

PLOS Science Wednesday: Hi Reddit, we're Drs. Malika Ihle, Wolfgang Forstmeier and Prof. Bart Kempenaers, behavioural ecologists here to discuss the fitness benefits of love... in birds – Ask Us Anything

PLOSScienceWednesday¹ and r/Science AMAs¹

¹Affiliation not available

April 17, 2023

Abstract

Hi Reddit, I am Dr. Malika Ihle and I am currently a post doctorate researcher at the University of Sheffield in the UK. I conducted my PhD at the Max Planck Institute for Ornithology (MPIO, Germany), under the great supervision of Dr. Wolfgang Forstmeier and Prof Bart Kempenaers, who will both be joining me today! Prof. Bart Kempenaers is the director of the MPIO and head of the Department of Behavioural Ecology and Evolutionary Genetics; Dr. Wolfgang Forstmeier is a researcher in this department, principal investigator of the evolution of sexual behaviour in zebra finches. We are all researching why and how female birds choose their partner, on what criteria, and also why some females are faithful to their partner while others are not. We recently published an article titled “The fitness benefits of mate choice for compatibility in a socially monogamous species” in PLOS Biology. We wanted to understand why female zebra finches differ in their mating preferences: do they pick compatible partners instead of high-quality ones? We compared the reproductive success of birds that bred with their chosen partner, to the fitness of birds that were forced to pair with the chosen partner of another bird. We found that individuals of chosen pairs had 37 percent more offspring than individuals of assigned pairs, not because they were genetically more compatible but because they were behaviourally more compatible: they were better at rearing chicks together. Individuals of chosen pairs were also more faithful to each other; females were more inclined to mate with their chosen partner, and males were more willing to invest into paternal care. Overall, it seems that each specific bird was, rather idiosyncratically, attracted and stimulated by their specific favourite mate, a phenomenon that some people might more commonly call love. In this case at least, ‘love’ did have fitness consequences. We will be answering your questions at 1pm EST (10am PST, 6pm UTC) – Ask Us Anything! Want to read about all the interesting results in an inspiring literary form? Read the synopsis written by PLOS Biology editor Roland Robert: “The fitness benefits of love”. Want to be able to explain the study to your friends, family or children? Read my PLOSable article “Benefits of being choosy”.

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PLOSSCIENCEWEDNESDAY [R/SCIENCE](#)

ABSTRACT

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We compared the reproductive success of birds that bred with their chosen partner, to the fitness of birds that were forced to pair with the chosen partner of another bird.

We found that individuals of chosen pairs had 37 percent more offspring than individuals of assigned pairs, not because they were genetically more compatible but because they were behaviourally more compatible: they were better at rearing chicks together. Individuals of chosen pairs were also more faithful to each other; females were more inclined to mate with their chosen partner, and males were more willing to invest into paternal care. Overall, it seems that each specific bird was, rather idiosyncratically, attracted and stimulated by their specific favourite mate, a phenomenon that some people might more commonly call love. In this case at least, 'love' did have fitness consequences.

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Is it true that swans (or other birds) can be "gay"?

[WRITE A REVIEW](#)

What does gay mean in the context of birds -- do they consciously seek out same-sex partners to the exclusion of other-sex partners, or is this more like an "Odd Couple" situation?

CORRESPONDENCE:

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[sonofabutch](#)

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Wolfgang: We also sometimes observe gay or lesbian couples in our captive zebra finches. When the birds are kept in same-sex groups for extended periods of time and then released into mixed-sex

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groups we see that some of the individuals really show clear homosexual preferences (strongly rejecting opposite-sex partners), leading to about up to 10% of all couples being same-sex couples. In contrast, when birds are always kept in mixed-sex groups, homosexual couples are much rarer (maybe 2%) but they still occur. Yet in wild zebra finches homosexuality has never been recorded, suggesting that the housing conditions play an important role.

Is it true that swans (or other birds) can be "gay"?

What does gay mean in the context of birds -- do they consciously seek out same-sex partners to the exclusion of other-sex partners, or is this more like an "Odd Couple" situation?

[sonofabutch](#)

Bart: you'll find answers in these two books (both published by Cambridge University Press): "Animal Homosexuality: A Biosocial Perspective" by Aldo Poiani "Homosexual Behaviour in Animals: An Evolutionary Perspective" edited by Volker Sommer and Paul L. Vasey

This study was presumably done in the lab. Does that mean that all your birds were "high quality" animals with access to lots of resources? In the wild there is a lot of variation in nutrition, status and other measures of quality. Do you expect that this 37% increase in offspring would be similar in the wild and in the low end of the quality range?

