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A taste for the familiar: explaining the inbreeding paradox

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Abstract:	<p>The negative consequences of inbreeding have led animal biologists to assume that mate choice is generally biased against relatives. However, inbreeding avoidance is highly variable and by no means the rule across animal taxa. Even when inbreeding is costly, there are numerous examples of animals failing to avoid inbreeding or even preferring to mate with close kin. We argue that selective and mechanistic constraints interact to limit the evolution of inbreeding avoidance, notably when there is a risk of mating with heterospecifics and losing fitness through hybridization. Further, balancing inbreeding avoidance with conspecific mate preference may drive the evolution of multivariate sexual communication. Studying different social and sexual decisions within the same species can illuminate trade-offs among mate-choice mechanisms.</p>

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1 **A taste for the familiar: explaining the inbreeding paradox**

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10 ABSTRACT: The negative consequences of inbreeding have led animal biologists to assume that
11 mate choice is generally biased against relatives. However, inbreeding avoidance is highly
12 variable and by no means the rule across animal taxa. Even when inbreeding is costly, there are
13 numerous examples of animals failing to avoid inbreeding or even preferring to mate with close
14 kin. We argue that selective and mechanistic constraints interact to limit the evolution of
15 inbreeding avoidance, notably when there is a risk of mating with heterospecifics and losing
16 fitness through hybridization. Further, balancing inbreeding avoidance with conspecific mate
17 preference may drive the evolution of multivariate sexual communication. Studying different
18 social and sexual decisions within the same species can illuminate trade-offs among mate-
19 choice mechanisms.

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24 **Keywords:** Inbreeding avoidance, assortative mating, conspecific mate preference, mate choice

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1 **Inbreeding avoidance is not ubiquitous**

2 Animal researchers often assume **inbreeding avoidance** (IA; see Glossary)— i.e., a preference
3 for unrelated partners before, during, or after mating —is the norm [1]. This stems largely from
4 observing **inbreeding depression** (ID), or reduced fitness of inbred offspring, in humans and
5 beyond [2]. If mating with close relatives incurs a substantial fitness cost, selection is expected
6 to favor mechanisms for avoiding such matings [3].
7

8 However, two new meta-analyses [4,5] suggest IA in mate choice is relatively uncommon.
9 Correcting for publication bias across 139 studies, de Boer and colleagues [4] found no overall
10 evidence for IA, with several studies even suggesting sexual preferences for close relatives [5-
11 11]. Subsequently, Pike et al. [12] argued that IA is common when there is ID *and* relatives often
12 interact as breeding adults. Unless both of these conditions are satisfied, choosers tend to show
13 no preference for non-kin, and may even choose kin as mates.
14

15 But even when inbreeding is costly and close relatives interact, many animals still fail to show IA
16 (Table 1) – the so-called '**inbreeding paradox**' [13-16]. Several recent studies fail to detect an
17 effect of kinship on mate choice [17-20], or even show mating preferences for kin [21, 22], even
18 when relatives encounter each other and show ID [13, 14, 23].
19

20 We argue that the inbreeding paradox stems from weak or variable selection for inbreeding
21 avoidance at any one stage of mate choice, operating against constraints imposed by **kin**
22 **selection** and selection against **outbreeding depression**. In particular, the evolution of
23 inbreeding avoidance is constrained by selection promoting mechanisms for self-similar
24 association, specifically **conspecific mate preference** (CMP) and nonsexual **kin affiliation**.
25

26 **Weak and variable selection for inbreeding avoidance**

27 As Pike et al. [12] suggested, inbreeding avoidance should only evolve when encounters
28 between adults result in ID. When there is such selection against mating with relatives, it may
29 operate at different stages of mate choice (fig. 1A) in ways that relax selection for behavioral IA
30 before mating. There are three main factors that weaken selection for IA at any one stage:
31

32 **1. *Inbreeding is not always costly*** The overall genetic consequences of mating with close
33 relatives should be negative: inbreeding increases genetic homozygosity of offspring, thereby
34 exposing deleterious recessive alleles and reducing intragenomic diversity [2]. As de Boer et al.
35 [4] and others have pointed out [24-27], inbreeding depression is often taken as a given [4], and
36 its negative consequences assumed to inevitably select for IA. However, the magnitude of ID
37 depends on a population's history of selection [28]. For example, prior inbreeding can function
38 to expose deleterious alleles to selection, reducing their frequencies within contemporary
39 populations (i.e., "purging"); thus, reducing costs associated with inbreeding and relaxing
40 selection for IA [26, 29].
41

1 Another reason inbreeding is not always costly is because its costs can be offset by phenotypic
2 and indirect genetic benefits of mating with relatives [24-27] via kin selection. Inbreeding
3 increases **inclusive fitness** because parents are more related to inbred relative to outbred
4 offspring, thus a greater proportion of parents' alleles are transmitted [1, 24, 25]. Further, kin
5 selection may favor preferences for relatives, as suggested in cichlids (*Pelvicachromis taeniatus*)
6 [30], by reducing sexual conflict over parental investment [31]. Increased investment in inbred
7 offspring can counterbalance the harmful effects of inbreeding [14, 31, 32] and may be
8 facilitated by cooperative parental care among relatives. Nonsexual cooperation among kin may
9 thus weaken selection for IA.

10
11 Though inbreeding may be costly, the alternative can be worse. More generally, preferences for
12 unrelated mates mean that choosers may incur fitness loss not only from outbreeding with
13 conspecifics [33-35], but from hybridization [36]. Thus, selection for IA may also be weakened if
14 it is more costly to mate with a heterospecific than it is to mate with a close relative.

15
16 **2. No opportunity to mate with relatives** Weaken selection for IA can also result from sex-
17 biased dispersal [37], environmental sex determination [38], sequential hermaphroditism [39],
18 skewing offspring sex ratio [40], and sexual dimorphism in life-history (e.g., sex differences in
19 maturation time) [41] which can all reduce inbreeding without behavioral mechanisms (fig. 1A).
20 If breeding relatives do not interact, there should be little to no selection for or against "active"
21 IA.

22
23 **3. Inbreeding avoidance can occur before, during, or after mating** IA can occur at any stage of
24 mate choice; even if close relatives fail to avoid mating, IA can occur through biased gamete
25 transfer, fertilization, and embryo retention [42, 43]. However, redundant IA mechanisms
26 across the process of mate choice may be costly and selection may favor IA at one particular
27 stage rather than another [26, 43].

28
29 Theory suggests that the evolution of inbreeding avoidance hinges on more than the genetic
30 costs of ID. Rather, it depends on dynamic cost-benefits: the potential advantages of inbreeding
31 and the costs of rejecting relatives as mates [25-27]. For example, if there is a net fitness benefit
32 to inbreeding, selection will favor mating with kin. Therefore, the spectrum of selection on
33 inbreeding and outbreeding suggests that so-called inbreeding strategies [25], of which IA is a
34 special case, may vary across different stages of mate choice.

35 36 37 **Constraints on inbreeding avoidance mechanisms**

38
39 Selection for "active" inbreeding avoidance requires a mechanism that biases against sexual
40 interactions with kin at some stage of mate choice. Like other mate-choice mechanisms, IA is
41 shaped by selective pressures within and outside the context of mating [44, 45]. Constraints on
42 mate-choice mechanisms may make IA challenging to achieve, for two primary reasons. First,
43 sexual reproduction requires coordination between individuals who share genetic ancestry.
44 Second, nonsexual cooperation often involves proximity and affiliative behaviors among close

1 kin. Inbreeding avoidance, by contrast, requires an individual to avoid one specific affiliative
2 behavior – mating – with individuals who are similar, familiar, and safe.

3
4 *Conspecific mating preferences promotes homotypic mating*

5
6 Inbreeding and outbreeding depression, including hybrid inviability, are special cases of genetic
7 (in)compatibility [3], whereby offspring fitness depends on interactions between the genomic
8 contribution of the two parents [45, 46]. Thus, both CMP and IA involve accepting compatible
9 mates and particularly rejecting incompatible ones.

10

11 The minimum and universally necessary mechanism for compatible, sexual reproduction is a
12 molecular interaction at the egg-sperm interface. From this cellular interaction to sophisticated
13 multimodal communication, signal-receiver coevolution generates systems, including CMP,
14 whereby affiliative interactions, mating, and ultimately fertilization are biased towards self-
15 similar individuals, termed **homotypic mating** [47] (fig. 1B).

16

17 Numerous mechanisms favor cues of self-similar, conspecific sexual partners, from sensory
18 filters at the earliest stages of mate choice [48], to integration of multimodal signals in the brain
19 [49], through the egg-sperm interface and beyond [3]. The most-studied cues involved in
20 conspecific mate recognition are often low-dimensional and vary little within a species, such as
21 color differences [50], acoustic frequency differences [51], or chemical ratios [52, 53]. If there
22 are significant differences between these cues and other stimuli in the environment, as in
23 humans and hihi (*Notiomystis cincta*), where no closely related species exist (Table 1), a single
24 filter – whether a membrane receptor molecule, an auditory tuning curve, or categorical
25 perception – can discriminate homotypic from heterotypic stimuli (fig. 2).

26

27 A single filter can generate sexual selection within conspecifics if some trait values are more
28 attractive than others; alternatively, choosers may be very permissive – within conspecifics and
29 well beyond – if the cost of a mistaken mating is low (fig. 2A). But even Australian jewel beetles
30 (*Julodimorpha bakewelli*) mating to death with beer bottles [54] are doing so within bounded
31 stimulus parameters. Preferences for bounded homotypic stimuli are genetically and
32 phenotypically correlated with species-typical signals or cues present in choosers or in
33 opposite-sex relatives, and these cues can be used to identify potential mates via **phenotype**
34 **matching** [55]). In addition, early learning [56], whereby individuals prefer cues learned from
35 parents or siblings, provides a powerful mechanism for genetic coupling and co-divergence of
36 homotypic traits and preferences.

37

38 The problem is harder when homotypic and heterotypic courtiers resemble each other and the
39 cost of a mistaken mating is high [57]. Therefore, selection against heterospecific mating often
40 yields **peak shift**, whereby choosers prefer cues displaced away from a stimulus to be avoided
41 (fig. 2B). Peak shift occurs in contexts ranging from learned sexual preferences [58] to
42 reproductive character displacement over evolutionary time [3, 59] and can result in divergent
43 preferences between sympatric and allopatric populations (e.g. [60, 61]). For example,
44 choosers may choose less-attractive, conspecific courtiers when the risk of hybridization is high

1 despite lower fitness benefits [57]. If traits overlap, a single filter cannot include all conspecifics
2 without including some heterospecifics, nor vice versa (fig. 2B). Selection therefore favors the
3 evolution of receivers who integrate responses to multiple cues [62] along multiple stages of
4 mate choice, pre- and postmating.

5

6 *Inbreeding avoidance: heterotypic mating within a homotypic envelope*

7

8 In contrast to CMP, inbreeding avoidance requires a mechanism that promotes **heterotypic**
9 **mating** – in other words, rejecting not just a subset of homotypic individuals but those most
10 like oneself (Box 1). Inbreeding avoidance, therefore, requires sexual rejection of individuals
11 that are too self-similar or too familiar (fig. 2C), conflicting with and constrained by selection
12 favoring homotypic mating (fig. 2A). And it must coexist with a mechanism, however broad, for
13 CMPs (fig. 2B).

