RUNAWAY SEXUAL SELECTION LEADS TO GOOD GENES

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Mate choice and sexual displays are widespread in nature, but their evolutionary benefits remain controversial. Theory predicts these traits can be favored by runaway sexual selection, in which preference and display reinforce one another due to genetic correlation; or by good genes benefits, in which mate choice is advantageous because extreme displays indicate a well-adapted genotype. However, these hypotheses are not mutually exclusive, and the adaptive benefits underlying mate choice can themselves evolve. In particular, examining how and why sexual displays become indicators of good genes is challenging in natural systems. Here, we use experimental evolution in "digital organisms" to demonstrate the origins of condition-dependent indicator displays following their spread due to a runaway process. Surprisingly, handicap-like costs are not necessary for displays to become indicators of male viability. Instead, a pleiotropic genetic architecture underlies both displays and viability. Runaway sexual selection and good genes benefits should thus be viewed as interacting mechanisms that reinforce one another.

KEY WORDS: Fisherian runaway, good genes, indicator traits.

For many organisms, mate choice is a risky affair. Assessing potential mates, and signaling or displaying to attract mates, requires time and energy and can increase exposure to predators and parasites (Pomiankowski 1987a; Zuk and Kolluru, 1998). Identifying the selective benefits counteracting these costs is an important problem for which a complete answer has proved elusive. In some species, these costs are offset by direct benefits received from mates, such as nuptial gifts or parental care (Gwynne 1982; Andersson 1994), but in others, no resources besides gametes are exchanged during courtship and mating. In these cases, indirect genetic benefits are hypothesized to explain the evolution of mate choice. Two of the most frequently invoked mechanisms are: (1) runaway sexual selection; and (2) good genes benefits or indicator traits. According to the former, mate choice is self-reinforcing;

mate preferences are selected indirectly due to a genetic correlation that builds up with male displays (Lande 1981; Kirkpatrick 1982), and females preferring males with elaborate sexual ornamentation may also benefit indirectly by having attractive sons (Weatherhead and Robertson 1979; Curtsinger and Heisler 1988; Pomiankowski et al., 1991). (For convenience, we will refer to choosy females and ornamented males, although these roles may be reversed in some species.) In the latter, choosy females benefit because the ornamented males they select tend to carry alleles conferring, for example, higher viability, which are then passed on to their offspring (Zahavi 1975; Pomiankowski 1987b; Iwasa et al. 1991; Andersson 1994; Rowe and Houle 1996). In particular, condition-dependent ornaments (i.e., displays that are expressed more strongly in individuals of higher condition) can lead to the

spread of mating preferences by providing information about the quality of potential mates (Andersson 1986; Iwasa et al. 1991).

In addition to a solid theoretical foundation (Lande 1981; Kirkpatrick 1982; Iwasa et al. 1991; Pomiankowski et al. 1991; Andersson 1994; Kokko et al. 2002; Mead and Arnold 2004; Kokko et al. 2006), both runaway sexual selection and good genes models enjoy empirical support (Jones et al. 1998; Welch et al. 1998; Wilkinson et al. 1998; Head et al. 2005). However, this evidence derives mostly from studies examining the current adaptive benefits of mate choice. Yet, the selective advantages maintaining a trait can differ from those that drove its origin, and theory predicts that adaptive benefits of mate choice in particular can change (Kokko et al. 2002). Moreover, although some studies suggest sensory biases can lead to the origins of new mating preferences (Rodd et al. 2002; Egger et al. 2011), testing how and why novel preferences spread in natural systems is challenging.

Here, we instead use Avida (Ofria and Wilke 2004), a digital evolution software environment containing populations of self-replicating, evolving "digital organisms," to explore how good genes and runaway sexual selection interact with one another when the benefits underlying adaptive mate choice are themselves allowed to evolve. We show that novel mating preferences and sexual displays can spread initially due to runaway sexual selection, but that these sexual displays quickly evolve into indicator traits, providing good genes benefits as well. Surprisingly, this outcome occurs even when displays are not costly, implying that "handicaps" are not necessary for the evolution of indicator displays. Instead, sexual displays share a common genetic basis with non-sexual components of fitness, consistent with theory predicting the evolution of condition-dependent indicator traits (Rowe and Houle 1996). Runaway sexual selection and good genes benefits should thus be viewed as complementary and coexisting mechanisms that reinforce one another (Andersson 1994; Kokko et al. 2002).

Methods
THE AVIDA SYSTEM
The details of Avida have been described elsewhere (Ofria and Wilke 2004). Briefly, a digital organism consists of a virtual hardware machine and a haploid circular genome, itself composed of a list of CPU instructions. Organisms copy their genomes and divide, obtaining metabolic resources (CPU cycles) by performing computational tasks, analogous to metabolic reactions. Populations have a user-defined spatial structure (in this case, a 60 × 60 grid, yielding a maximum size of 3600 organisms); when an organism reproduces, its offspring is placed at a random location in the population, killing the previous occupant of that position (if present). Because this system is characterized by (1) competition for limited resources (space and CPU cycles), (2) heritable variation in fitness, and (3) mutation, evolutionary processes arise naturally. As an independent instance of an evolving system, Avida can reveal general evolutionary principles not contingent upon the physical and chemical properties of life on earth. It also offers unprecedented power to measure organismal genotypes and phenotypes (including fitness) and to manipulate key experimental variables (e.g., cost of mate choice). Importantly, many processes that must be assumed in analytical or even some simulation models emerge on their own in Avida (admittedly, at the expense of some control over the processes operating in our populations). For example, a bias toward mutations that diminish male displays, which seems to be crucial for the evolution of costly preferences (Pomiankowski et al. 1991), is an inherent consequence of the mutational and evolutionary processes already present in this system, just as in nature (and some simulation-based explicit genetic models, such as that used in Lorch et al. 2003), whereas this feature must be intentionally incorporated into purely analytical models. Thus, evolution in Avida is open-ended, sometimes leading to surprising conclusions (Wilke et al. 2001) that might be missed in models lacking key elements such as mutational bias.

