

# Assets and tactics in a mating market: Economic models of negotiation offer insights into animal courtship dynamics on the lek

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**Abstract** Economists study negotiation as a series of events—partner choice, information gathering, bargaining, etc.—with each step of the process affecting the outcome of the next, and the optimal decision at each stage depending on the player's bargaining power. The context in which these negotiations occur—the market—is critical, since players can adjust their behaviors in response to outside offers. Animals similarly are faced with sequential decisions regarding courtship: who to court, how to approach a potential mate, at what level to display, when to give up, etc. Thus economic models of negotiation in a market provide a framework in which we can view not just the outcome of courtship (assortative mating), but also the process, where each sex can use tactics to improve their negotiating outcome, using the assets that they have available. Here we propose to use negotiation as a conceptual framework to explore the factors promoting tactical adjustments during sequential stages of courtship in lekking species. Our goal is to discuss the utility of negotiation as a heuristic tool, as well as the promise and peril of co-opting game theoretic models from economics to understand animal interactions. We will provide a brief overview of a few areas where we see promise for using negotiation as a framework to understand animal courtship dynamics: choice of a display territory, tactical partner choice for negotiation, approaching a potential partner and courtship haggling [*Current Zoology* 57 (2): 225–236, 2011].

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Watching a female animal cross a lek of displaying males can call to mind a tourist walking through a bazaar: surrounded by eager merchants, each with their wares displayed, promoting the high quality of their merchandise, and adjusting their prices according to the competitors surrounding them and the perceived interest and resources of potential buyers. Any merchant knows that success in such a market is determined by negotiation skills—such as choice of a buyer to target and responsiveness to market and buyer feedback—as well as the assets that the merchant has to work with—the quality of his merchandise and resources to invest in advertising. Yet we tend to view leks as more static, where each seller has a certain underlying quality (i.e. good condition and/or preferred genes) that determines his advertisement (i.e., his signal quality) and therefore attractiveness (Lande, 1981; Grafen, 1990; Számadó, 2011). We typically leave out the dynamic and tactical nature of negotiations in the marketplace. While there is an increasing consideration for how markets may affect sexual selection (Noë and Hammerstein, 1994; 1995),

there are still relatively few studies addressing the importance of tactical skills during the negotiations in the marketplace of the lek.

We argue that competition over mates on a lek requires two interacting components: access to assets (signal quality, size, energetic reserves, etc.) and a strategy for how to deploy these assets effectively (courtship tactics)(Fig. 1). Males use assets to invest in the quality of their signals, just as merchants invest in merchandise and advertisements. With condition-dependent indicator traits, males adjust their investment according to their underlying condition, by diverting energy to the bright coloration, muscles and/or brain tissue which determine the maximum attractiveness of the male's signals (Grafen, 1990; Getty, 1998; Griffith and Sheldon, 2001; Számadó, 2011). Once signals are produced, males do not automatically gain matings according to their quality; males must tactically deploy these signals in the mating market during courtship negotiations. These negotiations involve short-term plasticity throughout the day and during each courtship bout

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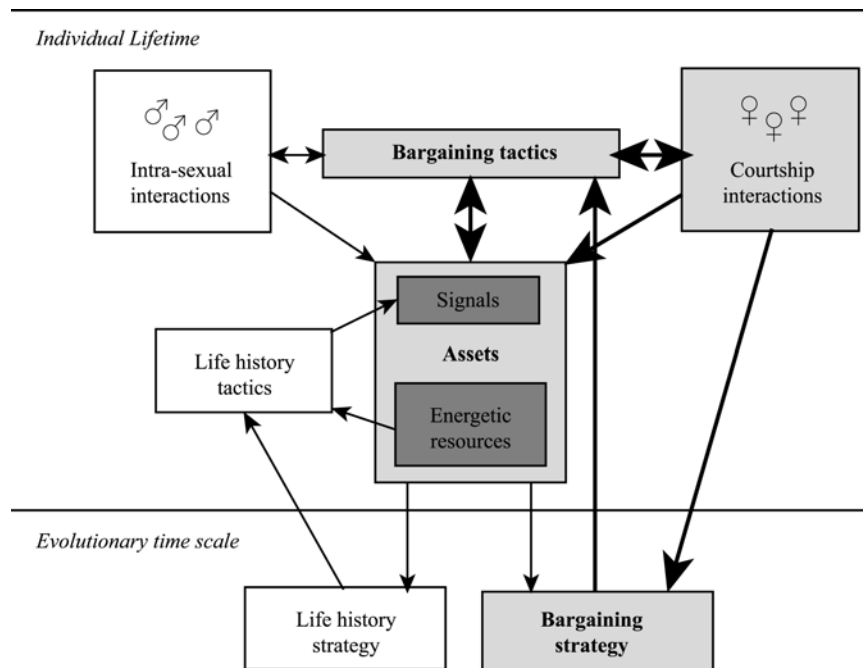
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as males interact with others in the market: for example, males must choose whether to display next to more or less attractive competitors, which females to target, and the intensity and duration of signaling.