14

15 Whether IA occurs through communication between individuals or gametes, it automatically
16 requires additional processes beyond those involved in accepting a conspecific signal (figs. 2B-
17 2C), because close relatives express conspecific cues. Within the envelope of CMP, then, how
18 can one choose a compatible mate with respect to the genetic consequences of inbreeding (Box
19 1)?

20

Box 1. Are there trade-offs between IA and CMP? Inbreeding avoidance requires sexual rejection of individuals that are too self-similar or too familiar, in direct conflict with selection favoring homotypic mating (fig. 2A). And it requires avoidance of activities that lead to mating, in direct conflict with selection favoring affiliative behaviors with kin (fig. 2b). This means that preferences for heterotypic or novel phenotypes may invariably go checked by preferences for self-similar individuals. How might CMP and IA interact?

Often, CMP is the foremost of a set of **hierarchical preferences**, whereby sexual cues are filtered by a set of criteria before further evaluation [51]. For example, in túngara frogs (*Engystomops pustulosus*), females share species-typical preferences for time-frequency characteristics of the "whine" call, rejecting males with atypical whines [49]. Among appropriately whining males, however, females are permissive: adding almost any detectable acoustic ornament makes a call more attractive. Females fail to avoid relatives based on acoustic cues [63], as expected if females share permissive preferences bounded by CMP.

Table 1 lists systems with measured inbreeding depression and studies of both IA and CMP. ID is summarized from recent meta-analyses [4, 12] with empirical evidence of ID both evidence of ID, and with information on both IA and CMP. Only 16 species meet all three criteria, and only 11 of these have direct tests of assortative mating. Only one species with demonstrated ID – two-spotted crickets – has been tested for both IA and CMP both before and after mating. Of five species tested for IA at multiple stages of mate choice, two showed IA at both stages, one failed to show IA at either stage, and two showed IA in one but not the other. The data summarized in Table 1, therefore, suggest that just examining one mate-choice stage may underestimate total IA.

It is suggestive that of the eight species with premating preferences for conspecifics (Table 1), five showed no evidence of inbreeding avoidance when tested. This is noteworthy given publication bias against negative results on IA [4]. Even species with robust mate-choice mechanisms in one context, therefore, may often fail to express them in another. Unraveling any trade-offs between IA and CMP requires many more studies of both tasks across mate-choice stages in the same populations.

- 1
- 2 For CMPs, phenotype matching and early learning shape sexual *preferences* for self-similar
- 3 individuals; in the context of IA, they shape sexual *avoidance* of self-similar individuals. For
- 4 example, self-incompatibility alleles in angiosperms reject the most self-similar genotypes,
- 5 limiting the most intense form of inbreeding [64]. The *t* allele system in mice also reduces
- 6 inbreeding: female mice carrying the recessive-lethal *t* locus avoid *t* males, a case of heterotypic
- 7 mating [65]. Importantly, heterotypic mating with respect to one cue must occur alongside
- 8 homotypic mating with respect to another, at all stages of mate choice. Examples are
- 9 conspecific pollen precedence [66] or pollinator-mediated premating barriers [67] co-occurring
- 10 with self-incompatibility in flowering plants, or conspecific sperm precedence [66] and

1 pre-mating preferences [68] co-occurring with self-avoidance in mammals. Therefore, we expect
2 that IA and CMP might have overlapping mechanisms but address different sets of partner cues.

3
4 The critical difference between IA and CMP is that while CMP cues are under stabilizing or
5 directional selection for homotypic mating [69], successful IA requires avoiding kin without
6 rejecting conspecifics altogether. Inbreeding avoidance, therefore, relies on cues that are
7 variable within a population and therefore distinct in unrelated individuals (Fig. 2). For example,
8 the vertebrate MHC complex of immune proteins is a popular candidate for linking genes under
9 diversifying selection to olfactory cues used to identify kin and reject related mates [70], likely
10 through effects of host MHC haplotype on the scent-producing microbiome [71]. Therefore,
11 selection for genetic compatibility may be a widespread driver of multimodal and
12 multidimensional complexity in sexual communication because antagonistic fitness benefits are
13 expected to favor distinct traits in different sensory modalities for IA versus CMP.

14 *Inbreeding avoidance, kin recognition, and domain-specific antipathy*

15
16
17 As noted above, preference for dissimilar phenotypes is bounded by CMP, whether selecting
18 conspecific mates is easy or difficult. If choosers simply make decisions based on novelty versus
19 familiarity, or similarity versus dissimilarity, this will invariably lead to some combination of kin
20 mating, heterospecific mating, and rejecting suitable conspecifics. Many organisms, however,
21 have mechanisms that label close kin differently from other conspecifics: **kin recognition**.

22
23 Discriminating among individuals by kinship, like CMP, is accomplished by behaving differently
24 towards individuals with a self-similar trait or individuals or stimuli experienced early in life
25 [72]. Kin recognition is more commonly studied not in the context of individuals avoiding kin,
26 but cooperating with them. And importantly, avoidance of related individuals is mainly useful in
27 one specific social context: sex.

28
29 In addition to the problem of sexual compatibility, there is, therefore, the additional problem of
30 decoupling sexual from nonsexual behavior with close social partners. Kin selection often favors
31 affiliative interactions between relatives, including care of young, with gametic exchange as the
32 noteworthy exception. Indeed, individuals often spend more time close to relatives than
33 nonrelatives, including intimate activities like food sharing, preening, and genital sniffing [73-
34 75] characteristic of sexual courtship when directed at non-kin. Indeed, kin may show
35 courtship-like behavior toward relatives during ontogeny but later form stable pair bonds only
36 with nonrelatives [74]. Successful IA around kin requires **domain-specific antipathy**: aversion to
37 kin, limited to contexts that increase the risk of mating. Therefore, naively measuring
38 proceptive or affiliative behaviors as proxies for sexual preferences may complicate measures
39 of inbreeding avoidance.

1

2

Major taxon	Species	Evidence for inbreeding depression	Premating IA	Postmating IA	Premating CMP	Postmating CMP	References
Insecta	<i>Bicyclus anynana</i> (African butterfly)	[76]	No	-	Yes	-	[19, 76, 77]
Insecta	<i>Drosophila melanogaster</i> (fruit fly)	[78]	No	No	Yes	-	[78-81]
Insecta	<i>Callosobruchus chinensis</i> (bean weevil)	[82]	No	Yes	No	-	[82-84]
Insecta	<i>Gryllus bimaculatus</i> (two-spotted cricket)	[85]	Yes	Yes	Yes	Yes	[85-89]
Teleostei	<i>Poecilia reticulata</i> (Trinidadian guppy)	[90]	Yes	Yes	No opportunity	No opportunity	[90, 91]
Teleostei	<i>Gasterosteus aculeatus</i> (Three-spined stickleback)	[92]	Yes	-	Yes	-	[92-94]
Aves	<i>Ficedula albicollis</i> (collared flycatcher)	[95]	No	-	Yes	-	[60, 95, 96]
Aves	<i>Melospiza melodia</i> (song sparrow)	[16]	No	-	Yes	-	[16, 97, 98]
Aves	<i>Notiomystis cincta</i> (hihi)	[99]	-	Yes	No opportunity	No opportunity	[99, 100]
Aves	<i>Passer domesticus</i> (House sparrow)	[101]	No	-	-	No	[101, 102]
Aves	<i>Taeniopygia guttata</i> (Australian zebra finch)	[103]	No	-	Yes	-	[8, 103, 104]
Mammalia	<i>Homo sapiens</i> (modern human)	[105]	Yes	-	No opportunity	No opportunity	[11, 105]
Mammalia	<i>Ovis canadensis</i> (bighorn sheep)	[106]	No	-	No opportunity	No opportunity	[106]
Mammalia	<i>Microtus ochrogaster</i> (prairie vole)	[107]	Yes	-	Yes	-	[107-109]
Mammalia	<i>Mus musculus</i> (house mouse)	[110]	No	Yes	Yes	-	[110-113]
Mammalia	<i>Lycaon pictus</i> (African wild dog)	[114]	Yes	-	No opportunity	No opportunity	[114]

Table 1. Table 1. Inbreeding avoidance and conspecific mate preference across animal taxa with demonstrated inbreeding depression. Included studies were taken from studies included in recent meta-analyses [4,12] that met three criteria: (1) evidence of inbreeding depression; (2) tested, before or after mating, for IA; and (3) either tested for CMP, or assumed to be under relaxed selection to recognize conspecifics because they do not currently coexist with any congeneric species ("No opportunity"). These included five studies [96, 97, 100, 101, 106] that were filtered from [4] because they were observational. (-) indicate that no studies could be found.

1 **Concluding Remarks: Inbreeding avoidance, mate-choice mechanisms, and sexual evolution**

2

3 The conventional wisdom surrounding inbreeding avoidance is largely incorrect. Not only is
4 there no overall evidence for IA across animals [4, 12], but patterns of IA across species and
5 sexes fail to conform to our assumptions. Inbreeding is usually costly, but selection for IA may
6 be weak if related individuals rarely encounter each other as breeding adults (fig. 1A). The
7 mechanistic challenges of IA – swimming upstream, as it were, against CMP and kin affiliation –
8 may favor sexual dimorphism in dispersal or maturation schedules that minimize the need to
9 make decisions; however, “active” inbreeding avoidance can occur across any stage of mating.
10 Experimental studies often focus on isolating a specific stage of mate choice at the expense of
11 understanding how stages of mate choice might interact to drive mating outcomes. For
12 example, multiply-mated female red jungle fowl (*Gallus gallus*) discriminate against related
13 sperm under natural mating conditions; however, this effect disappears with artificial
14 insemination, suggesting it is triggered by total chooser-courter interaction across stages of
15 mate choice [115]. It may be premature to generalize about how constraints on IA operate
16 across stages of mate choice (see Outstanding Questions).

17

18 Further, decisions to avoid inbreeding may be especially challenging when individuals
19 encounter heterospecifics with whom they may mate. Inbreeding avoidance mechanisms –
20 phenotype matching and early learning used to avoid relatives or prefer nonrelatives – all have
21 in common that they should increase the risk of preferring heterospecific traits in opposition to
22 preferences for self-similar conspecifics. Like inbreeding, hybridization can have advantages
23 that are dependent on time and space [116], but both generally have negative consequences.
24 Choosers may be faced with a dilemma: to inbreed or hybridize. Selection favoring CMP may
25 act to relax IA, even when inbreeding is costly, because choosing a heterospecific is worse (see
26 Outstanding Questions). This may resolve the 'inbreeding paradox'. Conversely, hybridization
27 may be facilitated by IA mechanisms favoring novelty and dissimilarity. It would be instructive
28 to see more systems where chooser preferences are assayed before and after mating across a
29 broad array of contexts, particularly in species that occur across gradients of hybridization and
30 inbreeding risk (see Outstanding Questions).

