



Review

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Author for correspondence:

Yitzchak Ben Mocha

e-mail: yitzchakbm@gmail.com

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Why do human and non-human species conceal mating? The cooperation maintenance hypothesis

Yitzchak Ben Mocha^{1,2,3,4}

¹Department of Anthropology, Zürich University, Winterthurerstrasse 190, 8057 Zürich, Switzerland

²Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

³Max Planck Institute for Ornithology, Seewiesen, Germany

⁴Department of Collective Behavior, Max Planck Institute for Animal Behavior, Konstanz, Germany

YBM, 0000-0002-9946-1936

Despite considerable cultural differences, a striking uniformity is argued to exist in human preferences for concealing sexual intercourse from the sensory perception of conspecifics. However, no systematic accounts support this claim, with only limited attempts to understand the selective pressures acting on the evolution of this preference. Here, I combine cross-cultural and cross-species comparative approaches to investigate these topics. First, an analysis of more than 4572 ethnographies from 249 cultures presents systematic evidence that the preference to conceal mating is widespread across cultures. Second, I argue that current anthropological hypotheses do not sufficiently explain why habitual concealment of mating evolved in humans but is only seldom exhibited by other social species. Third, I introduce the cooperation maintenance hypothesis, which postulates that humans, and a specific category of non-human species, conceal matings to prevent sexual arousal in witnesses (proximate explanation). This allows them to simultaneously maintain mating control over their partner(s) and cooperation with group members who are prevented from mating (ultimate explanations). I conclude by presenting a comparative framework and predictions to be tested across species and human cultures.

1. Introduction

Despite the extraordinary cultural diversity that has evolved in the human species, humans from distinct cultures have been reported to take active precautions to conceal sexual intercourse from the sensory perception of others [1]. During the last century, scholars argued that the preference for concealed mating represents a 'human universal' [2–7] and is also uniquely human [1,8]. Others speculated this had a significant effect on the evolution of human emotions (e.g. shame [3,6]) and cognitive skills (e.g. self-awareness, managing social relationships [3]).

Despite this long-standing interest, systematic research on concealed mating is virtually non-existent [3]. Specifically, two fundamental questions remain unanswered. First, is the preference to conceal legitimate mating from the sensory perception of conspecifics a 'human universal'? Second, what evolutionary pressures have selected for this preference? Here, I take evolutionary, cross-cultural and cross-species, comparative perspectives to investigate these questions.

Importantly, I focus on *legitimate mating* and *sensory concealment* (table 1). I examine legitimate mating (i.e. sexual intercourse that is approved of by the social norms of a pair's culture) since its concealment cannot be explained by punishment avoidance (unlike interactions that are prohibited by social norms, for example, extramarital sex [9]). I focus on sensory concealment, that is, whether pairs try to conceal the visual and/or auditory and/or odour stimuli of mating from the sensory perception of conspecifics (e.g. by postponing mating until co-residents are asleep). I did not investigate whether pairs

Table 1. Glossary.

glossary	
sensory concealment of mating	efforts to hide visual and/or auditory and/or odour stimuli of mating (i.e. sexual intercourse) from the sensory perception of conspecifics
non/legitimate mating (in humans)	sexual intercourse against/according to the customary social norms (e.g. incest/normative sexual intercourse between married couples)
mating between dominant/subordinate animals	mating between individuals that cannot/can physically be stopped by group members (e.g. mating between the alpha/beta male and the alpha female)
control of mating access to partner(s)	individual tries to prevent all/specific group members from <i>mating</i> with his/her partner(s) during all/specific times (e.g. when the female ovulates); mechanisms that prevent post-copulatory fertilization by other males (e.g. copulatory plug) are not regarded as means to control mating access
dependency on cooperation	at least one of the sexual partners depends on cooperation with group members that are prevented from mating with his/her partner

conceal the *fact* that they are engaged in legitimate mating, as it is evident that humans know that married pairs have legitimate sexual relationships [10].

In the first section of this review, I present systematic evidence for the wide prevalence of mating concealment across human cultures. Second, I take an evolutionary perspective to review existent hypotheses for concealed mating in humans and demonstrate that they do not explain why concealed mating evolved as the norm in humans, but is only seldom exhibited by other social great apes. Third, I review the phenomenon of concealed mating in non-human species. Fourth, I present the cooperation maintenance hypothesis, which postulates that concealed mating is a behavioural strategy used to concurrently maintain mating control over partner(s) and cooperation with group members. I conclude with predictions to test this hypothesis across social species and human cultures.

