proportional, conformist, anticonformist, and mixed copying behaviors. Conformist (or anticonformist) copying is understood as a disproportionate tendency to copy the majority (or minority). Although conformity and anticonformity can be defined mathematically in several ways, we restrict our analysis to two broad classes of copying functions, Type I and Type II, described in *Materials and Methods*. Type I functions are analytically tractable, allowing for exact solutions of the system's fixed points for multiple male morphs. Whereas Type II functions are more complex but capture a wider range of possible copying behaviors. Fig. 1 illustrates the two types of copying functions we use in our model.

From Binary Choice to Multiple Morphs

Two Morphs. We begin our analysis with the case of two morphs to exemplify the model dynamics. We solve Eq. **1** for two male morphs with different qualities q_1 and q_2 to understand the long-term dynamics of the system. Let y be the frequency of the lower-quality morph (with quality q_1). For any value of the copying probability γ, the system always has two boundary fixed points: $y = 0$ (stable) and $y = 1$ (unstable).

We find that a third, polymorphic equilibrium state appears in the presence of mate copying (Fig. 2) when the following condition is satisfied:

$$C_1(y) = \frac{A(r-1)+r}{1+r}, \qquad [3]$$

where $A = (1-\gamma)/\alpha\gamma$ and $r = q_2/q_1$. We know that $A \geq 0$ since $\gamma, \alpha > 0$. Here, $C_1(y)$ is a function of only the lower quality morph frequency because it is a one-dimensional system. If the polymorphic equilibrium state exists, then it is unstable for conformist copying and stable for anticonformist copying. In the conformist case, this means that the lower-quality morph can fix in the population due to the existence of an unstable polymorphic state. In the anticonformist case, both morphs coexist at a stable equilibrium (Fig. 2). We see that the polymorphic equilibrium is always ≥ 0.5 for conformist copying and ≤ 0.5 for anticonformist copying (for both Type I and Type II copying functions).

For Type I copying functions (described in *SI Appendix, Type I Copying Functions*), the polymorphic fixed point is given by,

$$y_{\mathrm{I}}^{*} = \frac{1}{k^{1/\beta}+1}, \qquad [4]$$

where k is a constant that depends on the relative morph quality r:

$$k = \frac{r+1}{A(r-1)+r} - 1. \qquad [5]$$

Note that we always take the ratio of the higher quality to the lower one, so $r > 1$.

In scenarios with many morphs where no single morph exceeds a frequency of 0.5, Type I functions become biologically unrealistic, which motivates our use of the more flexible Type II framework. Due to the nature of Type II copying functions, the equilibrium state in this case is defined piecewise. For the Type II conformist case, the equilibrium state is as follows for copying probabilities lower than the value given in *SI Appendix*, Eq. **SI.25**:

$$y_{\mathrm{II}}^{*} = \frac{1/(k+1) - f}{1-f} \qquad [6]$$

For higher copying probabilities, the equilibrium is at $y_{\mathrm{II}}^{*} = 0.5$. For Type II anticonformist copying, we observe the fixed point given in Eq. **6**, which is unstable, as well as an equilibrium at 0.5, which is stable. A special case is Type II mixed copying, which is conformist only below a male morph frequency threshold of T_2 for two morphs (and T_3 for three morphs). The default value of T_2 is 0.7, chosen to match the empirical observations from ref. 25 where flies maintained approximately 70% copying of the majority even as the majority frequency increased beyond this threshold. In the two-morph case, the copying function is anticonformist for $y > T_2$. Therefore, the equilibrium is given the piecewise definition in *SI Appendix*, Eq. **SI.27**. For a detailed derivation of the equilibrium states for Type II copying, see *SI Appendix, Equilibria in the two-morph system*.

With the boundary conditions $0 \leq y^{*} \leq 1$, we can find an upper bound on the value of the relative male morph quality r. If $1 < r < 1 + \alpha\gamma/(1-\gamma)$, then the polymorphic fixed point exists. Similarly, we obtain bounds on the copying probability. For a given set of parameters, the lowest value of γ for which the polymorphic fixed point exists is called γ_c (critical copying probability), and it can be obtained using Eqs. **4**–**6** (*SI Appendix, Bifurcation point*),

$$\gamma_c = \frac{r-1}{\alpha+r-1} \qquad [7]$$

If the copying probability is greater than the critical copying probability, then it is enough to allow the lower-quality morph to