31

32 Even still, the challenge of rejecting distasteful sexual signals of relatives while retaining sexual
33 preferences for unrelated conspecifics is compounded by the widespread benefits of kin
34 affiliation. This means that avoiding relatives must be domain-specific: antipathy for relatives in
35 a sexual context but not in a nonsexual one. Multiple cues conveying "multiple messages" [62]
36 for integration by receivers may be necessary to effectively avoid inbreeding (see Outstanding
37 Questions).

38

39 Research on mate-choice mechanisms could be more extensive as well as more intensive. We
40 need more studies of CMP and IA in the same systems across diverse taxa. The studies in Table
41 1 show the usual bias towards vertebrates and a few tractable insects [117] and omit
42 hermaphrodites, broadcast spawners, and many other taxa that could be used to test
43 predictions about inbreeding and hybridization. Choosing compatible mates is among the most
44 important decisions an individual can make. To avoid sexual interactions with relatives,

1 individuals may need to navigate a narrow course shaped by selection for social decisions in
 2 other contexts. Constraints on inbreeding avoidance mechanisms imposed by CMP and kin
 3 affiliation may have far-ranging consequences across the life cycle, from dispersal to parental
 4 care to mate choice.

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Glossary

Conspecific mate preference	Mating preference for members of one's species
Domain-specific antipathy	An aversive response to a trait in a specific context
Heterotypic mating	Mating with a phenotypically dissimilar or distinct individual to oneself
Hierarchical preferences	A preference in which one stimulus is only effective if values of another stimulus are within a given range.
Homotypic mating	Mating with a phenotypically similar individual to oneself
Inbreeding avoidance	Non-random mate choice for unrelated individuals before, during, or after mating
Inbreeding depression	The fitness reduction of offspring that are products of matings between related individuals
Inbreeding paradox	The co-occurrence of ID and the absence (presence) of evolved traits for inbreeding avoidance (preference)
Inclusive fitness	The proportion of alleles in a population directly passed down by an individual and indirectly passed down via relatives
Kin affiliation	Biased spatial and temporal proximity with related individuals
Kin recognition	The ability to discriminate biological relatives from unrelated individuals
Kin selection	Selection resulting from the combined fitness effects of relatives

Outbreeding depression	The fitness reduction of offspring that are products of matings between two genetically distant individuals
Peak shift	A behavioral response bias that occurs after discrimination learning wherein individuals respond toward extreme values of a stimuli
Phenotype matching	A mechanism for identifying individuals based on the correlation between genetic and phenotypic similarity

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References

- 1
- 2
- 3
- 4 1 Kokko, H. (2017) Give one species the task to come up with a theory that spans them all: what
5 good can come out of that? *Proc. R. Soc. B.* 284, 20171652
- 6 2 Charlesworth, D. and Willis, J.H. (2009) The genetics of inbreeding depression. *Nat. Rev.*
7 *Genet.* 10, 783-796
- 8 3 Rosenthal, G. (2017) *Mate Choice: The Evolution of Sexual Decision Making from Microbes to*
9 *Humans*. Princeton University Press
- 10 4 de Boer, R.A., *et al.* (2021) Meta-analytic evidence that animals rarely avoid inbreeding. *Nat.*
11 *Ecol. Evol.*, 1-16
- 12 5 Tuni, C., *et al.* (2019) Mate choice in naturally inbred spiders: testing the role of relatedness.
13 *Anim. Behav.* 157, 27-33
- 14 6 Butts, I.A.E., *et al.* (2012) Ovarian fluid enhances sperm velocity based on relatedness in lake
15 trout, *Salvelinus namaycush*. *Theriogenology* 78, 2105-2109.e2101
- 16 7 Thünken, T., *et al.* (2014) "Armpit effect" in an African cichlid fish: self-referent kin
17 recognition in mating decisions of male *Pelvicachromis taeniatus*. *Behav. Ecol. Sociobiol.* 68, 99-
18 104
- 19 8 Slater, P. and Clements, F. (1981) Incestuous mating in zebra finches. *Z Tierpsychol* 57, 201-
20 208
- 21 9 Valsecchi, P., *et al.* (2002) Influence of kinship and familiarity on the social and reproductive
22 behaviour of female Mongolian gerbils. *Ethol. Ecol. Evol.* 14, 239-253
- 23 10 Pillay, N. (2002) Inbreeding in Littledale's whistling rat *Parotomys littledalei*. *J. Exp. Zool.* 293,
24 171-178
- 25 11 Marcinkowska, U.M., *et al.* (2013) An experimental test of the Westermarck effect: sex
26 differences in inbreeding avoidance. *Behav. Ecol.* 24, 842-845
- 27 12 Pike, V.L., *et al.* (2021) Why don't all animals avoid inbreeding? *Proc. R. Soc. B.* 288,
28 20211045
- 29 13 Townsend, A.K., *et al.* (2019) Apparent inbreeding preference despite inbreeding depression
30 in the American crow. *Mol. Ecol.* 28, 1116-1126
- 31 14 Wells, D.A., *et al.* (2020) Inbreeding depresses altruism in a cooperative society. *Ecol. Lett.*
32 23, 1460-1467
- 33 15 Sakaluk, S.K., *et al.* (2019) Effects of inbreeding on life-history traits and sexual competency
34 in decorated crickets. *Anim. Behav.* 155, 241-248
- 35 16 Reid, J.M., *et al.* (2015) Resolving the conundrum of inbreeding depression but no
36 inbreeding avoidance: estimating sex-specific selection on inbreeding by song sparrows
37 (*Melospiza melodia*). *Evolution* 69, 2846-2861
- 38 17 Hu, Y., *et al.* (2017) Inbreeding and inbreeding avoidance in wild giant pandas. *Mol. Ecol.* 26,
39 5793-5806
- 40 18 Collet, M., *et al.* (2020) Insects and incest: Sib-mating tolerance in natural populations of a
41 parasitoid wasp. *Mol. Ecol.* 29, 596-609
- 42 19 Robertson, D.N., *et al.* (2020) Lack of sibling avoidance during mate selection in the butterfly
43 *Bicyclus anynana*. *Behav. Processes* 173, 104062

- 1 20 Vuarin, P., *et al.* (2018) No evidence for prezygotic postcopulatory avoidance of kin despite
2 high inbreeding depression. *Mol. Ecol.* 27, 5252-5262
- 3 21 Schausberger, P. and Çekin, D. (2020) Plastic female choice to optimally balance (k) in-and
4 out-breeding in a predatory mite. *Sci. Rep.* 10, 1-8
- 5 22 O'Brien, D.M., *et al.* (2019) Female choice for related males in wild red-backed toadlets
6 (*Pseudophryne coriacea*). *Behav. Ecol.* 30, 928-937
- 7 23 Haikola, S., *et al.* (2004) Has inbreeding depression led to avoidance of sib mating in the
8 Glanville fritillary butterfly (*Melitaea cinxia*)? *Evol. Ecol.* 18, 113-120
- 9 24 Puurtinen, M. (2011) Mate choice for optimal (k) inbreeding. *Evolution* 65, 1501-1505
- 10 25 Szulkin, M., *et al.* (2013) Inbreeding avoidance, tolerance, or preference in animals? *Trends*
11 *Ecol. Evol.* 28, 205-211
- 12 26 Duthie, A.B. and Reid, J.M. (2016) Evolution of inbreeding avoidance and inbreeding
13 preference through mate choice among interacting relatives. *Am. Nat.* 188, 651-667
- 14 27 Kokko, H. and Ots, I. (2006) When not to avoid inbreeding. *Evolution* 60, 467-475
- 15 28 Hedrick, P.W. and Garcia-Dorado, A. (2016) Understanding inbreeding depression, purging,
16 and genetic rescue. *Trends Ecol. Evol.* 31, 940-952
- 17 29 Benesh, D.P., *et al.* (2014) Lifetime inbreeding depression, purging, and mating system
18 evolution in a simultaneous hermaphrodite tapeworm. *Evolution* 68, 1762-1774
- 19 30 Thünken, T., *et al.* (2007) Active inbreeding in a cichlid fish and its adaptive significance. *Curr.*
20 *Biol.* 17, 225-229
- 21 31 Duthie, A.B., *et al.* (2016) Inbreeding parents should invest more resources in fewer
22 offspring. *Proc. R. Soc. B: Biol. Sci.* 283, 20161845
- 23 32 Gow, E.A., *et al.* (2019) Testing predictions of inclusive fitness theory in inbreeding relatives
24 with biparental care. *Proc. R. Soc. B.* 286, 20191933
- 25 33 Shields, W.M. (1982) *Philopatry, inbreeding, and the evolution of sex*. SUNY press
- 26 34 Teixeira, J.C. and Huber, C.D. (2021) The inflated significance of neutral genetic diversity in
27 conservation genetics. *Proc. Natl. Acad. Sci.* 118
- 28 35 Peer, K. and Taborsky, M. (2005) Outbreeding depression, but no inbreeding depression in
29 haplodiploid ambrosia beetles with regular sibling mating. *Evolution* 59, 317-323
- 30 36 Dagilis, A.J., *et al.* (2019) The evolution of hybrid fitness during speciation. *PLoS Genet.* 15,
31 e1008125
- 32 37 Li, X.-Y. and Kokko, H. (2019) Sex-biased dispersal: a review of the theory. *Biol. Rev.* 94, 721-
33 736
- 34 38 JANZEN, F.J. and PHILLIPS, P.C. (2006) Exploring the evolution of environmental sex
35 determination, especially in reptiles. *J. Evol. Biol.* 19, 1775-1784
- 36 39 Ghiselin, M.T. (1969) The evolution of hermaphroditism among animals. *Q. Rev. Biol.* 44,
37 189-208
- 38 40 Husseneder, C., *et al.* (2006) Genetic diversity and genotypic differentiation between the
39 sexes in swarm aggregations decrease inbreeding in the Formosan subterranean termite.
40 *Insectes Soc.* 53, 212-219
- 41 41 Pusey, A. and Wolf, M. (1996) Inbreeding avoidance in animals. *Trends Ecol. Evol.* 11, 201-
42 206
- 43 42 Speechley, E.M., *et al.* (2019) Female guppies increase their propensity for polyandry as an
44 inbreeding avoidance strategy. *Anim. Behav.* 157, 87-93