2. How prevalent is the preference to conceal mating across human cultures?

Although the claim that all human cultures conceal mating was repeated during the last century [1–3,5,6,11], to my knowledge, there is a lack of systematic supporting evidence (but see [1,12]). To examine the prevalence of concealed mating across cultures, I thus analysed sexual practices in 249 cultures from 35 geographical regions by reviewing more than 4572 ethnographies from the electronic Human Relations Area Files World Cultures (hereafter eHRAF [13]; see electronic supplementary material, appendix S1 for detailed methodology, and electronic supplementary material, appendix S2 for worldwide distribution of cultures). From this, I established two datasets. The first is the survey dataset ($n = 249$ cultures), which was designed to identify any customs of public mating and concealment of legitimate mating. To this end, I reviewed all ethnographies included in the eHRAF regardless of the community and historical period described. The SCCS/EA dataset ($n = 172$ cultures) was created to control for inter-culture independency and within-culture variation. It was thus confined to cultures and ethnographies that are included in the standard cross-cultural sample [14] and ethnographic atlas [15]. These samples include the most reliable ethnographies that describe a distinct historical period and community of cultures that represent

human diversity. Since informants are often reluctant to discuss their sexual lives [4] (see also Turks in electronic supplementary material, appendix S3), sexual aspects are often poorly documented [10]. Yet, sufficient ethnographic data on the privacy of legitimate mating were found in 131 and 82 cultures from the survey and SCCS/EA datasets, respectively.

In many cultures, living conditions prevent complete sexual privacy (e.g. [16]), while in others, sexual privacy is not rigorously kept (see §4d(v) for examples). Nevertheless, pairs from virtually all cultures were reported to take measures to conceal (at least partly) their legitimate mating from the sensory perception of adult conspecifics (survey dataset: 130/131 cultures; SCCS/EA dataset: 81/82 cultures; table 2; electronic supplementary material, appendix S3). An exception is the Goajiro from Colombia, where pairs reportedly took no precautions to conceal legitimate mating. However, data on sexual norms of the Goajiro before contact with missionaries are poor and rigorous modesty post-contact prevents an in-depth investigation (table 2).

Customs of public sex under special circumstances were reported in 20 cultures. Examples for customs of public sex include religious ceremonies and sex training (see electronic supplementary material, appendix S6 for full account).

These results show that the preference to conceal legitimate mating from the sensory perception of conspecifics is, at the very least, widespread across human cultures. Nonetheless, conclusions from ethnographic analyses of sexual norms should be viewed cautiously. An unavoidable limitation is that informants may not practise liberal sexual behaviours in the presence of anthropologists that come from cultures where such behaviours are strongly disapproved of (for discussion and examples see [17,18]).

3. Hypotheses on the function of concealed mating in humans and their limitations

Widespread human behaviours are strong candidates for evolutionary adaptations. Their functions should therefore also be studied from an evolutionary perspective [5,19]. I thus now turn from an ethnographic survey on the prevalence of concealed mating to an evolutionarily based investigation of its function.

Table 2. Examples of concealment of legitimate mating. See electronic supplementary material, appendix S3 for full account and references.

region (sub-region)	culture	is legitimate mating concealed? (sample dataset)	examples of concealment
Africa (Central)	Mongo	yes (standard cross-cultural sample)	'A natural shame which makes them seek darkness and privacy for acts of this sort.'
Africa (Western)	Nupe	yes (ethnographic atlas)	'Any open reference to sex is severely shunned by the rather prudish Nupe. Sex and privacy go together.'
Asia (Caucasus)	Abkhazians	yes (standard cross-cultural sample)	'Extreme modesty is required at all times.'
Asia (Southeast)	Semang	yes (standard cross-cultural sample)	'Semang cohabit in the camp at night. It is said to be improper during the day because others would notice.'
Europe (Southeastern)	Bosnian Muslims	yes (survey)	'Husband and wife relations vary within the village, but in general, public display of affection is rare.'
Europe (Southeastern)	Croats	yes (survey)	'A husband and wife could only show affection, therefore, in the privacy of their own room.'
North America (Arctic and Subarctic)	Ingalik	yes (standard cross-cultural sample)	'Man and woman are seldom isolated from a social group for other than sexual reasons.'
North America (Eastern Woodlands)	Iroquois	yes (survey)	'Iroquoian peoples were modest in dress, often rather shy in public contacts with the opposite sex ... chastity and marital fidelity were publicly recognized ideals.'
Oceania (Melanesia)	Trobriand	yes (standard cross-cultural sample)	'Sex is regarded as naturally to be avoided in public.'
Oceania (Polynesia)	Hawaiians	yes (ethnographic atlas)	'Old time Hawaiians never "made love" in public, or even in the presence of relatives or friends.'
South America (Amazon and Orinoco)	Sirionó	yes (standard cross-cultural sample)	'Since privacy is almost impossible to obtain within the hut [...] more intercourse takes place in the bush than in the house.'
South America (Eastern)	Canela	yes (standard cross-cultural sample)	'A youth visits his betrothed in her platform bed, which she [...] shields from the sight of the other inmates by a partition of mats. However, nobody casts prying eyes in their direction, for in this regard the Timbira display exemplary discretion.'
South America (Northwestern)	Goajiro (traditional)	no (standard cross-cultural sample)	'Conjugal relations of a couple who are pure Indian are carried out openly [...] even in front of the smaller children.'
South America (Northwestern)	Goajiro (modern)	yes (standard cross-cultural sample)	'Exhibitionism of a sexual type is considered a punishable act.'

