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Opinion

# A taste for the familiar: explaining the inbreeding paradox

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**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.**

## Highlights

Individuals often mate with relatives, even when it is costly: the 'inbreeding paradox'.

Avoiding kin shares neural and molecular mechanisms with other social tasks, such as affiliative behavior and conspecific mate preference.

'Active' inbreeding avoidance battles against nonsexual kin affiliation.

Trade-offs between conspecific preference and inbreeding avoidance may constrain or facilitate hybridization.

## Inbreeding avoidance is not ubiquitous

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

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

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

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

## Weak and variable selection for IA

As suggested by Pike *et al.* [12], IA should evolve only when encounters between adults result in ID. When there is such selection against mating with relatives, it may operate at different stages of

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mate choice (Figure 1A) in ways that relax selection for behavioral IA before mating. There are three main factors that weaken selection for IA at any one stage:

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

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

Although inbreeding may be costly, the alternative can be worse. More generally, preferences for unrelated mates mean that choosers may incur fitness loss not only from outbreeding with conspecifics [33–35] but also from hybridization [36]. Thus, 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.

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

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

Theory suggests that the evolution of IA 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.

## Constraints on IA mechanisms

Selection for 'active' IA requires a mechanism that biases against sexual interactions with kin at some stage of mate choice. Like other mate-choice mechanisms, IA is shaped by selective pressures within and outside the context of mating [44,45]. Constraints on mate-choice mechanisms may make IA challenging to achieve, for two primary reasons. First, sexual reproduction requires

### Glossary

**Conspecific mate preference (CMP):** mating preference for members of one's own 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 effective only if values of another stimulus are within a given range.

**Homotypic mating:** mating with an individual phenotypically similar to oneself.

**Inbreeding avoidance (IA):** nonrandom mate choice for unrelated individuals before, during, or after mating.

**Inbreeding depression (ID):** 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 IA (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 stimulus.

**Phenotype matching:** a mechanism for identifying individuals based on the correlation between genetic and phenotypic similarity.

Table 1. IA and CMP across animal taxa with demonstrated ID

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

Studies were taken from those included in recent meta-analyses [4,12] that met three criteria: (i) evidence of ID; (ii) tested, before or after mating, for IA; and (iii) 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.
Dash indicates that no studies could be found.