- 1 43 Duthie, A.B., *et al.* (2018) Evolution of precopulatory and post-copulatory strategies of
2 inbreeding avoidance and associated polyandry. *J. Evol. Biol.* 31, 31-45
- 3 44 Rosenthal, G.G. and Ryan, M.J. (2022) Sexual selection and the ascent of women: Mate
4 choice research since Darwin. *Science* 375, eabi6308
- 5 45 Achorn, A.M. and Rosenthal, G.G. (2020) It's not about him: mismeasuring 'good genes' in
6 sexual selection. *Trends Ecol. Evol.* 35, 206-219
- 7 46 Neff, B.D. and Pitcher, T.E. (2005) Genetic quality and sexual selection: an integrated
8 framework for good genes and compatible genes. *Mol. Ecol.* 14, 19-38
- 9 47 Palumbi, S.R. (2009) Speciation and the evolution of gamete recognition genes: pattern and
10 process. *Heredity* 102, 66-76
- 11 48 Rosenthal, G.G. (2018) Evaluation and hedonic value in mate choice. *Curr. Zool.* 64, 485-492
- 12 49 Ryan, M.J., *et al.* (2019) 'Crazy love': nonlinearity and irrationality in mate choice. *Anim.*
13 *Behav.* 147, 189-198
- 14 50 Seehausen, O., *et al.* (2008) Speciation through sensory drive in cichlid fish. *Nature* 455, 620-
15 626
- 16 51 Gray, D.A. (2022) Sexual selection and 'species recognition' revisited: serial processing and
17 order-of-operations in mate choice. *Proc. R. Soc. B.* 289, 20212687
- 18 52 Adams, S.A., *et al.* (2021) Chemical species recognition in a *Tetragnatha* spider (Araneae:
19 Tetragnathidae). *J. Chem. Ecol.* 47, 63-72
- 20 53 Smadja, C. and Butlin, R. (2009) On the scent of speciation: the chemosensory system and its
21 role in premating isolation. *Heredity* 102, 77-97
- 22 54 Gwynne, D.T. and Rentz, D.C. (1983) Beetles on the bottle: male buprestids mistake stubbies
23 for females (Coleoptera). *Aust. J. Entomol.* 22, 79-80
- 24 55 Kopp, M., *et al.* (2018) Mechanisms of assortative mating in speciation with gene flow:
25 connecting theory and empirical research. *Am. Nat.* 191, 1-20
- 26 56 Yang, Y., *et al.* (2019) Imprinting sets the stage for speciation. *Nature* 574, 99-102
- 27 57 Pfennig, K.S. (2000) Female spadefoot toads compromise on mate quality to ensure
28 conspecific matings. *Behav. Ecol.* 11, 220-227
- 29 58 ten Cate, C., *et al.* (2006) Sexual imprinting can induce sexual preferences for exaggerated
30 parental traits. *Curr. Biol.* 16, 1128-1132
- 31 59 Pfennig, K.S. and Pfennig, D.W. (2009) Character displacement: ecological and reproductive
32 responses to a common evolutionary problem. *Q. Rev. Biol.* 84, 253-276
- 33 60 SÆTRE, G.P. and Saether, S.A. (2010) Ecology and genetics of speciation in *Ficedula*
34 flycatchers. *Mol. Ecol.* 19, 1091-1106
- 35 61 Rundle, H.D. and Schluter, D. (1998) Reinforcement of stickleback mate preferences:
36 sympatry breeds contempt. *Evolution* 52, 200-208
- 37 62 Candolin, U. (2003) The use of multiple cues in mate choice. *Biol. Rev.* 78, 575-595
- 38 63 Lampert, K.P., *et al.* (2006) No evidence for female mate choice based on genetic similarity in
39 the túngara frog *Physalaemus pustulosus*. *Behav. Ecol. Sociobiol.* 59, 796-804
- 40 64 Nasrallah, M.E., *et al.* (2004) Natural variation in expression of self-incompatibility in
41 *Arabidopsis thaliana*: implications for the evolution of selfing. *Proc. Natl. Acad. Sci. U S A* 101,
42 16070-16074
- 43 65 Manser, A., *et al.* (2015) Female house mice avoid fertilization by t haplotype incompatible
44 males in a mate choice experiment. *J. Evol. Biol.* 28, 54-64

- 1 66 Howard, D.J. (1999) Conspecific sperm and pollen precedence and speciation. *Annu. Rev. Ecol. Syst.* 30, 109-132
- 2
- 3 67 Kephart, S. and Theiss, K. (2004) Pollinator-mediated isolation in sympatric milkweeds
- 4 (*Asclepias*): do floral morphology and insect behavior influence species boundaries? *New*
- 5 *Phytol.* 161, 265-277
- 6 68 Cerveira, A.M., *et al.* (2019) Reproductive isolation between sister species of Iberian pine
- 7 voles, *Microtus duodecimcostatus* and *M. lusitanicus*. *Ethol. Ecol. Evol.* 31, 121-139
- 8 69 Ritchie, M.G. (2007) Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.* 38, 79-102
- 9 70 Daniel, M.J. and Rodd, F.H. (2021) Kin recognition in guppies uses self-referencing based on
- 10 olfactory cues. *Am. Nat.* 197, 176-189
- 11 71 Schubert, N., *et al.* (2021) How can the MHC mediate social odor via the microbiota
- 12 community? A deep dive into mechanisms. *Behav. Ecol.* 32, 359-373
- 13 72 Penn, D.J. and Frommen, J.G. (2010) Kin recognition: an overview of conceptual issues,
- 14 mechanisms and evolutionary theory. *Animal behaviour: Evolution and mechanisms*, 55-85
- 15 73 Jaeggi, A.V. and Van Schaik, C.P. (2011) The evolution of food sharing in primates. *Behav.*
- 16 *Ecol. Sociobiol.* 65, 2125
- 17 74 Liévin-Bazin, A., *et al.* (2019) Food sharing and affiliation: An experimental and longitudinal
- 18 study in cockatiels (*Nymphicus hollandicus*). *Ethology* 125, 276-288
- 19 75 Wemmer, C. and Fleming, M. (1974) Ontogeny of playful contact in a social mongoose, the
- 20 meerkat, *Suricata suricatta*. *Am. Zool.* 14, 415-426
- 21 76 Saccheri, I.J., *et al.* (1996) Severe inbreeding depression and rapid fitness rebound in the
- 22 butterfly *Bicyclus anynana* (Satyridae). *Evolution* 50, 2000-2013
- 23 77 Bacquet, P.M., *et al.* (2015) Selection on male sex pheromone composition contributes to
- 24 butterfly reproductive isolation. *Proc. R. Soc. B: Biol. Sci.* 282, 20142734
- 25 78 Putten, V. (1999) Environmental dependence of inbreeding depression and purging in
- 26 *Drosophila melanogaster*. *J. Evol. Biol.* 12, 1125-1137
- 27 79 Tan, C.K., *et al.* (2012) No evidence for precopulatory inbreeding avoidance in *Drosophila*
- 28 *melanogaster*. *Anim. Behav.* 83, 1433-1441
- 29 80 Ala-Honkola, O., *et al.* (2011) No evidence for postcopulatory inbreeding avoidance in
- 30 *Drosophila melanogaster*. *Evolution* 65, 2699-2705
- 31 81 Tomaru, M. and Oguma, Y. (2000) Mate choice in *Drosophila melanogaster* and *D.sechellia*:
- 32 criteria and their variation depending on courtship song. *Anim. Behav.* 60, 797-804
- 33 82 Harano, T. (2011) Inbreeding depression in development, survival, and reproduction in the
- 34 adzuki bean beetle (*Callosobruchus chinensis*). *Ecol. Res.* 26, 327-332
- 35 83 Harano, T. and Katsuki, M. (2012) Female seed beetles, *Callosobruchus chinensis*, remate
- 36 more readily after mating with relatives. *Anim. Behav.* 83, 1007-1010
- 37 84 Kishi, S., *et al.* (2009) Reproductive interference determines persistence and exclusion in
- 38 species interactions. *J. Anim. Ecol.* 78, 1043-1049
- 39 85 van Oosterhout, C., *et al.* (2000) Inbreeding depression and genetic load in laboratory
- 40 metapopulations of the butterfly *Bicyclus anynana*. *Evolution* 54, 218-225
- 41 86 Simmons, L. (1991) Female choice and the relatedness of mates in the field cricket, *Gryllus*
- 42 *bimaculatus*. *Anim. Behav.* 41, 493-501
- 43 87 Veen, T., *et al.* (2013) Diverse reproductive barriers in hybridising crickets suggests extensive
- 44 variation in the evolution and maintenance of isolation. *Evol. Ecol.* 27, 993-1015

- 1 88 Tyler, F., *et al.* (2013) Multiple post-mating barriers to hybridization in field crickets. *Mol.*
2 *Ecol.* 22, 1640-1649
- 3 89 Bretman, A., *et al.* (2009) Promiscuous females avoid inbreeding by controlling sperm
4 storage. *Mol. Ecol.* 18, 3340-3345
- 5 90 Johnson, A.M., *et al.* (2010) Inbreeding depression and inbreeding avoidance in a natural
6 population of guppies (*Poecilia reticulata*). *Ethology* 116, 448-457
- 7 91 Gasparini, C. and Pilastro, A. (2011) Cryptic female preference for genetically unrelated
8 males is mediated by ovarian fluid in the guppy. *Proc. R. Soc. B: Biol. Sci.* 278, 2495-2501
- 9 92 Frommen, J.G. and Bakker, T.C. (2006) Inbreeding avoidance through non-random mating in
10 sticklebacks. *Biol. Lett.* 2, 232-235
- 11 93 Rafferty, N.E. and Boughman, J.W. (2006) Olfactory mate recognition in a sympatric species
12 pair of three-spined sticklebacks. *Behav. Ecol.* 17, 965-970
- 13 94 Kozak, G.M. and Boughman, J.W. (2009) Learned conspecific mate preference in a species
14 pair of sticklebacks. *Behav. Ecol.* 20, 1282-1288
- 15 95 Kruuk, L.E., *et al.* (2002) Severe inbreeding depression in collared flycatchers (*Ficedula*
16 *albicollis*). *Proc. R. Soc. Lond. B: Biol. Sci.* 269, 1581-1589
- 17 96 Pärt, T. (1996) Problems with testing inbreeding avoidance: the case of the collared
18 flycatcher. *Evolution* 50, 1625-1630
- 19 97 Keller, L.F. and Arcese, P. (1998) No evidence for inbreeding avoidance in a natural
20 population of song sparrows (*Melospiza melodia*). *Am. Nat.* 152, 380-392
- 21 98 Schmidt, K.L., *et al.* (2013) Early-life stress affects the behavioural and neural response of
22 female song sparrows to conspecific song. *Anim. Behav.* 85, 825-837
- 23 99 Brekke, P., *et al.* (2010) Sensitive males: inbreeding depression in an endangered bird. *Proc.*
24 *R. Soc. B: Biol. Sci.* 277, 3677-3684
- 25 100 Brekke, P., *et al.* (2012) Postcopulatory mechanisms of inbreeding avoidance in the island
26 endemic hihi (*Notiomystis cincta*). *Behav. Ecol.* 23, 278-284
- 27 101 Billing, A.M., *et al.* (2012) Evidence of inbreeding depression but not inbreeding avoidance
28 in a natural house sparrow population. *Mol. Ecol.* 21, 1487-1499
- 29 102 Cramer, E.R., *et al.* (2014) Testing a post-copulatory pre-zygotic reproductive barrier in a
30 passerine species pair. *Behav. Ecol. Sociobiol.* 68, 1133-1144
- 31 103 Bolund, E., *et al.* (2010) Inbreeding depression of sexually selected traits and attractiveness
32 in the zebra finch. *Anim. Behav.* 79, 947-955
- 33 104 Burley, N., *et al.* (1982) Influence of colour-banding on the conspecific preferences of zebra
34 finches. *Animal Behaviour* 30, 444-455
- 35 105 Ceballos, F.C. and Álvarez, G. (2013) Royal dynasties as human inbreeding laboratories: the
36 Habsburgs. *Heredity* 111, 114-121
- 37 106 Rioux-Paquette, E., *et al.* (2010) No inbreeding avoidance in an isolated population of
38 bighorn sheep. *Anim. Behav.* 80, 865-871
- 39 107 Bixler, A. and Tang-Martinez, Z. (2006) Reproductive Performance as a Function of
40 Inbreeding in Prairie Voles (*Microtus ochrogaster*). *J. Mammal.* 87, 944-949
- 41 108 Lucia, K.E. and Keane, B. (2012) A field test of the effects of familiarity and relatedness on
42 social associations and reproduction in prairie voles. *Behav. Ecol. Sociobiol.* 66, 13-27
- 43 109 Pierce, J.D., *et al.* (1989) Conspecific preferences in prairie voles, *Microtus ochrogaster*, and
44 meadow voles, *M. pennsylvanicus*. *Psychon. Bull. Rev.* 27, 267-270