To date, only brief explanations have been suggested for the function of concealed mating (e.g. a few sentences or a footnote). To the best of my knowledge, the first explanation was proposed in 1930 by Malinowski, who argued that public mating ‘excites jealousy. Hence to make love or to eat in public is to invite rivals to seize that which is being enjoyed’ ([6], p. 179). Half a century later, Symons repeated a similar argument: ‘Ultimately, this [concealed mating] probably is the outcome of reproductive competition. Where food is scarce, and the sight of people eating produces envy in the unfed, eating is often conducted in private. While there are many societies in which everyone has enough to eat, there are no societies in which everyone can copulate with all the partners he or she desires [...] The seeking of privacy for sex probably has been uniformly adaptive and hence is virtually universal among humans’ ([2], p. 67).

Building on this interaction between jealousy and reproductive competition, Friedl posited the costly consequence of reproductive competition: ‘the value of hidden sex [is] to protect [the copulating pair] and the social group from the dangers of jealousy caused by competition [...] for mates, [as] a degree of social harmony is a prerequisite for an individual animal’s reproductive success’ ([3], p. 838). Similarly, van Schaik recently hypothesized that ‘the benefit for the man is that it prevents overt contest competition for access to potentially fertile mates, which would threaten male–male cooperation’ ([11], p. 184).

These explanations share the view that avoiding overt reproductive competition is the main function of concealed mating in humans, while differing in the importance ascribed to cooperation. Malinowski and Symons neglect the importance of cooperation altogether, Friedl invokes the cost of reproductive competition on ‘social harmony’, and van Schaik points out the importance of male–male cooperation. However, if these hypotheses were true, I would expect to find habitual concealment of matings in many other social species. Specifically, I would expect to find concealed matings in our phylogenetically closest living relatives, the social non-human great apes (bonobos *Pan paniscus*, chimpanzees *Pan troglodytes* and mountain gorillas *Gorilla beringei beringei*). In these species, within-group reproductive competition is common (electronic supplementary material, appendix S7), while social cohesion is crucial for between-group competition [20–22] and, at least among chimpanzees, male–male cooperation is vital [22]. Nevertheless, dominant individuals from these species seldom conceal matings from the view of conspecifics (electronic supplementary material, appendix S7; see §4d(iv) and §5 for explanations for occasional concealment in these species).

In conclusion, although the selective pressures proposed by current explanations may have played a role in the evolution of concealed mating, in my opinion, these explanations do not sufficiently explain why habitual concealment evolved in humans but is rarely exhibited in other social great apes. I propose that explaining the currently known taxonomic distribution of concealed mating should be the first touchstone for any hypothesis aiming to explain the function of concealed mating in humans.

4. The cooperation maintenance hypothesis

In this section, I discuss the cooperation maintenance hypothesis (hereafter ‘CMH’). I first review the phenomenon of concealed mating in non-human species, while emphasizing the Arabian babbler (*Turdoides squamiceps*), for which this hypothesis was

originally proposed [23]. Second, I develop a cross-species and cross-cultural account of the hypothesis. Third, I apply the CMH to explain the human case. Fourth, I present predictions to test the CMH across species and human cultures.

(a) Non-human species

In a wide range of species, subordinate animals conceal matings to avoid interference by more dominant group members. Dominant individuals, by contrast, often mate in full view of group members and seldom actively conceal matings (see electronic supplementary material, appendix S7 for review of 34 species and §4d(iv) and §5 for potential explanations). To my knowledge, *habitual* concealment of matings by individuals that are not subject to physical interruption by conspecifics has so far been documented in two species only: humans and Arabian babblers.

Arabian babblers are cooperative breeding birds living in the Middle East [24]. They live in stable, territorial groups (2–22 individuals) that include all combinations of age, sex and kin relations [24]. During days in which the alpha female ovulates, she is mate-guarded by the alpha male, who may use dominance displays when other males interact with her [25]. Consequently, the dominant pair produces 95% of the offspring [26]. Nonetheless, all group members participate in rearing offspring (e.g. transferring them between shelters [27]) and other cooperative interactions [28]. Helpers have therefore a significant effect on offspring survival [29].

Arabian babblers use discreet communication to initiate copulation [25]. Then, pairs sneak away and only mate in locations and/or times in which they are hidden from view of other group members [23]. Subordinate Arabian babblers are likely to conceal their matings since they risk attack if discovered by more dominant group members [23,25]. A subordinate bird, however, would not attack the dominant pair if it happened to interrupt the privacy of mating [23,25]. After presenting evidence against common explanations for inconspicuous matings in non-human species (see §5), Ben Mocha *et al.* [23] proposed that dominant Arabian babblers conceal visual stimuli of mating to (i) avoid triggering extra-pair matings by helpers and (ii) maintain alloparental care (by avoiding conflicts that would increase the probability of helpers challenging the alpha position or dispersing).