[Jobediah](#)

Bart: Yes, all birds have ad lib access to high-quality food, and to a nest site and nesting material. However, even if individuals do not differ in access to resources, they can still differ in genetic quality or compatibility. In the wild, forced pairings do not occur, and given that these birds live in groups, each individual probably has lots of potential partners to choose from.

In general, I would expect larger fitness effects in harsher environments, and hence they should be larger in the wild than in the lab. However, in the wild, it is not unlikely that fitness effects of mate choice are obscured by other effects that are independent of mate quality or compatibility, such as predation.

This study was presumably done in the lab. Does that mean that all your birds were "high quality" animals with access to lots of resources? In the wild there is a lot of variation in nutrition, status and other measures of quality. Do you expect that this 37% increase in offspring would be similar in the wild and in the low end of the quality range?

[Jobediah](#)

Wolfgang: It is a widespread opinion that captive conditions are benign, but this need not be the case. Some of the captive individuals may suffer from inbreeding depression and some individuals may perceive the captive environment as stressful already, and the additional stress of having a non-preferred partner may then lead to a more drastic effect than would be observed under absolutely ideal conditions. In the wild there is practically no inbreeding and no stress of captivity, but probably plenty of stress caused by raptors. Overall, I am not sure how big an effect our treatment would cause in the wild, and it could be more or less than 37%.

How do you judge the behavioral compatibility of finches? Was it like attracts like or different but

complimentary?

[firedrops](#)

Malika: This need a longer answer that the question let presume.

Due to a large cross-fostering experiment, we know that embryo mortality is determined by the biological parents but not by the incubating parents, and is therefore a sign of genetic incompatibility. To the contrary, chick mortality is entirely determined by the parents rearing the offspring and not anymore dependent on the biological parents. Chick mortality is therefore the result of behavioral incompatibility. In our experiment, chosen and assigned pairs had similar rate of embryo mortality: even females that could choose their partner could not reduce their embryo mortality rate: they could not select a genetically compatible mate. To the contrary, chick mortality was higher in assigned pairs, showing that parents suffered from behavioural incompatibility.

We had two hypotheses as to what is behavioural compatibility. And to try to favour one over the other we conducted exploratory analyses (which means: this needs further experimental work to particularly target that question)

1) Either parents could be better at coordinating activities or synchronizing them, and individuals that have for instance, similar personalities or, to the contrary, dissimilar personalities, could be better at doing this. I did not measure personality traits of individuals but I did score the synchrony and coordination of pairs in activities during breeding which could potentially result from the combination of the pair members' personalities, but this did not differ between the treatments. Therefore, although the method should be improved to particularly target the question of the personality match, these results are not so much favouring this hypothesis. I hope this somehow answer your question...

2) Alternatively, individuals could have specific sensory biases (due to random mutations) and specific phenotypic traits (also presenting variation due to random mutations); a specific male could for instance stimulate the senses of a specific female, which could make her invest more into reproduction. We have evidence that individuals of assigned pairs were less committed to each other, less faithful, less motivated to breed together. For instance, female were less incline in copulating with their assigned partner, male engaging more in extra-pair courtships and attending less their nest on days where chicks hatched, which are crucial days for chick survival. I feel (but these were exploratory analyses – and this requires more work) that this support more the hypothesis of individual-specific stimulation.

For a long time I thought birds had a poor sense of smell, but recently read this is not the case in several species.

Do you think the olfactory system plays a role in mate selection in birds like it does in mammals?

[TwerkWork](#)

Bart: T-maze experiments have shown that petrels can recognize their partner based on smell alone, but there is little evidence that olfaction is used in mate choice. I'm aware of only one case where potential partners seem to "sniff" each other: Julie Hagelin showed that crested auklets have a tangerine-like smell in the neck region, and part of the birds' courtship behaviour involves putting their bills in each others neck. Whether it actually plays a role in mate choice remains unknown.

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[TwerkWork](#)

Wolfgang: Smell has been suggested to play a potential role in zebra finch mate choice, but I think the evidence is really weak. What we do know almost for certain is that zebra finches have not evolved mechanisms to avoid inbreeding (e.g. kin recognition via smell) beyond the effect of direct familiarity (e.g. don't pair with your nest sib). More generally, across all birds, I think that smell plays much less of a role compared to mammals, but some exceptions to this rule may exist (some birds are highly olfactory).