Although Avida has previously been used to study evolution in microbe-like systems (Lenski et al. 1999; Wilke et al. 2001; Lenski et al. 2003; Chow et al. 2004; Misevic et al. 2006; Clune et al. 2011), we added new features resembling those found in more complex organisms, specifically the ingredients necessary for mate choice to evolve: sexual recombination (Misevic et al. 2006) with distinct mating types (males and females), and configurable sex-specific reproductive costs reflecting the differential investments (anisogamy) made by each sex in most animals; CPU instructions allowing organisms to develop display traits; and CPU instructions allowing females to exhibit directional mating preferences, analogous to sensory biases thought to trigger the evolution of new mate preferences (Fuller et al. 2005; Fuller 2009; Egger et al. 2011), with configurable costs for these mating preferences. Mating occurs in an area similar to a lek, with a number of competing males displaying at any given time, and females choosing among them. In this system, male fitness can be broken into a nonsexual component (hereafter referred to as "viability" for convenience, although it also includes other aspects of fitness such as efficiency at gathering CPU resources) and a sexual component (mating success).

In all experiments, we recorded at regular intervals: the average population viability; mating display values of successfully mating and unsuccessful males; female mate preferences; and genome sequences of all organisms in the population. Stochastic noise was included in mate assessments such that perceived display values were drawn from a normal distribution around the displayer's true value with a coefficient of variation of 0.15, but

allowing perfect mate assessment did not alter any experimental outcomes or conclusions in preliminary tests. In addition to the default instruction set and new instructions allowing organisms to set their mating type (male or female), develop mating displays, and set mating preferences, we also included instructions allowing organisms to alter their execution flow (analogous to regulating gene expression) depending on their own phenotypic mating type (if-male, if-female, and if-juvenile), permitting the evolution of sexual dimorphism.

Populations were initialized with a single male and a single female that performed no functions other than reproduction, thus requiring the evolution of signaling traits and mate choice. Unless otherwise stated, all populations were allowed to evolve for 500,000 updates (8000–45,000 generations), with one update defined as the amount of time needed for the average organism to execute 30 instructions. Genome sizes were fixed at 200 instructions, with a mutation rate of 0.0025 substitutions per site per generation (thus, children differed from their parents by 0.5 mutations on average). We imposed an additional reproductive cost of 200 CPU cycles on females (∼12–60% increase in reproductive costs relative to males), but different values led to similar outcomes. (Note that these costs affected only the parents; greater reproductive CPU costs for the parents do not necessarily imply more resources available to offspring at birth.) Unless otherwise stated, in each experiment we tested three costs of mate choice (0, 50, or 200 CPU cycles), each in two different environments. Environment 1 was Avida's default environment, providing resource rewards when organisms performed each of nine Boolean logic operations, with larger rewards (i.e., stronger selection) for more complex operations; each organism could only be rewarded for each type of operation once (Lenski et al. 2003). Environment 2 was similar, but each Boolean "task" could be rewarded up to four times, resulting in more ways for organisms to differ from one another in fitness-related phenotypes and a more complex fitness landscape. Each population took 10–15 h to run at Michigan State University's High Performance Computing Center.

All statistical analyses were performed in R version 2.13.2. We used Avida release 2.12.3; source code and instructions for running Avida are available at avida.devosoft.org. Data files, analysis scripts, and Avida configuration files for our experiments are available from the Dryad data repository (doi:10.5061/dryad.cq737).

EXPERIMENT 1 (TESTING GOOD GENES HYPOTHESIS)
In our system, females mate randomly by default, but can mate nonrandomly by executing instructions that confer directional mating preferences prior to reproducing. We allowed populations access to (in other words, gave them the ability to evolve) one of two such mate preference instructions: one allowing females to prefer males with higher "merit" (a measure of the CPU resources an organism has obtained, strongly correlated with viability); and one conferring a preference for higher values of an arbitrary sexual display that, in this experiment, was fixed at zero for all males (by disabling instructions that allow organisms to modify or set their displays). The former could be considered an honest indicator display, for example, analogous to body size in a species in which larger individuals exhibit higher survival. The latter, on the other hand, was a "dummy" display lacking any variation, serving as a negative control to provide a null expectation for the frequency of mate choice in the absence of any advantages to choosiness.

We tested three costs of mate choice (0, 50, or 200 CPU cycles), each in two different environments, with 20 replicate populations of each treatment. We predicted that, if preferences for indicator traits are favored by good genes benefits, mate choice should reach higher frequencies in populations allowed to use instructions conferring preferences for higher merit, than in negative control populations, in which only mutations to instructions conferring a preference for the "dummy" display were allowed.

EXPERIMENT 2 (TESTING RUNAWAY SELECTION)
In this experiment, we evolved populations using three different mate choice treatments. In the "display + preference" treatment, mutations to instructions conferring female preferences for higher values of a male display were allowed (analogous to a sensory bias toward brighter coloration). Males are born with a display value of zero, but in this treatment could alter their displays by executing an "increment-display" instruction (analogous to increasing investment in the production of bright pigments). For the "preference only" treatment, we used the same populations as the negative control in experiment 1, in which the preference was allowed but the "increment-display" instruction was disabled, preventing organisms from developing displays, and thus eliminating variation in the display. In the "display only" treatment, our second negative control, the "increment-display" instruction was enabled, but mutations causing mating preferences were turned off. We predicted that, if sexual displays and mate choice reinforce one another in a runaway process, then (1) mate choice would reach higher frequencies in the "display + preference" treatment than in the "preference only" treatment; and (2) that male displays would become more exaggerated in the "display + preference" treatment than in the "display only" treatment. As in experiment 1, we tested two environments and three different levels for the cost of choosiness.

TESTING THE EVOLUTION OF GOOD GENES BENEFITS
To test whether initially "arbitrary" sexual displays can evolve into indicators of good genes, we examined the relationship

between male displays and viability in the "display + preference" and "display only" treatments from experiment 2. To assess this relationship, we measured male displays and viability in a test environment, log-transformed viability values, and then standardized both displays and log-viability within each population. We used linear models to estimate the slope of the regression of standardized log-viability on standardized sexual display in each population. Finally, we tested for differences in this relationship among treatments by examining the average slope across all replicates within each treatment.

