SEXUAL SELECTION

Irrationality in mate choice revealed by túngara frogs

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Mate choice models derive from traditional microeconomic decision theory and assume that individuals maximize their Darwinian fitness by making economically rational decisions. Rational choices exhibit regularity, whereby the relative strength of preferences between options remains stable when additional options are presented. We tested female frogs with three simulated males who differed in relative call attractiveness and call rate. In binary choice tests, females' preferences favored stimulus caller B over caller A; however, with the addition of an inferior "decoy" C, females reversed their preferences and chose A over B. These results show that the relative valuation of mates is not independent of inferior alternatives in the choice set and therefore cannot be explained with the rational choice models currently used in sexual selection theory.

Evolutionary theory is tightly linked to traditional decision theory, which predicts consumer behavior by assuming individuals' decisions will lead to outcomes that maximize the chooser's subjective utility, in terms of satisfaction or benefit (1, 2). A rational individual is one who makes choices that obey the simple mathematical axioms of transitivity (if A > B and B > C, then A > C) and regularity (if A > B in the absence of C, then A > B in the presence of C). The simple nature of rational models is intuitively attractive; however, there has been much recent debate as to how valuable they are in predicting actual behavior (3–5). Human behavior commonly deviates from what is predicted by rational choice models, with individuals making seemingly suboptimal decisions regardless of outcome importance. One well-known violation of regularity is the "decoy effect" (6–8). For example, while shopping for a used vehicle, the buyer may value both low price and fuel efficiency. Of the two vehicles considered, one has a higher price tag but also better efficiency (A), whereas the second has a lower price but also lower efficiency (B). The buyer decides that he or she values lower prices over higher efficiency and so chooses B. At this point, the salesperson mentions that there is a third vehicle (C), which also has good fuel efficiency but a much higher price than both A and B. This causes the buyer to reconsider, despite no interest in the higher-priced vehicle. To the salesperson's delight, the buyer ultimately chooses A, spending more money for better fuel efficiency. This irrational behavior has been produced by the decoy effect.

Mate choice is one of the most important decisions an animal makes. In many species, these critical decisions occur in dynamic social environments (such as leks) containing multiple potential mates with complex traits. Comparable to human consumers maximizing utility, we expect animals to maximize their Darwinian fitness by making

rational mate choices. The preference function concept, central to sexual selection theory (9), assumes that mate choice rules obey formal rationality (2, 7). The results of the scant empirical studies that have tested this assumption were either inconclusive (2) or failed to reject the axioms of transitivity (10) and regularity (11). Thus, we designed a study to address the axiom of regularity using a decoy paradigm (6–8). We hypothesized that females exhibit decoy effects similar to those commonly observed in humans,

whereby the probability of choosing stimulus A over B is dependent on the presence of the inferior third option C [P(A|B) ≠ P(A|B,C)].

Mate choice behavior in our subject, the túngara frog (*Physalaemus pustulosus*), has been thoroughly studied for three decades (12). Males form lek-like aggregations and produce advertisement calls to attract females. Females exhibit a highly stereotyped and robust phonotactic response to speakers broadcasting stimuli that mimic male advertisement calls. Females generally prefer "static" call characteristics such as low dominant frequency and longer call durations, which are largely replicable within individuals, in addition to faster call rates, which change dynamically with the social conditions. For the current study (13), potential mates were represented by three acoustic stimuli (A, B, C) varying in two traits under selection by females: (i) static attractiveness [dimension 1 (DIM-1)] and (ii) call rate (DIM-2). The subjective values of each of these independent traits were determined by the actual measured preferences of 78 females from the same population in preliminary choice trials, which were completed before beginning our decoy experiments (Fig. 1, A and B; fig. S1; and tables S1 and S2). To represent variation in static attractiveness, we chose three natural male call variants from a previous study that demonstrated the range of multidimensional acoustic variation present in our study population (13, 14). Static attractiveness and call rate were inversely combined to
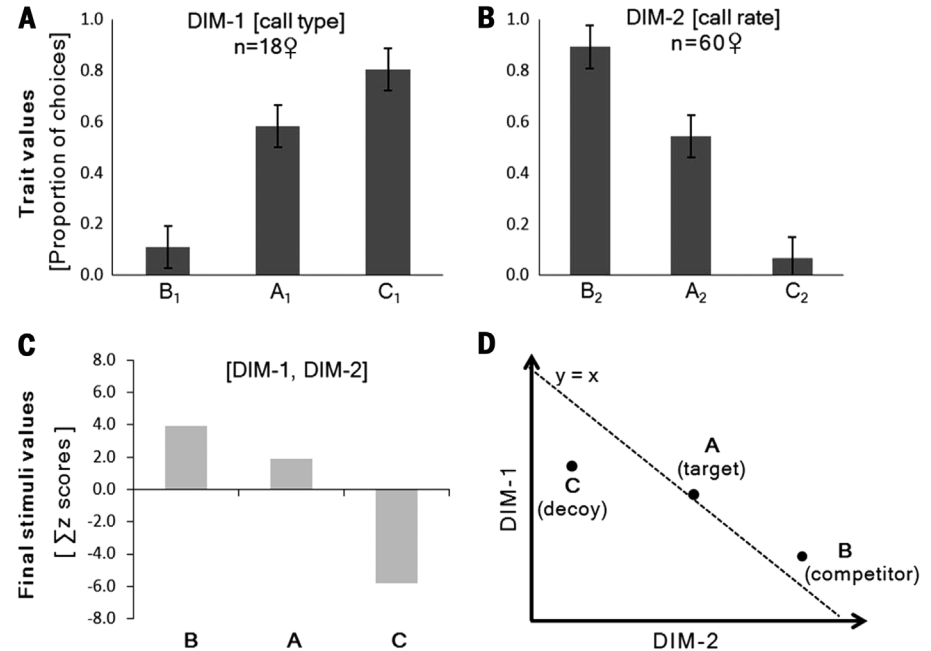