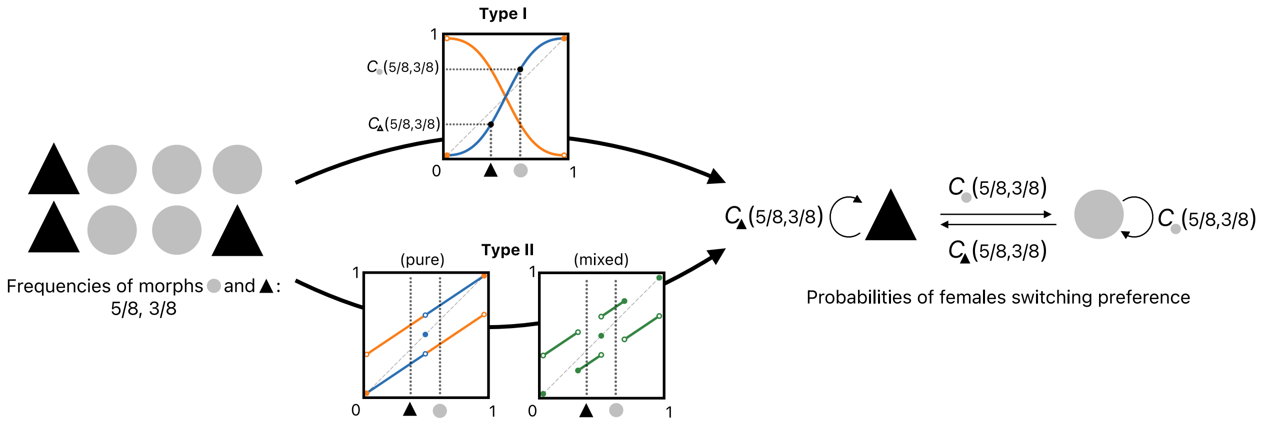

Fig. 1. Illustration of the copying function for two morphs. Here, the frequencies of two male morphs (circles and triangles) are 5/8 and 3/8. Type I (*SI Appendix*, Eq **SI.8**) and Type II (*SI Appendix*, Eq **SI.12**) copying functions give the probability of a female to switch preference to a given morph under conformist (blue), anticonformist (orange), or mixed (green) mate copying behaviors, as a function of male morph frequencies in the population. Mixed mating behaviors (conformist only for small majorities) are only modeled by Type II copying functions. Switching probabilities are conditional on the occurrence of mate copying. Type I conformist switching probabilities are shown on the *Right*. The probability of switching to morph i is denoted by $C_i(\mathbf{y})$ where $\mathbf{y} = (y_1, y_2, \ldots, y_i)$ is the frequency of all male morphs. If mate copying does not occur, then mating occurs according to the female's inherent preference, which is proportional to male morph qualities.

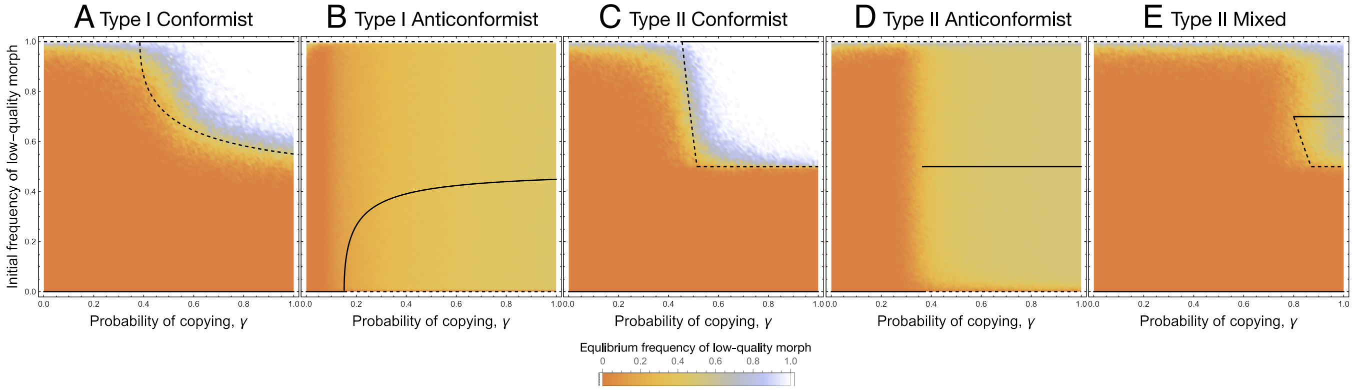

Fig. 2. Two male morphs. Analytically derived solutions for polymorphic and monomorphic equilibrium states (black lines) overlaid on simulation results (heatmap) for two male morphs. Five different forms of the copying function $C_i(\mathbf{y})$ are shown. The x-axis is the probability of mate copying, γ, and the y-axis is the initial frequency of the lower-quality morph. Solid and dashed black lines show analytical solutions for the stable and unstable equilibrium points respectively. The underlying heatmap shows simulation results as the long-run frequency of the lower-quality morph, averaged over 50 independent runs. (*A*) Type I conformist mate copying gives an unstable polymorphic state. $\alpha = 0.8, \beta = 2$. (*B*) Type I anticonformist mate copying gives a stable polymorphic state. When the polymorphic state exists, all initial frequencies lead to the same equilibrium frequency for a given copying probability γ. $\alpha = 2.8, \beta = -2$. (*C*) Type II conformist mate copying gives an unstable polymorphic state. $\alpha = 0.6, f = 0.83$. (*D*) Type II anticonformist mate copying gives a stable polymorphic state at 0.5. $\alpha = 1.1, f = 0.83$. (*E*) Type II mixed mate copying (with threshold $T_2 = 0.7$) leads to one unstable polymorphic state and one stable polymorphic state at T_2. $\alpha = 0.5, f = 0.83$. For all panels, the male morph qualities are $q_1 = 2$ and $q_2 = 3$. Other parameter values used to compute the solution and run the simulations are given in *SI Appendix*, Table SI.2.

reach fixation or stable coexistence. For the complete derivation of the two-morph case, see *SI Appendix*, *Equilibria in the two-morph system*.

In Fig. 2, we compare simulation results to the numerical estimate (obtained using our model) of the polymorphic equilibrium state for both Type I and Type II copying functions. As predicted by our model, the simulations verify that for high values of γ and $y(0)$, the lower-quality morph can reach fixation in the population with conformity. The boundary between the predominantly orange and white regions in Fig. 2 (corresponding to low and high equilibrium frequencies according to the simulation results) coincides with the analytical prediction of the polymorphic equilibria across the range of copying probabilities. This boundary, the separatrix, is defined by the set of polymorphic states. With anticonformity, the simulations exhibit a stable equilibrium state that coincides with our model predictions. We also run stochastic simulations to show that the equilibrium state solely depends on the relative morph quality and to verify the range of r for which polymorphic equilibria exist for a given copying probability γ (*SI Appendix*, Fig. SI.2).

The polymorphic state occurs when the difference in modified qualities equals 0. This is clearly observed in Eq. **1**. When the difference in modified qualities is high, there is a strong preference for one of the morphs due to mate copying or due to inherent preference via private information use. This results in a significant difference in growth rates of the two male subpopulations and faster fixation (*SI Appendix*, Fig. SI.3). When the quality difference is low, the growth rates are similar, resulting in more competition between the two male morphs.