To test whether a positive relationship between male displays and viability is accompanied by good genes benefits, for each evolved population, we generated 10,000 offspring from random pairings of male and female organisms. We then measured offspring viability in a test environment, and asked whether offspring viability is correlated with paternal sexual displays in each treatment, using the same approach as for the relationship between male displays and viability.

EXPERIMENT 3 (TESTING THE COSTS OF DEVELOPING SEXUAL DISPLAYS)

To test how display costs (handicaps) influence the evolution of indicator traits, we repeated the "display + preference" and "display only" treatments of experiment 2 with an altered genetic architecture underlying sexual displays. Specifically, we replaced the "increment-display" instruction with a "set-display" instruction, allowing organisms to immediately set their display to any value present in their CPU's internal memory, rather than needing to execute the "increment-display" instruction repeatedly. Thus, by using relatively few mathematical operations present in the default instruction set to generate a large number in their CPU's memory, and copying that value to their sexual displays, organisms using "set-display" can develop exaggerated displays while paying small CPU costs. Post-hoc tests confirmed that costs were correlated with display values using "increment-display" but not "set-display" (Fig. S1). Thus, these new displays are analogous to male calls or songs, with different song frequencies having similar costs (e.g., similar energy investment and equally attractive to predators).

TESTING THE PLEIOTROPIC EFFECTS OF MUTATIONS

To test whether mutations have correlated effects on male viability and sexual displays, in each evolved male genome from experiments 2 and 3, we generated a random point mutation. We measured the effects of each mutation on both viability and sexual displays, and within each population, estimated the slope of the regression of standardized viability effects on standardized display effects. We then averaged these slopes across all populations within each treatment to obtain estimates of the average pleiotropic effects of point mutations.
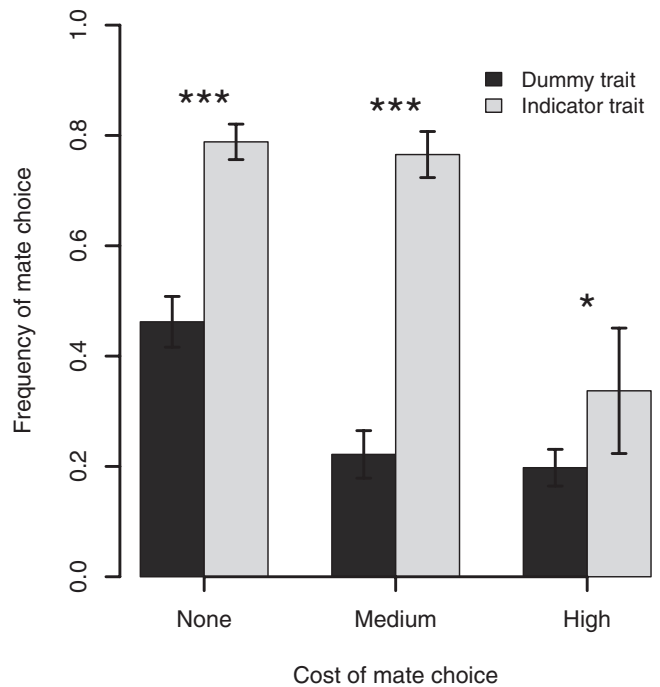
Figure 1. Directional mate choice for an indicator trait (experimentally forced to reflect male viability) reaches significantly higher frequencies than a preference for a "dummy" trait (lacking phenotypic variation), provided mate choice is not too costly, consistent with the good genes hypothesis. Bars show the average frequency of mate choice in populations ($n = 20$ per treatment) of digital organisms evolved for >8000 generations, in which females could express one of the two mating preferences. Results from environment 2 are presented. Error bars indicate mean frequency $\pm$ 2 SE. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

Results

EXPERIMENT 1 (TESTING GOOD GENES HYPOTHESIS)

As predicted, when females could base their mating decisions on a display indicating good genes, mate choice reached significantly higher frequencies than in negative control populations, in which we only allowed preferences for a "dummy" trait lacking male variation (Fig. 1). This result was consistent across different environments, but varied with the cost of mate choice: smaller costs maintained preferences at higher frequencies and for longer, whereas mate choice tended to decline after its initial spread when this cost was high (Fig. S2).

EXPERIMENT 2 (TESTING RUNAWAY SELECTION)