Hi! Thank you for doing this AMA. This may be a completely off-topic question, but I'm curious. I've had a male cockatiel for about 10 years. He is housed with multiple female cockatiels who have shown interest in mating with him, but that interest is not reciprocated by him. He does, however, show strong interest in mating with human hands (really anyone's hand). We, of course, do not encourage this behavior, but I'm wondering why he might choose to mate with something so different from his own species, when he is housed with interested mates of the same species. Thank you!

[SweetestDisposition](#)

Wolfgang: Not sure. Is it possible that this male has been hand-reared and has been sexually imprinted on human hands? There are such reports of hand-reared zebra finches attempting to copulate with human hands.

You briefly mention that the loss in fitness may be a result of stress or trauma, but dismiss trauma as unlikely because the number of partner losses doesn't correlate well with fitness.

Could a single partner loss simply have roughly the same traumatic effect as multiple partner losses? Could or has an experiment been done that would rule that out? I couldn't find any mating choice experiments with random assortment in your references, but I only skimmed them quickly. I realize random assortment has its own flaws, but combined with your own work it might suffice to rule out some alternate explanations.

[Sadnot](#)

Wolfgang: Yes, our experimental design is not ideal for ruling out this alternative, but there is one test (but low statistical power) that is informative: birds that got assigned to the "free-choice" treatment in both the first and second breeding season, but that were not allowed to keep the same partner over the two seasons. Hence those birds experienced one traumatic event, but still were doing fine in the second season. More generally, I would consider it unlikely that a species with high risk of adult mortality (due to sparrow hawks, falcons etc) evolves such a fragile psychology. In another experiment (unpublished data) where we were interested in examining the effect of pair-bond duration on clutch size, we have been swapping partners in half of the pairs, while others were allowed to continue with their partner (all of them force-paired in individual cages). There, we observed no difference between the treatments in clutch size, and swapping partners caused a delay of egg-laying of only 0.8 days on average (relative to those who kept the partner). Hence, it doesn't even take the birds an entire day to get over the loss of the partner and to make the best of the new situation.

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Malika: This is an interesting question. In fact we cannot completely rule out that the reduction in fitness is the result of a single trauma if, and only if, as you said, a single partner loss has the same traumatic effect as multiple partner losses.

The problem with random assortment between individuals that would not chose a partner (so that they don't experience the traumatic separation) is that this would include low quality individual (individual not chosen by anyone). And measuring the fitness outcome of mate choice for compatibility while controlling for quality effects was our first aim. For this we only used birds that were chosen by another bird. So that, in both groups, birds were on average of similar quality and only differ in their potential compatibility.

Maybe, an experiment where birds can be chosen but cannot choose would be the ultimate one? For instance if we use choice chamber devices with one way glass so that the bird in the center can spend time nearby its chosen partner, but that the chosen partner does not see it. But such an experiment would be extremely weird for other aspects: the lack of interactions which might be needed for choosing a partner.

Is something like mating fitness an adaptation that has evolved separately across many different species of birds?

On the flip side, is there any evidence that this trait is a genetic predisposition that has been in an ancient part of DNA of many groups of animals that manifests when conditions are right?

[jesus_lil_stinkr](#)

Wolfgang: Not sure I am getting your question right, but I will still give it a try. What I always thought must be an ancestral adaptation that is shared by all organisms with well-developed senses is that all females will prefer high-quality males and that all males will prefer high-quality females. To my very surprise I have a very hard time finding any evidence for that in our zebra finches (both domesticated and wild-derived birds). It really seems that they care about something that varies idiosyncratically between individuals, but there is little agreement among individuals about who is the most attractive, and the little agreement that exists does not seem to target the high-quality individuals (e.g. preferring healthy outbred males over crappy inbred ones). This I find very surprising and very interesting because this possibility is not covered by our text books on the evolution of mate choice.

What do you think about the "Tap-dancing" bird mating displays being investigated more recently with slow-mo video. Do the birds in your study also show mating displays you did not expect?

[lablizard](#)

Malika: In zebra finches, the courtship is also a stereotyped behaviour (not as impressive as in the tap dancing birds though):

the male start singing in an upright posture, the head looking directly at the female and nodding from left to right, the female hop in front of him and the male follows. if the female is inclined to copulate,

she hops while putting her tail on one side and then the other, and can even solicitate copulation by quivering her tail, the male then jumps on her back and pushes his cloaca towards hers.

What I maybe did not expect is that it seems that females were able to judge how well it would work out with one male only in the course of a few days.