Three Morphs. A system with three male morphs is more complex and harder to study experimentally and theoretically. Our model provides valuable insights into the dynamics of the male population, comprising three morphs with frequencies y_1, y_2, y_3 and qualities q_1, q_2, q_3, respectively. The interior of this phase space simplex is defined as the collection of all points (y_1, y_2, y_3) such that $0 < y_i < 1 (i = 1, 2, 3)$. The boundary of the phase space consists of points corresponding either to a two-morph system (edges) or to the fixation of one of the male morphs (vertices). Again, we solve Eq. **1** for three morphs to obtain the following conditions for the existence of a polymorphic state in the interior:

$$\frac{q_1 C_1(\mathbf{y}) - q_3 C_3(\mathbf{y})}{q_1^2 - q_3^2} = \frac{-A}{q_1 + q_2 + q_3} \qquad [8]$$

$$\frac{q_2 C_2(\mathbf{y}) - q_3 C_3(\mathbf{y})}{q_2^2 - q_3^2} = \frac{-A}{q_1 + q_2 + q_3} \qquad [9]$$

$$\frac{q_1 C_1(\mathbf{y}) - q_2 C_2(\mathbf{y})}{q_1^2 - q_2^2} = \frac{-A}{q_1 + q_2 + q_3}, \qquad [10]$$

where $A = (1 - \gamma)/\alpha\gamma$ and $C_i(\mathbf{y})$ is the copying function as defined in *SI Appendix*, *Copying function and the copying matrix*. Satisfying any two of the three conditions (Eqs. **8**–**10**) is sufficient for the existence of a polymorphic equilibrium state in the interior. The sign of the difference in qualities must be opposite that of the difference in $q_i C_i(\mathbf{y})$ between any two of the three male morphs. Furthermore, the relative value of the differences between $q_i C_i(\mathbf{y})$ and squared qualities must be the same for all pairwise combinations. These conditions are equivalent to setting the pairwise difference in modified qualities to zero (*SI Appendix*, *Equilibria in the three-morph system*).

Note that these conditions are similar to the condition for two morphs (Eq. **3**), but solving analytically for the fixed points in the three-morph case is challenging. In the two-morph case, we could obtain a one-to-one mapping from $C_i(\mathbf{y})$ to y_i. That is, given the values of $C_i(\mathbf{y})$, we could uniquely determine the frequencies of all male morphs. This one-to-one mapping is generally not possible without additional information or constraints for the three-morph case. Therefore, we solve this system numerically using Eqs. **8**–**10**. However, we can obtain approximate analytical estimates for Type I conformist copying functions. This is because, for Type I conformist copying functions, we can (with an approximation) decouple the population dynamics of the male morphs such that $C_i(\mathbf{y}) = C_i(y_i)$, i.e., the copying function depends only on the frequency of morph i, not on the frequencies of other morphs (see *SI Appendix*, *Copying function and the copying matrix* for more details). This holds true for the two-morph