Consistent with runaway sexual selection, when mutations altering both the display and preference were allowed in populations, mate choice reached significantly higher frequencies (Fig. 2A), and sexual displays were significantly larger (Fig. 2B), than populations with only mate preferences (for a dummy display) or only
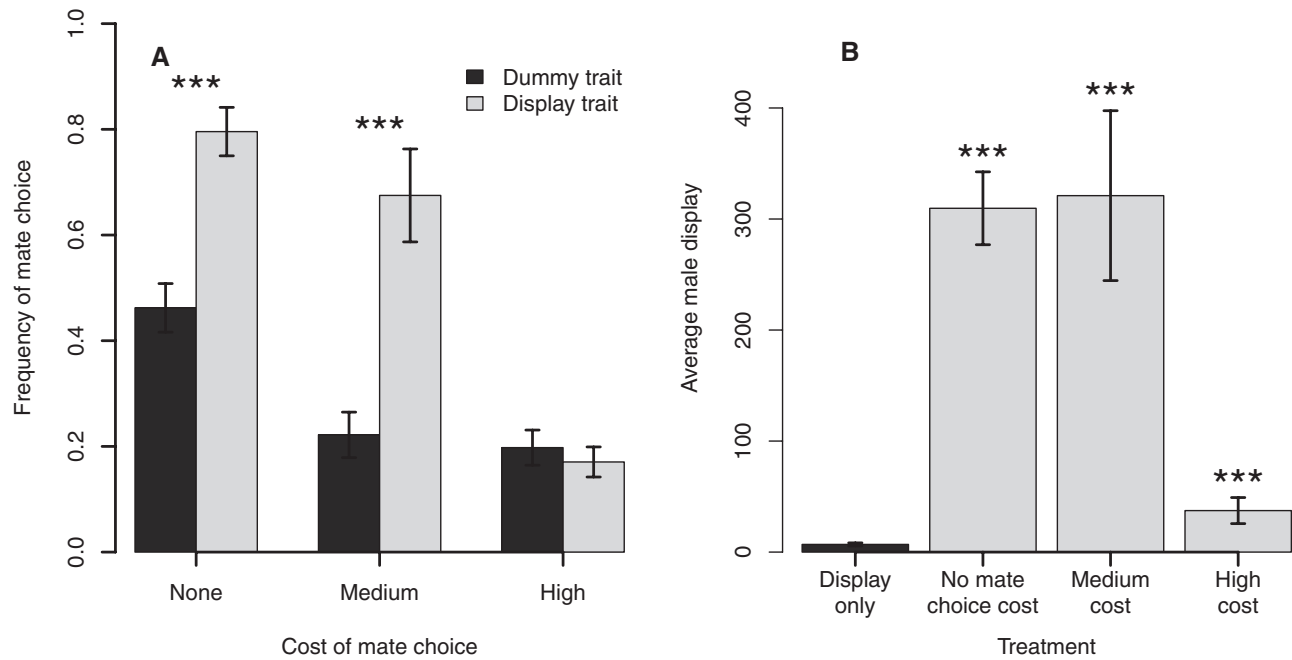
Figure 2. (A) The frequency of a directional female mate preference reaches significantly higher frequencies for displays with heritable variation than for a "dummy" display (lacking variation in males), provided the cost of mate choice is not too high, consistent with a self-reinforcing runaway process. (B) Male displays are significantly exaggerated in populations in which females are allowed to exhibit mate choice, relative to populations in which all females mate randomly. Bars show mean frequency of female mate choice (A) or male display value (B) across populations of digital organisms evolved for >8000 generations ($n = 20$ per treatment). Results from environment 2 are presented. Error bars indicate mean frequency ± 2 SE. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

sexual displays. Again, these results were consistent in different environments, but the frequency of choosy females declined if a cost to mate choice was introduced (Figs. S3 and S4). Results were also similar for different mutation rates and when populations were preadapted to the environment before mutations allowing mating preferences were permitted (Figs. S5–S7).

TESTING THE EVOLUTION OF GOOD GENES BENEFITS
To investigate the interaction between indicator and runaway mechanisms, we asked whether a novel sexual display initially uncorrelated with male viability could evolve such a correlation. In populations in which runaway sexual selection occurred, a significantly more positive, stable correlation between viability and display levels evolved (Figs. 3A, S5–S8). Furthermore, offspring viability was, on average, more strongly positively correlated with paternal display values in runaway selection populations than in negative control populations (Fig. 3B), although the strength of this correlation did depend on the environment (Fig. S9). Thus, although no relationship between sexual displays and male viability was experimentally enforced (unlike the treatment in experiment 1 in which displays directly reflected male "merit"), a positive correlation between them, and therefore good genes benefits, evolved in the presence of runaway sexual selection.

### EXPERIMENT 3 (TESTING THE COSTS OF DEVELOPING SEXUAL DISPLAYS)
When the "increment-display" instruction was replaced by "set-display," strongly diminishing the "handicap"-like costs associated with displays, a strong relationship between display intensity and viability still evolved (Figs. 3C, S8). Likewise, paternal display values were again positively correlated with offspring viability (Figs. 3D, S9). Such costs are therefore not necessary for the evolution of indicator traits.

TESTING THE PLEIOTROPIC EFFECTS OF MUTATIONS
Point mutations randomly inserted across the genome in individuals from the evolved populations of experiments 2 and 3 showed widespread pleiotropy, with significantly positively correlated effects on both viability and displays, and stronger correlations in conditions leading to a runaway process (Fig. 4). Sexual displays therefore indicate male viability because they share a common genetic basis.