To give you an idea of how the 'speed-dating' is taking place, here a description of my observations: a) when birds are unpaired (i.e. 'freshly' sexually mature) and are put into communal aviaries, males are courting many females intensively, and, at first, females are all responding to the males very negatively b) males focus their courtship on a few females, until one of them start to show willingness to copulate c) copulations happen between future partners, who then visit a nest box together and start building a nest d) they will usually stay together for their entire life.

Maybe, just like when you find somebody attractive because they stimulate your senses in a very particular way, the birds may be more drawn to a specific voice or a movement. This might also be what keeps them motivated in their relationship.

Hello, I had some zebra finches once, and I noticed that over time, the songs of the children began to vary widely from the older generations. Does song play a role in zebra finch society and pairing?

[zxcvbnm9878](#)

Wolfgang: Not sure, but this is exactly what we want to study next!

Thank you so much for doing this. I study human behavior and am beginning to think about what animal models can tell us, especially animal research conducted in an evo framework.

So: what are the implications of your research for research on human behaviors?

Thank you again, Fascinating stuff and congrats on a great pub!

[dachsl](#)

Malika: In fact zebra finches and humans share some similarities: they form socially monogamous pair bonds with one partner for their entire life and share the duty of parental care. In addition, in both species, extra-pair paternity concerns 2% of the young.

In that sense we could speculate that humans might also choose their partner based on behavioural compatibility criteria, either to match their personality or coordinate their behaviour, or because individuals are specifically (idiosyncratically) attracted by a particular partner, stimulated by him/her and therefore willing to invest into reproduction. This study could raise awareness on the importance of being stimulated/motivated by your specific partner in order to face the challenge of having a family.

Nevertheless, I think our experimental treatment do not reflect what happen in arranged marriages in humans. In our experiment, we specifically assigned to a female a male she could have interacted with and chosen (they were in the same pool of unpaired individuals to choose from) but that she did not prefer. In fact, another female from the same pool preferred that male. In humans, I believe the family (who may care about the happiness of their children) choose what they think would be a best match for their child, and they might actually know who would be a good or compatible partner.

Oh my gosh, an AMA by people whose work I've read?! I barely know what to do with myself right now! Okay, pull it together.

In your discussion, you briefly address stress as a potential factor in the reduced fitness in forced pairs. Did you consider monitoring stress hormones such as CORT during the pairing and nesting process? If so, what held you back? Seems to me that a pair of birds who are forced to breed together might have higher stress hormones, which may negatively impact their reproductive success. It would be interesting to see the numbers on that.

[nerdybirdie](#)

Bart: Interesting suggestion indeed. Behavioural endocrinologists should look into it!

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[nerdybirdie](#)

Malika: their dissatisfaction and lack of motivation could indeed be mediated by the chronic stress arising from being paired with a non-preferred partner, or a not stimulating one.

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[nerdybirdie](#)

Wolfgang: Yes, I fully agree that this would be interesting to see. We had been discussing this for a long time, but the practicalities of taking blood samples from 120 birds within less than 3 minutes of disturbing them put us off.

Hello!

behaviourally more compatible: they were better at rearing chicks together. Individuals of chosen pairs were also more faithful to each other; females were more inclined to mate with their chosen partner, and males were more willing to invest into paternal care.

For less compatible pairs, was there any obvious hostility of self destructive behavior? If so, would this behavior go away if the birds were separated?

[AsAChemicalEngineer](#)

Malika: no, there were no difference in aggressive behaviour between the two type of pairs, simply because aggressive behaviour in this species is pretty rare.

Hello, thank you for doing this AMA. I was wondering what your thoughts were on the trade off of fitness of a partner versus affection for them. It seems that the results point out many benefits for affection over fitness, but I am assuming there is some drawback. Thank you for your time!

[green_bumblebees](#)

Wolfgang: Yes, it is my general impression that zebra finches chose their partner mostly based on (for us unpredictable) affection, and less (or maybe not at all) on predictable quality indicators (e.g. preferring a healthy outbred partner over a crappy inbred partner). This really puzzles me, and I hope to do more experiments in the future that help us better understand this apparently random phenomenon of affection. Isn't this also an important factor in human mate choice (and quite unpredictable)?

How does pair-bonding in birds compare to pair bonding in humans and non-human mammals?

Unrelatedly, I'd be curious what effect individual mate preference has on extra pair copulations. For instance, are EPCs more likely to occur in forced matings? Are species that focus mate choice on mate quality rather than compatibility more likely to have EPCs?