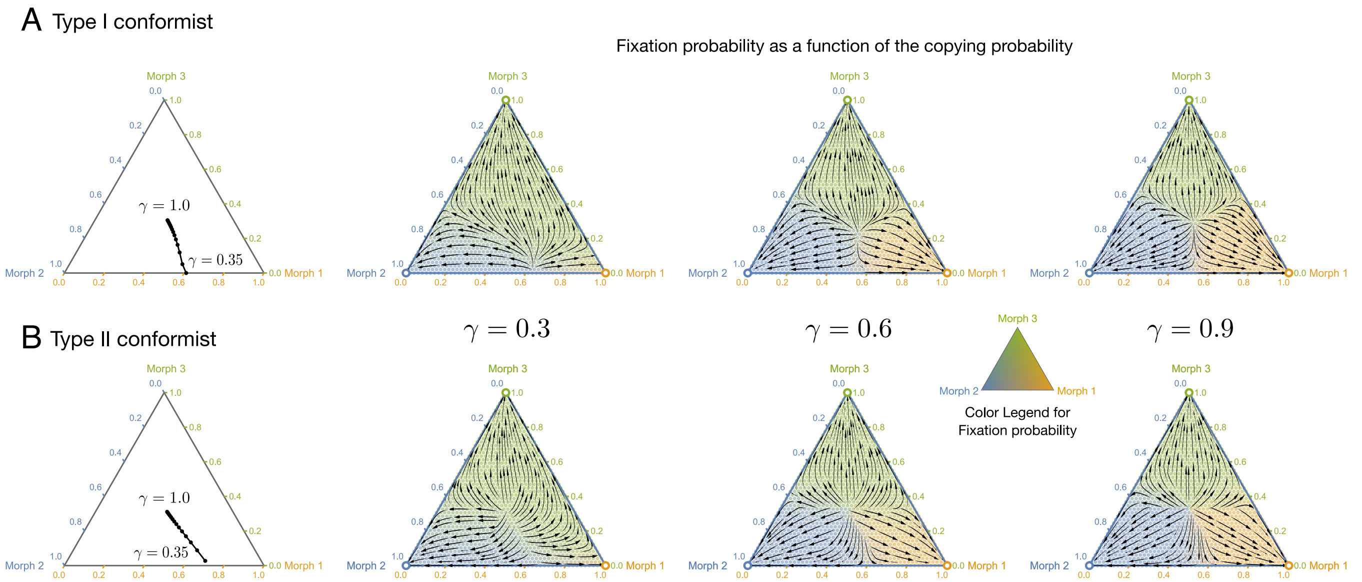

Fig. 3. Three male morphs. The leftmost column shows numerically derived solutions for polymorphic equilibrium states with different values of the copying probability γ in the three-morph system. As the value of γ increases, an equilibrium state appears in the interior of the simplex (around $\gamma = 0.35$ and persists till $\gamma = 1.0$). The remaining columns display numerically solved male-morph frequency dynamics (black arrows) overlaid on simulation results (heat map) for three different values of the copying probability γ. Simulation results are plotted as long-run frequency, averaged over 50 independent runs. This represents the probability of ending up in one of the three monomorphic states (vertices). The colors indicate which of the three probabilities is the highest. Morph 1 (orange) is the lowest-quality and Morph 3 (green) is the highest-quality morph. (*A*) Type I conformist copying, (*B*) Type II conformist copying. $q_1 = 2.0$, $q_2 = 2.5$, $q_3 = 3$, $\alpha = 0.8$, $\beta = 2$, and $f = 0.83$. Simulation parameters are listed in *SI Appendix*, Table SI.2.

case even without the approximation. For the three-morph case, this approximation is required to obtain a one-to-one mapping from $C_i(\mathbf{y})$ to y_i. This analytical approximation is particularly informative in determining the critical copying probability, above which a polymorphic state exists. For greater values of γ, the analytical estimate is not accurate.

Without mate copying ($\gamma = 0$), there is a single stable equilibrium, and any initial condition in the interior leads to the fixation of the highest quality morph. With an increase in the probability of mate copying with conformity, new unstable fixed points appear in the interior of the simplex, while the vertex points become stable fixed points (Fig. 3). The existence of unstable fixed points in the interior and stable fixed points on the vertices implies that any system starting from the interior will, in time, move toward one of the vertices. Depending on the initial conditions, any of the three morphs can fix in the population for high values of γ. Therefore, a higher conformist mate copying probability enables the fixation of lower-quality morphs. This result holds for both Type I and Type II copying functions.

Stochastic simulation results for the three morph system align with our model predictions. Using the simulations, we obtain equilibrium frequencies of the male morphs for different initial conditions (green, blue, and orange points in Fig. 3) and show the fixation of the lower-quality morph in the conformist case. In this case, the numerically determined polymorphic state coincides with the intersection of the three basins of attraction, or the set of initial points for which a morph has a high fixation probability according to the simulations.

If we track the polymorphic equilibrium state as we increase the copying probability γ, we see that it moves toward the center of the simplex (Fig. 3). It follows that with conformity, the basin of attraction of the lowest-quality male morph increases as the copying probability increases. We can therefore define two critical values of γ. The first (γ_1) marks the point at which a fixed point exists on the boundary of the phase space, consisting of two morphs. This is equal to the critical value of γ_c obtained for the corresponding two-morph system (*SI Appendix*, *Bifurcation point*). The second (γ_2) is when all male morphs, including the lowest-quality morph, are present at the equilibrium state. We focus here on γ_2, which is the minimum value of γ required for the polymorphic state to exist in the interior of the simplex. This can be obtained by numerically solving Eqs. **8** and **9**. For our default parameter values, $\gamma_2 = 0.38$, which is verified by the stochastic simulation results in Fig. 3. This is equal to the critical value of γ_c obtained for the two-morph system corresponding to the highest and lowest quality morph only. It is interesting to note that the value of γ_2 does not depend on the type of copying function we use or on the intermediate morph quality.

Multiple Morphs. We solve the model in Eq. **1** for M morphs (with frequencies $y_1, y_2, \ldots, y_M$) to obtain insights into the multiple morph system dynamics. Similar to the three-morph system, we define the interior of the phase space as the collection of all points such that $0 < y_i < 1 (i = 1, \ldots, M)$. In the M-morph case, the condition for the existence of a polymorphic state in the interior of the phase space is given by,

$$\frac{q_i C_i(\mathbf{y}) - q_j C_j(\mathbf{y})}{q_i^2 - q_j^2} = \frac{-A}{\sum_k q_k}, \quad \forall i, j \in \{1, 2, \ldots, M\}, \qquad \textbf{[11]}$$

where $A = (1-\gamma)/\alpha\gamma$ and $C_i(\mathbf{y})$ is the conformist copying function as defined in *SI Appendix*, *Copying function and the copying matrix*. Satisfying these conditions is equivalent to setting pairwise differences in modified qualities to zero (*SI Appendix*, Lemma 1). Since an M-morph system is $M-1$-dimensional, it is sufficient to satisfy any $M-1$ of the M conditions in Eq. **11**. Note that Eq. **11** is a generalized version of the conditions obtained for the two-morph and three-morph cases. We again conclude that the sign of the difference in qualities must be opposite to that of the difference in $q_i C_i(\mathbf{y})$ between any two male morphs. The relative value of the differences between $q_i C_i(\mathbf{y})$ and squared qualities must be the same for all pairwise combinations.

Stable Polymorphism with Conformity. Through our analysis of the two- and three-morph systems, we have demonstrated that stable polymorphism is not possible with conformity. While mate copying with conformity allows the lower-quality morph to fix in the population, only anticonformity allows the existence of a stable equilibrium state. In this section, we show that a stable polymorphism of male morphs with conformist mate copying is achievable when the copying probability evolves over time.