- 1 110 Lynch, C.B. (1977) Inbreeding effects upon animals derived from a wild population of *Mus*
2 *musculus*. *Evolution*, 526-537
- 3 111 Barnard, C. and Fitzsimons, J. (1988) Kin recognition and mate choice in mice: the effects of
4 kinship, familiarity and social interference on intersexual interaction. *Anim. Behav.* 36, 1078-
5 1090
- 6 112 Firman, R.C. and Simmons, L.W. (2015) Gametic interactions promote inbreeding avoidance
7 in house mice. *Ecol. Lett.* 18, 937-943
- 8 113 Smadja, C., *et al.* (2004) Strong premating divergence in a unimodal hybrid zone between
9 two subspecies of the house mouse. *J. Evol. Biol.* 17, 165-176
- 10 114 Becker, P.A., *et al.* (2012) Inbreeding avoidance influences the viability of reintroduced
11 populations of African wild dogs (*Lycaon pictus*). *PLoS One* 7, e37181
- 12 115 Løvlie, H., *et al.* (2013) Cryptic female choice favours sperm from major histocompatibility
13 complex-dissimilar males. *Proc. R. Soc. B: Biol. Sci.* 280, 20131296
- 14 116 Chen, C. and Pfennig, K.S. (2020) Female toads engaging in adaptive hybridization prefer
15 high-quality heterospecifics as mates. *Science* 367, 1377-1379
- 16 117 Rosenthal, M.F., *et al.* (2017) Taxonomic bias in animal behaviour publications. *Anim.*
17 *Behav.* 127, 83-89
- 18 118 Olsen, K.C., *et al.* (2021) Lessons from the study of plant mating systems for exploring the
19 causes and consequences of inbreeding in marine invertebrates. *Mar. Biol.* 168, 1-12
- 20 119 Lehtonen, J. and Kokko, H. (2015) Why inclusive fitness can make it adaptive to produce
21 less fit extra-pair offspring. *Proc. R. Soc. B: Biol. Sci.* 282, 20142716
- 22
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1 Figure Legends:
2

3 **Figure 1. Selection, inbreeding avoidance, and conspecific mate preference.** Inbreeding and
4 outbreeding both have variable costs and benefits. Both can be avoided through processes that
5 make it unlikely that sexually-mature adults will encounter each other. When individuals are
6 faced with mating decisions, they may show biases against relatives or heterospecifics before,
7 during, and after mating. **(A) The evolution of inbreeding avoidance (IA):** (1) Female (light
8 brown) mates with a close relative (dark brown). Inbreeding can be beneficial due to kin-
9 selected benefits and/or low overall costs associated with inbreeding resulting in little selection
10 for IA. (2) Breeding adults may never encounter relatives; however, when they do and it is
11 costly, selection favors IA at the (3) pre- and/or (4) postmating stage (blue, unrelated sperm is
12 preferred over the more distal orange, related sperm). **(B) The evolution of conspecific mate
13 preference (CMP):** Female (light brown) mates with heterospecific male (striped). (1)
14 Outbreeding can be beneficial because it introduces novel alleles, for example. Notably,
15 inbreeding and outbreeding exist on a continuum, with heterospecific mating at the extreme
16 end of outbreeding. Under conditions where hybridization is beneficial, selection for CMP is
17 expected to be weakened. (2) Homotypic mating may occur simply because breeding adults
18 never encounter heterospecifics or genetically distant individuals, for example through host
19 plant or microhabitat preference (3) When heterospecifics encounter each other and
20 outbreeding is costly, CMP evolves at the (3) pre- (striped males are heterospecifics) and/or (4)
21 postmating stage (orange, conspecific sperm is preferred over heterospecific sperm). Created
22 with BioRender.

23 **Figure 2. Selection on mate-choice mechanisms when inbreeding is costly.** **(A)** Chooser
24 preferences (arbitrary units) for conspecific color. In the absence of similar heterospecific
25 signals, preferences may be directional (solid line) or permissive (dashed line) among
26 conspecifics. **(B)** When mating with heterospecifics is costly, selection favors narrower
27 preferences (solid black line) or peak shift away from heterospecifics (dashed line). **(C)** Chooser
28 preferences among conspecifics for a variable trait, call frequency. Squiggly arrows represent
29 "stepping into" another dimension of courter traits. If inbreeding is costly, selection should
30 favor avoidance of trait values present in relatives (solid line). In this example, there is a
31 hierarchical interaction between preference for conspecific color signals and preference for
32 acoustic signals of unrelated conspecifics: only choosers with acceptable color traits are
33 evaluated for call frequency. In this example, evaluation is sequential but could happen
34 simultaneously or in reverse. Created with BioRender.

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Figure 1

A The Evolution of Inbreeding Avoidance

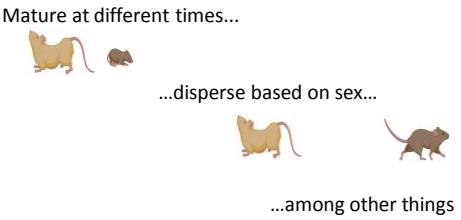


1. There may be little cost or even a benefit to inbreeding



But when inbreeding is costly...

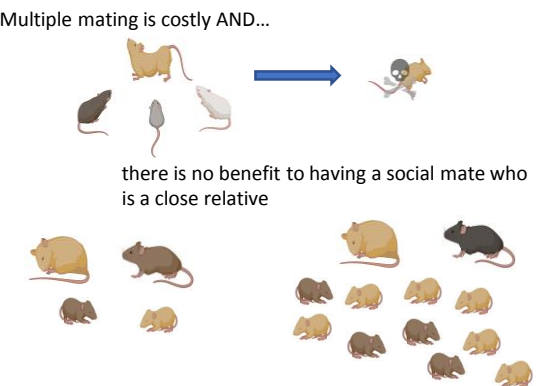
2. Close relatives may rarely meet to mate if they:



When inbreeding is costly AND close relatives risk mating...



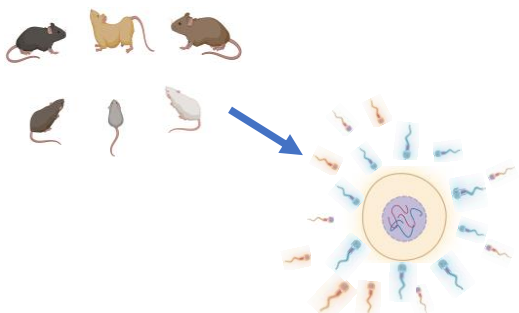
3. Selection favors the evolution of premating inbreeding avoidance when:



When inbreeding is costly AND individuals mate with BOTH relatives and nonrelatives...

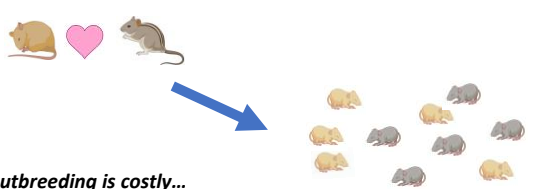


4. Selection favors the evolution of postmating inbreeding avoidance



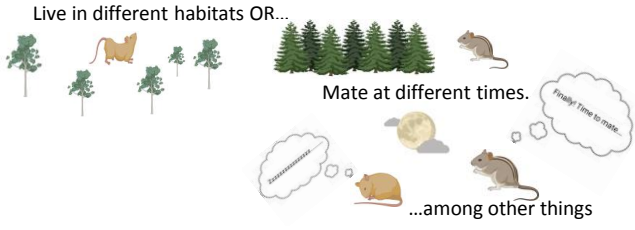
B The Evolution of Conspecific Mate Preference

1. There may be little cost or even a benefit to outbreeding

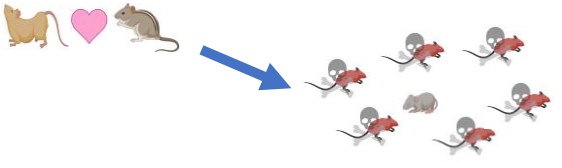


But when outbreeding is costly...

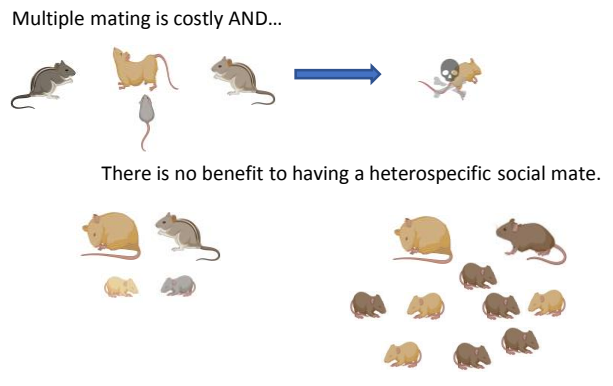
2. Heterospecifics may rarely meet when mature if they:



When outbreeding is costly AND heterospecifics risk mating...



3. Selection favors the evolution of premating conspecific preference when:



When outbreeding is costly AND individuals mate with BOTH conspecifics and heterospecifics...