Despite the potentially-complex interplay between assets and tactics, studies of sexual selection tend to focus on signals and their relationship to fitness, leaving out courtship tactics. But this approach may miss much of the action, since courtship tactics may have significant impacts on male fitness. For example in satin bowerbirds ~30% of the variation in male courtship success was explained by the average intensity of male behavioral displays, and another ~30% was explained by the male's ability to adjust his display intensity in response to female signals during courtship (Patricelli et al., 2002). Therefore by examining only how fitness is related to male signals and not to how these signals are tactically deployed, we may see only *half* the picture, and more importantly, we may be missing an entire arena of adaptive decision making. Examples of adaptive courtship tactics have been found in a wide variety of taxa, including arthropods, fish, herps, birds and mammals (e.g., Evans et al., 2002; Kelso and Verrell,

2002; Patricelli et al., 2002; Shine et al., 2003; Sockman et al., 2006; Wong et al., 2007; How et al., 2008; Wong and Svensson, 2009; Bro-Jørgensen, 2010; Patricelli and Krakauer, 2010)—suggesting that these capabilities are widespread. But only a handful of studies have measured their fitness consequences, thus we know little about how selection acts on courtship tactics and the factors that might constrain their evolution. Further, we lack a framework in which to investigate the relationship between assets and courtship tactics, and how they change with the mating market.

One of the hindrances to empirical studies on courtship tactics is the paucity of available theory. Which models are appropriate to bridge this gap? Game theoretic models from economics have provided important perspectives for the study of animal behaviors (Maynard Smith, 1982; McNamara et al., 1999). An appropriate set of economic models for this case are those describing the use of assets and tactics in *negotiation in a market*. Negotiation in business involves a series of events—partner choice, information gathering, haggling, etc.—with each step of the process affecting the outcome of the next, and the optimal decision at each stage



**Fig. 1 Assets and tactics**

Competition over mates on a lek requires both assets (e.g., signal quality and energetic reserves) and tactics. Within their lifetime, males use resources to invest in the quality of their signals, just as merchants invest in merchandise and advertisements. With condition-dependent indicator traits, life-history tactics determine how males adjust their investment according to their energetic resources (i.e., condition). Once signals are produced, males tactically deploy these signals in the mating market, which happens on a shorter time scale: during a season, a day and a courtship bout. The male's assets and tactics feed back on each other via the direct cost of the tactic and the outcome of his social interactions. The success of individual males affects the relative frequencies of different life history and bargaining strategies to change in the population on an evolutionary time scale. This, in turn, affects the composition of the market, which may affect which assets and strategies are favored. Tactical interactions discussed in this review are highlighted with bold arrows and gray boxes.

depending on the players' bargaining power. The context in which these negotiations occur (i.e., the market) is critical, since players can adjust their demands in response to those of other players (Hammerstein and Hagen, 2005). The economic theory of negotiation can similarly provide a framework to view courtship as a series of interdependent tactical decisions—where to display, who to court, when to give up, etc.—made in the social context of a mating market.

Here we discuss the utility of negotiation as a conceptual framework for understanding tactical behaviors in lekking animals, as well as the promise and peril of co-opting game theoretic models from economics to formalize this model. We will then provide a brief overview of a few areas where we see promise for using negotiation as a framework to understand animal courtship dynamics: choice of a display territory, tactical partner choice for negotiation, approaching a potential partner and courtship haggling. This review will focus on males displaying to choosy females on a lek, however most of these models are equally valid for animals with different mating systems or sex-role reversal. Further, we will focus on male tactical choices here, but courtship in many species involves complex mate-selection tactics by females as well (Real, 1990; Luttbeg, 1996). We will discuss a number of these female tactics, but a review of female tactical choices at each stage of the negotiation—and how they may interact with male tactical choices—is beyond the scope of this paper.