VARIATION IN MATE CHOICE FREQUENCY AND INDICATOR DISPLAYS
To assess variation in outcomes among runs within each treatment, we measured the frequency of mate choice and the
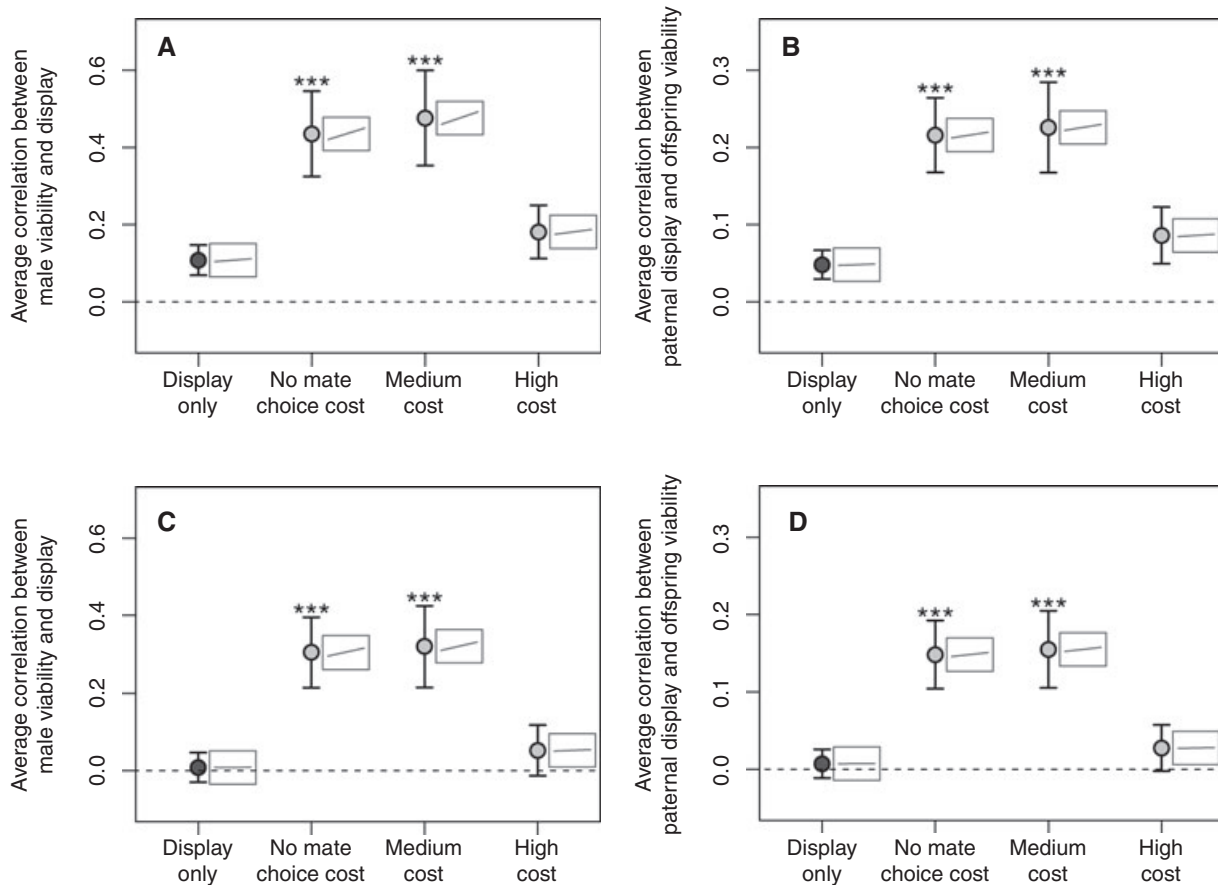
Figure 3. "Good genes" benefits from mate choice for sexual displays that initially evolved because of runaway sexual selection. (A, C) Average correlation between male display values and viability in digital organisms evolved for >8000 generations ($n = 20$ populations per treatment), using two different architectures for organisms to produce sexual displays (A: increment-display instruction; C: set-display instruction). (B, D) Average correlation between paternal display and offspring viability in the same populations (10,000 offspring generated per population; B: increment-display; D: set-display). Inset plots depict the average relationship between male displays and either male viability or offspring viability in each treatment. Asterisks indicate significant differences between treatments with mate choice (with varying costs of choosiness) and the appropriate negative control treatment (male displays but no mate choice). Results from environment 2 are presented. Error bars indicate mean ± 2 SE. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

relationship between male displays and viability in each population after 500,000 updates. The frequency of choosiness was positively correlated with the slope of male viability on displays (Fig. 5), in treatments with (using "increment-display") and without (using "set-display") costs of displaying (with costs: slope = 1.97, 95% CI = 1.24–2.70, $P = 1.2 \times 10^{-6}$; without costs: slope = 2.29, 95% CI = 1.48–3.10, $P = 4.9 \times 10^{-7}$). Thus, variation in how well displays evolve to indicate male viability can be partially explained by variation in the frequency of mate choice.

Discussion

While theory has provided a number of predictions regarding the evolution of sexual displays and mating preferences (Lande 1981; Kirkpatrick 1982; Iwasa et al. 1991; Pomiankowski et al. 1991; Andersson 1994; Kokko et al. 2002; Mead and Arnold

2004; Kokko et al. 2006), nature has provided few opportunities to test them directly in a tractable biological system. Here, we adopt an alternative approach: experimental evolution in an artificial system. Although the user has control over many important variables, evolution in Avida is much more open-ended than in analytical or numerical simulation models. For example, there is no explicit fitness function; evolution instead occurs as a consequence of mutation, heritability, and competition inherent in Avida. Likewise, certain properties that must be deliberately assumed in theoretical models, such as directionally biased mutation (Pomiankowski et al. 1991), arise on their own in Avida. Thus, this system can yield unexpected outcomes that would be missed if experimenters failed to incorporate these assumptions.

