**Are high-quality mates always attractive?**

**State-dependent mate preferences in birds and humans**

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Sexual selection theory posits that females should choose mates in a way that maximizes their reproductive success. But what exactly is the optimal choice? Most empirical research is based on the assumption that females seek a male of the highest possible quality (in terms of the genes or resources he can provide), and hence show directional preferences for indicators of male quality. This implies that attractiveness and quality should be highly correlated. However, females frequently differ in what they find attractive. New theoretical and empirical insights provide mounting evidence that a female’s own quality biases her judgement of male attractiveness, such that male quality and attractiveness do not always coincide. A recent experiment in songbirds demonstrated for the first time that manipulation of female condition can lead to divergent female preferences, with low-quality females actively preferring low-quality males over high-quality males. This result is in line with theory on state-dependent mate choice and is reminiscent of assortative mating preferences in humans. Here we discuss the implications of this work for the study of mate preferences.

Birds of a Feather Flock Together: State-Dependent Preferences in Zebra Finches

Holveck & Riebel manipulated adult phenotypic quality in zebra finches (Taeniopygia guttata) by rearing nestlings in experimental broods that contained either few or many siblings. This brood-size manipulation is known to have measurable effects on adult physiology, morphology and behavior,[14] with birds from smaller broods faring better than those from large broods. Instead of showing a uniform preference for males of superior quality, adult females preferred males whose quality matched their own. Quality-matched pairs also showed a much shorter latency to breeding than non-matched pairs, suggesting a reproductive advantage: zebra finches in their natural habitats have to breed quickly if they want to take full advantage of the rare rainfalls.[7]

Although divergent preference functions (i.e., the order in which prospective mates are ranked[9]) based on the chooser’s own quality had previously been shown in fish[9] and spiders,[10] these earlier studies relied on naturally occurring variation in quality, which could be correlated with genetic differences. Furthermore, they measured choice in interactive situations, which complicates interpretation due to the feedback between male and female courtship behavior. The study by Holveck & Riebel circumvented both issues, by showing that divergent preferences were a direct response to (experimentally altered) phenotypic quality, and using a non-interactive choice test to measure female preference directly without any confounding influence of the male’s preference. Similar methods had been used by others (e.g., ref. 11) to show that females in poor condition typically have weaker preferences,[12] but this was the first demonstration that differences in phenotypic quality can generate preferences in completely opposite directions.

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**Key words:** assortative mating, state-dependent mate choice, choosiness, preference function, condition, humans, birds, zebra finch, attractiveness, constrained and unconstrained choice

Submitted: 02/15/10

Accepted: 02/16/10

Previously published online: www.landesbioscience.com/journals/cib/article/11557

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Addendum to: Holveck M-J, Riebel K. Low-quality females prefer low-quality males when choosing a mate. Proc R Soc Lond B 2010; 277:153–60; PMID: 19812084, DOI: 10.1098/rspb.2009.1222.
males at the first choice opportunity they mously preferred the songs of low-quality Nonetheless, low-quality females unani-
they chose between pre-recorded songs. In the unconstrained choice situation
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growing evidence that attractiveness
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expected for high-quality mates. (B)
state-dependent preferences or from a uniform,
directional preference for high quality in
individuals (be they birds or humans) prefer
a mate who is similar to themselves.26-28
For example, internal physiological
alternatives pairing off first, leaving low-quality
choice will lead to high-quality individu-
individuals who are too choosy may
fail to find a mate and be forced to forego
reproduction altogether; while those who
are unselective may end up with a mis-
mated partner, resulting in low parental
investment29 and a high risk of desertion
or divorce.19 These factors could make it
advantageous for individuals to mate
assortatively.

However, positive assortative mat-
ing does not necessarily imply that indi-
viduals (be they birds or humans) prefer
a mate who is similar to themselves.26-28

**Figure 1.** Different underlying processes can lead to assortative mating. (A) Divergent, state-de-
dependent preferences in both sexes (high-quality individuals prefer high-quality mates, while low-
quality individuals prefer low-quality mates). (B) Uniform, directional preference for high-quality
mates in both sexes. Due to mutual choice and competition for mates, low-quality individuals are
left with only low-quality mates to pair up with. Low-quality individuals will typically spend more
time and energy in finding a mate.

What explains these divergent pref-
ences? Theoretical models of state-
dependent mate choice point out that
indivduals in poor condition should be
less attracted to high-quality mates when
they cannot defend them.13,14 risk being desereted by them15 or are unlikely to be
accepted by them in the first place.16 If
pursuing these mates is likely to waste
time or energy, it may pay to avoid high-
quality mates altogether and target low-
quality partners instead.13 Holbeck &
Riebel’s work1 provides the first empiri-
cal evidence for this prediction, showing
that high-quality males are not the most
attractive mates for all females. Together
with studies on other species9-11 this adds
to growing evidence that attractiveness
judgments may be closely related to the
chooser’s own state.

