Covert Sexual Signaling: Human Flirtation and Implications for Other Social Species

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Abstract: According to signaling theory and a large body of supporting evidence, males across many taxa produce courtship signals that honestly advertise their quality. The cost of producing or performing these signals maintains signal honesty, such that females are typically able to choose the best males by selecting those that produce the loudest, brightest, longest, or otherwise highest-intensity signals, using signal strength as a measure of quality. Set against this background, human flirting behavior, characterized by its frequent subtlety or covertness, is mysterious. Here we propose that the explanation for subtle and ambiguous signals in human courtship lies in socially imposed costs that (a) vary with social context and (b) are amplified by the unusual ways in which language makes all interactions potentially public. Flirting is a class of courtship signaling that conveys the signaler’s intentions and desirability to the intended receiver while minimizing the costs that would accompany an overt courtship attempt. This proposal explains humans’ taxonomically unusual courtship displays and generates a number of novel predictions for both humans and non-human social animals. Individuals who are courting should vary the intensity of their signals to suit the level of risk attached to the particular social configuration, and receivers may assess this flexible matching of signal to context as an indicator of the signaler’s broader behavioral flexibility and social intelligence.

Keywords: communication, courtship, courtship signals, flirtation, honest signaling, sexual selection

Introduction

In species with high female parental investment, because females benefit by choosing mates of high quality, males appear to have been selected to broadcast signals that reliably correlate with—and therefore advertise—their quality. This idea was famously formalized by Grafen’s (1990) mathematical analysis of the evolutionary stability of honest
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According to this analysis, a male should be expected to present the most intense signal that he is able to produce and defend. The cost of emitting these intense signals—energy, increased risk of predation, etc.—is offset by the benefit of being chosen as a mate. Empirical work substantiates these predictions: Across the range of display traits and performances that have been studied in the context of signaling theory and sexual-selection theory, signals communicate maximum quality when expressed to the greatest degree (Cronin, 1993; Searcy and Nowicki, 2005). From the speed of a long-legged fly’s (Dolichopodidae) aerial display (Zimmer, Diestelhorst, and Lunau, 2003), to the amplitude and pitch of an American bison’s (Bison bison) bellow (Wyman, Mooring, McCowan, Penedo, and Hart, 2008), to the duration of a firefly’s (Photinus ignitus) pulse (Lewis and Cratsley, 2008), higher intensity signals improve reproductive chances. In this context, the subset of human courtship signals we know as “flirting” is an anomaly.

Why is Flirting Coy?

Although humans also advertise their quality with intense signals of various kinds (Miller, 2000), archetypal human flirting—the coy glance, the loaded invitation to “grab coffee sometime”—has a covert quality that stands in sharp contrast to non-human animal displays. Human courtship includes a range of behaviors that might correspond to the bison’s bellow—from the eloquent reverence of love poetry to the blunt aggression of catcalling—but few people would say that Cyrano de Bergerac is “flirting” when he declaims below Roxane’s balcony. Instead, flirtation is marked by “mixed signals”: sidelong glances and indirect overtures. The human ethologist Irenäus Eibl-Eibesfeldt, synthesizing decades of comparative study of human social behavior, reported that flirtatious gestures and expressions are cross-culturally consistent. He found that partially obscured actions such as quick looks and coy giggles behind a hand were common elements of flirtation in cultures from pastoral Africa to urban Europe to Polynesia. “Turning toward a person and then turning away,” he wrote, “are typical elements of human flirting behavior” (Eibl-Eibesfeldt, 1971, p. 50). That indirect flirtation is recognizable as its own category of signaling suggests it might require a separate functional explanation. What do courting humans gain by making some courtship signals oblique?

Here we propose that the explanation for the subtlety of human courtship lies in the potential costs imposed by both intended and unintended receivers of courtship signals, either in the form of damage to social capital or of interference and intervention by third parties. This paper proposes a social-cost-based model of human courtship signaling. The model starts with the premise that sexual overtures among humans are inherently risky, with most of the potential costs coming from the social realm. It further proposes that, because the social risks of courtship signaling vary depending on details of the social context, signalers will be most successful when they modify signal intensity in response to the relevant social cues. Whereas the standard model of sexually selected courtship signaling suggests that maximum intensity is always favored, we propose flexibility as an alternative route to reproductive success. Signalers who skillfully assess and adjust to social context (i.e., good flirts) display their quality not through high-intensity displays that index physical prowess and condition, but through sensitive signal-to-context matching that
indicates behavioral flexibility and social intelligence.

**What are the Costs of Human Courtship Signals?**

Animal-communication theorists divide the costs of courtship signaling into two categories that apply broadly to human and non-human courtship: “receiver-independent” costs of signal production (Vehrencamp, 2000) and costs of performance externally imposed by intended or unintended receivers once the signal has been transmitted (Searcy and Nowicki, 2005). Total signaling cost can be distributed evenly or unevenly across these categories; a widowbird’s (*Euplectes progne*) elaborate tail involves an energetic investment in building and displaying a large and heavy structure, the weight and visibility of which can also expose the bird to increased risk of predation (Andersson, 1994).