First, our experiments provide strong support that both good genes benefits and runaway sexual selection can promote the spread of novel mate preferences (Figs. 1, 2): in experiments
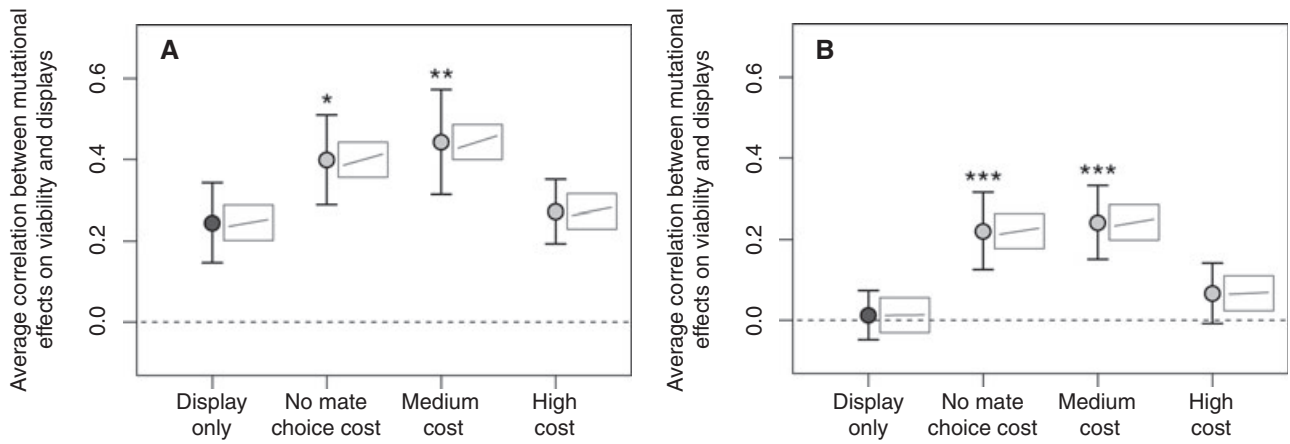
Figure 4. Point mutations have more strongly correlated effects on male viability and sexual displays when runaway sexual selection is operating. (A) Populations in which organisms developed displays using the "increment-display" instruction. (B) Populations in which organisms developed displays using the "set-display" instruction. Inset plots depict the average relationship between mutational effects on viability and displays in each treatment. Asterisks indicate significant differences between treatments with mate choice (with varying costs of choosiness) and the appropriate negative control treatment (male displays but no mate choice). Results from environment 2 are presented. Error bars indicate mean ± 2 SE. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.
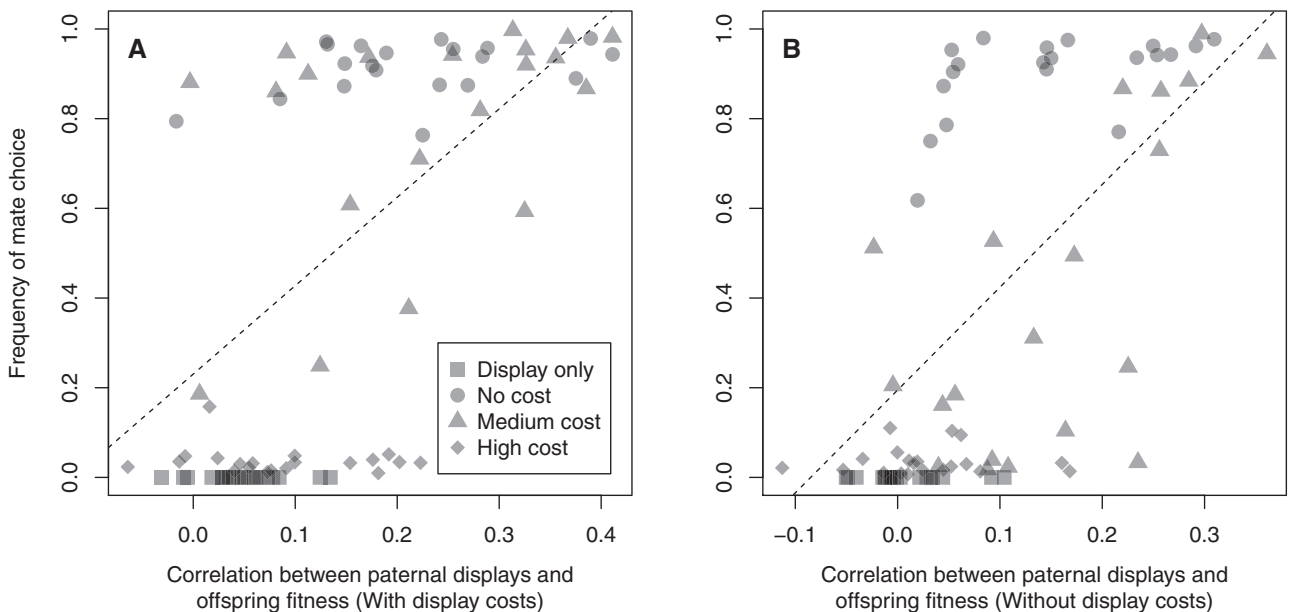
Figure 5. Among populations, the frequency of mate choice is positively correlated with the strength of the relationship between male viability and displays. (A) Populations in which organisms developed displays using the "increment-display" instruction. (B) Populations in which organisms developed displays using the "set-display" instruction.

testing both mechanisms, mate choice consistently reached higher frequencies than in negative control populations, in which only preferences for a nonvariable "dummy" display were allowed. Outcomes were robust to experimental conditions, including the selective environment, mutation rate, and preadaptation to the environment prior to the appearance of mating preferences (Figs. S5–S7); mate preferences were only limited when they were prohibitively costly. Thus, in many cases, novel mate preferences can spread quite easily, once they appear. In nature, however, the

appearance of new preferences may be a more limiting factor than in our populations: even in our negative control populations, mate choice reached non-negligible frequencies, probably due to new mutations causing "choosiness" (Figs. 1, 2, S2, S3, S5–S7). While there is some evidence that mate preferences can evolve from sensory biases selected in other contexts (Rodd et al. 2002; Fuller 2009; Egger et al. 2011), these sensory biases probably arise less frequently in nature than they did in our populations (because a single mutation to a set-mate-preference instruction at nearly any

locus in an Avidian genome could hypothetically cause such a sensory bias), perhaps explaining why such strong mate choice is not as widespread as our results would otherwise suggest. Recombination rates might also affect the frequency with which runaway processes could arise. In our system, a single recombination event occurred during each mating (i.e., a single continuous genomic segment was swapped between the two parental genomes; Misevic et al. 2006), but higher recombination rates would likely slow a runaway process by impeding the buildup of linkage disequilibrium (and thus genetic correlation) between preferences and displays.

More importantly, our results illustrate how new indicator traits evolve. After a mate preference spreads due to a runaway process, it is likely to evolve additional "good genes" benefits, as well. Our results suggest that these benefits do not derive from a purely epistatic "handicap" display (Iwasa et al. 1991; Smith 1991). Such displays are expressed unconditionally but are disproportionately more costly (or provide lesser benefits; Getty 2006) for individuals of low quality. Surviving adults with the display are therefore more likely to be of high quality than those lacking the display, and females are more likely to choose a high-quality mate if they prefer ornamented males. This scenario is unlikely to explain the good genes benefits observed in our populations, because we were able to drastically reduce the costs of sexual displays by making a set-display instruction available to organisms, permitting them to immediately develop greatly exaggerated displays with virtually no costs (experiment 3; Fig. S1). Even in these cases, more intense paternal displays were correlated with increased offspring viability.

Instead, displays in our populations evolved into condition-dependent indicators of male "quality" (Andersson 1986; Iwasa et al. 1991; Rowe and Houle 1996). Our results show that mutations frequently had pleiotropic, correlated effects on sexual displays and the nonsexual component of male fitness (Fig. 4). Sexual displays and viability, in other words, seem to be regulated by common genetic mechanisms. We propose that a process somewhat analogous to Haldane's sieve (Haldane 1924) selects for such condition-dependent indicator displays: preferences for displays that, by chance, happen to be associated with viability, are likely to be the most strongly favored, because they provide females with both runaway and good genes advantages. As a result, displays that happen to be associated with viability are also more strongly favored in males. In our populations, genetic variance in both displays and viability is likely maintained by pleiotropic mutations.