[Kenley](#)

Bart: in our experiment, broods of non-chosen pairs were indeed more likely to have extra-pair offspring, and females of non-chosen pairs tended to have more extra-pair copulations.

How would you determine whether species focus mate choice more on quality than on compatibility?

Re the question about pair bonding in birds versus mammals (including humans): fundamentally, the process of mate choice may be similar, but one can expect large differences between species/populations in terms of number of potential mates that can be sampled, competition for mates, duration of courtship, and in the relevant and available information on which the choice is based.

Wow, this is really interesting. Do you guys have any plans for further experimentation?

[youflow](#)

Malika: the study now raises the questions: how can a pair of individuals be more behaviorally compatible than another pair? Is it a matter of personality matching, synchronisation/coordination of activities ? or a matter of stimulation/motivation by your partner in investing all the work it takes to raise a family, as our exploratory analyses tend to suggest ? how the variation in mate preferences is maintain? is this variation adaptive? how heritable are those individual-specific preferences? is this variation the raw material for speciation to happen?

Therefore, new studies could measure more precisely the provisioning behaviour and the personalities of the birds to dig into the behavioural coordination hypothesis better. In addition, to be able to study further individual-specific preferences, we need proper replicates of individuals. Therefore, ideally, a new study should be conducted with clones (e.g. identical twins).

You say that some zebra finches are monogamous (faithful) while others are not. Is there a social consequence for them if they are not faithful?

More generally, when a species (especially in birds) is identified as having "monogamous" mating

pairs, does that strictly apply or are there non-monogamous pairs like with zebra finches?

[siltstridr](#)

Bart: We typically differentiate between social monogamy and genetic monogamy. Most bird species are socially monogamous, that is, one male and one female form a pair for one or more breeding seasons and raise offspring together. However, this does not necessarily mean that the partners are faithful: both the male and the female may copulate with others ("extra-pair copulations") and this often leads to multiple paternity in broods. For example, about half of all blue tit pairs (socially monogamous) have at least one extra-pair offspring in their nest.

Long-lived birds are more likely to be strictly monogamous (less extra-pair paternity) than short-lived birds.

How do bird species, where the males and females look the same (non sexual dimorphic), tell the sex of other birds?

[intawsomenary](#)

Bart: Interestingly, sometimes it looks like they cannot tell the sex of another individual, at least not immediately. In some species (e.g. ruffs), there are so-called "sneaker" males, that look like and behave like females. They are not treated aggressively by other males and they may "sneak" copulations by getting in between the male and the real female. In a related species, the sexually monomorphic buff-breasted sandpiper, males can play both the male "role" (behave aggressively to other males and display to females) and the "female" role (pretend to be a female and "sneak" copulations).

This is really interesting!

I'm wondering, why did you decide to work on this species, rather than another?

[lilikiwi](#)

Bart: zebra finches are a good model system for this type of studies for practical and for biological reasons. Practical: they are easy to keep in large numbers and they breed very well in captivity (and year-round). Biological: in the wild they form life-long pair bonds, so finding the right partner seems important!

My understanding is that many/most birds choose mates based not on compatibility, but more-so on status as measured by fitness indicative characteristics (brightness of plumage, length of tail, etc). Further, female birds of low status will cuckold their mates to mate with higher status birds to secure better genes for the next generation. How does this research factor into this concept?

[digitalis303](#)

Bart: If choice is based exclusively on quality-indicator traits, then all females should prefer the same males. However, individuals may for example also avoid mating with a sibling to avoid inbreeding depression, even if the sibling would be of high quality. That would be an example of choice based on (in)compatibility. Our experiment was designed to eliminate effects of mate choice for quality, because all males involved in the study were "preferred males", that is, they were chosen by a female.

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[digitalis303](#)

Malika: In fact, your description match most people understanding. This is because, usually, studies on mate choice in animal focus on the preference expressed for a particular measurable trait, neglecting a bit the variation present among individuals.

On a theoretical point of view, there are four types of different benefits from choosing a mate (Fig. 1). Direct benefits are those the bird can get directly from a mate, such as resources like food or territory. Indirect benefits are those that are only expressed in the offspring, like good genes increasing offspring survival (which a female can also get for her offspring via extra-pair copulations). But individuals of high quality, with good genes and good behaviour, are not necessarily the best match for everyone. Compatible genes and compatible behaviour are also potential benefits from choosing the right mate. Here, one original point of the study is to focus only on this 'idiosyncrasy' in mate preferences, i.e. on individual-specific preferences.