## 1 The Promise and Peril of Economic Models of Negotiation

As in nearly every aspect of game theory, economists have preceded biologists, thus there is a lot we can usefully borrow from the economic study of negotiation. In economics, modern game theoretic approaches to negotiating, or “bargaining,” begin with Nash's (1950) paper. The model in that paper is fairly narrow, yet Nash suggests in the first line that bargaining and negotiation is any situation that involves “individuals who have the opportunity to collaborate for mutual benefit in more than one way.” From that perspective, essentially all social interaction is bargaining. Binmore (1985) argues, for example, that negotiation models offer a successful framework for studying the formation of coalitions, essentially mirroring—and sometimes pre-dating—the development of skew theory in biology (Vehrencamp, 1983; Johnstone, 2000). Yet the historical course of economic bargaining theory (as models of negotiation are usually called in economics) has lead to the accre-

tion of terminology and to models that may be confusing and misleading, once borrowed into evolutionary biology (for an excellent review of bargaining for biologists, see Binmore, 2010). In this section, we provide a very short commentary on the interface between economic models of negotiation and the theoretical study of negotiation in evolutionary ecology.

For a long time, prominent economists felt that game theory had little to contribute to the study of negotiation (Roth, 1985) due to the perceived complexity of human psychology as well as the complexity of early model outcomes, such as Nash (1953), which found an infinite number of possible agreements to a bargaining problem. But depending upon the details, it is possible for negotiation models to produce unique and testable predictions. Rubenstein (1982) showed that two players sequentially negotiating over how to divide a resource, but doing so under time pressure, such that the size of the resource shrinks with each rejected proposal, can reach a unique agreement (see also Rubenstein and Wolinsky, 1985).

Since Rubenstein's pioneering models, bargaining theory in economics has tackled a dizzying number of scenarios, but these models build from a common structure (Muthoo, 2000). Buyers and sellers both have some valuation of the possible outcomes, which may or may not be known to the other party; the parties then haggle, each trying to get as close as possible to their preferred outcome. These models also share a sensitivity of negotiated outcomes to both strategic options as they occur in time and space and the individual strengths and opportunity costs of individuals (Muthoo, 1999; Binmore, 2007). Further, they are sensitive to the symmetry of information among the partners—who knows what and when (e.g., Harsanyi and Selten, 1988). This sensitivity to model assumptions and structure suggests that we will be better served by thinking hard about the relevant details of each biological case and investing in new models, rather than simply borrowing off-the-shelf models from economics. There are, however, a number of valuable generalizations and modes of analysis that we think provide a productive outline of what evolutionary models of negotiation, in context of courtship, will resemble.

One of the key components of the study of negotiation in economics has been the so-called Nash program, which is an attempt to justify or improve the predictions of simple action-response models (“cooperative” game theory) using extensive-form games that explicitly model the process of negotiation (“non-cooperative”

game theory). The majority of first generation evolutionary games were action-response games—two or more players simultaneously choose from a set of available strategies and fitness payoffs can be calculated purely from the combination of strategies chosen (Maynard Smith, 1982). Indeed, most current models relevant to sexual signaling on the lek are action-response models, and do not address the dynamic interaction between males and females as they proceed through the steps leading to rejection or copulation (Számádó, 2011; but see Payne and Pagel, 1996; Payne, 1998). While these models are appropriate in some cases, most interactions between conspecific animals involve multiple stages before the “game” is resolved. For biologists, extensive-form games provide ways of conceptualizing short-term behavioral tactics as well as the evolutionary time scale, and have been used to model a variety of behavioral contexts (Enquist and Leimar, 1983; Dugatkin and Reeve, 1998; McNamara et al., 1999; McElreath and Boyd, 2007). In order to build an extensive-form game of signaling or other behaviors, one must be explicit about how individuals interact, in which order, for how long, and which actions are possible for each player at each point in time. Behavioral choice can be contingent on previous behavior, and so a much richer strategy set becomes available. For example, can males signal to multiple females at once, or must they rather interact with a single female at a time? Can females evaluate multiple males or once, or is there an attention limit that constrains female strategy? Building models that include variations of these assumptions may reveal the roles of cognitive constraints on both behavioral dynamics seen in mating markets as well the evolutionary dynamics of signaling strategies (McNamara and Houston, 2009). These questions are hard to ask when we adopt a classical strategic-form game, which includes no explicit time scale for behavioral negotiations.