Human verbal or gestural courtship signals are energetically inexpensive to produce. However, the socially imposed performance costs that attend human courtship can be high. Both within the signaler-receiver dyad and in the larger social network, initiating courtship involves risks that vary widely in scale and scope. Jealous mates and rivals can impose physical costs ranging from a shove to serious injury or death. The costs to reputation and social capital can be as minor as a small demotion in the receiver’s esteem, or as large as the complete loss of benefits that the signaler derived from his relationship to the receiver or to a potentially vast network of others who may disapprove of—or actively oppose—a particular courtship attempt.

*Second-party costs of performance*

Within the bounds of a dyadic exchange, courtship signaling can alter the relationship between signaler and receiver to produce an array of deleterious effects, depending on the nature of that relationship and how robustly it responds to the introduction of a sexual element.

Studies of opposite-sex friendship dyads have found that when one member expresses romantic desire for the other, a corresponding increase in “relationship uncertainty” can destabilize the friendship (Guerrero and Chavez, 2005; Weger and Emmett, 2009). This loss of stability represents a potentially sizable cost, insofar as friends represent important exchange partners and allies (Bleske and Buss, 2000; DeScioli and

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1 It is tempting to think of embarrassment itself as a low-end cost. Research reviewed by Baumeister and Leary (1995) describes a host of emotional, social, and mental-and-physical health costs that follow from social rejection, ranging from immediate anxiety to longer-term depression. However, the emotional reaction to rejection is probably best considered as a proximate mechanism designed to recalibrate oneself to the social world. Recent work in cognitive science has shown that social rejection triggers the same “neural alarm system” in the anterior cingulated cortex that is responsible for processing physical pain (Eisenberger and Lieberman, 2004; Eisenberger, Lieberman, and Williams, 2003). That social rejection causes emotional or even physical pain is analogous to the way that starvation causes intense hunger pangs: Both sensations are there to help individuals avoid conditions that directly reduce fitness. In human courtship, such risks to fitness accrue primarily in the social realm.
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Kurzban, 2009; Holt-Lunstad, Uchino, Smith, and Hicks, 2007; House, Landis, and Umberson, 1988; Lewis et al., 2011).

Even if a courtship attempt does not dissolve a standing relationship, it can produce losses in social capital by changing the dominance relations between signaler and receiver. This is starkly apparent in cases where flirtation is seen as a moral, social, or professional violation, such as between teacher and student, old and young, boss and employee, or members of different social classes. Individuals on both ends of these power spectra who initiate a sexual negotiation can risk a loss of status (comprising elements of prestige and dominance) and associated deference (Henrich and Gil-White, 2001), or some degree of moral punishment (as discussed in, e.g., Kurzban, DeScioli, and O’Brien, 2007). An individual who initiates courtship risks such losses even if the target is amenable, because acceptance can mean a sexual or romantic realignment that equalizes two people who previously held distinctly different places in their shared hierarchy. A professor who propositions a student empowers that student to expect preferential academic treatment; a poor acquaintance who accepts a wealthy admirer’s advances can demand entry to his social circles.

Third-party costs of performance

Third parties constitute an additional source of potential courtship costs. Theories of the evolution of signaling behavior, based primarily on animal communication, divide third-party costs into two categories. “Interception” occurs when a third party detects a signal and procures some information from it, as when a predator uses a prey animal’s mating call to locate the caller (e.g., the location of Túngara frogs, *Engystomops pustulosus* by fringe-lipped bats, described in Searcy and Nowicki, 2005, p. 182). “Eavesdropping” occurs when third parties gather information about participants from an interaction between a signaler and an intended receiver (McGregor, 1993; Searcy and Nowicki, 2005). For instance, a territorial dispute between two males could have consequences for the participants’ future interactions if listening females alter their assessments of the participants’ attractiveness or if male witnesses recalculate their relative dominance ranks (Bergman, Beehner, Cheney, and Seyfarth, 2003; McGregor, 1993; Searcy and Nowicki, 2005). The capacity and tendency for third parties within a shared “communication network” (McGregor, 1993) to apprehend and use social information captured from interception and eavesdropping has been found in a wide range of species. Fish (Johnsson and Åkerman, 1998; Oliveira, McGregor, and Latruffe, 1998), songbirds (Mennill and Ratcliffe, 2004; Naguib, Fichtel, and Todt, 1999), and baboons (Cheney and Seyfarth, 1999), among others, have been shown to eavesdrop on competitive interactions and adjust their own competitive behavior towards participants depending on the outcomes of those interactions. A particularly relevant form of this type of behavior is mate-choice copying: Females of many species increase their interest in pairing with a male when they observe him successfully courting other females (e.g., Galef and White, 2000; White and Galef, 1999).