As far as zebra finches are concerned, we do not know of any traits that are generally attractive for the group, birds show individual specific preferences which I call idiosyncratic only because I can't predict them: we do not know which variable traits are targeted by individuals to obtain a (behaviourally) compatible partner. I would say, it is usually not obvious what makes a male attractive in any species, specifically when talking about those individual-specific preferences.

To come back to the selection for high quality partner you describe, I still think this should happen at each generation. But this does not have to be through mate choice necessarily: predator can also take care of weak individuals.

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[digitalis303](#)

Wolfgang: From my reading of text books and scientific literature I fully agree with what you say. From my own experiences of doing research on mate choice in zebra finches (13 years) I couldn't disagree more with what the text books (and scientific literature) say. Maybe it is the zebra finches that are really weird, but maybe it is also that our research has been biased into seeking confirmation for sexual selection theory without ever daring to challenge the general ideas. I agree that conceptually the text books make sense, but in the specific case of my study system, the concept of constant sexual selection for traits that indicate quality (good genes) is probably misleading. Nevertheless, most scientific literature even on the zebra finch would largely disagree with my view. I think the literature is heavily biased towards stories of "success", i.e. studies that confirm what people believed in to begin with.

for a more on topic question:

In your study, did the birds always pair off, or did situations occur in which a birds choice was not reciprocated? If these situations occurred, how were they dealt with?

also,

How closely do you believe this to correlate to humans in situations such as arranged marriages?

[RN1985](#)

Malika: I am not sure which situation you are referring to. I can think of two:

1) during the free choice period: As a biparental care species, it is very likely that mate choice is mutual. I judge preferences by the frequency of allopreening (an individual cleaning another). This is an affiliative behavior mostly shared between future breeding partners. If not exclusive to one opposite sex individual, very often the 'favorite allopreening partner' of a female is a male that also prefers this female as his 'favorite allopreening partner'. When this was not the case, I focused on the female side. In the paper I therefore talk about the consequences of female preferences, but in fact this very often includes preferences of both sexes.

2) in the period of breeding where some pairs were force-paired (i.e. after they had spent a few months in cage with only this one potential partner) Some pairs divorced as soon as they were put in communal breeding aviary. Maybe, those pairs were the least compatible ones. Birds that divorced were discarded from the analysis.

Regarding your question on arranged marriages in humans, please refer to my answer to 'dachsi'.

Do the birds also get jealous if their chosen pair is having a bird affair?

I have an African grey parrot who gets crazy jealous of my wife sometimes.

[orangejulius](#)

Bart: Jealousy is hard to measure, but males can surely be aggressive if they have witnessed their mate copulating with another male. During the female's fertile period, males of many species closely guard their mate, and/or attempt to copulate frequently. This will help avoid that they care for offspring that are sired by other males.

How did you prevent extra-pair paternities in the naturally forming pairs? were they isolated once the pairs formed?

[happy-little-atheist](#)

Malika: we did not prevent extra-pair behaviour. Chosen pairs were by themselves more faithful to their partners than were non-chosen pairs.

The protocol went as follows: 1) free choice in large communal aviary 2) pairing in cages (so that assigned pairs would form pair bonds) 3) breeding in communal aviaries with 3 pairs of each treatment -> plenty of opportunities for extra-pair relationships.

Scheme of that can be found in the original paper, Fig. 4; and in the PLOSable article Fig.2

IIRC something similar to your work was done with cockatiels where the quantity of synchronised behaviours were used as an index of pair bond strength. Did you notice any obvious behavioural differences in the pairs of different treatments?

[happy-little-atheist](#)

Malika: in fact I use this protocol developed by Spoon et al 2006 that you describe, to perform all our focal pair watches. Chosen pairs were a bit more lovey dovey than non-chosen pairs during the first week in communal breeding aviary (just before nest material was added): individuals of chosen pairs stayed closer together and behaved more synchronously than those of non-chosen pairs. But during breeding (the next 4 months), no differences were observed regarding our 'pair harmony' measurement.

This is awesome, thank you. After reading the synopsis, I had a few questions:

- 1) I've read about a number of bird species that are reported as monogamous. Is it common to see the same kind of deviations from this pattern in most species as in the finches?
- 2) There are a lot of different types of courtship displays (like bowerbirds with their color-separated arrangements or club-winged manakins with their sonations). Do you think some are more or less likely than others to result in a compatibility or fitness mate selection?