Another helpful concept key to the bargaining literature is the consideration of outside options (Rubenstein and Wolinsky, 1985; Muthoo, 1999; Cant and Johnstone, 2009). In a bargaining context, an outside option represents a choice to terminate negotiation with a current partner or partners and instead pursue payoffs in another context. Outside options may be alternative buyers or sellers, or in our context alternative potential mates on the lek. In game theoretic models, the presence or absence of outside options can affect the outcome strongly. Typically, the individual with the best outside option has the most power in bargaining, because that individual

will be willing to terminate the negotiation first. This means that the individual with better outside options can essentially force their bargaining partner to accept a worse deal, because such a deal will still be better than their inferior outside options. However, having an outside option no better than what can be gained through continued bargaining will not affect the outcome; therefore the quality of other partners is more important than the quantity alone. Further, the importance of outside options will increase when there is a low cost to switching partners (Rubenstein and Wolinsky, 1985). On most leks, the cost of switching partners is likely to be low; indeed, Alexander (1975) proposed that leks may have evolved by female preference for low-cost switching and comparison among aggregated males. Therefore, outside options are likely to be an important consideration for both males and females on the lek.

While we see great promise in illuminating biological negotiation with extensive-form games inspired by economic models, there are reasons to be very careful in doing so (Binmore, 2010). First, a major area of distinction between evolutionary and economic game theory, which is often overlooked, is the realm of solution concepts. How are we to “solve” the model, to figure out what it predicts? In evolutionary theory, fitness provides a natural currency. Economists, in contrast, spend a healthy amount of time discussing different solution concepts (e.g., Nash, perfect, sub-game perfect and Bayesian solutions) because the vagaries of “rationality” and the reality of variable preferences (Selten, 1978) make it difficult to decide what a model predicts (Binmore, 2007). This is not a flaw with game theory, but rather a deficit in our understanding of rationality. Furthermore, “rational” predictions can differ markedly from evolutionary ones. For example, in classical game theory, no distinction was made between evolutionarily stable equilibria (ESS's, Maynard Smith, 1982) and unstable equilibria—they are all Nash equilibria. Therefore one has to be careful not to merely lift predictions from an economic model, without first considering whether an evolutionary analysis would generate the same prediction.

With due caution, however, there is great potential for concepts originally explored in economic bargaining models to help in the study of animal courtship. Since no model developed in economics will fit the biology quite right, we think new theory development is the right approach. But in the shorter term, the most immediate value is in nominating behavioral aspects of mate choice on leks—extensive-form in structure—which

may be viewed in this framework.

## 2 Negotiation on the Lek

The following is a brief overview of a few areas where we see promise for using negotiation in a market as a conceptual framework to understand animal courtship dynamics on leks: choice of a display territory, tactical partner choice for negotiation, approaching a potential partner and courtship haggling. In each case, we highlight some of the many ways in which male tactical decisions may affect male fitness. Further, we discuss economic models related to negotiation—including, but not restricted to bargaining models—which may serve to guide further development of theory in this area.

### 2.1 Choice of a display territory

Similar to a merchant choosing a location to establish a business, a displaying male may consider many factors when deciding where to display. These decisions will have important effects on the quantity and quality of females that will be available—the male's outside options, as well as the competitors against which the seller will be compared—the female's outside options. These outside options in turn will affect the bargaining power available to both partners during courtship, and thus the outcomes of negotiation (Rubenstein and Wolinsky, 1985).

Retail location theory includes several classes of models to predict the location and density of business or other human institutions (reviewed in Brown, 1989). To predict how businesses should distribute themselves on a landscape, these models highlight factors such as travel distance (central place theory; Christaller, 1966), accessibility-attractiveness trade-offs for consumers (spatial interaction or gravitation theory; Reilly, 1953), and differential costs and benefits to prime locations (bid rent theory; Alonso, 1964). Additionally, business location may be influenced by the location of similar establishments; the principle of minimum differentiation (i.e., Hotelling's law; Hotelling, 1929) considers factors such as comparison shopping, uncertainty reduction, and customer spillover to explain retail clustering, synergistic interactions, and neighbor effects. There is a rich theoretical and empirical literature on lek settlement which draws from (or is analogous to) economic models of retail location (Bradbury and Gibson, 1983; Wiley, 1991; Höglund and Alatalo, 1995), for example, relating lek settlement and male display to female home ranges (e.g., "hotspots"; Bradbury and Gibson, 1983), resources important for females (McNaughton, 1988), predation (Ryan et al., 1981), harassment (Clutton-Brock