Fig. 1. Independent valuation of call traits. (A) Static attractiveness (DIM-1) is a composite trait of acoustic characters inherent to a given natural call variant (B_1, A_1, C_1). (B) Calls were presented at three different call rates (DIM-2): C_2 = 1/4, A_2 = 1/2, B_2 = 1/1 (in calls per second). Females' relative preferences for the three variants of each trait were measured in preliminary phonotaxis trials: (A_t, B_t), (B_t, C_t), (A_t, C_t). The trait value is the proportion of females' choices out of the total possible. Each stimulus variant (e.g., A_t) was presented in two of the three pairwise tests; thus the sum of proportions for the three stimuli was 1.50, whereas the maximum possible for a given stimulus is 1.0. Error bars indicate ±SE of the binomial distribution. (C and D) Differences in DIM-2 are discriminated more by females than differences in DIM-1, leading to an asymmetric relation among final stimuli (A, B, C) in total value, as calculated by the sum of binomial z ratios for each trait.

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produce an inferior decoy stimulus (C) among the final three stimuli (Fig. 1, C and D). We then measured females' relative mate preferences for each set of paired calls [(A, B), (A, C), and (B, C)] and for the trinary choice set (A, B, C). Based on compromise effects in other decoy experiments, we predicted that the relative preference for the intermediate stimulus A (target), with respect to the highest-value stimulus (competitor), will increase when C (decoy) is present.

In experiment one, we tested 40 females repeatedly on each of the four choice sets, using a grouped-speaker configuration that allowed females to choose the decoy option during the trinary test (Fig. 2A). Experiment two was identical to experiment one, with the important exception that during the trinary set, the decoy stimulus was broadcast from a speaker directly above the females' starting position to make it perceptible but inaccessible (Fig. 2B). The influence of unavailable decoys, referred to as the phantom decoy effect (15), has been shown to shift preferences toward the asymmetrically dominated target; thus, the prediction is the same as in experiment one. This experimental design also makes it possible to avoid complications potentially arising from the relative spatial positions of the speakers, such as a preference for centrally positioned males. Eighty females completed both the binary (A, B) and trinary (A, B; in the presence of C) choice sets. Fifty of these 80 females were also tested with the two additional binary tests [(A, C) and

(B, C)] to verify the inferior status of stimulus C in this configuration (experiment two).

Results were consistent in both experiments. As predicted by independent trait valuation of the three stimuli (Fig. 1, C and D), stimulus C (decoy) was inferior to both A and B in all tests [experiment one: C < B, $P = 0.007$; C < A, $P < 0.001$; P(C, trinary) = 0.175, $P = 0.042$; all $n = 40$ females; experiment two: C < A, $P < 0.001$; C < B, $P = 0.034$, all $n = 50$]. In all binary tests, but not the trinary tests, the preferred stimulus in the pair was that with the fastest call rate [DIM-2] (Fig. 2, C and D). In the trinary tests, females were significantly more likely to choose the intermediate target A in the presence of the decoy regardless of the availability of the decoy as an option (Fig. 2, C and D). Female túngara frogs reversed their preferences in the presence of an irrelevant alternative in two separate experiments and thus violate a key assumption of mate choice models derived from decision theory.