Among courting humans, the most straightforward interception costs involve physical violence related to jealousy: Courting someone who already has a partner or admirer can bring swift and direct consequences if one is observed by that rival (or the
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rival’s allies). Jealousy is cross-culturally common, if not universal. For men, evidence from psychology and anthropology suggests that the detection of or even suspicion of another man’s attempt at sexual access to one’s partner is often met with extreme anger and even lethal violence (Buss, 2000). For instance, a study of conflict in Irish and American bars found that “conflict over the opposite sex” was one of the top three catalysts of physical violence (Felson, Baccaglini, and Gmelch, 1986). Whereas jealousy among women less frequently leads to physical violence, it can nonetheless be an important consideration because physical violence is not the only means by which heavy costs can be imposed on a potential interloper (Hess and Hagen, 2006; see Sagarin et al., 2012, for a recent review of sex differences in this area).

Indeed, physical violence is only a small subset of the total costs that third parties can impose. Eavesdroppers may respond to courtship signals in ways that threaten all of the same types of social resources at risk in dyadic courtship interactions, but on a larger scale: threats to valuable relationships; to moral, legal, or professional status; or to other forms of social capital. There is also evidence that humans engage in mate-choice copying (Miller and Todd, 1998; Waynforth, 2007). For instance, Jones, DeBruine, Little, Burriss, and Feinberg (2007) found that women showed a preference for a man’s face when other women’s faces were facing the man with positive (as opposed to neutral) expressions. To the extent that observers are using information about others’ mate choices in making their own decisions, being known to have failed at one courtship attempt might lower thecourter’s chances for future success.

The unique implications of language for the costliness of human courtship signaling

For animal signalers, the pool of potential eavesdroppers or interceptors is limited to other creatures that happen to perceive the original exchange of signals. This may diminish the relative selective influence of third-party costs (vs. those imposed by intended receivers) on the form of animal courtship signals. Among humans, however, the performance costs that third parties can impose on courtship signaling are omnipresent. The property that the linguist C.F. Hockett (1960) called “displacement” —language’s capacity to free information from the constraints of time and space—extends the reach of an exchange between two people to include all other members of each participant’s social sphere. Language allows the information contained in a signal or conversation to travel indefinitely. This property underlies the old observation (Goffman, 1959) that humans always compose their behavior for an unseen public. Perhaps especially in a flirtatious conversation, where a new relationship between signaler and receiver may be emerging, the speaker has no guarantee that his comments won’t be communicated to others later on. Information about a courtship attempt can spread rapidly and broadly (Christakis and Fowler, 2010).

Because language substantially weakens the boundary between “private” (dyadic/second-party) and “public” (third-party) spheres of communication, we can assume that the design of human courtship signals has been shaped by the full range of socially imposed pressures.
Social Variability Calls for Variable Signaling

Even if third-party costs shadow all human courtship signaling, not all courtship attempts are equally risky. Different degrees of risk will attend a given courtship signal depending on the second- and third-party context surrounding that courtship attempt. Consequently, courtiers have to decide not only whether to send a courtship signal, but also how strong a signal to send. Figure 1 illustrates the distribution of risk for a given courtship signal, which will vary within two basic dimensions: the expected value of the benefits of signaling (the size of the benefit times the chance of success) and the expected value of the costs (the size of these costs and the chance they will be imposed).

**Figure 1.** Socially imposed risk in courtship signaling

Movement along the benefit axis reflects both the mate value of the target and the probability that (s)he will be receptive to courtship, ranging from a weakly desirable, likely uninterested receiver to a highly valued and seemingly receptive one. Movement on the cost axis reflects the range of possible social penalties that could be imposed by either the target or third parties, ranging from minor, transient damage to one’s reputation or physical wellbeing at the low end, to significant and lasting loss of status or relationship benefits, serious physical harm, or a wide-ranging reduction in one’s perceived desirability as a mate. The chance of these costs being imposed depends on factors such as the nature of the preexisting relationship between the signaler and the target and the characteristics of third parties that are either physically present or likely to hear about the signaling event. Third parties may be more or less interested or able to impose costs. They may, for example, be friends or enemies, large or small in size or number, and relatively powerful or powerless in the signaler’s social or professional milieu.

The total predicted risk for sending a courtship signal represents the yoked...
relationship between the magnitude and likelihood of the possible benefits, and the magnitude and likelihood of the possible costs. For example, consider the case of a teacher who contemplates propositioning a student, illustrated very basically (we will build on this figure later in the paper) in Figure 1. If the student has previously indicated some degree of sexual interest in the teacher, and the teacher perceives the student as exceptionally attractive in some way, the teacher may believe the probability and desirability of successful courtship are high (marked as “A” in Figure 1). However, members of the teacher’s wider social network are unlikely to respond favorably if they learn that he has made an advance on a student, and the penalties that could be assigned in that larger context are significant. He may also suspect that students are unlikely to vigilantly protect the reputations of their superannuated suitors, and linguistic displacement means that once he makes an advance, the teacher will have to contend with the possibility of public exposure even years after the student graduates and moves on in life. So the teacher ought to assess his total risk as something closer to “A1.”