In our model so far, copying probability is a female phenotype that is fixed for a given population. However, it is plausible that the copying probability evolves over time in response to the changes in male morph frequencies. This is because the copying phenotype can be beneficial or detrimental to females, depending on the frequencies of male morphs. For example, if copying females mate with the lower-quality morph due to a preference for commonality, it confers an overall advantage to the noncopying females, since their inherent preference is proportional to male quality. This, of course, depends on how the copying phenotype is inherited or learned. Here, we consider a simple addition to our two-morph system to represent the dependence of copying probability on the dynamics of male morphs. If $\dot{y} > 0$:

$$\dot{\gamma} = \begin{cases} -G & ; 0 < \gamma \le 1 \\ 0 & ; \gamma = 0 \end{cases} \qquad [12]$$

If $\dot{y} < 0$:

$$\dot{\gamma} = \begin{cases} G & ; 0 \le \gamma < 1 \\ 0 & ; \gamma = 1, \end{cases} \qquad [13]$$

where y is the frequency of the lower-quality morph in the two-morph system and G is a constant. According to this equation, γ increases with time at a constant rate if the frequency of the higher-quality male is increasing with time. Consider a situation in which the lower quality morph is in the majority. Conformist mate copying would increase its frequency further, so γ will decrease, reducing the amount of copying. This will allow the higher-quality morph to increase, which will in turn increase the copying probability, allowing the lower-quality morph to grow. Therefore, with the addition of Eqs. **12** and **13** to the two-morph system, we see the possibility of maintaining polymorphism in the phase space (Fig. 4). We observe the stable coexistence of low- and high-quality morphs for a range of initial conditions.

We do not see the same coexistence in our stochastic simulation results. While the fixation time increases as male morph frequencies and γ fluctuate around the expected equilibrium frequency and expected equilibrium copying probability, one morph eventually fixes in the population. A possible reason for the absence of coexistence in the simulations is the way we model stochasticity. Since our simulations employ an event-based approach with multiple generations, each with numerous matings, the timescale of change in frequency and γ may not align, thereby breaking the feedback loop necessary for stability. With a rate-based simulation approach, we would expect to see stable coexistence.

With the limitation that the stable polymorphism is only exhibited in the numerical solution of the analytical model, we show that it may be possible to achieve it in the presence of conformist mate copying with a dynamic copying probability.

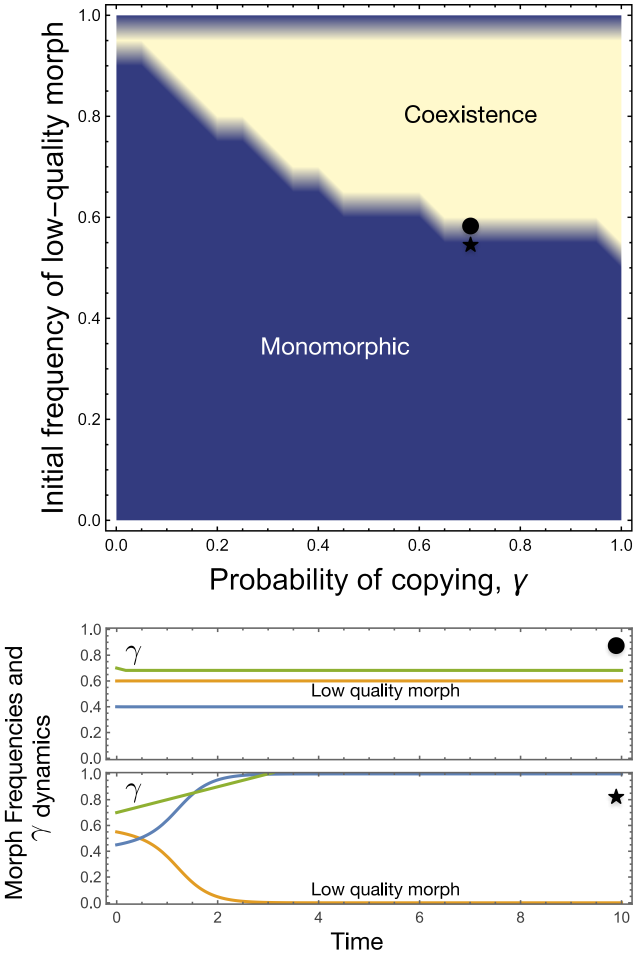

Fig. 4. Dynamic copying probability. Results from the modified model with a dynamic γ (Eqs. **12** and **13**) and Type I conformist copying. The modified model can lead to stable coexistence via a stable internal polymorphic state, even in the presence of conformist copying. The heat map illustrates the nature of equilibrium for a range of initial γ values (x-axis) and initial frequencies of the low-quality morph (y-axis). The example trajectories below show the dynamics of male morph frequencies (blue and orange lines) and γ (green line). Two initial conditions are shown, denoted by the star ($y_1 = 0.55, \gamma = 0.7$) and circle ($y_1 = 0.6, \gamma = 0.7$) symbols.

Discussion

In this study, we examined the effect of female mate copying on populations with multiple male morphs, a topic that has received little attention in both theoretical and empirical studies of mate copying. Our findings provide a theoretical framework that can inform experiments on mating systems with multiple morphs. We demonstrated that even a costly or "low quality" morph can reach fixation or stable coexistence in the presence of mate copying and derived explicit conditions under which a polymorphic state occurs (Eq. **11**).

To obtain our results, we captured the interplay between cultural preference and inherent preference through the concept of modified qualities, which integrates both intrinsic male morph quality and the effects of mate copying (Eq. **2**). This equips us with a powerful and generalizable tool for analyzing mating dynamics influenced by social learning. Using the modified qualities as a proxy for male fitness, we derived fixed points from Eq. **1** to find polymorphic states. The number and stability of these fixed points depend on the copying probability γ and the specific form of the copying function $C_i(\mathbf{y})$, which quantifies mate copying.

We studied conformist, anticonformist, and mixed behaviors in the context of mate copying by modifying $C_i(\mathbf{y})$ and considering two types (Type I and Type II) of copying functions.