[fleursdubon](#)

Wolfgang: re 1) About 90% of all birds are socially monogamous, but the great majority of them shows some level of extra-pair mating. re 2) I think that really extreme (exaggerated) display traits are likely to arise from strong directional selection (due to consensus among females). In contrast, displays that are less extreme and maybe more variable (like zebra finch song) could indicate that females differ in what they prefer.

First of all, thank you for taking the time and effort to answer all of our (ridiculous?) questions. It shows a great commitment to your work and a desire to share your knowledge, which are both admirable traits.

I did have a question which might not be in your wheelhouse (or might be covered in your paper; I haven't had time to read it yet): What, if any, genetic benefit is there to the species/society of these idiosyncratic pairs as opposed to more "genetically compatible" mates or higher-quality ones? I mean, does it increase genetic diversity in a meaningful way, or allow potentially beneficial traits to survive, or something else useful? Or is the primary benefit in the quality of the parenting?

[Duke Paul](#)

Wolfgang: Yes, as far as we understand the system, the benefit (if any) lies in the quality of the parenting. We are a bit puzzled that such choosiness has evolved at all, but maybe it does not serve a function (just arising from random genetic mutation leading to differences in tastes), or maybe it facilitates a stronger pair bond and better parenting (assuming that, in the wild, birds could always find a well-matching partner). At the genetic level, we did not find what we were looking for (mate choice for genetic compatibility leading to higher embryo viability).

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[Duke_Paul](#)

Malika: if I reformulate your questions as I understand them, here is my answer (if you realize I did not please reformulate and I will try again!)

Is it adaptive in any way to exhibit such idiosyncratic individual specific preferences, which do not target at genetic compatibility?

It is in fact maladaptive not to invest as much as you can with the partner you breed for your entire life. Those assigned birds that did agree to breed should have done their best and they probably did, but as they show lack of motivation/commitment (e.g. female were less inclined in copulating with their assigned partners, assigned male were spending more time in seeking extra-pair copulations and were attending less their nest on the days where chicks hatched), I sometimes talk about 'psychological constraints'. In fact, being choosy is here maladaptive, they should just not care and breed as much as they can with anyone.

Where do these preferences come from then?

My best guess (this is speculative) is that there are random variations in the sensory systems of individuals that lead, as a by-product, to a variation in the latent preferences or tastes of individuals. These individual specific sensory biases (I call them 'idiosyncratic because they are hard to predict) could in turn induce differential investment: if being with the partner who better stimulates one's senses can also mechanistically stimulate individuals in investing in reproduction, we would get a higher fitness in those phenotypically compatible pairs. Just to give you an example of what it could mean: in the zebra finch, we have some evidence that male undirected song stimulates females in investing nutrient in the yolk of the egg, but here what I suggest is that, for instance this maternal effect, happens particularly in certain combinations of pairs.

If it is maladaptive, why are those random mutations not counter selected?

Choosiness should be counter selected (because those that would not end up with their favourite partner would have a lower reproductive success, and therefore this trait should disappear) but it might be that in this gregarious species flocking in huge numbers, they mostly have the choice of their mate... So selection might be weak. In addition, counter selection of preferences might be weak if their heritability is low (which is the case in the animal kingdom in general, and in the zebra finch in particular). Low heritability could be due to complex epistatic interactions or environmental variation.

Alternatively, it could still be that mate choice for behavioural compatibility is based on personality matching for instance. In this case, one could think that this variation in personality is there for other adaptive reasons and that mate choice is related to it. Although our exploratory analyses do not point into that direction, it requires more studies.

To summarize, the adaptive significance of the variation in preferences still remains speculative: it could only be due to random variation in the sensory system of individuals which would not be efficiently counter selected (and this interpretation is also speculative).

You mention the word 'love' in your synopsis. This is obviously a loaded word, and one that is anthropomorphic to the extreme, as you surely are aware.

Given that the observation upon which this is based is that individuals mate more successfully with individuals they have chosen themselves, wouldn't an equally valid explanation arise from 'hate' rather than 'love'? What I mean is this: couldn't you equally conclude that they just hate their assigned partner, and don't hate their chosen partner?

What about your data pushes you towards invoking love rather than disdain?

I recognize that you didn't use the word love in your paper, but all the press seems to take that angle, rather than alternative interpretations. Does this bother you?

[tarzanandcompany](#)

Malika: as you said, we do not have this angle in the paper, but this is how people perceived it. But are they wrong? To be honest, now I am personally starting to embrace it a bit.

to me (this is my humle opinion, I insist) love is a peculiar attraction toward a specific individual that is not necessarily shared by the other choosing individuals. In that sense I qualify this type of preferences as idiosyncratic or individual-specific.