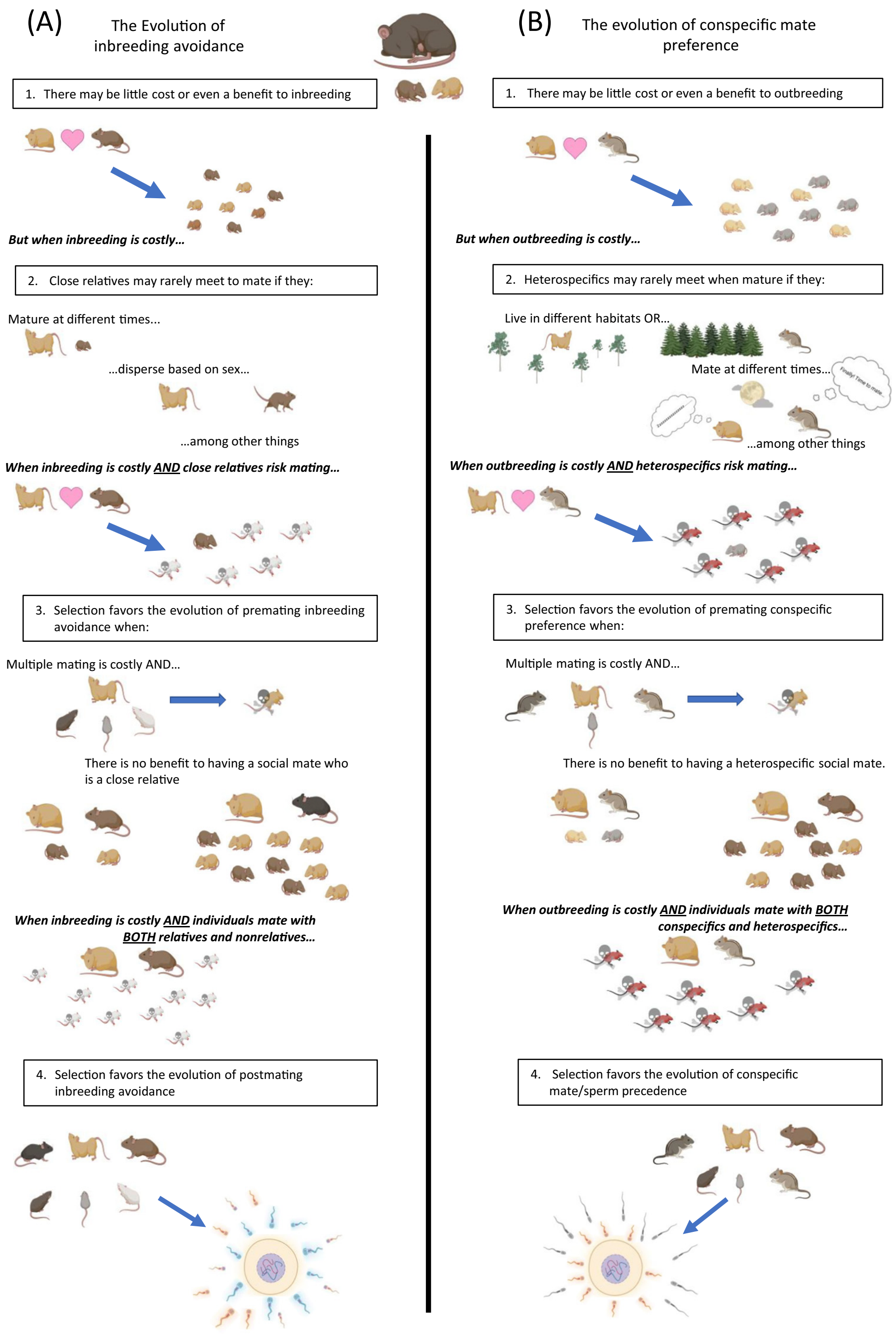
coordination between individuals who share genetic ancestry. Second, nonsexual cooperation often involves proximity and affiliative behaviors among close kin. IA, by contrast, requires an individual to avoid one specific affiliative behavior (mating) with individuals who are similar, familiar, and safe.

## CMP promotes homotypic mating

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

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

Numerous mechanisms favor cues for self-similar, conspecific sexual partners, from sensory filters at the earliest stages of mate choice [48], to integration of multimodal signals in the brain [49], through the egg–sperm interface and beyond [3]. The most studied cues involved in conspecific mate recognition are often low-dimensional and vary little within a species, such as color differences [50], acoustic frequency differences [51], or chemical ratios [52,53]. If there are substantial differences between these cues and other stimuli in the environment, as in humans



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:

Mature at different times…

…disperse based on sex…

…among other things

***When inbreeding is costly <u>AND</u> close relatives risk mating…***

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

Multiple mating is costly AND…

There is no benefit to having a social mate who is a close relative

***When inbreeding is costly <u>AND</u> individuals mate with <u>BOTH</u> relatives and nonrelatives…***

4. Selection favors the evolution of postmating inbreeding avoidance

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:

Live in different habitats OR…

Mate at different times…

…among other things

***When outbreeding is costly <u>AND</u> heterospecifics risk mating…***

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

Multiple mating is costly AND…

There is no benefit to having a heterospecific social mate.

***When outbreeding is costly <u>AND</u> individuals mate with <u>BOTH</u> conspecifics and heterospecifics…***

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

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Figure 1. Selection, inbreeding avoidance (IA), and conspecific mate preference (CMP). Inbreeding and outbreeding both have variable costs and benefits. Both can be avoided through processes that make it unlikely that sexually mature adults will encounter each other. When individuals are faced with mating decisions, they may show biases

*(Figure legend continued at the bottom of the next page.)*

and hihi (*Notiomystis cincta*), where no closely related species exist (Table 1), a single filter – whether a membrane receptor molecule, an auditory tuning curve, or categorical perception – can discriminate homotypic from heterotypic stimuli (Figure 2).