Regardless of the form of the copying function, our main condition for the existence of polymorphism (Eq. **11**) remained structurally unchanged. The condition states that polymorphism arises when the pairwise differences in modified qualities among all morphs are zero. This implies that a high-quality male morph would need to have a lower preference due to mate copying, such that its modified quality is equal to that of lower-quality morphs. Thus, achieving polymorphism requires that mate copying sufficiently compensates for the difference in male morph quality. The greater the difference in morph qualities, the higher the required probability of mate copying to observe polymorphism. We showed that this polymorphism is always unstable when mate copying is conformist and stable when it is anticonformist. To complement our analytical results, we conducted stochastic simulations for two- and three-morph systems (*SI Appendix, Simulations*) and observed strong agreement with the theoretical predictions.

As we began by developing intuition through the two-morph case, we showed that the existence and frequency of polymorphic states in this case depend on the ratio of male morph qualities, rather than their absolute values (*SI Appendix,* Fig. SI.2). We found the range of relative male morph qualities that allow a polymorphism to exist for a given copying probability. For a fixed ratio of male morph qualities, we found the critical copying probability, which is the minimum probability of copying required for the existence of the polymorphic state. Extending this to the three-morph system, we showed that the critical copying probability required for a polymorphic state involving all male morphs is equal to the copying probability required for a polymorphism in a two-morph system consisting of the highest and lowest quality morphs. The study of two- and three-morph cases allowed us to illustrate two key insights about the critical copying probability: 1) it is independent of the intermediate qualities and 2) it is the same for the two types of copying functions we consider.

After showing that conformist mate copying typically leads to an unstable polymorphic state, we next discussed a plausible scenario in which temporal changes in the copying probability could lead to a stable polymorphism with conformity. Conformist copying confers a benefit to copying females when the common phenotype is of high quality, while being disadvantageous when it is of low quality. On the other hand, noncopying females are conferred a benefit relative to copying females when the low-quality morph is in the majority. This is because, in our model, inherent preference is proportional to the quality of male morphs. These opposing selective pressures suggest that the proportion of copying females could evolve toward a stable equilibrium, as previously proposed (16). We demonstrated that altering the copying probability in response to changes in male morph frequencies can enable a feedback loop that maintains polymorphism in a population with conformist mate copying. Our results serve as a first step in exploring coevolution with mate copying and can be used in further studies to understand the interaction of female copying behavior and male morph frequencies. However, a careful analysis of the costs and benefits of copying behavior is required to further incorporate temporal changes in the probability of copying.

Our model takes a phenomenological approach to frequency-dependent copying probability, tracking the consequences of such behavior rather than modeling its evolutionary origins. This complements previous work that has examined when and how copying strategies evolve. For instance, ref. 24 demonstrated using dynamic programming that mate copying can evolve when young females are poor at discrimination and need to learn what high-quality males look like. Similarly, ref. 22 modeled the evolution of frequency-dependent mate choice under varying ecological conditions. Our approach differs in that we ask: Given that copying probability is frequency-dependent (as observed empirically by ref. 25), what are the consequences for male morph diversity? This phenotypic modeling framework is broadly applicable, regardless of whether frequency dependence arises through genetic evolution, learning, or plasticity. An important direction for future work would be to explicitly model the coevolution of male morphs and female copying strategies, examining whether selection would favor the evolution and maintenance of the frequency-dependent copying patterns we assume here.

Another rich avenue for future work is to examine the extent of (anti)conformity, represented by β and f in our model. Prior studies have shown that varying conformity coefficients over time can lead to significantly different evolutionary dynamics (34, 35). Depending on the expected level of conformity, stochastically locally stable equilibria can be observed, which are not possible in the deterministic case of conformist mate copying, as demonstrated by our model. On the other hand, the instability of the polymorphic state with conformity suggests a mechanism by which mate copying could facilitate speciation, as proposed in previous work (31). Investigating such dynamics across ecological contexts could yield insights into the role of social learning in diversification.

Previous theoretical work has predominantly focused on mate copying in two-morph systems (20, 25, 36, 37). Our model enhances the existing literature by incorporating the more natural condition of multiple morphs, offering general insights into their dynamics through a simple yet versatile dynamical model, supported by simulations. Furthermore, the concept of modified qualities is adaptable—other factors influencing mating preferences, such as ornamentation or intrasexual competition (38), can be easily integrated into our framework. Our simulations are also readily extendable to systems with more than three morphs, making the approach broadly applicable. An example are lek mating systems, where females have the opportunity to easily compare potential mates by gathering private information about the competitive courtship displays of multiple males, as well as observing the mate choice of other females (39). Our simulations could help answer the long-standing question of how male polymorphism is maintained despite strong female preferences.

In summary, our model helps understand how mate copying can contribute to the maintenance of male polymorphisms under a process of sexual selection and whether its effect varies with two, three, and more than three morphs in the population. Using the model, we can modify/add parameters in the expression for modified quality to account for mating preferences, both positive/negative and inherent/socially learned. Simple conditions for characterizing polymorphism can be derived with modified qualities. This exposition and further possibilities for an expanded analysis help us move beyond a single copying style and situate our results within a broader and empirically grounded space of social learning strategies. There are many avenues to be explored in modeling mating behavior, such as mate copying. For instance, the effect of the spatial distribution of the population, where females are more likely to copy individuals that are closer in space (19). The age, reputation, and reliability of model females could further affect the frequency of copying (23, 40, 41). The delay between consecutive observations and the nature of information obtained clearly affect the production of copying behavior (27, 42, 43). Future models could consider the effect of intergenerational learning with overlapping generations and the interplay of multiple observations (30, 42) with multiple morphs. There is still much to explore in mate copying studies in a coevolutionary context of multiple male morphs and female preferences and types. Combining our model's flexibility with the complexities presented above will be crucial in deriving the joint effects of biological and cultural impacts on mate choice and population dynamics in species showing such complex mating behavior.