In decision theory, predictions are based on the expected outcomes of individual behavior, and no assumptions are made about the underlying cognitive processes. Given the similarity of our results to systematic biases exhibited by human consumers, mate choice models might benefit from behavioral economics insights that employ psychological concepts such as perceptual biases or limited cognitive resources to explain irrational choices. Economic rationality does not account for reference dependence, which

is inherent to perceptual systems during rapid comparative evaluations (16, 17). In socially complex situations such as frog choruses, rational decisions could be time-consuming, potentially resulting in lost mating opportunities or the risk of further exposure to predators. Decision rules might evolve to include loss aversion (4, 18, 19), mitigating the risk of costly errors, which are more likely when there are extreme alternatives and in uncertain environments. Such heuristics could lead to stabilizing selection on male traits and maintenance of genetic variation. Moreover, as human consumers are susceptible to manipulation by salespeople, context-dependent choice rules may make female frogs vulnerable to behavioral exploitation by competing males; for instance, if males are selective of their nearest neighbors (20, 21).

Although it is clear that female choice patterns do not coincide with the consistent valuation predicted by traditional models in sexual selection, it is far from clear whether perfect formal rationality is mutually compatible with optimal evolutionary fitness (22–24). Closer inspection is required to determine whether inconsistencies revealed by decoy effects are, in fact, suboptimal in the context of fitness maximization. Variation of female mate choice in different social contexts might reflect adaptations for using additional sources of information (25), resulting in the expression of more complex but predictable choice patterns.

Fig. 2. Mate preference reversal for two stimuli (A, B) with the addition of an inferior decoy option (C). (**A**) Experiment one: The decoy was available as a third option in the trinary test. (**B**) Experiment two: The decoy was broadcast from a ceiling speaker and so was perceptible but unavailable. (**C** and **D**) Relative preferences were dependent on the presentation of the decoy in both experiments. Experiment one: binary ($n = 40$ females) versus trinary ($n = 33$, excludes choices to stimulus C), $X^2 = 3.765$, $P < 0.05$; experiment two: binary versus trinary ($n = 77$, excludes no choice data), $X^2 = 14.700$, $P < 0.001$. Error bars indicate ±SE of the binomial distribution. ns, not significant. *, $P < 0.05$; ***, $P < 0.001$.
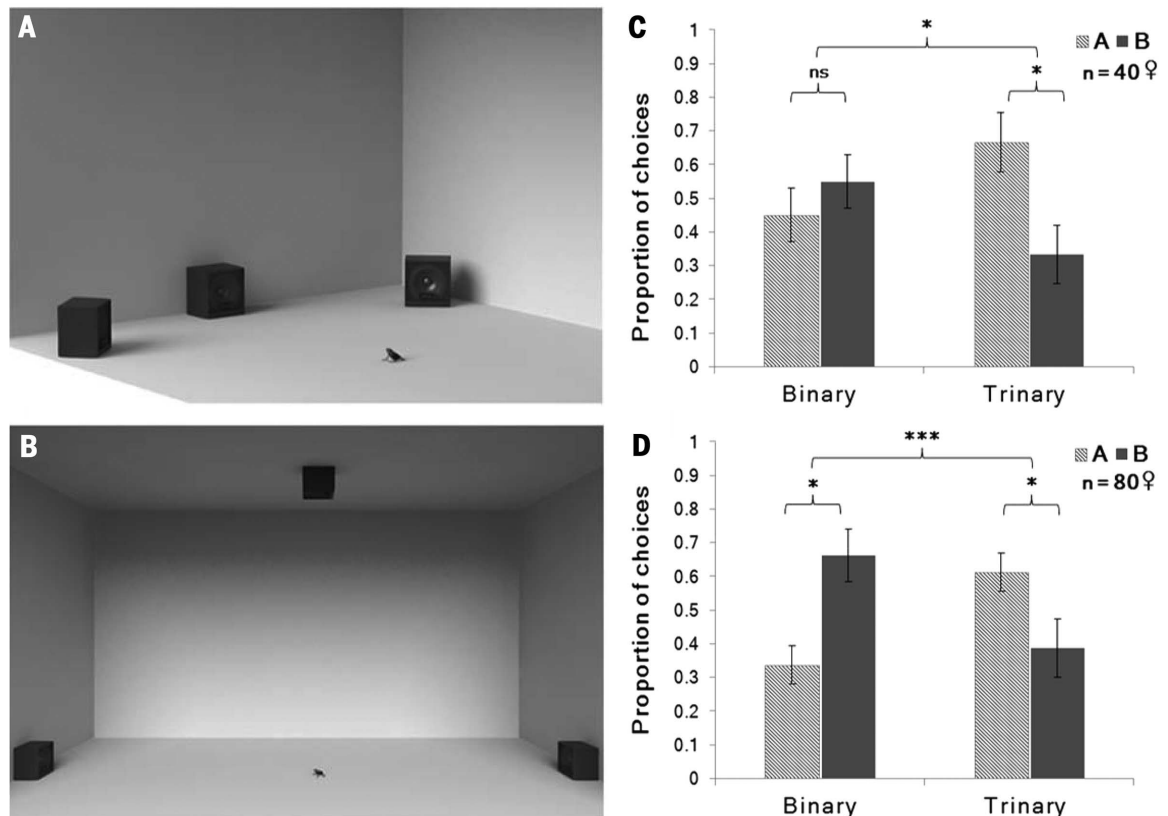
Growing empirical evidence suggests we lack a coherent understanding of the decision rules governing mate choice. Rational choice models have proven fruitful for static or otherwise simple selection scenarios, and yet may prove inadequate for generating accurate predictions of how sexually selected male traits evolve by female mate choice in the socially dynamic sexual marketplace. Further elucidating complex but predictable mate choice patterns would generate valuable insight into the evolution of decision-making and the coevolutionary processes of sexual selection.

