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Multiple cues in mate selection: The sexual interference hypothesis

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Abstract   Animals use multiple cues when choosing mates, but it is not yet clear why a single signal would not suffice. In this paper, drawing support from predation and ''noise'' effects on mate choice, marketing economics, and multiple signals models, a new hypothesis explaining multiple sexual signals is proposed: the sexual interference hypothesis. The hypothesis is based on three well-supported premises: (1) selectivity decreases when mate assessment costs increase, (2) assessment costs increase when the propagation or reception of sexual signals is more difficult, and (3) males not only exploit such circumstances by courting females when choice is more difficult, but actively interfere with females' preferences by making choice more difficult. The hypothesis argues that additional sexual signals evolve as a way for males to hinder female mate choice by interfering with the propagation and reception of other males' sexual signals. Females respond by evolving the ability to glean meaningful information from signals despite males' attempts at obfuscation. In turn, males respond by producing better interference signals and signals that are not so easily blocked. This co-evolutionary process increases the costs of assessment for females and the costs of signal production for males, and leads to a temporary equilibrium of honest advertising via multiple signals.
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Darwin [1] recognised that females use several cues when choosing mates, but hypotheses addressing why selection would favour multiple over single signals were not forthcoming until the late 20th century. There are four main hypotheses; the first two emphasise the current adaptive function whereas the latter two also address the evolutionary origin of multiple signals. The multiple messages hypothesis [2] posits each signal provides information about a different aspect of quality, and either females assess all signals to arrive at an overall estimate of male quality, or each female has different preferences and focuses on different signals. The redundant signal hypothesis [3] argues that every signal gives an overall measure of quality, and females assess multiple signals to minimise errors that might occur if they relied on just one cue. The unreliable

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signal hypothesis [2] proposes that signals evolve to exploit pre-existing female preferences [4], and hence these signals do not necessarily reflect male quality. Finally, the chase-away sexual selection hypothesis [5] agrees that sexual signals originate to exploit pre-existing female biases [4] and posits that males, in their perpetual efforts to seduce females, continuously evolve new signals, while females, in their constant efforts to limit wanton male seduction, continuously evolve resistance to formerly effective signals, in the process decreasing the signals' efficacy as tools of seduction and favouring the evolution of new signals.

Hence, the first two hypotheses view signal multiplicity as being driven primarily by female choice. The third one turns the tables and views females as being duped by opportunistic males over evolutionary time. The last one views both sexes as drivers of an antagonistic co-evolutionary process. Support for these hypotheses is still ambiguous [reviewed by Ref. [6]]. Here I propose an alternative new hypothesis: the sexual interference hypothesis. It states that additional sexual signals evolve to interfere with female choice; females respond by evolving the ability to glean meaningful information from all available cues, and males by producing signals that are more resistant to interference; these selection pressures increase the cost of both female assessment and male display, and gradually produce multiple honest signals.

First, I briefly summarise the effects of assessment costs on choosiness [7], approaching the idea from four perspectives: marketing and product selection by humans, effects of predation, multiple signals models, and the effects of noise. Then, I examine behaviours that males use to interfere with female choice and propose that sexual signals can also be viewed in this context. Finally, I describe and discuss the sexual interference hypothesis, and present several predictions unique to the hypothesis.

Product selection and marketing

Optimal foraging models and empirical work indicate that increases in assessment costs lead to decreases in foraging selectivity [8—15]. An analogous and perhaps more pertinent situation occurs when consumers select manufactured products. Like food items and potential mates, the degree to which consumer products are chosen depends not only on their intrinsic qualities but also on their marketing. Furthermore, from the consumer's perspective the problem remains the same: seeking, assessing and selecting a resource given information that might be incomplete, deceitful, conflicting and/or irrelevant [16].

In marketing, the term ''meaningless differentiation'' refers to the observed and experimentally demonstrated changes in consumer preference resulting from the inclusion of irrelevant attributes in a product's advertisement [17,18]. Examples include advertising that instant coffee crystals are flaked as opposed to granular, which has no effect on the product's actually quality [19], or that a highly technical product is ''computer designed'', as if it were not necessarily obvious. Including meaningless attributes in advertising is costly in terms of print space and air time, space and time that could be used to advertise more relevant attributes. Meaningless differentiation is usually explained in the marketing literature by invoking the consumer's cognitive processes, experience and motivation [20,18,21]. However, a more parsimonious explanation surfaces when one considers the effects of increased assessment costs on consumer choice.