Materials and Methods

Here, we describe the mathematical details of the two types of copying functions introduced in the main text. These functions capture conformist, anticonformist, and frequency-proportional mate copying behaviors. We distinguish between two classes of anticonformity: weak and strong. Weak anticonformist functions correspond to the conventional inverse-S shape anticonformity described by Boyd and Richardson (26). Strong anticonformity arises when the lower-frequency morphs are preferred even over higher-frequency morphs. Although we discuss weak anticonformity in *SI Appendix*, this study primarily focuses on strong anticonformity. Throughout the main text, the term anticonformity refers to strong anticonformity. This choice is motivated by the fact that weak anticonformity produces dynamics that are qualitatively similar to those observed under conformity (*SI Appendix*, Fig. SI.4).

A comprehensive analysis of these copying functions and their impact on the equilibria and their stability in the two- and three-morph systems is provided in *SI Appendix*.

Type I Mate Copying. This class of copying functions are simple and mathematically tractable. We choose the function described in *SI Appendix, Type I copying functions*, with a single parameter β to track the extent of conformity or anticonformity. Under this formulation, $\beta > 1$ corresponds to conformist behavior, $\beta < -1$ to strong anticonformity, $0 < \beta < 1$ implies weak anticonformity, and $\beta = 1$ gives us frequency-proportional copying. Unless specified otherwise, we set $\beta = 2$ and $\beta = -2$ as default values for conformist and anticonformist copying, respectively.

A limitation of Type I functions is that the definition of "majority" is fixed at 0.5, regardless of the number of morphs. For example, with three male morphs, one would expect the threshold to shift so that $C_i(\mathbf{y}) > y_i$ when $y_i > 1/3$ and $C_i(\mathbf{y}) < y_i$ when $y_i < 1/3$, but Type I copying functions do not capture this property.

Type II Mate Copying. The advantages of introducing the more complex Type II copying functions are two-fold. First, they allow us to shift the threshold for the majority depending on the number of male morphs in the population. Second, they are more flexible and can capture mixed behaviors that correspond better to empirical observations. For example, mate copying behavior in *D. melanogaster* (25) is best described as conformity for small majorities, i.e., there can be an exaggerated tendency for individuals to copy the majority unless the majority is too big (26, 44). Type II copying functions, along with the (anti)conformity conditions they follow, are described in *SI Appendix, Type II copying functions*. They are adapted from the probabilities of adopting polychotomous traits as given in ref. 45.

We define the parameter $f > 0$ to modulate the extent of (anti)conformity. We get frequency-proportional mate copying for $f = 0$, and the greater the value of f, the higher is the extent of (anti)conformity. For Type II copying, we can only define weak anticonformity in the two- morph case.

Data, Materials, and Software Availability. Figure-generating codes are available on Zenodo https://doi.org/10.5281/zenodo.18268587. Code data have been deposited in Zenodo (DOI: https://doi.org/10.5281/zenodo.18268587) (46).

ACKNOWLEDGMENTS. C.S.G. acknowledges the visiting fellowship from the Institute for Advanced Study in Toulouse.

Author affiliations: [a]Division of Theoretical Systems Biology, German Cancer Research Center, Heidelberg 69120, Germany; [b]Indian Institute of Science Education and Research, Pune 411008, Maharashtra, India; [c]Department of Animal Ecology, Martin-Luther-University Halle-Wittenberg, Halle (Saale) 06120, Germany; and [d]Chair for Computational and Theoretical Biology, Julius-Maximilians University, Würzburg 97074, Germany