(b) The cooperation maintenance hypothesis: cross-species and cross-cultural account

The CMH is based on the following argument:

If:

- (i) Sensory stimuli of mating between conspecifics evokes sexual arousal and trigger mating behaviour in witnesses (hereafter, the sexual arousal premise).
- (ii) X (a male and/or a female) tries to control mating access to his/her partner(s) (hereafter, the mating control premise).
- (iii) X depends on cooperation with group members that he/she prevents from mating with his/her partner(s) (hereafter, the cooperation dependency premise).

Then:

Public mating between X and his/her partner will evoke sexual arousal in group members (males and/or females).

This, in turn, will increase the likelihood that aroused witnesses will attempt to initiate mating with X's partner when possible (the sexual arousal premise). These attempts will violate X's efforts to control mating access to his/her partner (the mating control premise) and will trigger social conflicts that will harm the cooperation between X and his/her group members (the cooperation dependency premise; figure 1).

By contrast, sensory concealment of X's mating with his/her partner will not evoke sexual arousal in group members. Hence, the act of mating will not induce extra-pair mating with X's partner and will not affect X's cooperation with other group members (figure 1). I therefore suggest that concealed mating by individuals whose mating is not subject to physical interruption by conspecifics is a relatively non-costly strategy for avoiding unnecessary sexual arousal in group members (proximate explanation). At the ultimate level, concealed mating allows an individual to maintain two needs that would otherwise conflict: mating control over his/her partner(s) and cooperation with those group members that are prevented from mating with these partner(s).

Thus, the CMH elaborates factors that were previously proposed to select for concealed mating—jealousy [2,6], reproductive competition [2,3,11] and social harmony/male–male cooperation [3,11]—and combines them as necessary premises of a coherent argument. According to the CMH, explanations that rely solely on avoiding reproductive competition [2,6] are not sufficient, since the question of concealed mating is only applied to individuals who do not expect interference from conspecifics (e.g. dominant individuals). In addition, in social systems without cooperation, dominant animals settle conflicts with aggression and often mate in public (e.g. Rocky Mountain bighorn sheep *Ovis Canadensis* [30]). But where competitors also cooperate, aggression may eliminate future cooperation (for ethnographic examples in Yanomamö see [31]). The CMH differs from previous explanations by requiring both a specific form of reproductive competition (i.e. attempting to prevent group members from mating with one's partner) and reliance on cooperation between group members. It thereby highlights the need to manoeuvre between these conflicting motives as the crucial selective pressure.

The CMH further stands up to evolutionary critiques that previous explanations failed to address. Namely, it can explain why dominant individuals of non-human great apes seldom conceal mating: because they rarely monopolize a specific partner (bonobos and chimpanzees use other forms of reproductive competition, e.g. sperm competition [32]; electronic supplementary material, appendix S7) or they do not depend on cooperation with subordinate group members (mountain gorillas; electronic supplementary material, appendix S7)—at least not to the same extent as humans and Arabian babblers (but see §4d(iv)).

(c) Explaining the human case

In the following, I discuss the evidence that supports the three premises of the CMH in humans.

(i) Sensory stimuli of mating between conspecifics evoke sexual arousal and trigger mating behaviour in witnesses

Visual [33] and auditory [34] stimuli of mating activate the reward system in the human brain and trigger mating

behaviour in males and females via mirror neurons. For ethnographic examples, see the Goajiro [35] and Lesu [16].

Knowing that a desired group member has a legitimate mating tie with another person may also trigger jealousy (see the Muria for ethnographic examples [18]). Yet, the sensory stimulus of mating is another powerful trigger of sexual arousal that can be prevented by sensory concealment. The benefits of sensory concealment therefore do not rely on individuals being ignorant of the existence of mating ties between group members.

(ii) X (a male and/or a female) tries to control mating access to his/her partner(s)

Various scholars have claimed that in virtually all cultures, husbands and/or wives try to control mating access to their spouse(s)—at least to a certain degree [1,2,9,36]. Three clarifications should be made regarding this claim. First, mating control should not be confused with monogamy. For instance, a man/woman may marry several wives/husbands and forbid them to have extramarital sex. Second, it has been argued that even in cultures where some extramarital sex is allowed (e.g. in cultures with 'shared paternity'), husbands and/or wives are still entitled to restrict the trysts of their spouse(s) to specific individuals and/or limit extramarital sex to the greatest possible extent [9]. Third, this premise requires an attempt, not a success, to control mating access to X's spouse(s). As adultery is evident across human societies [10], this emphasizes the importance of behavioural strategies to reduce its occurrence.