When assessment costs are considered, the primary issue becomes not whether the information is trivial with respect to the product's quality, but rather whether the individual consumer deems it to be meaningless. If the information is deemed meaningless, a consumer will immediately dismiss it and selectivity will not be affected. Otherwise, if the information is not deemed to be totally meaningless, a consumer will try to assess the meaning and validity of the said information, which might or might not yield any additional information but will increase assessment costs and, in doing so, decrease the net benefits of choosiness. Hence, the best products are more likely to be selected when assessment is crystal-clear and assessment costs are as low as possible, and the use of trivial attributes is beneficial to products that would otherwise have a smaller share of the market [22,20,18,23]. This general phenomenon also explains the zeal with which top products guard their logos; an easily recognisable brand is an assurance of quality, which, in essence, decreases assessment costs. Another manifestation of this effect is that brand slogans with multiple meanings increase preference for a product, but only among consumers who instantly recognise the multiple meanings, and not among consumers who are only aware of one meaning [24]. Obfuscation increases assessment costs and hence it is beneficial to otherwise sub-optimal products.

Predation risk and choosiness

When individuals choose among prospective mates in the presence of predators, essentially the same phenomenon, whereby increased assessment costs decrease selectivity, has been predicted [25—27] and observed [28,29]. Crowley et al. [30] developed a life-history model that predicted predation risk would decrease selectivity, a prediction that has been supported by several studies. Female sand gobies (*Pomatoschistus minutus*) [31] and guppies (*Poecilia reticulata*) [32,33] prefer larger and more colourful males in the absence of predators, but these preferences wane in the presence of a predator. In pipefish (*Syngnathus typhle*), a species with ''reversed'' sex roles, males prefer larger females in the absence of predators, but choose randomly in the presence of a predator [34]. In crickets (*Gryllus integer*), female preference for long-bout calls decreases when the perceived risk of predation increases [35]. Therefore, whether viewed from a life-history or risk-assessment perspective, predation can make assessment of males more difficult for females, which leads to lower selectivity [36,14,37].

Multiple signals models

Mathematical models on the costs of mate choice offer similar insights. Pomiankowski [38] reckoned costly choice causes choosiness to collapse in a Fisherian system, but stability is theoretically attainable when selection is based on a condition-dependent trait. A model by Schluter and

Price [39] posited that female preference for a given male trait is inversely proportional to the cost of choice, and directly proportional to the trait's honesty and detectability, and to the benefit accrued from choosing. The model argued that when several traits are involved, the relative detectability of male traits can differ between habitats, and sometimes less honest traits with higher detectability might end up being preferred. Iwasa and Pomiankowski [40] countered by arguing that female preference for multiple sexual ornaments could evolve only if the cost of choice does not increase significantly by the use of multiple traits, despite the fact that there would be more signals to assess. This theoretical difficulty is solved if costs to the signaller also increase along with the costs of choice or if different signals indicate different aspects of quality [41]. Overall, these models suggest that multiple condition-dependent signals can evolve, production costs are linked to assessment costs, and females become less choosy as assessment costs increase [25−27].

"Noise" and choosiness

Signal broadcast and detectability differ among environments, and affect mating selectivity, both in artificial and natural situations. For example, pheromone disruptors are sometimes used instead of conventional pesticides against species with chemically-based mate selection [42−44]. Pheromone disruptors can be actual pheromones, slightly modified analogues, or cues that cause pheromone release. Some disruptors cause males to signal too early, when females are not yet receptive, and leave less pheromone available for a more appropriate time. When a signal is composed of several chemicals released simultaneously, a disruptor might work by changing the component ratio, thus confusing the receiver. Finally, the sheer over-abundance of artificial pheromones might make detection of actual pheromones more difficult or decrease female responsiveness, due to habituation [43−45]. Therefore, pheromone disruptors essentially work by creating a noisy environment and making it more difficult for females to locate and assess males.

In natural situations, a noisy habitat can lead to convergence in the types of signals produced by different species [46], and differences in background noise can lead to divergence in the signals produced by a single species [47,48]. Schluter and Price [39] noted this phenomenon and its possible effects on speciation; a more modest but not fully explored implication is that lower-quality males would have a greater chance of being selected by females in conditions that hinder signal propagation or reception. These conditions would include noisy sites for sound-based systems, and turbidity, clouds, mist, fog, or poor light for visual systems. To summarise the previous four sections, noise, chemicals, predators, and other factors can increase assessment costs for females and decrease their choosiness; in these situations, although high-quality males are invariably more likely to be selected than low-quality males, the variability in female choice is higher, and lower-quality males have a better chance of being selected than otherwise they would have.