4. Selection favors the evolution of conspecific mate/sperm precedence

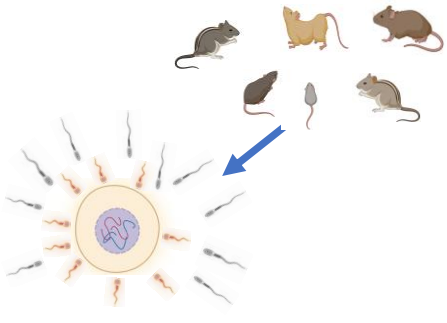
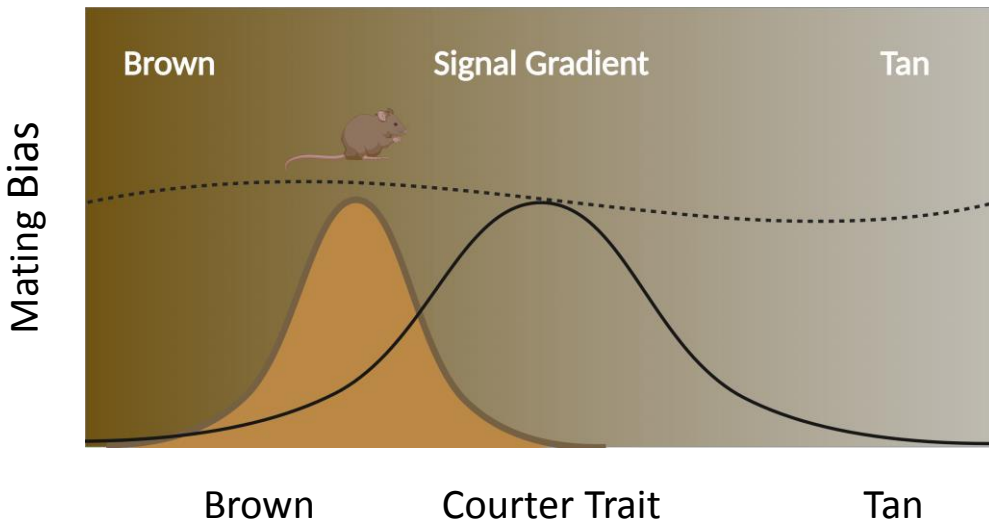
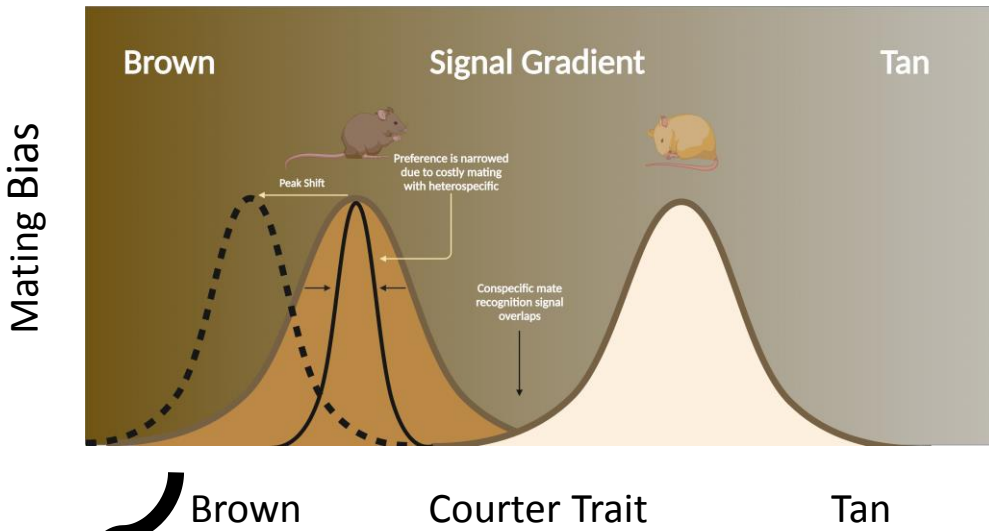


Figure 2

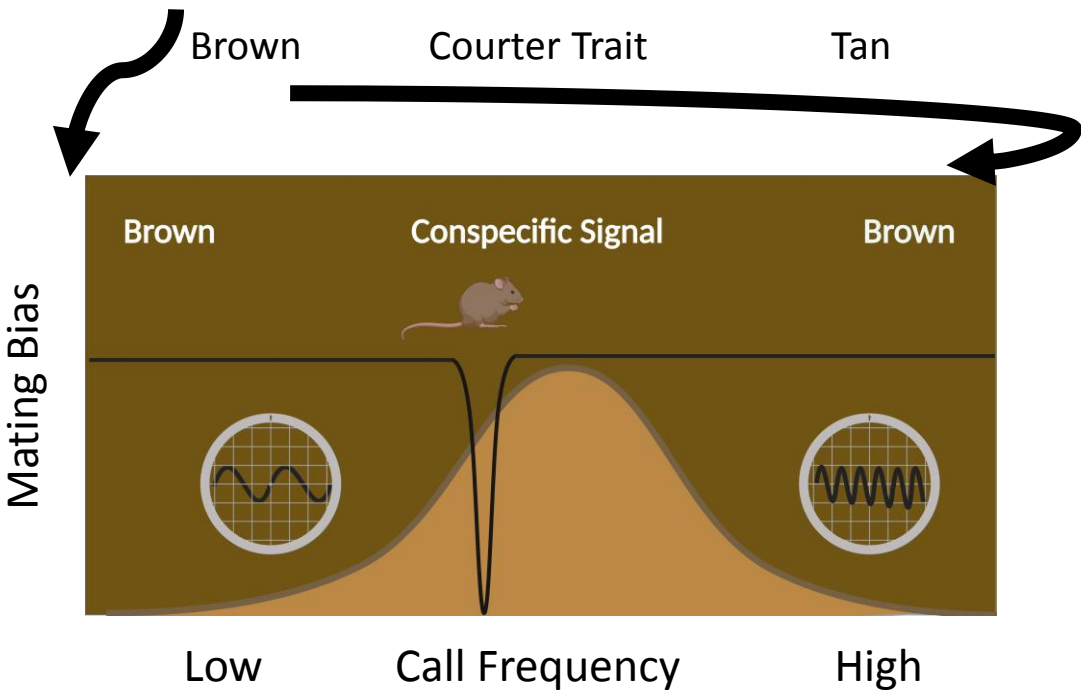
A.



B.



C.



Outstanding Questions

Does postmating IA evolve more readily because of the constraints imposed by kin affiliation?

We expect that postmating Inbreeding avoidance evolves more readily due to the benefits of physical proximity to kin and the complexity of premating inbreeding avoidance. Molecular postmating, rather than premating mechanisms of inbreeding avoidance, is the norm rather than the exception in flowering plants and, perhaps, the same for animals.

Does selection on hybrids facilitate or inhibit inbreeding avoidance? Inbreeding avoidance should evolve most readily when the fitness consequences of potential hybridization are zero (e.g., when closely related species are absent) or positive (e.g., heterosis with incompletely isolated lineages). These patterns would be most easily observed by comparing the strength of inbreeding avoidance across populations along an allopatry gradient.

Does the trade-off between inbreeding avoidance and conspecific mate preference explain the evolution of multivariate sexual communication? The balance between inbreeding avoidance and conspecific mate preferences provides a plausible mechanism for the "multiple messages" hypothesis. Restricting mates to individuals who fall outside the parameters of a variable cue for kin recognition, and within those of conspecifics, may provide a ubiquitous explanation for one aspect of signal complexity.

Ref.: TREE-D-22-00074R1
Sept. 2, 2022

Dear Dr. Stephens,

We are grateful for your feedback and the reviewers'. We are glad that reviewer 1 was positive about our revisions and grateful for reviewer 3's constructive comments, which we believe have greatly improved the manuscript while also helping us trim the manuscript to 2655 words, as appropriate for an Opinion piece.

We respond to reviewer 3's specific comments in ***bold italics*** below.

Thanks again to you and the reviewers for your time and thoughtful comments.

Best wishes,

Owen Dorsey and Gil Rosenthal

Reviewer #3: In general, I found this paper chock full of important and thought-provoking ideas. How do animals thread the needle between inbreeding avoidance, conspecific mate preference, and kin affiliation? In particular, the ideas that stood out were (1) the hypothesis that a conflict between IA and CMP/KA favors multimodal signaling, (2) that measuring affiliation in dichotomous "mate choice" tests may not be a good measure of CMP, especially if there is domain-specific kin affiliation, (3) the hypothesis that different stages of mating may have different fitness consequences of avoiding or affiliating with close relatives, leading to different dynamics of selection for/against IA and CMP/KA at different stages, and (4) the corollary hypothesis that postmating IA is the path of least resistance and thus most likely to manifest it.

We are excited that the reviewer found the ideas important and thought provoking and are gratified by this synthesis, which captures the message we were trying to convey.

That said, I had a hard time following the logical flow of the paper and offer suggestions for clarity, by Page (P) and Line (L) number.

P2L21 and throughout: The phrase "selection on" is used throughout the manuscript, and I find it confusing. Selection can result from both advantageous and disadvantageous alleles, increasing or decreasing their frequency, respectively, so it can be said to be "for" or "against" them. The preposition "on" is therefore ambiguous. I tried to infer it to mean "for or against," but I'm not sure that was the authors' intent in every case, because "selection on" often connotes "selection for". This is especially important on P2L29-31, because that sentence sets the stage for the rest of the section, and it is not clear if "weaken selection on IA" means that IA becomes more neutral and is therefore free to vary, or if selection will disfavor IA mechanisms. Clarity with respect to selection would be most helpful. One suggestion is to reframe arguments about selection whenever possible to indicate when IA/CMP/KA is expected to have fitness

consequences rather than using the phrase "selection on", for example, "When there is selection on mating with relatives..." could be rephrased as "When mating with relatives has fitness consequences, selection may operate at different stages of mate choice in ways that... reduce the (deleterious?) fitness consequences of IA (?) at any one stage" Again, I'm not entirely sure what is meant here by "weaken selection on IA" but I think that's right.

We have now explicitly stated when IA/CMP/KA is selected “for” or “against,” where appropriate, to clear up ambiguity.

P2L25: The subject of the sentence here is "selection" but the verb is "overlap"... this subject/verb combination should be clarified here.

We thank the reviewer for catching this and have now rewritten the sentence for clarity. The sentence now reads, “The evolution of inbreeding avoidance is constrained by selection promoting mechanisms for self-similar association, specifically conspecific mate preference (CMP) and nonsexual kin affiliation.”

P3L4 and throughout: Topic sentences that clearly link the previous paragraph to the current paragraph and to the subheading title would go a long way in improving the logical flow of the ms. For example, a helpful topic sentence here might be "Another reason inbreeding is not always costly is that its costs can be offset by..."

We have made the change as suggested, and rewritten paragraphs for clarity as appropriate throughout the manuscript.

P3L7: should be "alleles" instead of "genes".

Fixed.

P3L13: As above, does this mean that IA has less fitness consequence (becomes more neutral), or that its fitness consequences become more negative? Also see P3L20.

We now rewrite as “Selection for IA may also be weakened if it is more costly to mate with a heterospecific than it is to mate with a close relative.”(page 3 line 13-14).

P3L15: A topic sentence that clearly links to the section heading "inbreeding is not always costly" would be helpful, e.g., something like "Inbreeding may be costly but not as costly as the alternative..."

Thank you for this suggestion. We have updated this on page 3 line 11 in the revised manuscript for a smoother transition.

P3L27: In this case we'd expect little to no selection for OR against IA.

Exactly! We have rewritten this on page 3 line 20 for clarity.

P3L34: I had a hard time envisioning what might be a "low-cost stage" of mate choice. Can you give some examples?

We have rewritten the sentence (page 3 line 25-27) for clarity. We just mean that selection may favor IA at one stage of mate choice rather than another.

P3L36: It seems like we're talking about the spectrum of selection that results from both inbreeding and outbreeding, not just inbreeding here, no?