Although it has been claimed repeatedly that restrictive sexual norms are virtually universal, there is a dearth of supporting evidence (but see [1,9]). Hence, I analysed whether social norms in this study's dataset entitle husbands and/or wives to at least some control over mating access to their spouse(s), or, in contrast, if both spouses are allowed to have unrestricted extramarital sex (see electronic supplementary material, appendix S1 for methodology). I found social norms that entitle mating control over spouse(s) in 100% of cultures for which data were available (survey dataset: $n = 210$; SCCS/EA dataset: $n = 145$; see electronic supplementary material, appendix S8 for full account). Cultures had diverse norms of sexual control; for instance, norms that forbid both spouses to have extramarital sex (e.g. orthodox Jews [37]); cultures where wives are required to stay faithful to their husbands, but husbands are allowed to have extramarital sex (e.g. Malekula [38]); and cultures where husbands and/or wives are allowed to have extramarital sex, but only with specific partners (e.g. Huaorani [39]). I found no culture in which social norms entitle both husbands and wives unrestricted freedom to engage in extramarital sex. These norms suggest that in virtually all human societies, group members are prevented (sometimes or always) from mating with spouses of others.

(iii) X depends on cooperation with group members that he/she prevents from mating with his/her partner(s)

Humans depend on cooperation with group members in various aspects, such as hunting and between-group competition (e.g. [31]). Furthermore, an individual's fitness critically depends on systematic alloparental care from kin and non-kin [40]. For example, the survival of parents and offspring in hunter–gatherers Hiwi (Venezuela) and Ache

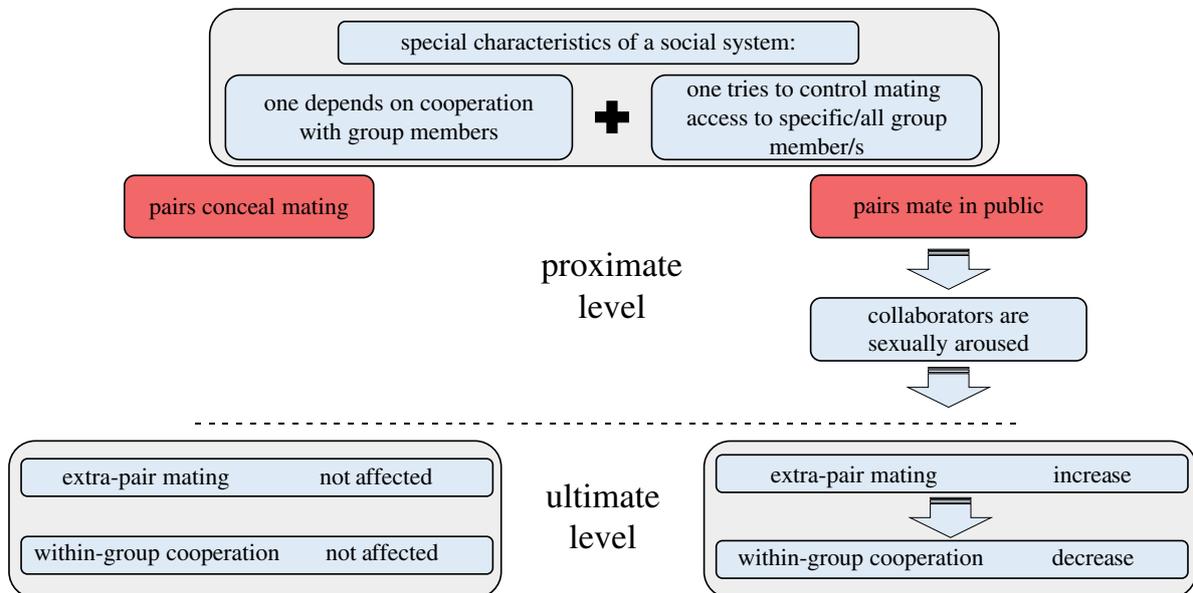


Figure 1. The predicted consequences of concealed and public mating in social systems where an individual tries to control mating access to all or specific partner(s), while also dependent on cooperation with group members that are prevented from mating with his/her partner(s). (Online version in colour.)

(Paraguay) depends on food obtained by young, unrelated males [41]; infants of the Aka people in central Africa are carried by kin and non-kin helpers for roughly 30% of the time [42]. Humans are thus considered a communal, and even cooperatively breeding, species [40].

(iv) Summary

In conclusion, visual and audile stimuli of human mating trigger sexual arousal and sexual behaviour in both male and female observers [33,34]; across cultures, husbands and/or wives attempt to control mating access to their spouse(s) (electronic supplementary material, Appendix S8, [9]); humans live in social systems where fitness crucially depends on cooperation between group members [40,41]. I therefore suggest that the habitual concealment of legitimate mating in humans is a relatively non-costly behavioural strategy to prevent unnecessary sexual arousal in group members (proximate explanation). This simultaneously maintains control over mating access to their spouse(s) as well as cooperation with group members that are prevented from mating with their spouse(s) (ultimate explanations).