1. E. Danchin, L. A. Giraldeau, T. J. Valone, R. H. Wagner, Public information: From nosy neighbors to cultural evolution. *Science* **305**, 487–491 (2004).
2. F. Mery *et al.*, Public versus personal information for mate copying in an invertebrate. *Curr. Biol.* **19**, 730–734 (2009).
3. D. J. White, Influences of social learning on mate-choice decisions. *Anim. Learn. Behav.* **32**, 105–113 (2004).
4. B. Galef, D. White, Evidence of social effects on mate choice in vertebrates. *Behav. Process.* **51**, 167–175 (2000).
5. J. Höglund, R. V. Alatalo, R. M. Gibson, A. Lundberg, Mate-choice copying in black grouse. *Anim. Behav.* **49**, 1627–1633 (1995).
6. B. Galef, D. White, Mate-choice copying in Japanese quail, coturnix coturnix japonica. *Anim. Behav.* **55**, 545–552 (1998).
7. J. P. Swaddle, M. G. Cathey, M. Correll, B. P. Hodkinson, Socially transmitted mate preferences in a monogamous bird: A non-genetic mechanism of sexual selection. *Proc. R. Soc. B Biol. Sci.* **272**, 1053–1058 (2005).
8. R. I. Bowers, S. S. Place, P. M. Todd, L. Penke, J. B. Asendorpf, Generalization in mate-choice copying in humans. *Behav. Ecol.* **23**, 112–124 (2012).
9. B. Galef, T. Lim, G. Gilbert, Evidence of mate choice copying in Norway rats, Rattus norvegicus. *Anim. Behav.* **75**, 1117–1123 (2008).
10. L. A. Dugatkin, Interface between culturally based preferences and genetic preferences: Female mate choice in *Poecilia reticulata*. *Proc. Natl. Acad. Sci. U.S.A.* **93**, 2770–2773 (1996).
11. K. Witte, M. J. Ryan, Mate choice copying in the sailfin molly, *Poecilia latipinna*, in the wild. *Anim. Behav.* **63**, 943–949 (2002).
12. M. Santos, M. Matos, S. A. M. Varela, Negative public information in mate choice copying helps the spread of a novel trait. *Am. Nat.* **184**, 658–672, PMID: 25325749 (2014).
13. M. Santos, M. Sapage, M. Matos, S. A. M. Varela, Mate-choice copying: A fitness-enhancing behavior that evolves by indirect selection. *Evolution* **71**, 1456–1464 (2017).
14. S. Nöbel, E. Danchin, G. Isabel, Mate-copying for a costly variant in *Drosophila melanogaster* females. *Behav. Ecol.* **29**, 1150–1156 (2018).
15. S. Bikhchandani, D. Hirshleifer, I. Welch, A theory of fads, fashion, custom, and cultural change as informational cascades. *J. Polit. Econ.* **100**, 992–1026 (1992).
16. F. Dubois, D. Drullion, K. Witte, Social information use may lead to maladaptive decisions: A game theoretic model. *Behav. Ecol.* **23**, 225–231 (2012).
17. J. D. Reynolds, M. R. Gross, Costs and benefits of female mate choice: Is there a lek paradox. *Am. Nat.* **136**, 230–243 (1990).
18. M. Monier, S. Nöbel, G. Isabel, E. Danchin, H. e. D. Bierbach, Effects of a sex ratio gradient on female mate-copying and choosiness in *Drosophila melanogaster*. *Curr. Zool.* **64**, 251–258 (2018).
19. M. Sapage, S. A. M. Varela, H. Kokko, Social learning by mate-choice copying increases dispersal and reduces local adaptation. *Funct. Ecol.* **35**, 705–716 (2021).
20. A. F. Agrawal, The evolutionary consequences of mate copying on male traits. *Behav. Ecol. Sociobiol.* **51**, 33–40 (2001).
21. M. Kirkpatrick, L. A. Dugatkin, Sexual selection and the evolutionary effects of copying mate choice. *Behav. Ecol. Sociobiol.* **34**, 443–449 (1994).
22. H. Kokko, M. D. Jennions, A. Houde, Evolution of frequency-dependent mate choice: Keeping up with fashion trends. *Proc. R. Soc. B Biol. Sci.* **274**, 1317–1324 (2007).
23. T. Uehara, H. Yokomizo, Y. Iwasa, Mate-choice copying as Bayesian decision making. *Am. Nat.* **165**, 403–410 (2005).
24. S. Stöhr, Evolution of mate-choice copying: A dynamic model. *Anim. Behav.* **55**, 893–903 (1998).
25. E. Danchin *et al.*, Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science* **362**, 1025–1030 (2018).
26. R. Boyd, P. J. Richerson, *Culture and the Evolutionary Process, Culture and the Evolutionary Process* (University of Chicago Press, Chicago, IL, US, 1985), pp. viii, 331.
27. T. J. H. Morgan, A. Acerbi, E. J. C. v. Leeuwen, Copy-the-majority of instances or individuals? Two approaches to the majority and their consequences for conformist decision-making. *PLoS One* **14**, e0210748 (2019).
28. L. M. Aplin *et al.*, Counting conformity: Evaluating the units of information in frequency-dependent social learning. *Anim. Behav.* **110**, e5–e8 (2015).
29. M. Somveille *et al.*, Movement and conformity interact to establish local behavioural traditions in animal populations. *PLoS Comput. Biol.* **14**, e1006647 (2018).
30. K. K. Denton, Y. Ram, U. Liberman, M. W. Feldman, Cultural evolution of conformity and anticonformity. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 13603–13614 (2020).
31. S. A. M. Varela, M. Matos, I. Schlupp, The role of mate-choice copying in speciation and hybridization. *Biol. Rev.* **93**, 1304–1322 (2018).
32. S. Nöbel *et al.*, Conformity in mate choice, the overlooked social component of animal and human culture. *Biol. Rev.* **98**, 132–149 (2023).
33. E. Heinrich Mora, K. K. Denton, M. E. Palmer, M. W. Feldman, Conformity to continuous and discrete ordered traits. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2417078122 (2025).
34. K. K. Denton, U. Liberman, M. W. Feldman, On randomly changing conformity bias in cultural transmission. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2107204118 (2021).

35. K. K. Denton, U. Liberman, M. W. Feldman, On random conformity bias in cultural transmission of polychotomous traits. *Theor. Popul. Biol.* **156**, 5–11 (2024).
36. S. Gavrilets, G. Arnqvist, U. Friberg, The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 531–539 (2001).
37. H. Kokko, Treat 'em mean, keep 'em (sometimes) keen: Evolution of female preferences for dominant and coercive males. *Evol. Ecol.* **19**, 123–135 (2005).
38. V. R. Venkateswaran, C. S. Gokhale, Evolutionary dynamics of complex multiple games. *Proc. R. Soc. B Biol. Sci.* **286**, 20190900 (2019).
39. M. Andersson, *Sexual Selection* (Princeton University Press, 1994).
40. J. Vukomanovic, F. H. Rodd, Size-dependent female mate copying in the guppy (*Poecilia reticulata*): Large females are role models but small ones are not. *Ethology* **113**, 579–586 (2007).
41. J. Amlacher, L. Dugatkin, Preference for older over younger models during mate-choice copying in young guppies. *Ethol. Ecol. Evol.* **17**, 161–169 (2005).
42. M. Lachmann, G. Sella, E. Jablonka, On the advantages of information sharing. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **267**, 1287–1293 (2000).
43. T. J. H. Morgan, B. Thompson, Biased transformation erases traditions sustained by conformist transmission. *Biol. Lett.* **16**, 20200660 (2020).
44. E. Lappo, K. K. Denton, M. W. Feldman, Conformity and anti-conformity in a finite population. *J. Theor. Biol.* **562**, 111429 (2023).
45. K. K. Denton, U. Liberman, M. W. Feldman, Polychotomous traits and evolution under conformity. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2205914119 (2022).
46. S. Patil, S. Nöbel, C. S. Gokhale, tecoevo/matecopying_multiplemorphs: Revision 2. Zenodo. https://zenodo.org/records/18268587. Deposited 16 January 2026.