Yes, we mean the spectrum of selection resulting from both. We have revised this on page 3 line 33-34

P3L36-37: We should talk about inbreeding strategies instead of what?

We have rewritten this section as follows: "Theory suggests that the evolution of inbreeding avoidance hinges on more than the genetic costs of ID. Rather, it depends on dynamic cost-benefits: the potential advantages of inbreeding and the costs of rejecting relatives as mates [25-27]. For example, if there is a net fitness benefit to inbreeding, selection will favor mating with kin. Therefore, the spectrum of selection on inbreeding and outbreeding suggests that so-called inbreeding strategies [25], of which IA is a special case, may vary across different stages of mate choice."

P3-4L43-3: The point of this paragraph was not clear to me. Was it a summary of the section? I'm not sure it's necessary.

This paragraph has been removed from the manuscript.

P4L5: I could not parse the logic of this subsection heading. Is "under selection" necessary here?

We have removed "under selection" from the section title.

P4L5: Throughout this section, all section headings and topic sentences of each paragraph should be modified to clearly refer in some way to constraints, since that is the point of this section.

We have titled the revised subsection accordingly and now refer to constraints throughout the manuscript.

P4L13-17: This paragraph proposes a framework for understanding the relationship between mate choice and inbreeding avoidance. This framework is only helpful if the remainder of the section explicitly refers back to it, i.e., if subsequent points embellish

and flesh out the framework, but I didn't see that. I would also suggest that this paragraph be combined with the previous.

We have combined and extensively rewritten the paragraphs for clarity, we believe they now flow more clearly with the rest of the ms and Box 1.

P4L25: Why is IA a more constrained problem than conspecific mate preference?

We agree this was confusing as written and now unpack this question on pages 4 and 5.

P5L16: Did the authors mean to limit the discussion to males here? Perhaps "courtiers" is more appropriate here.

We have changed "males" to "courtiers".

P5L23: I wasn't sure what "such evolutionary changes is preferences" was referring to...just peak shifts? If so, then this paragraph could be combined with the previous. If not, listing the relevant evolutionary changes would be helpful, like a summary.

We have revised this paragraph to refer to peak shift (page 4 line 40-42).

P6L2-3: This is a fundamentally important hypothesis stemming from this manuscript, but it is stated as an assertion. We know that plants and animals exhibit both self-incompatibility/IA at the same time as CSP/CMP, but the novel point being raised here is about "cues" - suggesting that the focus is on communication. Is there evidence showing that CMP is mediated by different phenotypes ("cues") than IA within a single taxon/population? Phrasing this as a hypothesis seems more appropriate, and/or making clear links between the examples at the end of the paragraph and the concept of "different sets of partner cues".

We rewrite as "...we expect that IA and CMP might have overlapping mechanisms but address different sets of partner cues." (page 7 line 1-2)

P6L30: As in previous comment, this seems better stated as a hypothesis - something like "Antagonistic fitness benefits are expected to favor distinct traits in different sensory modalities for inbreeding avoidance versus CMP" or "we hypothesize that..." Perhaps I'm overstating the novelty of your approach—if you're not the first to propose this hypothesis, perhaps you could cite others that do.

We have now stated this as a hypothesis (page 7 line 10 - 13) using this suggestion.

P7L16-18: This is a very important point, thank you!

We appreciate this!!

P7L20: This subject heading refers to "other social decisions" but seems to refer only to CMP, and thus seems a bit redundant with an earlier section. I would recommend making explicit how this section differs from above statements about the trade-off between IA and CMP.

We have now integrated this section into Box 1 to underscore one of the main points of our argument – in some cases, animals have to decide between inbreeding and hybridizing – and the conclusion of Table 1.

P7L28-30: This is also a very important point. Is this the conclusion of Table 1? It seems like a stronger statement about what we can take from Table 1 could be made here (what's the take-home message of the table?), if only to rephrase the last statement as "The data summarized in Table 1 therefore suggest that examining one stage of mate choice may thus underestimate..."

We have revised Box 1 to reflect this suggestion and reiterated in the concluding remarks! Thank you!

Table 1 legend: should read across "animal" taxa.

Changed.

P9L9: It is not clear how hierarchical preferences in a CMP context impact our understanding of the trade-off between IA and CMP.

We now discuss hierarchical preferences in Box 1, which focuses on the trade-off between IA and CMP.

P9-10: The concluding remarks were rather long and mostly redundant, although some novel points were raised. It seems like this section should be streamlined and hit only the main points from the text.

We have extensively rewritten the concluding remarks as suggested and cut about 30% of the text.

P9L18: This statement contradicts an earlier point (p6) about how IA promotes a diversity of signals.

In this example (moved to Box 1, page 6), we illustrate the converse point, that signal distribution and receiver biology are consistent with an observed lack of IA.

Glossary: Inclusive fitness should be stated in relative fitness terms, so the "proportion of alleles in a population" rather than the "sum of the number of genes," and should say

alleles rather than genes.

We have made this change.

Glossary: The definition of kin selection didn't quite sit right. Selection is a change in a population's allele or phenotype frequencies due to the differential fitness of those alleles/phenotypes. In that context, perhaps a better definition of kin selection is selection resulting from the combined effects of the fitness of close relatives.

We now adopt this definition in the glossary. We use 'kin selection' in the manuscript to mean selection resulting from inclusive fitness.

Glossary: The definition of phenotype matching here doesn't reflect statements in the text. In the text, a preference for relatives' phenotypes is called "early learning" and it's distinguished from "phenotype matching," which is used to refer only to self-referential phenotype matching.

We have modified the definition and the text so that they are in agreement.

Outstanding Questions: The second point is a hypothesis (and a good one!) rather than a question.

This outstanding question has been rephrased as a question instead of a hypothesis.

Highlights: The third point really wasn't developed in the text—is this a vestigial highlight from a previous version?

The revised highlights are now congruent with the main take aways from this ms as articulated by the reviewer.

In sum, I hope these comments weren't overwhelmingly picky—I think this will be a great addition to the literature.

Thank you for this encouraging comment!

- Responses to Reviewers' Comments

Reviewer #1: This is an interesting and engaging opinion piece that seeks to explain the inbreeding paradox - namely, that many animals do not avoid mating with relatives even though inbreeding is costly. The authors argue that inbreeding avoidance may not occur as much as one might expect due to weak or variable selection and functional constraints on avoidance mechanisms. Moreover, the authors argue that selection for conspecific preference during mate choice limits the scope for kin avoidance and highlights the contrasting selective forces at play when animals are interacting with kin in sexual and non-sexual contexts (kin association). The link with potential hybridization potential is very interesting and well described. These ideas are set within the framework of an ongoing re-think in the field regarding the ubiquity of inbreeding avoidance in animals generally. Therefore, this opinion piece does a good job in highlighting and ongoing shift in the field while also describing a clear framework to further the field. As such, I think there is a lot to like about this work.

- ***We are delighted by this reviewer's overall assessment and grateful for their constructive feedback.***

However, despite my general positive reception of this work, I do think there is scope for the authors to clarify a few aspects of their arguments. These include:

1. Treatment of the literature

This is a complex and wide-ranging topic and I wouldn't expect an exhaustive treatment of the literature. Nevertheless, there were some odd uses of the literature that are worth reflection.

The text is framed around two recent meta-analyses that demonstrated i) limited evidence for inbreeding avoidance generally and ii) that inbreeding avoidance only occurred under a narrow set of circumstances. Yet after this initial introduction the remainder of the text overlooks the findings from these meta-analyses.

- ***We acknowledge this point and have carefully considered the two meta-analyses. We have responded to specific criticisms below.***

For example, the authors argue later that postcopulatory inbreeding avoidance should be more common than precopulatory inbreeding avoidance (e.g. pg 6 lines 41-42 and elsewhere). While I agree with their argument generally, my understanding is that de Boer et al. compared the strength of inbreeding avoidance during these two episodes of sexual selection and did not find a difference between them.

One could argue that the available data in this meta-analysis were not up to the task of differentiating them. But in this case the authors ignore relevant information that goes against one of the main points they are trying to make.

- ***We now cite this comparison in pg. 9, lines 38, noting that this comparison is likely to be susceptible to publication bias, and now conclude our piece by calling for more***

powerful comparisons through studies of pre- and postmating IA within the same organism.

Similarly, the authors state that this is one of the outstanding questions in the field (Q2 in the Outstanding Questions box), without any reference to the fact that this has been examined. I agree that this is an outstanding question but it needs to be better integrated into the existing literature.

- ***We now point out why we think experimental design issues make it premature to conclude that there is no difference in inbreeding avoidance across mating stages (pg 10, lines 6-8).***

Another example comes on pg 3 line 32 when the authors suggest that preference for kin as mates is only found before mating and cite one study to support this idea. Couldn't you verify this by looking at the effect sizes in these recent meta-analyses? I'm not sure what the pattern will look like but it does seem like there is scope to improve your argumentation here by relying more on the information in these recent meta analyses.

- ***We thank the reviewer for this point and have removed the reference to the lone study.***

Similarly, the authors summarize evidence of inbreeding avoidance, depression and conspecific preference in Table 1. This table is generally fine, but it falls into the standard pitfalls of a narrative review (e.g. biased choice of specific studies) that these recent meta-analyses have helped clarify. To take one example that jumped out at me - humans. In Table 1, the authors argue that there is evidence for premating inbreeding avoidance in humans. Yet this evidence is mixed at best depending on how data are examined. Many genomic studies have addressed this issue in couples and the results vary depending on countries and populations examined. Again, I may misremember, but didn't the de Boer et al. meta-analysis look at human inbreeding avoidance and compare this with animals, finding no effect in both cases? This is just to illustrate that there are cases where the empirical evidence may not be as clear cut as is being illustrated here. I recommend the authors clarify their choice of studies and acknowledge some of the ambiguity in the literature where it exists.

- ***We now note the limitations of the table and that this is an example list of species from the meta-analyses. We now include the criteria for inclusion in the caption for the table; this is a small but comprehensive subset of studies examined in the two recent meta-analyses. With regards to humans specifically, brother-sister mating is taboo in the overwhelming majority of cultures (Maryanski, A. and Turner, J. (2018) Incest, Theoretical Perspectives on. The International Encyclopedia of Anthropology, 1-14). We were unable to identify the comparison set to nonhuman animals in the deBoer et al. meta-analysis.***

2. Clarifying the sensory perception argument.

The abstract highlights the role of integration of signals beyond the sensory periphery and the

role of multivariate sexual communication as useful avenues for future work. I agree. Yet these topics are get precious little treatment in the manuscript. For example, I would have loved to read more about hoe hierarchical processing of cues could influence inbreeding avoidance and lead to domain-specific antipathy, but his topic was only dealt with in a single sentence (pg 7, lines 10-12). Similarly, the importance of multivariate sexual communication was mainly dealt with in the Outstanding Questions box without much relevant background in the main text.