The corollary is that high-quality males would prefer to avoid low-quality males and situations in which assessment costs are high, and they try to: they arrive first to the breeding grounds [49,50], sing earlier in the morning [51,52], and create exclusive enclaves [53,54]. However, quality is a relative term, so even if low-quality males could be completely excluded, a hierarchy would still exist among high-quality males. Furthermore, although sexual selection models rest on the assumption of consistent individual female preferences for specific male phenotypes [55], data are not always consistent with theory [reviewed by Ref. [7]]. Female preferences can also be affected by a myriad of other factors, including competition, noise, and (the risk of) predation or parasitism, to name a few. Finally, some male traits might be consistently preferred by females, but other traits fall victim to the vagaries of individual female preferences [56]. As a result of this inter- and intra-individual variability in female preference, for males being "high-quality" is nothing more than an ephemeral condition between bouts of mediocrity. Usage of the term "high-quality", here and in the literature, is simply a conceptual aid, not a stern refusal to acknowledge reality, and it actually means "relative high-quality, temporarily". Nevertheless, given that "low-quality" males have a better chance of being selected when assessment costs are high, they should not only seek such situations, but might actually create them by actively increasing assessment costs for females, which is the basis of the sexual interference hypothesis.

The sexual interference hypothesis

Sexual interference, any process whereby mate selection is hindered, obstructed or impeded, is common and it can take many forms. For example, in the water boatman (*Palmacorixa nana*), although larger groups of males call more and attract more females, at high densities male intrasexual aggression increases and the number of copulations per caller decrease and become more spread among males [57]. In Guianan cock-of-the-rock (*Rupicola rupicola*) leks, males interrupt 30% of all female visits and matings, which causes females to change their courtship and mating patterns to the benefit of males who are the most active disruptors [58]. In a study with sand gobies (*P. minutus*), female preference was estimated by the amount of time females spent near one of two males who were allowed to interact with each other at three levels: none, visually and physically; females were subsequently allowed to spawn, and although they tended to do so with their preferred males, their preference was stronger in the first condition, when males had not been allowed to interact [59]. In ruffs (*Philomachus pugnax*), males interfered with 11% of all copulation attempts; females whose copulations had been interrupted were more likely to subsequently mate polyandrously, and half of these subsequent polyandrous matings were the interfering male [60]. Other forms of sexual interference include mate guarding, sexual coercion, Machiavellian manipulation, scent over-marking, sperm plugs, penises designed to remove previously deposited sperm, etc. For some of these examples, it is difficult to determine where unhindered, open competition ends and where sexual interference begins, but it is clear that interference works. Male interference increases female assessment costs and, in so doing, decreases female selectivity.

The sexual interference hypothesis simply suggests that sexual signals ought to be included within the array of morphological, physiological and behavioural adaptations that males use for the purposes of sexual interference. The suggestion that sexual signals are a form of sexual interference might be new, but it should not be a major paradigm change, and it leads to the novel idea that additional signals might have evolved to affect female choice by interfering with the dissemination and reception of other sexual signals.

Under this framework, sexual signals would be subject to several selection pressures. First, whereas an over-abundance of signalling males might obfuscate female assessment [61–63] and benefit ''low-quality'' males, not all males would be expected to compete using the same type of signals, or at least, not all the time. Males might sometimes resort to producing interference signals. A critical assumption is that for some males, some of the time, the net benefits of switching to interference signals would be higher than investing in ''standard'' or ''original'' signals. Just as with other forms of sexual interference or alternative reproductive strategies, it is unlikely that the benefits of producing interference signals would be greater, but the costs might be lower; it would depend on the shape of the benefit vs. cost relationships for original and interference signals. These interference signals would not have to directly compete with standard sexual signals; they would have to merely exploit [64] or disrupt them, making it more difficult for females to detect, localise or assess potential mates. Second, ''high-quality'' males would respond by producing signals that are not so easily blocked, which could be accomplished by making changes to existing signals or producing qualitatively different signals. The use of interference signals and changes to the original signals would result in multiple sexual signals.