The observation that populations with a higher frequency of mate choice have "better" indicator displays (i.e., a steeper positive slope for the relationship between male displays and viability; Fig. 5) is consistent with this hypothesis. Although this correlation alone does not reveal the direction of causation, mating preferences appear to invade more quickly than indicator displays (Figs. S5–S7), suggesting that the runaway process has facilitated the evolution of these indicator displays, rather than the other way around. Interestingly, at least for populations using the "set-display" instruction, increasing the cost of mate choice in females from zero to a moderate level seems to promote the evolution of more reliable indicators for a given mate choice frequency, and thus mating preferences that confer stronger "good genes" advantages (triangles tend to appear to the right of circles in Fig. 5B). This is consistent with the finding by (Kokko et al. 2002) that when mate choice is inexpensive, females benefit indirectly mainly through the increased mating success of their sons, whereas when mate choice is costly, their offspring enjoy increased viability.

Our results suggest that indicator traits evolve in stages. First, a novel mate preference appears in a population, perhaps due to a new mutation or newly evolved sensory bias (Fuller 2009; Egger et al. 2011). Runaway sexual selection maintains and amplifies this preference and the corresponding sexual display. Finally, the sexual display becomes genetically correlated with nonsexual fitness components, and thus an indicator of good genes, providing additional indirect genetic benefits that further maintain mate choice. This model contrasts with Fisher's original formulation (Fisher 1915, 1930), in which good genes benefits precede runaway sexual selection: in our populations, the relationship between male viability and display intensity evolved more slowly than the spread of the mate preference (evident in Figs. S5–S7). This is not to say that good genes benefits must always be preceded by a runaway process. Both mechanisms could simultaneously support a novel preference from its initial appearance if the display it acts on happens to be an indicator of condition; many nonsexually selected traits are already condition dependent (Rowe and Houle 1996; Cotton et al. 2004a). However, our results do lend support to the hypothesis that sexual selection, even if it is initially triggered by a runaway process, can lead to the evolution of heightened condition dependence (Cotton et al. 2004b).

Our findings underscore the inseparability of good genes benefits and runaway sexual selection, which are often pitted against each other as competing hypotheses, but which have also been recognized as endpoints along a single continuum (Kokko et al. 2002). Our work extends this conclusion by showing that runaway processes can also facilitate the evolution of condition-dependent indicator displays, even if those displays do not impose "handicap"-like costs. We propose that future work should test this result in biological systems, especially taking an experimental evolution approach in a tractable model (Rogers and Greig 2009; Smith and Greig 2010). The Avida system will also be useful for addressing questions about the evolutionary consequences of sexual selection, for example, its effects on rates of adaptation and speciation (Proulx 1999; Whitlock 2000; Agrawal 2001; Proulx

2001; Siller 2001; Holland 2002; Proulx 2002; Ritchie 2007; Hollis et al. 2009; Maan and Seehausen 2011).

LITERATURE CITED

Agrawal, A. 2001. Sexual selection and the maintenance of sexual reproduction. Nature 411:692–695.

Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. Evolution 40:804–816.

———. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

Chow, S. S., C. O. Wilke, C. Ofria, R. E. Lenski, and C. Adami. 2004. Adaptive radiation from resource competition in digital organisms. Science 305:84–86.

Clune, J., H. J. Goldsby, C. Ofria, and R. T. Pennock. 2011. Selective pressures for accurate altruism targeting: evidence from digital evolution for difficult-to-test aspects of inclusive fitness theory. Proc. R. Soc. Lond. B 278:666–674.

Cotton, S., K. Fowler, and A. Pomiankowski. 2004a. Heightened condition dependence is not a general feature of male eyespan in stalk-eyed flies (Diptera: Diopsidae). J. Evol. Biol. 17:1310–1316.

———. 2004b. Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? Proc. R. Soc. Lond. B 271:771–783.

Curtsinger, J., and I. Heisler. 1988. A diploid sexy son model. Am. Nat. 132:437–453.

Egger, B., Y. Klaefiger, A. Theis, and W. Salzburger. 2011. A sensory bias has triggered the evolution of egg-spots in Cichlid fishes. PLoS One 6:e25601.

Fisher, R. A. 1915. The evolution of sexual preference. Eugen. Rev. 7:184–192.

———. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

Fuller, R. C. 2009. A test of the critical assumption of the sensory bias model for the evolution of female mating preference using neural networks. Evolution 63:1697–1711.

Fuller, R. C., D. Houle, and J. Travis. 2005. Sensory bias as an explanation for the evolution of mate preferences. Am. Nat. 166: 437–446.

Getty, T. 2006. Sexually selected signals are not similar to sports handicaps. Trends Ecol. Evol. 21:83–88.

Gwynne, D. 1982. Mate selection by female katydids (Orthoptera: Tettigoniidae, *Conocephalus nigropleurum*). Anim. Behav. 30:734–738.

Haldane, J. 1924. A mathematical theory of natural and artificial selection. Part I. Proc. Camb. Philos. Soc. 23:19–41.

Head, M. L., J. Hunt, M. D. Jennions, and R. Brooks. 2005. The indirect benefits of mating with attractive males outweigh the direct costs. PLoS Biol. 3:e33.

Holland, B. 2002. Sexual selection fails to promote adaptation to a new environment. Evolution 56:721–730.

Hollis, B., J. L. Fierst, and D. Houle. 2009. Sexual selection accelerates the elimination of a deleterious mutant in *Drosophila melanogaster*. Evolution 63:324–333.

Iwasa, Y., A. Pomiankowski, and S. Nee. 1991. The evolution of costly mate preferences. II. The "handicap" principle. Evolution 45:1431–1442.