- ***This is an aspect of the paper we are very excited about, and the revised version develops these concepts extensively on pages 6 and 7, and in figure 2.***

Specific comments:

Pg 3, line 19: please reconsider the use of the word 'cooperation'. I think you are referring to cooperative behaviours in a non-sexual context here. If so it may be worth stating this refers to non-sexual cooperative behaviours. As written this section blurs the line between sexual here between sexual and non-sexual cooperation and this harkens back to the Roughgarden's critique of sexual selection which I think will distract from the main points you are making here.

- ***We have added the qualifier “non-sexual” to clarify (p. 3, line 12).***

Table 1 and pg 3, lines 24-29, pg 6, lines 11-13: ideas are introduced here without much development.

- ***We now develop these ideas in detail in the sections before we introduce the table.***

Can you expand on why humans, hihi, bighorn sheep, guppies and African wild dogs have **limited** scope for conspecific preferences?

- ***We explain in the table caption that this is because they have no opportunity to encounter closely related heterospecifics.***

Similarly, no information is provided for how inbreeding avoidance or conspecific preference was tested, which makes it harder to work thought this table.

- ***We began to parse through studies but struggled with a way to keep the table readable. We discuss methodological issues extensively now in the Concluding Remarks.***

The same issue comes up when introducing hybridization risk in flycatchers (pg 6, lines 12-13) but here the authors provide just enough context to allow the reader to follow their point.

- ***We thank the reviewer for pointing it out; upon reflection we think the flycatcher example is unnecessarily confusing and have omitted it.***

I realize there may be space constraints but a few sentences would go a long way to making this interesting table more accessible to a general audience.

We now discuss the table extensively on page 7.

Page 5, line 39: should this read: '...nonrelatives than in related conspecifics'?

- ***This has now been rewritten.***

Page 6, line 1-2: This human reference seems out of place here as this paragraph is focused on the gametic level. Recent work in humans suggests that postcopulatory mechanisms can influence sperm quality metrics depending on MHC similarity (e.g.

<https://royalsocietypublishing.org/doi/full/10.1098/rspb.2020.1682>) which seems more relevant for this paragraph. Even if this isn't what you were going for, the Westermarck effect being introduced here seems odd for a paragraph focused on the gametic level.

- ***We've replaced the reference and now have introduced the Westermarck effect in the context of premating inbreeding avoidance.***

Pg 6, line 22: consider changing to 'who HAVE a phenotype' as share implies that unrelated individuals will have to have the same phenotype that differs from relatives, while I think you mean that they should have a different phenotype from relatives (i.e. as long as it is different).

- ***The original section has been extensively rewritten.***

Pg 7, line 23: consider adding a citation to Box 1 after 'may confer advantages'.

- ***Box 1 has now been merged into the main text per the reviewer's suggestion. The benefits of mating with kin are now addressed on page 3.***

Outstanding questions box: Please see my comment about Q2 above. Also, for Q2 the authors argue that postmating mechanisms are the norm in flowering plants. It is worth stating here that plants lack equivalent premating avoidance mechanisms from animals, so it wasn't clear if this comparison with animals is apt. There may be more scope for precopulatory selection in plants than I'm aware of and the authors would know more about this than I do. But nevertheless some clarification would help here.

- ***We now refer to pollinator-mediated premating barriers (pg. 6, line 11). The importance of premating choice varies hugely among animals, and we still consider this point to be pertinent for flowering plants and other sessile organisms.***

The legend for figure 2 could be clarified. I struggled to follow these plots. The green line was not described, and the black line/grey curves could be explained in more detail to make it clear what is happening. For example, in B it isn't clear why the curve is inverted above the text 'Variable cue'. More detail in the figure caption would help. As it is I don't think these figures

are as useful as the authors may want them to be.

- ***Figure 2 has been entirely redesigned; please see responses to reviewer 2.***

Also, in figure 1, the thought bubble overlaps with the text 'When outbreeding is costly and heterospecifics risk mating...'. It would be good to correct this.

- **This has been fixed**

Reviewer #2: Thanks for the opportunity to read this interesting manuscript. I think there are some really valuable ideas here that deserve to be out there in the literature, but I also found that there are some pretty substantial details missing regarding the table and figures that make it hard to follow what's going on in several places. The manuscript would also benefit from a little more "roadmapping" to set up expectations of what's next in the article and how the findings/points differ from those made in the recent meta-analyses cited. In general, I think the authors can deal with these issues in a revision. I hope my comments are helpful.

- **The rewritten introduction now provides a roadmap on pg. 2, lines 22-26.**

Highlights:

It's not immediately clear to me what these "functional constraints on mate choice mechanisms" might be. The sentence making (I think) the same point in the abstract was much more intuitive.

- ***We have rewritten this to "Avoiding kin shares neural and molecular mechanisms with other social tasks, like affiliative behavior and conspecific mate preference" for clarity.***

Page 2, Line 12: should this say in preference? Or kin avoidance?

- ***This section has been extensively rewritten and we no longer use the term "kin preference".***

Page 2, Line 12: should references 4 and 5 be cited after Pike et al? It looks like 4 is the de Boer et al. 2021 paper.

- ***Thank you for this catch. We have updated the reference to only include Pike et al.***

Page 2, Line 24-27: Given this is an opinion piece, and you've just described two very recent reviews on this topic, I think it would help the reader to understand what new information they'll gain from this opinion - perhaps some minor wording changes here would help the reader to distinguish what you're doing here from those very recent reviews. Is it that you're offering explanations for the patterns they uncovered that were not discussed in those

reviews?

- ***In contrast to recently proposed adaptive explanations, we argue the “inbreeding paradox” arises from selective constraints on inbreeding avoidance mechanisms involved in other social and sexual interactions. We suggest these constraints may play a role in the evolution of complex communication and of passive mechanisms to avoid inbreeding. We hope we have made this clearer throughout the manuscript.***

Page 2, Line 39: missing the word "and"

- ***This has been addressed.***

Page 2, Line 28: I found this section on weak or variable selection on inbreeding avoidance a little thin, given that this is one of the two mechanisms you're going to talk about in the paper. In particular, I wonder if the content in the box needs to be a box? What's the benefit of pulling that out? I also think the important point that selection on sibling-sibling mating may "in ways that may relax, and perhaps at times reverse, selection favoring inbreeding avoidance at any one stage" was underdeveloped. And I left this section wondering what mechanisms were relaxing or reversing selection on inbreeding avoidance. Figure 1 helped a little bit, but more in terms of the different stages of mating at which selection may act. It would help to then really spell out for the reader which of these are relaxing/reversing selection on inbreeding avoidance.

- ***Box 1 has been integrated into the manuscript's main text to provide more substance to this section. We have also pointed out where selection on inbreeding avoidance may be relaxed in each subsection.***

Box 1: This box makes a number of great points. I wonder too if there is literature on selection on inbreeding avoidance under certain demographic circumstances - e.g. very biased sex ratios or in very small populations? It seems likely that there would be benefits to not avoiding mating with siblings under these conditions (if the alternative is no mate at all...).

- ***We thank the reviewer for this insight, and now address this point on pg. 10, lines 43-44.***

Figure 1: This is a pretty great figure, but the figure legend lacks some detail. Please expand to indicate what the colors/body shapes/patterns of animals are indicating (males and females?, different morphs?, different species?, kin or non-kin?). Also, what are the green things on the left under the word microallopatric (under Figure 1b)? Are these just a different kind of tree, spread out to indicate microallopatry? Or is the microallopatry indicated by the two different habitat types and species on the left and right? If the latter, maybe spread the two habitat types out a bit more to make that a little more clear - give the pictures some room to breathe.

- ***We have edited Fig. 1 and updated the caption to clarify these points.***

Page 3, line 22: Please wrap this point up a bit for clarity, ie "So, both selection for both conspecific mate prefs and cooperation may act in opposition to that on inbreeding avoidance (trade off)" or whatever.

- ***We now reiterate this key message at the end of each section.***

Page 3, line 24: While describing what's in Table 1, it would help the reader to know WHY you are including Table 1 here - why was this collated? How does it help make your point?

- ***Table 1 is intended broadly to present conspecific mate preference and inbreeding avoidance as part of a unified problem in mate choice and social decision making, and specifically to point out that (a) when tested, inbreeding avoidance is often absent at a given stage of mate choice and (b) inbreeding avoidance is often absent even in systems with mate choice in the form of preferences for conspecifics.***

Table 1: I don't see any information at all about how the studies summarized in this table were collected/searched for. Is this an exhaustive list? What searches were used etc? How did you determine which species on this list have no sympatric congeners? And, if it's absence of a test for conspecific mate preference that was used to determine likelihood of having sympatric congeners, how do we know it isn't just a lack of time/money/interest in studying that particular concept in that particular species? Please explain.

- ***The criteria for inclusion are now explained in detail in the table caption. This is a comprehensive list of studies filtered from those cited by one or both of the two recent meta-analyses, including XX observational studies excluded from their statistical analyses. Studies were selected if they met three criteria: evidence for inbreeding depression, tests of inbreeding avoidance at any stage, and tests of conspecific mate preference against sympatric congeners at any stage. If there were no sympatric congeners, as in humans and hihi, we referenced these as "no opportunity" to exercise preferences for or against conspecifics and assumed relaxed selection on conspecific mating preferences.***

Also, consider not using red and green as some will have difficulty with this color scheme.

- ***We've changed the color scheme to gray and white.***

Table 1 caption: The second sentence in this caption is not a complete sentence. What does the "-" mean? No data?

- ***We have rewritten this caption extensively and clarified that "-" means no studies could be found.***

Page 3, line 31: I'm not sure why the word 'only' is in this sentence.

- ***We have removed only from this phrasing.***

Page 3, line 36-37: This is really interesting!

- ***Thank you! We now expand on the net benefits of inbreeding on page 3, lines 4-14.***

Figure 2: This figure also needs some additional description in the figure caption. In a, for instance, please write out what is in yellow (what is meant by frequency?), indicate the peak shift you're trying to draw our attention to, and describe what an imprinted phenotype has to do with this - none of that is in the figure caption, so it's not clear what the reader should pay attention to here. What about something like show two preference functions with different peaks (an average function and an individual's function after experience/imprinting - if that's what is meant by peak shift). I think part of the issue I'm having with this is that the phenotype of the familiar relatives isn't shown. Is the imprinted phenotype the peak shift? In b, I can't even begin to figure out what's happening here because the yellow and blue distributions aren't defined in the caption. Finally, in C-F there are some labels that seem out of place - "conspecific preference favored" is shown twice, but once way off center from the x-axis of part D, inbreeding avoidance is also listed twice etc. I think some of these are meant to be a color legend, but the placement is odd and it's not clear what's going on.

- ***We have gone back to the drawing board with this figure and hope that fig. 2B explains peak shift more clearly.***

Page 6, line 39+: Again, super interesting point!

- ***Thank you! We now develop this point more fully on pages 5-6.***

On pages 6 and 7 the authors are describing various things that are shown graphically in Figure 2, but the figure is only referred to once, in the context of talking about part 2a only. Please refer to the parts of this figure as needed and see additional notes above about more fully describing the graphics in the figure caption. For example, Fig 2b should be referred to on line 8 of page 7, correct?

- ***We have revised figure 2 extensively, and believe the figure and caption are now consistent with the text.***

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