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

The problem is harder when homotypic and heterotypic courters resemble each other and the cost of a mistaken mating is high [57]. Therefore, selection against heterospecific mating often yields **peak shift**, whereby choosers prefer cues displaced away from a stimulus to be avoided (Figure 2B). Peak shift occurs in contexts ranging from learned sexual preferences [58] to reproductive character displacement over evolutionary time [3,59] and can result in divergent preferences between sympatric and allopatric populations (e.g., [60,61]). For example, choosers may choose less attractive, conspecific courters when the risk of hybridization is high despite lower fitness benefits [57]. If traits overlap, a single filter cannot include all conspecifics without including some heterospecifics, nor vice versa (Figure 2B). Selection therefore favors the evolution of receivers who integrate responses to multiple cues [62] along multiple stages of mate choice, pre- and post-mating.

### IA: heterotypic mating within a homotypic envelope

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

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

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against relatives or heterospecifics before, during, and after mating. (A) The evolution of IA: (1) female (light brown) mates with a close relative (dark brown). Inbreeding can be beneficial due to kin-selected benefits and/or low overall costs associated with inbreeding resulting in little selection for IA. (2) Breeding adults may never encounter relatives; however, when they do and it is costly, selection favors IA at the (3) pre- and/or (4) post-mating stage (blue, unrelated sperm is preferred over the more distal orange, related sperm). (B) The evolution of CMP: female (light brown) mates with heterospecific male (striped). (1) Outbreeding can be beneficial because, for example, it introduces novel alleles. Notably, inbreeding and outbreeding exist on a continuum, with heterospecific mating at the extreme end of outbreeding. Under conditions where hybridization is beneficial, selection for CMP is expected to be weakened. (2) Homotypic mating may occur simply because breeding adults never encounter heterospecifics or genetically distant individuals: for example, through host plant or microhabitat preference. (3) When heterospecifics encounter each other and outbreeding is costly, CMP evolves at the pre-mating (striped males are heterospecifics) and/or (4) post-mating stage (orange, conspecific sperm is preferred over heterospecific sperm). Figure was created with BioRender.

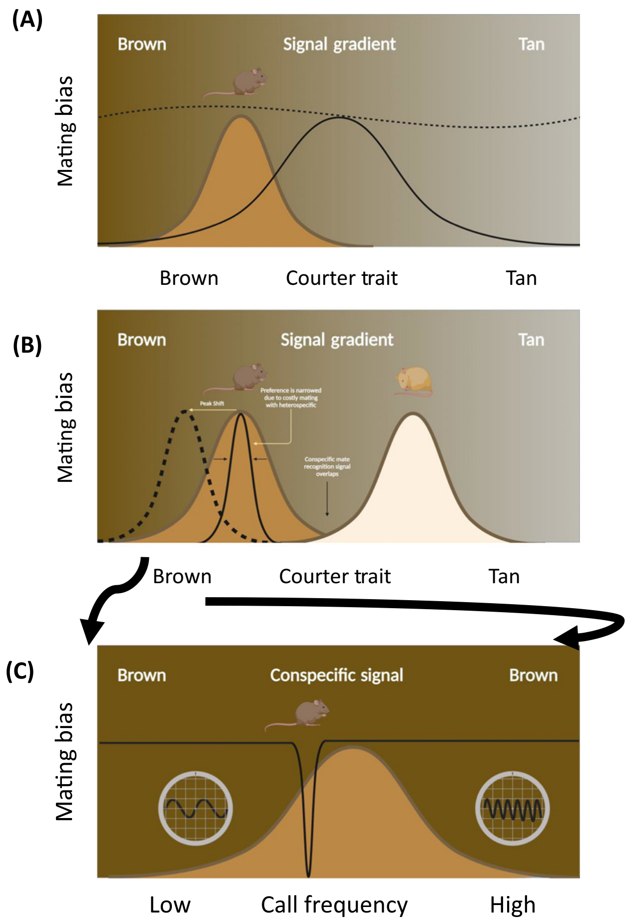

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Figure 2. Selection on mate-choice mechanisms when inbreeding is costly. (A) Chooser preferences (arbitrary units) for conspecific color. In the absence of similar heterospecific signals, preferences may be directional (solid line) or permissive (dashed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