Females would not be passive participants in this process. Females would have to evolve awareness of and sensitivity to the new interference signals, and to changes in the original, presumably condition-dependent signals, and would be selected to glean meaningful information from both types of signals. This process would lead to an increase in the costs of assessment, which better quality females would better able to pay [65], and to an increase in the costs of producing all signals, causing prior interference signals to gradually become honest indicators of male quality [66]. A temporary equilibrium of multiple honest signals might be achieved, depending on the rate at which new interfering signals evolve.

Assumptions and predictions

The sexual interference hypothesis of signal multiplicity is based on three generally well-accepted premises. First, female selectivity decreases as assessment costs increase. This does not mean that females cease to be choosy and mate randomly, but rather that they mate under a different set of constraints. Second, ''noise'' increases assessment costs and hence decreases selectivity. The type of noise would depend on the system: turbidity, clouds, mist, fog, for visual systems, movement or lack thereof for seismic systems, chemicals or strong currents for pheromone systems, etc. The corollary is that low-quality males are more likely to be selected in noisy environments, in a ''smoky bar'' where choice is relatively difficult, rather than in hypothetical or artificial noise-free conditions, where choice would be unequivocal. Finally, males not only exploit such circumstances by courting females when choice is more difficult, but also actively interfere with females' preferences and make choice more difficult. Although all these assumptions have already received ample theoretical and empirical support, it might be useful to re-examine them for a given system before embarking on more thorough tests of the sexual interference hypothesis' predictions.

The novelty of the hypothesis comes in viewing sexual signals as another form of sexual interference. The first prediction is that the presence of additional signals will make assessment by females more costly. This prediction could be tested by excluding certain signals from an animal's repertoire, for example, with the use of blocking chemicals, filtered light, modified auditory stimuli, or substrates with different vibrational properties. Second, and along the same lines, the presence of competing signalling males will increase assessment costs for females. Third, the hypothesis predicts that ''low-quality'' males will be more likely to resort to interference signals, the purpose of which is to specifically hinder mate assessment. Compared to standard signals, the costs of producing interference signals would be lower, and they would be specifically structured to disrupt or exploit standard signals. Different individuals could adopt different strategies or a single individual could alternate between them. Fourth, female selectivity will decrease due to the presence of interference signals, particularly for females unable to bear the increased cost of assessment. Finally, ''high-quality'' males will respond by producing costlier, signals that are more resistant to interference; this would be accomplished quantitatively, by changing the frequency or intensity of the signal, or qualitatively, by switching to different types of signals, adding to their repertoire, or switching to a completely different signalling modality.

The hypothesis also yields the several inter-population or inter-specific predictions, which could be tested in any system in which the degree of sexual ornamentation differs markedly between populations, such as in the Trinidadian guppy, or between closely related species, such as in the now classic swordfish system. First, the costs of signal production by males and assessment by females should be lower in species or populations with less complex sexual ornaments. Second, the effectiveness of a novel trait should decrease over evolutionary time, not because of a decrease in female attraction for the trait, as predicted by the chase-away model [5], but rather because of an increase in the quality of information females glean from the trait. This is a crucial difference between the two hypotheses. The chase-away hypothesis predicts that females cease to pay attention to a new signal and evolve the ability to ignore it despite their pre-existing biases. The sexual interference hypothesis predicts that females pay increasingly more attention to a new signal and evolve the ability to glean more information from it. Third, the sexual interference hypothesis is the only one of the multiple signals hypotheses that predicts novel traits eventually become condition-dependent [66]. Over evolutionary time,

the usefulness of a novel trait in hindering female choice will decrease; increased assessment ability by females and increased display costs incurred by males will change interference signals into honest signals. Until new interference signals evolve, a temporary equilibrium of multiple honest signals will be maintained.

Conclusion

The hypothesis presented here is based on three premises. First, that female choosiness decreases when assessment costs increase. Second, that hindering the propagation or reception of sexual signals will lead to increased assessment costs. Finally, that males will take advantage of decreased female selectivity both by seeking environments in which female choice is more difficult, and more importantly, by actively interfering with female choice. The hypothesis proposes that, congruent with other forms of sexual interference, sexual signals can be used and have evolved to confuse and hinder female choice. The process leads to the evolution of higher assessment costs for females and to the production by males of additional, costlier signals that are more resistant to interference, and hence, to the evolution of multiple honest sexual signals. A shift in perspective is suggested, whereby we begin to consider the fact that sexual signals can interfere with each other and probably have been selected to do so. The implications of this minor shift, however, offer an alternative hypothesis and compel us to re-examine the evolutionary origin and maintenance of sexual signals.

Conflict of interest

The author has no conflict of interest to disclose.

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