(d) Testable predictions

As a post hoc hypothesis, the CMH was developed to explain the currently known taxonomic distribution of concealed mating in humans and non-human species (presence and absence). Its scientific strength thus lies in its ability to generate testable predictions for species with unknown mating behaviours [43]. To this end, I first modify the terms of legitimate mating and mating control to enable a cross-species comparison. Second, I present the principal prediction of the CMH and discuss its applications across species and human cultures.

(i) Cross-species comparative terms

I propose that legitimate mating in humans is comparable to matings between the most dominant individuals in a social group of non-human animals (table 1) since both phenomena raise the same question: why do individuals, whose matings are not subject to physical interruption by conspecifics, conceal

it from the sensory perception of others [23]? This question on concealed mating is therefore only relevant for social species with distinct dominance hierarchies where subordinates are not capable of interfering with the alpha pair's mating (see the social interference hypothesis in §5).

The mating control premise (i.e. X tries to control mating access to his/her partner(s)) often takes different forms in humans and non-human species. In humans, social norms entitle X's complete or partial control over mating access to his/her specific spouse(s). In non-human species, X usually attempts to monopolize mating access across specific/all opposite-sex group member(s) during their ovulation (electronic supplementary material, appendix S7). The important commonality among these various forms is that X's mating control results in the presence of group members who are prevented from mating with partners they may desire.

(ii) Principal prediction

The CMH has three necessary premises: (i) the sexual arousal premise; (ii) the mating control premise; and (iii) the cooperation dependency premise. Its principal prediction is that concealed matings (by legitimate human pairs and dominant animals) will only be found in species that fulfil all three premises and absent in species that do not (figure 2).

Importantly, it is possible to exhibit different degrees of mating control and dependency on cooperation. Thus, a more precise formulation of this principal prediction is that the extent to which dominant individuals try to control mating access to their partner(s) and the extent to which they depend on cooperation with other group members determine the extent to which mating is concealed. Specifically, dominant individuals in social systems that exhibit no/medium/high extent of mating control *and* cooperation dependency is predicted to exhibit no/context-dependent/habitual concealment of matings, respectively (figure 2).

In the following, I discuss these three categories of species and specific predictions for humans. Note that this discussion assumes that the sexual arousal premise is true for social mammals and birds. This assumption is based on research showing

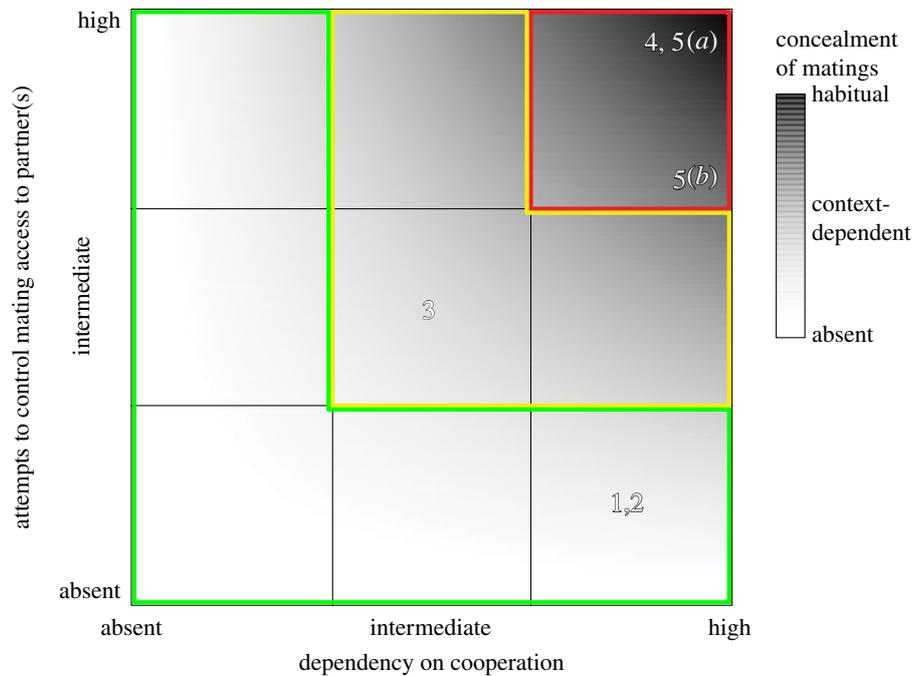


Figure 2. The predicted concealment of matings based on the interaction between attempts to control mating access to partner(s) and dependency on cooperation. Dominant individuals from social systems in the green/yellow/red areas are predicted to not conceal matings/present a context-dependent concealment of matings/conceal matings habitually, respectively. Numbers indicate examples of non-human species and human cultures according to the known extent of mating control, dependency on cooperation and concealment: (1) brown-mantled tamarins; (2) Tasmanian native hens; (3) geladas; (4) Arabian babblers; and (5) humans: (5a) Siwai; (5b) Huaorani.

that mirror neurons trigger sexual arousal in human [33] and non-human [44] primate observers of mating, and that mirror neurons exist in birds [45]. Future research should, nonetheless, examine the overall applicability of this premise in specific non-human species.