In our study we show that bird vary in their preferences and that these idiosyncratic preferences do lead to fitness consequences. Our results also show that this came about behavioral compatibility advantages but had nothing to do with genetic compatibility.

Our exploratory analyses, conducted to have a first idea of what could make some birds behaviourally or phenotypically more compatible, suggest that birds were not more coordinated in their activities but were more committed to their relationships; for instance we observed higher female within-pair responsiveness, lower male extra-pair courtship rate, and higher male nest attendance.

Therefore it seems that chosen pairs, those 'love marriages', invested more into reproduction, were more committed, more faithful, and more motivated to raise their family.

to me, it could be that 'love' is simply a stimulation (e.g. a brain reward of a song you like) by a specific male that fit the specific sensory biases of a female (and vice versa). This stimulation could in turn activate a physiological mechanism that makes you invest more into reproduction.

In my scenario, those sensory biases would be due to random mutations and therefore hardly predictable, isn't that what we say about love?

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[tarzanandcompany](#)

Wolfgang: Yes, I think you have a valid point and I am grateful for the reminder. Unfortunately it is very time-consuming to study the preferences of an individual in sufficient depth in order to be able to distinguish between two extreme scenarios: say female A really loves 3 out of 10 possible partners and finds the other 7 intermediate, while female B finds 7 partners acceptable (intermediate) but really dislikes the other 3 males. Most likely, a mix of both phenomena (love and disdain) will exist, but still very interesting to investigate this! Thanks again.

Sorry if this has already been asked but why did you choose zebra finches as opposed to another

monogamous bird species?

Also Thank you so much for doing this reasearch! Confirms what I've seen in my pigeons for years! Choosing a mate isn't arbitrary, each bird is an individual and has it's own preferences and personality traits. It makes perfect sense that they would be likely to choose a partner that they get along well with.

[Primarycoverts](#)

Bart: zebra finches are a good model system for this type of studies for practical and for biological reasons. Practical: they are easy to keep in large numbers and they breed very well in captivity (and year-round). Biological: in the wild they form life-long pair bonds, so finding the right partner seems important!

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Bart: What do you mean with bird law?

hmm.. why?

looks like you and many other researchers get money for absolutely not important researches. ok they love each another.. wow! birds love each another.. what a huge step for human kind!

[ariel222](#)

Malika: I see where you are coming from. You shouldn't believe we do not think about these considerations. Although I believe this is not the place to discuss the potential importance of fundamental science, here is part of the answer, as far as this study is concern.

This study is relevant for behavioural ecologists who want to understand how mate choice take place, a new research question for them is what makes individuals more behaviorally compatible; relevant for evolutionary biologists who want to understand the evolutionary causes and consequences of variation in mate choice (in term of speciation for instance); it will also be of particular interest to researcher working on humans, where addressing the fitness consequences of pairing with a preferred and a non-preferred partner is impossible; and finally, the study has raised the general public interest as it essentially aims at explaining what love is.

hmm.. why?

looks like you and many other researchers get money for absolutely not important researches. ok they love each another.. wow! birds love each another.. what a huge step for human kind!

[ariel222](#)

Bart: I am curious about animal behaviour. I respect that you do not find that important, but I find it wonderful and full of mysteries. if you want to get a taste, I can recommend "Cuckoo: cheating by Nature" written by behavioural ecologist Nick Davies.

hmm.. why?

looks like you and many other researchers get money for absolutely not important researches. ok they love each another.. wow! birds love each another.. what a huge step for human kind!

[ariel222](#)

Wolfgang: Much of our research focuses on understanding the genetic causes of embryo mortality. Pregnancy loss is very common in humans (2 out of 3 fertilized eggs die before birth), but its genetic causes are still poorly understood, particularly from an evolutionary point of view (how can such a wasteful system evolve?). Our research on embryo mortality in zebra finches might also help understanding the causes of pregnancy loss in humans. The current study was designed to find out whether zebra finches are able to identify and select a partner with whom they would reach higher embryo viability. This was not the case: chosen pairs had 20% of their embryos dying while forced pairs had 22% dying (clearly not significantly different). However, we do know that the rate of embryo mortality strongly depends on the combination of males and females, but apparently zebra finches have no way of foreseeing with whom they would be genetically compatible. Hence, for us this was an important study to do, to get better insights into what is behind their reproductive problems.

What are you working on...?