Jones, T. M., R. J. Quinnell, and A. Balmford. 1998. Fisherian flies: benefits of female choice in a lekking sandfly. Proc. R. Soc. Lond. B 265:1651–1657.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1–12.

Kokko, H., R. Brooks, J. M. McNamara, and A. I. Houston. 2002. The sexual selection continuum. Proc. R. Soc. Lond. B 269:1331–1340.

Kokko, H., M. D. Jennions, and R. Brooks. 2006. Unifying and testing models of sexual selection. Annu. Rev. Ecol. Evol. Syst. 37:43–66.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78:3721–3725.

Lenski, R., C. Ofria, T. Collier, and C. Adami. 1999. Genome complexity, robustness and genetic interactions in digital organisms. Nature 400:661–664.

Lenski, R., C. Ofria, R. Pennock, and C. Adami. 2003. The evolutionary origin of complex features. Nature 423:139–144.

Lorch, P., S. Proulx, and L. Rowe. 2003. Condition-dependent sexual selection can accelerate adaptation. Evol. Ecol. Res. 5:867–881.

Maan, M. E., and O. Seehausen. 2011. Ecology, sexual selection and speciation. Ecol. Lett. 14:591–602.

Mead, L. S., and S. J. Arnold. 2004. Quantitative genetic models of sexual selection. Trends Ecol. Evol. 19:264–271.

Misevic, D., C. Ofria, and R. Lenski. 2006. Sexual reproduction reshapes the genetic architecture of digital organisms. Proc. R. Soc. Lond. B 273:457–464.

Ofria, C., and C. Wilke. 2004. Avida: a software platform for research in computational evolutionary biology. Artif. Life 10:191–229.

Pomiankowski, A. 1987a. The costs of choice in sexual selection. J. Theor. Biol. 128:195–218.

———. 1987b. Sexual selection: the handicap principle does work—sometimes. Proc. R. Soc. Lond. B 231:123–145.

Pomiankowski, A., Y. Iwasa, and S. Nee. 1991. The evolution of costly mate preferences. I. Fisher and biased mutation. Evolution 45:1422–1430.

Proulx, S. 2001. Female choice via indicator traits easily evolves in the face of recombination and migration. Evolution 55:2401–2411.

———. 2002. Niche shifts and expansion due to sexual selection. Evol. Ecol. Res. 4:351–369.

Proulx, S. R. 1999. Matings systems and the evolution of niche breadth. Am. Nat. 154:89–98.

Ritchie, M. G. 2007. Sexual selection and speciation. Annu. Rev. Ecol. Evol. Syst. 38:79–102.

Rodd, F. H., K. A. Hughes, G. F. Grether, and C. T. Baril. 2002. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? Proc. R. Soc. Lond. B 269:475–481.

Rogers, D. W., and D. Greig. 2009. Experimental evolution of a sexually selected display in yeast. Proc. R. Soc. Lond. B 276:543–549.

Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. Proc. R. Soc. Lond. B 263:1415–1421.

Siller, S. 2001. Sexual selection and the maintenance of sex. Nature 411:689–692.

Smith, C., and D. Greig. 2010. The cost of sexual signaling in yeast. Evolution 64:3114–3122.

Smith, J. M. 1991. Theories of sexual selection. Trends Ecol. Evol. 6:146–151.

Weatherhead, P., and R. Robertson. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis." Am. Nat. 113:201–208.

Welch, A., R. Semlitsch, and H. Gerhardt. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. Science 280:1928–1930.

Whitlock, M. C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. Evolution 54:1855–1861.

Wilke, C., J. Wang, C. Ofria, R. Lenski, and C. Adami. 2001. Evolution of digital organisms at high mutation rates leads to survival of the flattest. Nature 412:331–333.

Wilkinson, G., D. Presgraves, and L. Crymes. 1998. Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression. Nature 391:276–279.

Zahavi, A. 1975. Mate selection—a selection for a handicap. J. Theor. Biol. 53:205–214.

Zuk, M., and G. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. Q. Rev. Biol. 73:415–438.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Average correlation between male display values and "gestation time," a measure of the number of CPU instructions executed over the course of an organism's lifetime.

Figure S2. Frequency of female mate choice for either a dummy trait (lacking phenotypic variation) or an indicator trait (experimentally forced to reflect a male's fitness) through time in evolving populations of digital organisms.

Figure S3. Frequency of female mate choice for either a dummy trait (lacking phenotypic variation) or an arbitrary male display trait through time in evolving populations of digital organisms.

Figure S4. Average male display values in evolving populations of digital organisms allowed to exhibit both an arbitrary male sexual display and a directional female preference for the display (blue lines), or only the sexual display with no female mating preferences (red lines).

Figure S5. Frequency of mate choice (left column), average male sexual displays (middle column), and average correlation between male displays and viability (right column) over time in populations evolved for one million updates with a reduced mutation rate of 0.0005 substitutions per site per generation, for three different levels of the cost of choosiness.

Figure S6. Frequency of mate choice (left column), average male sexual displays (middle column), and average correlation between male displays and viability (right column) over time in populations preadapted to their environment 5×10^6 updates prior to enabling mutations causing mate preference, for three different levels of the cost of choosiness.

Figure S7. Frequency of mate choice (left column), average male sexual displays (middle column), and average correlation between male displays and viability (right column) over time in populations preadapted to their environment 5×10^6 updates prior to enabling mutations causing mate preference, and with a reduced mutation rate of 0.0005 substitutions per site per generation, for three different levels of the cost of choosiness.

Figure S8. Average correlation between male display and fitness in populations of digital organisms evolving over time, in two different environments, with three different costs of mate choice (none, medium, high), and with two different architectures underlying male sexual displays (increment-display and set-display).

Figure S9. Average correlation between paternal display value and offspring viability in populations of digital organisms evolved for > 8000 generations (10,000 offspring generated per population), with varying costs of mate choice, in two different environments, and with two different architectures underlying male sexual displays (A, C: increment-display; B, D: set-display).

Supporting Information may be found in the online version of this article.

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