A Model of Courtship Signaling In Response to Socially Imposed Costs

Context-dependent variation in the risks that attend sexual signaling presents humans with an adaptive problem: how to indicate sexual interest (with the obvious attendant potential benefits) while avoiding the social costs of courtship – a problem made especially thorny by the complexity of human social systems and the language-enabled ubiquity of eavesdropping. One solution would be to produce a signal that is overt enough to open a sexual negotiation with a receptive target, but covert enough to minimize the likelihood of detection or penalties from unsympathetic receivers or in situations with inherently high social risks. Figure 2 illustrates the proposed inverse-correlational relationship between the potential costliness of making a courtship attempt in a given set of circumstances (on the x-axis) and the overtness of the ideal courtship signal (on the y-axis).

We propose that skilled sexual signaling (represented by the descending bisecting line), and especially flirting, solves the human courtship-signaling problem by flexibly adjusting signal intensity to suit the social context.

We can anchor the line with examples, at its low and high ends, of courtship signals that are not flirtation. In the upper left quadrant of the signaling space, the risk of social penalties for signaling about sex is extremely low, and signals can be correspondingly direct, as in sexual signals exchanged between members of an established couple where one partner’s sexual access to the other is uncontested (“I’m about to put the baby down for a nap, so we’ve got half-an-hour to ourselves. Let’s have sex.”). This is proficient signaling about mating, but it is not flirting. In the lower right corner, where courtship signaling is highly inappropriate and consequently suppressed, are very covert signals, such as a brief glance between two people who are married, but not to one another. The act may carry information about sexual interest and perhaps intent, but it is too small and subtle to be called flirtation.
On the line, and in the center of the plot, where a signaler wants to woo a receiver but is cognizant of the risks, there will be flirting: a wink across a crowded bar, an invitation to coffee that seems more-than-casual, or a “joke” about finding a coworker attractive.

The human social environment is complex and fluid, and different social configurations will demand different levels of signaling from the same individual. An attractive young man might flirt brazenly with a comparably attractive woman, somewhat less so if he’s a waiter and she is his wealthy customer, significantly less so if she’s dining with her rich husband.

The question remains, however: How do ambiguous signals confer an advantage on the flirt? For an answer, we can draw on theoretical work in linguistics, social psychology, and human decision-making.

**Indirect Signaling Mitigates Social Costs via Plausible Deniability**

What is the property of indirect (or “coy” or “ambiguous”) courtship signaling that makes it adaptive within the circumstances described above? Both the second- and third-party costs attending courtship present a common problem to would-be signalers: how to signal one’s sexual interest while minimizing exposure to socially imposed costs. Within a signaler-receiver dyad this could mean opening the question of a sexual relationship while minimizing risk to the stability of the existing relationship and its attendant benefits; within a social network, it would mean signaling sexual interest to one’s intended target without attracting third-party attention where such attention could bring physical, moral, professional, or other penalties.
A potential solution lies in “implicature” (Grice, 1975), a type of speech act that contains more meaning (via implication) than what is strictly present in the words used. The key quality of Gricean implicature—for the flirt—is that it allows speakers to claim two distinct meanings at once: the surface meaning as well as the implied one. For example, the question, “Do you want to grab coffee sometime?” can be both an innocent invitation to drink coffee and a sexual overture. The mechanics of implicature place some of the burden of assigning meaning onto the receiver; this shift in responsibility, and the ambiguity of multi-meaning utterances, allows speakers to maneuver around the risks that attend certain utterances in certain social spaces.

Grice proposed that indirect statements succeed in getting implied meanings across because of the ritualized way that they appear to violate a general “cooperative principle” of conversation—essentially that conversation partners will reliably do their best to make themselves understood, by confining their speech to utterances that are pertinent to the subject at hand and comprehensible to the listener. Speakers fulfill this mandate to communicate cooperatively by adhering to four “maxims”: Under the maxim of Quantity, speakers will make their contributions neither more nor less informative than required. Under Quality, they will be truthful. Under Relation, speakers will simply “be relevant.” Under Manner, they will be as brief, orderly, and clear as possible.