(iii) Which species are predicted to not conceal matings or to conceal matings habitually?

The most straightforward way to test the CMH is to contrast species that are predicted to exhibit absence versus habitual concealment of matings. Species that are predicted to not conceal matings are those in which dominant individuals do not fulfil the mating control premise and/or the cooperation dependency premise. For example, although Tasmanian native hens (*Tribonyx mortierii*) and brown-mantled tamarins (*Saguinus fuscicollis*) are cooperative breeding species, males share the matings with the breeding female in the group and copulate with her in view of each other without interference (electronic supplementary material, appendix S7).

By contrast, species in which dominant individuals attempt to achieve strict mating monopolization, while heavily relying on cooperation with group members (e.g. cooperative breeders), are predicted to conceal matings habitually. I suggest that Florida scrub jays (*Aphelocoma coerulescens*), pied babblers (*Turdoides bicolor*), superb starlings (*Lamprolornis superbus*), white-winged choughs (*Corcorax melanorhamphos*), common marmosets (*Callithrix jacchus*), pygmy marmosets (*Cebuella pygmaea*) and meerkats (*Suricata suricatta*) are particularly strong candidates for testing this prediction, as they are cooperative breeding species where within-group matings are strongly skewed in favour of dominant individuals (at least during ovulation). Surprisingly, although habituated and individually marked populations of these species are extensively studied, matings between alpha pairs are very

rarely observed (see electronic supplementary material, appendix S7 for references).

(iv) Which species are predicted to exhibit context-dependent concealment?

In species that fulfil the mating control or the cooperation dependency premises only to a limited extent (e.g. when within-group mating is moderately skewed and/or where the link between cooperation and fitness is weaker compared to cooperative breeders), dominant individuals are predicted to conceal mating only when a greater degree of mating control and/or cooperation is needed (e.g. when trying to completely monopolize an ovulating female or when inter-group conflicts require stronger intra-group cooperation). For instance, geladas (*Theropithecus gelada*) usually form social units where a single male monopolizes several females (i.e. high mating control but no cooperation dependency). Occasionally, subordinate males join a dominant male's unit, help him defend it against other males and consequently sire about 17% of the unit's offspring (i.e. limited extent of mating control and dependency on cooperation [46]). In terms of concealment, a dominant male in these collaborative units is more likely to inhibit his mating calls when the social terms with the subordinate males are unstable versus when they are stable [47] (figure 2).

Abundant data about the extent of mating control and dependency of cooperation are available for many species that belong to this category (electronic supplementary material, appendix S7). Limited data, however, are available on the mating behaviour of dominant individuals and whether concealment may be correlated with a greater need for mating control and/or cooperation. Promising avenues for future research could be chimpanzees, chacma baboons (*Papio ursinus*) and spider monkeys (*Ateles belzebuth chamek*), where dominant males rely on cooperation with other males, occasionally act to

monopolize matings with a female and show variation within and between individuals with regard to the concealment of mating (electronic supplementary material, appendix S7).

(v) Humans

Since humans rely on systematic alloparental care, I speculate that dependency on cooperation is high across cultures. However, the extent of mating control is highly variable across cultures, with some cultures exhibiting relatively mild constraints regarding extramarital sex (see [10] and electronic supplementary material, appendix S8 for examples). I therefore predict that in cultures where extramarital sex is strictly forbidden for at least one of the spouses, matings will be concealed rigorously. By contrast, concealment will be mild in cultures where limited extramarital sex is approved of for both spouses (figure 2). Testing this prediction requires a cross-cultural comparison that is beyond the scope of this review. Nonetheless, the ethnographic surveys in electronic supplementary material, appendices S3 and S8 present several examples supporting this prediction: among the Mbuti and Khoi from Africa, Manchu from Asia, Lesu from Oceania, and the Canela and Huaorani [39] from South America, social norms allow both spouses to engage in extramarital sex with specific partners. In these cultures, spouses are also reported to not insist on rigorous privacy during matings.

5. Alternative hypotheses for non-human species

As different species may conceal mating for different reasons, alternative functions should be investigated for each species. Here, I present four functions that were suggested for inconspicuous mating in non-human species, testable predictions for future studies and evidence against these explanations in Arabian babblers and humans.