**Beauty is in the Eye of the
Beholder in Zebra Finches and
Humans**

In the unconstrained choice situation
used by Holbeck & Riebel, females did
not experience direct rejection by males or
competition with other females, because
they chose between pre-recorded songs.
Nonetheleess, low-quality females unani-
mously preferred the songs of low-quality
males at the first choice opportunity they
had as adults.1 This implies the existence
of mechanisms that alter females’ mating
decisions in relation to their own phe-
notypic quality.17 Such state-dependent
choice is highly reminiscent of mate pref-
rencias in humans: people who consider
themselves unattractive tend to show
weaker preferences for the most sought-
after mates and for traits presumed to
indicate mate quality.18-20 Sensitivity to
one’s own quality or attractiveness may be
useful in species with mutual choice, as a
way of deciding which mates are unattain-
able and therefore not worth courting.1,18,21
But while questionnaire-based studies ask
people to reflect consciously on their own
attractiveness, in a real choice situation
entirely subconscious mechanisms could
be at work, in humans as well as in zebra
finches. For example, internal physiologi-
cal monitoring might inform individuals
about their body condition6 and lead to
adjustment of their preferences. Likewise,
individuals may gain feedback about their
quality relative to conspecifics from previ-
ous non-sexual social experiences17 and
be sensitive to the level of interest they
receive from the opposite sex,16 which
could precipitate hormonal changes22,23
and subsequently drive changes in choice.
Thus in both species, individuals may
change their preferences in response to
physiological and social feedback without
directly perceiving their own attractiveness (cf. refs. 17, 18).

**Assortative Mating in Humans and
Birds**

The mating systems of humans and pas-
serine birds share important features: both
show pronounced plasticity in relation to
ecological conditions, but there is a high
prevalence of stable pair formation and
joint parental care.24 The considerable
parental investment by males as well as
females means that mutual mate choice
is common. In such systems, the time
and energy costs of searching for a mate
are typically high, and mate-choice deci-
sions can strongly affect reproductive suc-
cess. Individuals who are too choosy may
fail to find a mate and be forced to forego
reproduction altogether; while those who
are unselective may end up with a mis-
matched partner, resulting in low parental
investment29 and a high risk of desertion
or divorce.19 These factors could make it
advantageous for individuals to mate
assortatively.

However, positive assortative mat-
ing does not necessarily imply that indi-
viduals (be they birds or humans) prefer
a mate who is similar to themselves.26-28

**Figure 1** illustrates how quality-matched
pairs could result from divergent, state-
dependent preferences or from a uniform,
directional preference for high quality in
both sexes. In the latter case, mutual mate
choice will lead to high-quality individu-
als pairing off first, leaving low-quality
individuals as the last resort, perhaps
after prolonged search and rejections.
This may be compounded by variation in
choosiness (i.e., the effort invested in mate
assessment8), since directional preferences
for high-quality individuals should favor
reduced choosiness in low-quality individu-
als, or at least its gradual decrease with
search time.13 Thus, assortative pairing
between individuals of the same quality
does not imply that preferences are state-
dependent.

**Quality and Attractiveness are Not
Synonymous**

Evidence from several taxa suggests that
individual variation in state can favor
preferences for quality-matched rather than superior mates, such that low-quality females actively prefer low-quality males. Genetic compatibility (e.g., based on the major histocompatibility complex), ecological context, and the particular subset of males available during choice are additional factors that can further disrupt the link between male quality and female mate preferences. Consequently, when discussing attractiveness we should be aware that this is a measure of how much a particular male is preferred by a particular female, which may be related in different ways to the quality of both individuals. High-quality males are therefore not always the most attractive.

Viewed in this light, attractiveness is not an inherent property of a particular male phenotype; rather, it is a combined outcome of the male’s phenotype and the female’s response. Females may vary in their responses, in which case the same male is attractive to one female but unattractive to another. Despite this, females may still agree on which male has the highest quality. This may explain why verbally expressed preferences did not match actual choices in human speed dating or why female zebra finches consistently laid bigger eggs when mated to high-quality males, despite preferring males of their own quality in choice tests.

**Conclusions**

Preferences measured in mate-choice experiments are rarely uniform among the tested subjects; a female’s current state, influenced throughout her development by genetic and non-genetic factors, can affect the direction and strength of her choices. Unraveling the extent to which variation in female preferences can be attributed to state-dependent effects is a major challenge for future studies of sexual selection.

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