For CMPs, phenotype matching and early learning shape sexual preferences for self-similar individuals; in the context of IA, they shape sexual avoidance of self-similar individuals. For example, self-incompatibility alleles in angiosperms reject the most self-similar genotypes, limiting the most intense form of inbreeding [64]. The *t* allele system in mice also reduces inbreeding: female mice carrying the recessive-lethal *t* locus avoid *t* males, a case of heterotypic mating [65]. Importantly, heterotypic mating with respect to one cue must occur alongside homotypic mating with respect to another, at all stages of mate choice. Examples are conspecific pollen precedence [66] or pollinator-mediated pre-mating barriers [67] co-occurring with self-incompatibility in flowering plants, or conspecific sperm precedence [66] and pre-mating preferences [68] co-occurring with self-avoidance in mammals. Therefore, we expect that IA and CMP might have overlapping mechanisms but address different sets of partner cues.

The critical difference between IA and CMP is that while CMP cues are under stabilizing or directional selection for homotypic mating [69], successful IA requires avoiding kin without rejecting conspecifics altogether. IA, therefore, relies on cues that are variable within a population and therefore distinct in unrelated individuals (Figure 2). For example, the vertebrate major histocompatibility complex (MHC) of immune proteins is a popular candidate for linking genes under diversifying selection to olfactory cues used to identify kin and reject related mates [70], likely through

### Box 1. Are there trade-offs between IA and CMP?

IA requires sexual rejection of individuals that are too self-similar or too familiar, in direct conflict with selection favoring homotypic mating (Figure 2A in main text). And it requires avoidance of activities that lead to mating, in direct conflict with selection favoring affiliative behaviors with kin (Figure 2B in main text). 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 (in main text) lists systems with measured ID and studies of both IA and CMP from recent meta-analyses [4,12]. 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 (in main text), therefore, suggest that just examining one mate-choice stage may underestimate total IA.

It is suggestive that of the eight species with pre-mating preferences for conspecifics (Table 1 in main text), five showed no evidence of IA 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.

effects of host MHC haplotype on the scent-producing microbiome [71]. Therefore, selection for genetic compatibility may be a widespread driver of multimodal and multidimensional complexity in sexual communication because antagonistic fitness benefits are expected to favor distinct traits in different sensory modalities for IA versus CMP.

## IA, kin recognition, and domain-specific antipathy

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

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

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

## Concluding remarks: IA, mate-choice mechanisms, and sexual evolution

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

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

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

Research on mate-choice mechanisms could be more extensive as well as more intensive. We need more studies of CMP and IA in the same systems across diverse taxa. The studies in Table 1 show the usual bias towards vertebrates and a few tractable insects [117], omitting hermaphrodites, broadcast spawners, and many other taxa that could be used to test predictions about inbreeding and hybridization. Choosing compatible mates is among the most important decisions an individual can make. To avoid sexual interactions with relatives, individuals may need to navigate a narrow course shaped by selection for social decisions in other contexts. Constraints on IA mechanisms imposed by CMP and kin affiliation may have far-ranging consequences across the life cycle, from dispersal to parental care to mate choice.

## Outstanding questions

Does post-mating IA evolve more readily because of the constraints imposed by kin affiliation? We expect that post-mating IA evolves more readily due to the benefits of physical proximity to kin and the complexity of pre-mating IA. Molecular post-mating, rather than pre-mating mechanisms of IA, is the norm rather than the exception in flowering plants and is perhaps the same for animals.

Does selection on hybrids facilitate or inhibit IA? IA 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 IA across populations along an allopatry gradient.

Does the trade-off between IA and CMP explain the evolution of multivariate sexual communication? The balance between IA and CMP 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.

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### Declaration of interests

No interests are declared.

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