Grice’s principle and its maxims not only describe how speakers are able to communicate clearly and directly, but also how listeners are able to interpret utterances that seem unclear or indirect (cf Sperber and Wilson, 1986). If a comment seems on its face to violate the maxims—to be irrelevant, or overly detailed, or blatantly untrue—the listener can look for an implied meaning that would bring the comment back into alignment with cooperative conversation. If Jane asks her father, “What do you think of the new guy I’m dating?” and her father answers, “He’s got great hair,” Jane can infer his overall opinion is not favorable. By violating the Gricean imperative to answer Jane’s question in a relevant and informative way, her father has cued Jane to infer the implicature behind his words.

Pinker, Nowak, and Lee (2008) proposed a game-theoretic model of indirect speech to explain how implicature alters the cost-benefit landscape for many classes of risk-laden exchanges. They offer the example of a motorist stopped for speeding. In a world without Gricean indirect speech, the driver would face a certain cost (the price of a ticket) and the choice to either accept that cost or gamble on the chance that the officer is dishonest and offer a bribe: “If you let me go without a ticket, I’ll pay you $50.” If he gambles in this implicature-free reality, the outcome would rest entirely on the probability that the cop happens to be dishonest. The worst-case cost—arrest and prosecution by an honest cop—is prohibitively high, and only a desperate gambler would take on such risk to avoid a $50 fine.

However, in a Gricean world with indirect speech, the driver can change the costs and payoffs for this matrix by asking, “Is there some way we can settle this here, officer?” In this case, his question has the quality of plausible deniability. Most reasonable listeners would conclude confidently that this wording contains the same offer as the direct one, but the possibility that the driver’s surface meaning was genuine leaves room for the claim that he was merely making an innocent inquiry. Though the driver’s true intentions are identical in either phrasing, the indirect formulation is a vastly better signal because, Pinker
proposes, honest and dishonest cops will have different thresholds for deciding to act on the implicit meaning based on the distinct sets of costs and payoffs that each of these receivers brings to the exchange. For the dishonest cop looking to make a bit of extra money, that threshold is likely to be comparatively low. She can send back her own indirect signal—“What do you suggest?”—and begin assessing the chances of a bribe with little chance of penalty (as the chances that this is a sting are low) and a likely $50 payoff. The honest cop’s threshold for choosing the implied meaning is higher, because the costs of escalating a routine traffic stop into an arrest and prosecution are high, especially given that the driver will undoubtedly fall back on plausible deniability in his claim of innocence. The indirect overture exploits the space between these two decision thresholds with a signal that is overt enough to meet the corrupt officer’s lower criterion for negotiating a bribe, yet covert enough to fall below the honest one’s criteria for initiating an arrest—a proposition that Lee and Pinker (2010) went on to support experimentally.

The proposal that unreceptive and hostile receivers will have higher thresholds for initiating conflict than receptive and friendly ones will have for negotiating cooperation matches a central tenet of evolutionary game theory as it deals with the escalation of animal-signaling contests. Symbolic competitive exchanges, as in the classic example of the parallel walk and belling contests of male red deer (Clutton-Brock and Albon, 1979; Clutton-Brock, Albon, Gibson, and Guinness, 1979), allow individuals to assess one another without having to incur the costs of physical combat. In the case of conspecifics seeking to determine dominance, the risks associated with more direct action come from the participants themselves, whereas the potential costs to the driver and cop would come from third parties. But the basic situation is the same. Hostile receivers such as honest cops and jealous boyfriends typically incur costs when they arrest motorists or start fights, respectively, so the choice to postpone a decision that demands escalating conflict will often be favorable up to a point. Even a sympathetic but unreceptive receiver—the friend who wants to stay just friends—will similarly endure higher costs if she decides to interpret an ambiguous overture as a sexual advance (as in the destabilization of mutually beneficial relationships discussed above). So receptive and unreceptive receivers of sexual overtures should provide a similar “sweet spot” for a well-placed indirect signal (Lee and Pinker, 2010).

However, it is not obvious that the decision thresholds of receptive and unreceptive targets should always fall out this way, with receptive receivers setting the lower bound and hostile ones setting the upper bound of the optimal-signaling space. If that target space were static, any moderate-strength signal would solve the problem. Adept courtship would be the equivalent of speaking in a soft voice when you know that your friend has sharp hearing and your enemy is a little deaf. In reality, however, some promising receivers may need more overt coaxing; some hostile ones may be quicker to infer sexual content.

Implicature addresses the problem of the moving target by splitting communicated meanings into two parts. Some informational content is in the signal itself and some is derived from knowledge shared between signaler and receiver. The same signal can therefore communicate two different meanings, either (a) simultaneously, to two different receivers who share different amounts of background knowledge with the signaler, or (b) over the course of a multi-step interaction, as the shared knowledge between receiver and
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signaler changes. A man who asks his coworker to coffee in front of the boss can trust that his target will perceive the flirtatious intent (and the boss will miss it) if they stood unusually close to one another in the elevator earlier. A man who wants to court a woman with a possessively jealous boyfriend might begin with a very subtle signal, such as prolonged eye-contact. The shared knowledge that her boyfriend has a low decision threshold for ascribing sexual intent would boost the communicative power of the signal; any direct attention under threat of hostility suggests special interest.