(a) The predation hypothesis

Matings may be concealed to avoid predation. High vulnerability during matings may result from the pair's attention being focused on the act (e.g. Richardson's ground squirrels *Spermophilus richardsoni*; electronic supplementary material, appendix S7) or difficulty to separate from the partner (e.g. due to 'copulatory tie' in Canidae [48]). In species that conceal mating to avoid predation, I predict that individuals (i) will mate primarily inside shelters (e.g. burrows, thick vegetation) and (ii) will not conceal the solicitation of mating from conspecifics. These predictions are not fulfilled in Arabian babblers [23], nor humans [1].

(b) The social interference hypothesis

In social systems with no significant dominance differences, dominant and subordinate group members conceal their mating to avoid physical interference from others (see examples for non-human species in electronic supplementary material, appendix S7, with this hypothesis suggested also for humans [6,7,36]). In species where avoiding social interference is the primary function of concealment, I predict that individuals will (i) interrupt others' mating behaviour when possible and (ii) conceal the solicitation of mating from conspecifics. These predictions are not fulfilled in Arabian babblers [23], nor in humans, where pairs often reveal the time and/or location of future matings (79% of cultures in the SCCS/EA sample, $n = 43$; electronic supplementary material,

appendix S11) and group members frequently help pairs to achieve privacy for legitimate mating, rather than interfere with it (for examples, see Albanians, Wogeo and Khoi in electronic supplementary material, appendices S3 and S6).

(c) The mating exclusiveness hypothesis

A male may isolate a female from competitors to achieve an exclusive mating relationship during her fertile period (e.g. Rocky Mountain bighorn sheep; electronic supplementary material, appendix S7). I predict that in species that use this strategy, pairs will be isolated from conspecifics during the majority of the ovulation period (e.g. consortships). This prediction does not hold true for Arabian babblers since mating pairs usually isolate themselves for several minutes only (Y.B.M. 2019, personal observations) [27], nor for humans (since ovulation is concealed from women and men [3]).

(d) The paternity confusion hypothesis

If females conceal all their matings, they control their partners' perspectives about their reproductive share [49]. Females can thus decrease the probability of infanticide by relatively neglected males and/or receive benefits from several males (e.g. parental care). In species that use this strategy, I predict that (i) matings are concealed only from males, not from females (for evidence against this prediction in Arabian babblers see [23]); (ii) matings will not be concealed in family-based groups since there is no competition over paternity; (iii) infanticide will occur occasionally and neglected males will be more prone to infanticide; (iv) neglected males will not provide parental care; and (v) in species that produce litters/clutches with multiple offspring, mixed paternity will occur frequently (for evidence against this prediction in Arabian babblers see [26]).

Note that although the paternity confusion hypothesis and the CMH postulate that concealed mating is used to maintain benefits from group members, they differ with regard to their underlying mechanisms. The paternity confusion hypothesis requires *factual ignorance* by males about their true share in mating, while the CMH emphasizes the prevention of *sexual arousal* in collaborators. Thus, while the paternity confusion hypothesis can explain why women conceal extramarital mating (e.g. to benefit from parental care by lovers and husbands), it does not explain why women conceal sensory stimuli of mating with their husbands (since their extramarital partners are often aware of these legitimate mating ties).

6. Conclusion

- (1) The ethnographic and zoological literature reviewed here provides two constructive conclusions. First, that the concealment of legitimate mating is a widespread human preference. This prevalence emphasizes the importance of also studying the phenomenon from an evolutionary perspective [19]. Second, the current hypotheses on the functions of concealed mating do not sufficiently explain why habitual concealment of matings evolved in humans and Arabian babblers but is absent in other social species.
- (2) I propose two touchstones for any scientific hypothesis on the function of mating concealment in humans. First, it should explain why habitual concealment evolved in humans but is only seldom exhibited by social non-human great apes. Second, it should present testable predictions [43].

- (3) The cooperation maintenance hypothesis postulates that concealed mating in distantly related species, such as humans and Arabian babblers, is a behavioural strategy to prevent sexual arousal in group members (proximate explanation), and that it has evolved by convergent evolution driven by the need to manoeuvre between two conflicting pressures: maintaining mating control over partner(s) while relying on cooperation with group members who are prevented from mating with these partner(s) (ultimate explanations).
- (4) The scientific strength of the cooperation maintenance hypothesis lies in its ability to generate testable predictions. A particular testable prediction is that habitual concealment of matings by dominant individuals will be found in cooperative breeding species with high within-group mating skew.
- (5) As concealed mating may be an overlooked phenomenon in many species, I urge systematic data collection from non-human species, as well as in-depth analyses of ethnographies. Such comparative datasets can be used to test the cooperation maintenance hypothesis and, if disproved, to generate data-driven alternative hypotheses.
- (6) I propose that the importance of research on concealed mating may go far beyond revealing 'sexy' truths about our human species. It may rather provide essential insights regarding the cognitive abilities required for deception, the evolution of cooperation and the strategies employed to maintain it in a competitive world.

Data accessibility. All data reported in this review are available in the electronic supplementary material.

Competing interests. We declare we have no competing interests.

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