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LIFE HISTORY

Age-related mortality explains life history strategies of tropical and temperate songbirds

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Life history theory attempts to explain why species differ in offspring number and quality, growth rate, and parental effort. I show that unappreciated interactions of these traits in response to age-related mortality risk challenge traditional perspectives and explain life history evolution in songbirds. Counter to a long-standing paradigm, tropical songbirds grow at similar overall rates to temperate species but grow wings relatively faster. These growth tactics are favored by predation risk, both in and after leaving the nest, and are facilitated by greater provisioning of individual offspring by parents. Increased provisioning of individual offspring depends on partitioning effort among fewer young because of constraints on effort from adult and nest mortality. These growth and provisioning responses to mortality risk finally explain the conundrum of small clutch sizes of tropical birds.

Life history strategies of virtually all taxa vary along a slow-fast gradient. Slow strategies are characterized by slow growth, low total parental effort for fewer offspring but high effort per offspring [i.e., high parental investment (*1*)], and long life (*2*). Fast strategies are characterized by the opposite (*2*). This slow-fast gradient is particularly well defined for songbirds of different latitudes, with tropical songbirds typically on the slow end and northern temperate birds falling toward the fast end (*3–7*). An extensive body of work and theory has attempted to explain the drivers of this pattern of life history variation, yet no consensus has emerged (*8–13*).

An early perspective on latitudinal variation in life history strategies proposed that stable tropical environments allow habitats to become "saturated" with individuals, thereby favoring slow life history strategies that improve competitive abilities (*10*, *11*). Yet the life history traits of coexisting tropical songbird species can vary as much or even more (*5*, *14*) than those of temperate species, and this variation is difficult to explain by the simple argument that competition is greater in the tropics. Other hypotheses invoking latitudinal differences in food limitation or nest predation have also failed to explain latitudinal variation (*4–6*). Differences in parental effort within and among latitudes have been addressed in part by classic theories based on age-specific or season-specific mortality [e.g., (*8*, *9*, *12*, *13*)]. However, an explanation is lacking for why effort may be partitioned among differing numbers of young and how this integrates with enigmatic growth strategies among species and latitudes. In short, the causes of variation in growth strategies, parental provisioning rates, and clutch size within and among latitudes remain unclear.

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Here, I provide a conceptual framework for within- and across-latitude variation in life history strategies based on mortality risk across life stages (Fig. 1). I base this on empirical evidence from extensive field studies of 20 to 30 coexisting songbird species in each of three locations: north temperate Arizona, USA, and tropical Malaysia and Venezuela.

An initial enigma is presented by the slow growth of tropical songbirds. Predation causes the vast majority of mortality for songbird offspring in the nest (nestlings) (*15*). Higher risk of nest predation favors faster growth (Fig. 2A and table S1A) in order to reduce time in the nest (nestling period) and exposure to nest predators (Fig. 1) (*5*, *16*). Yet tropical birds exhibit slower growth rates than temperate species for similar or even higher nest predation rates (Fig. 2A and table S1A), which has been perceived as a paradox (*9*). Moreover, this paradox was reinforced by the inability of an assumed longevity benefit to explain the slower growth of tropical birds (*17*).

This apparent paradox may reflect the way that growth rates have been viewed and estimated. Traditional growth rate estimates (*5*, *7*, *17*) provide estimates of peak growth (*18*). Slower peak growth rates of tropical birds have been implicitly assumed to reflect slower overall growth. Yet nestling periods of tropical species are 2 to 6 days shorter for the same peak growth rates (K_i) as temperate species (Fig. 2B and table S1B). If slower peak growth reflects slower overall growth, it should cause tropical offspring to leave the nest (fledge) at smaller relative sizes and earlier developmental states relative to temperate species (Fig. 3A, dashed versus yellow curves). Yet reduced development at fledging increases subsequent mortality (*19*). Tropical species might minimize such costs by extending the nestling period, but that increases nest predation risk (*16*) and is not reflected by the relationship of nestling period with peak growth rates (Fig. 2B). I suggest that this conundrum can be resolved by considering a