Implicature can even allow for one meaning to be conveyed to only a single individual when a signal is completely public. A newspaper article or blog post might contain a set of key words or phrases that have a particular meaning to a target, while seeming innocuous to every other reader. By carefully choosing words that are meaningful to exactly one other person—perhaps because of a unique and shared experience with the author—writers can pack their prose with meaning that only the intended reader will decode. In this way, secret courtship signals can safely be sent to a prospective mate even when the potentially jealous boyfriend (husband, fiancé, etc.) might well have access to the article or post.

So flirtation offers an adaptive signaling repertoire for risky courtship. Yet flirting occurs even in contexts where the immediate risks of signaling seem to be trivially low. One reason for this, discussed above, is the potential for gossip to transfer knowledge of a courtship attempt beyond the context where it was initially performed. In the next section we discuss another explanation.

Adept Flirtation Can Be a Quality Signal

So far, we have focused on the idea that socially imposed costs are sufficient to exert selective pressure on human courtship. But if flirtation fulfills Grafen’s basic requirements for an honest biological signal, it ought to respond both to the constraints imposed by costs and to the signaler’s need to be perceived as high quality. How might an adept performance of flirtatious signals enhance a receiver’s perception of the signaler’s value as a mate?

The ethological study of display (usually male) and choice (usually female) as they function in sexual selection has tended to focus on male ornaments and the selective processes that lead those ornaments to ever larger and more elaborate forms (Andersson, 1994). However, the skill and vigor with which males display can also demonstrate quality, providing evidence for the strength of multiple genetic and condition-dependent traits. Byers and colleagues (Byers, Hebets, and Podos, 2010) have suggested that the critical role of this “performance” dimension has been under-weighted in studies of courtship signaling. While vigor may largely attest to physical condition, skill can be a measure of cognitive ability (2010). Human signalers, whose fitness is linked to social intelligence, might need to advertise their quality in terms of cognitive and behavioral traits that facilitate success in the social environment.

Many display behaviors demonstrate quality because their basic components are intrinsically challenging physical acts (e.g., running, jumping, flying). The same follows for displays of cognitive fitness: In the case of birdsong, experimental work has shown that
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the highly precise singers that females prefer can be those whose juvenile neurocognitive development was healthiest (Nowicki, Peters, and Podos, 1998; Nowicki, Searcy, and Peters, 2002a,b). Indirect speech offers a similar performance opportunity. There is some evidence from neuropsychology and psycholinguistics that simply producing or interpreting implicature is challenging cognitive work (discussed in Shetreet, Chierchia, and Gaab, 2013). Moreover, the complexity—and consequent showiness—of implicature is clear in its essential structure. Whereas direct speech merely reports informational content, implicature manipulates meaning by playing that content off of the implicit knowledge shared between speaker and audience.

General intelligence is not the only quality one can demonstrate through indirect speech. Signaling subtly in appropriate situations can convey the signaler’s social awareness and adeptness, his cognizance of the potential costs attached to the sort of transaction he is proposing, his ability to skillfully reduce those costs, and, therefore, his worthiness as a partner. A discretely offered bribe not only opens a negotiation but shows that the aspiring briber knows how to avoid attracting attention. By the same token, the suitor who subtly approaches a woman with a jealous boyfriend does more than simply protect himself from physical assault. He shows his sensitivity to his target’s circumstances. If she is looking for an alternative partner, the subtle signaler may simultaneously broadcast both his basic sexual interest and the qualities that make him a superior option as a mate. A slightly more transparent sexual signal might be optimal if the suitor wants to convey not only that he has the social intelligence to be moderately subtle, but also the implicit physical confidence to take on the risk of a fight with the boyfriend. Of course, a completely overt signal (one we would not call flirting) would do the most to demonstrate that quality of fearlessness. This might be a winning strategy at times, but only in cases where the target female was assessing mate quality only on the basis of physical prowess.

If skilled flirtation signals quality, then there is a third feature of our model: signal-to-context matching. Figure 3 illustrates the augmented model, which fills in the remaining quadrants of the signaling space with courtship signals that are marked by poor matching and consequent indication of poor quality. In the upper right is the highly overt, socially inappropriate signaling that we call boorishness (e.g., making crude advances to a friend’s partner). Another sort of bad match, found in the lower left of the plot, is signaling weakly when the risks attached to a sexual advance are quite low, as in the shy mumbling of a high-schooler who knows his current companion is interested in him but still can’t manage to make a move. The zone of flirtation is now bounded on four sides. Skilled courtship signaling (again, the bisecting line) moves out of this zone when the costs are low enough to allow complete overtness or high enough to demand complete covertness; unskilled signaling is orthogonal to the line in the direction of inappropriate bluntness or shy obliqueness.

Human social contexts encompass multiple hierarchies at once. For example, we assess our dominance rank on multiple scales – a lowly waiter might feel empowered to flirt more openly with a rich customer’s wife if he were younger, taller and better looking than the husband (cf Sell, Tooby, and Cosmides, 2009). Calibrating one’s signal-intensity to the right pitch of flirtatiousness may require a blend of social awareness, behavioral
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flexibility, and precision analogous to the skillfulness that Byers et al. (2010) describe for more corporeal displays.

Indeed, being a “good flirt” is attractive above and beyond other personal traits that contribute to one’s desirability (Miller, 2000). As with other displays of cognitive ability that influence an individual’s perceived attractiveness, such as creativity (Haselton and Miller, 2006) and humor (Bressler and Balshine, 2006), flirtation’s strange ornateness is less puzzling when we consider that displays of superior social intelligence can confer a reproductive advantage on the performer.

Figure 3. Cost-overtness matching in courtship signals

Implications for Animal Behavior

This model is potentially applicable to courtship signaling in any system where signalers face performance costs imposed by members of their own social groups. Our model suggests covert signaling can arise wherever there is social risk attached to courtship and individuals can adjust their signal intensity. However, animal behaviorists and behavioral ecologists have so far devoted comparatively little attention to the possible role of flexible signaling in promiscuous reproduction.

As evidence has mounted that covert promiscuity plays an important role across a range of overtly polygynous, polyandrous, and monogamous mating systems (Alberts, Watts, and Altmann, 2003; Westneat, Sherman, and Morton, 1990; Worthington Wilmer, Allen, Pomeroy, Twiss, and Amos, 1999), ethologists have increasingly focused on the topic of “alternative reproductive strategies.” Most of this research deals with pathways to reproductive success that span entire life histories or stages, as in the scholarship on frequency-dependent “sneaky” body morphs (among, e.g., fish: Taborsky, 2008; reptiles: Evolutionary Psychology – ISSN 1474-7049 – Volume 12(3). 2014.
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Calsbeek and Sinervo, 2008; and birds: Kruger, 2008) or behaviors like helping-at-the-nest that let individuals whose age or status constrains their reproductive access make “the best of a bad job” (per Dawkins, 1980). Even among primatologists, research has focused on umbrella strategies such as “territorial” vs. “nomadic” approaches to seeking mates (Setchell, 2008), while descriptions of strategic responses to particular social moments are rare (but see Crockford, Wittig, Seyfarth, and Cheney, 2007). As such there is little in the animal literature that deals with flexible courtship signaling behaviors that might parallel human flirtation (but see Patricelli, Coleman, and Borgia, 2006). The most common account of how surreptitious matings proceed is that they happen when no one else is around (Davies, Hartley, Hatchwell, and Langmore, 1996; Dickinson, Kraaijeveld, and Smit-Kraaijeveld, 2000; Hayakawa, 2007; Oliveira, Taborsky, and Brockmann, 2008). However, for animals that live in dense and well-connected social groups, if courtship is a critical part of the mating process, then it follows that surreptitious signaling might sometimes precede covert mating.

Anecdotal accounts of covert signaling do exist. Dickinson (1997) noted a previously undiscovered and cryptic “tch-tch” call given by intruder male Western bluebirds into the territories of mated pairs; the call appeared to be designed only to be heard from nearby and preceded the intruders’ attempts to solicit extrapair copulations with the resident female when the male was not present. Dickinson pointed out that the sound was soft enough to be nearly undetectable to mate-guarding bluebird males and researchers alike. Hayakawa’s (2007) 4-year study of mating patterns in Japanese macaques documented that females moved to the periphery of the group when pursuing copulations with low-ranking or non-troop males; Hayakawa noted that “before moving, the female sometimes glanced at the male, raising her tail and soliciting him to copulate” (2007, p. 89). Carosi and Visalberghi (2002) and Lynch Alfaro (2005) have documented similar “furtive visual signaling” in the proceptive behavior of female capuchin monkeys.

A recent experiment with brown-headed cowbirds (Molothrus ater) offers evidence that at least one non-human animal responds to changes in competitive mating pressure by adjusting the overtness of its courtship signal. Gersick and White (2014) found that male cowbirds can perform more attractive and less attractive versions of the same courtship songs (as measured by “potency”: a song’s capacity to elicit copulation-solicitation displays from females in separate playback experiments). The males produced less attractive songs when they could hear other males singing nearby but could see only a lone female target; they sang the more attractive versions when they could see an adjacent male competitor. The behavior makes sense in light of a prior finding that male cowbirds are selectively drawn to investigate high-quality male song (Snyder-Mackler and White, 2011). In the context of cowbird breeding flocks, singing a just-good-enough song to a lone female might be an adaptive strategy for courting without attracting other males to the scene; conversely, direct competition might require a male to offer his best possible courtship signal to the evaluating female.

The generalizability of this finding is unclear, but, as Dickinson (1997) pointed out in reference to the bluebird’s “tch-tch,” covert signals might be rare or merely rarely observed. Across many species, the lack of evidence for subtle courtship signaling might be due to methodological constraints. The model proposed here suggests that if researchers
focus on capturing and quantifying the signals that support surreptitious mating, a whole new class of alternative mating strategies may be identified in species whose primary mating systems have already been documented.

Predictions of the Model

The present model explains three principal features of human courtship signaling: the variable subtlety of flirtatious signals, the influence of social context on the perceived attractiveness of those signals, and the discrete value that “being a good flirt” can add to a signaler’s total perceived desirability. Other models of courtship (e.g., of courtship as a trust-building ritual: Bergstrom, Kerr, and Lachmann, 2008; sexual strategies theory: Buss and Schmitt, 1993; stage and filter models of courtship: Cate and Lloyd, 1992; or script theory: Laner and Ventrone, 2000) do not transparently explain these phenomena. In particular, the present model makes the following predictions:

Signalers will adjust the overtness of their sexual overtures in response to changes in the social context.

- Within-individual differences in signal intensity (overtness) should correlate with between-context differences in the social risks attached to a courtship attempt. Contextual parameters such as the presence of rivals, the potential for an advance to be considered inappropriate, or the higher social status of the receiver should typically induce signalers to be flirtatious rather than overt.
- Signaling will be direct (and not flirtatious) in contexts in which social risks are extremely low, and most indirect (and also not flirtatious) in contexts where social risks are extremely high.
- Individuals who are more socially skilled or experienced in general should be more adept at varying their courtship approaches to match varying social contexts.

 Receivers’ assessments of particular signals will not be static, and their assessments of signalers will take into account the adeptness with which they flirt:

- Receivers will judge the appeal of flirtatious signals on how well those signals match particular social scenarios.
- Receivers should perceive “good flirting,” characterized by a balance between daring and subtlety, as an attractive trait in itself, distinct from other traits that determine attractiveness (e.g., physical appearance).

 Receivers who judge a particular signaler to be a “good flirt” will correspondingly increase their assessment of the signaler’s overall social intelligence.

- Receivers should take “good flirting,” as defined above, as evidence that the signaler possesses broader underlying intelligence.
- Receivers may also be expected to treat a signaler’s strong or weak performance as a flirt as predicting his likely abilities in other areas of performance that index the same underlying cognitive skill set, such as humor or creativity.
Testing these hypotheses experimentally, particularly the critical prediction that the same signaler should vary his overtness by the level of risk in a given context, requires a method for measuring and controlling social risk with reasonable confidence. Even in imaginary scenarios such as experimental vignettes, the same set of social circumstances might be read as intimidating to some and comfortable to others. Differences in areas such as individuals’ self-assessments, their real-world reproductive status (single, married, etc.) or their ability to respond to simulated social “risk” in naturalistic ways will present serious experimental challenges. Nevertheless, within-subject study designs and careful manipulation of a small number of contextual variables might be sufficient. The prediction that the same signal will be perceived as more or less attractive by receivers depending on the context may also be tractable.

Finally, we are agnostic on the important question of whether sexual dimorphism should be expected in this behavior. Both male and female humans exercise some amount of mate choice, and female proceptive signals play a comparable role to male display in courtship. In such cases², sexual dimorphism in signaling behaviors might be subtler or more complex than in the sorts of classic sexually selected ornaments that are the exclusive province of one sex or another. Rather than predicting how such dimorphism ought to manifest in flirtation, we hope that the model proposed here offers a useful framework for considering the parameters that might differ for male and female signalers, and the corresponding phenotypic variance one might expect in male and female flirtation.

Conclusion

Starting with the observation that the coyness of human flirting seems to be an outlier among courtship signals, this paper proposes a model for flexible courtship signaling that might be applicable beyond the sphere of human flirtation. Animals living in complex social groups will constantly encounter changes in social context that create variation in the potential costs attached to courtship attempts. We should look for correspondingly variable courtship behavior wherever individuals attempt to mitigate those costs. For many social species, we can expect to find surreptitious signaling where individuals seek mating opportunities that subvert the reproductive control of pair-mates and dominants. Among humans, the class of indirect signals that we perceive as flirtatious might be pervasive because the potential for social risk around courtship is itself pervasive, even when that courtship is not directly opposed by a particular rival. Subtle flirtation may also be a quality signal, indicating the signaler’s social awareness and behavioral flexibility. Regardless of the level of risk surrounding any particular courtship attempt, these qualities are desirable because they mediate fitness in complex human societies.

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² Other examples include capuchin monkeys of the *Sapajus* genus (Lynch Alfaro, Silva and Rylands, 2012).
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