et al., 1992), nepotism (Kokko and Lindstrom, 1996), environmental conditions (Uy and Endler, 2004; Martin, 2010), and lek size (Widemo and Owens, 1995; Hernandez et al., 1999). Variation in these factors can be important determinants of male mating success, and to the extent that males differ in their ability to assess each of these conditions and adjust display location and behavior accordingly, these tactical skills that may also contribute to variance in male fitness.

In addition, males make tactical choices on a smaller scale—in choosing to settle near, or allow settlement by, particular competing males within the lek. Males may benefit, for example, by reduced aggression if they settle near relatives (Reynolds et al., 2009), or they may increase female traffic by permitting unrelated associate males on their territory (van Rhijn, 1983). A question with particularly interesting parallels to economic models is how the relative quality of surrounding males should influence male settlement. The "hotshot" model suggests females search primarily for high quality males; lower quality males therefore should surround these males to intercept females or otherwise benefit from spill-over of female traffic (Beehler and Foster, 1988), a hypothesis that has received mixed support (e.g., Höglund et al., 1993; Drone, 1994; Young et al., 2009). However, it is not clear that males should always settle next to the highest quality male they can find. For example, bid rent models from economics (Alonso, 1964), as well as social queuing models from biology (Kokko et al., 1998), would predict male quality declining as males settle farther from the lek center, since only older and more aggressive males can 'afford' a more central territory. In contrast, Hotelling's law might predict males of similar quality would cluster together (Nelson, 1958; Brown, 1989).

Just as retail settlement models have considered consumer behavior, optimal settlement decisions should also depend on female cognitive processes such as the decision rules used to evaluate potential mates—for example, whether females compare males to an endogenous acceptance threshold or compare multiple males to each other (i.e., best of  $n$ ; Real, 1990; Luttbegg, 1996). If males are compared only to each other, then unattractive males may benefit from clustering with other unattractive males to improve their relative attractiveness (Bateson and Healy, 2005; Oh and Badyaev, 2010); this will also limit female outside options for a better partner. Where a male sets up shop as well as the behavior of the surrounding males will influence subsequent stages of negotiation, as discussed further below.

## 2.2 Tactical partner choice by lekking males

Before negotiation can begin, partners must be chosen. Early economic studies of negotiation ignored this fact, assuming random pairing in models and enforcing random assortment in experiments. More recent studies which allow partner choice have found significantly different outcomes, suggesting that partner choice may be equally important to other tactics in determining how negotiations progress (e.g., Tenbrunsel et al., 1999; Bazerman et al., 2000; De Fraja and Muthoo, 2000). Similarly, game-theoretic and genetic models of behavioral evolution have found very different outcomes when players can choose to interact with particular partner types (e.g., Wolf et al., 1999; McNamara et al., 2009a) and when market dynamics are considered (Noë and Hammerstein, 1994; 1995; Cant and Johnstone, 2009).

Males in lekking species typically are not considered to be choosy (Trivers, 1972; Emlen and Oring, 1977), but courtship and mating activity is temporally clumped in many lekking species (Höglund and Alatalo, 1995), and thus top males may find a group of females simultaneously seeking courtship. Selection may therefore favor males that exert partner choice, allocating their courtship effort according to female reproductive value, as has been found in many non-lekking species (e.g., Shine et al., 2003; Sockman et al., 2006; Ruiz et al., 2008; Wong and Svensson, 2009). For example, survivorship of offspring may change with the age of the female (Schroeder et al., 1999), selecting for males with a corresponding preference for female age. Further, if young females copy the mating choices of older females, as has been found in guppies (Dugatkin and Godin, 1993), then males may increase the probability of further copulations by courting older females. However, female reproductive value may not be the only consideration; unattractive males may benefit from directing courtships toward younger females if these less experienced females are less choosy (i.e., having a lower threshold of courtship stimulation required for mating or more likely to make a "mistake" in mate choice; Gibson and Höglund, 1992). This may select for different partner-choice tactics in attractive versus unattractive males.

Male partner choice tactics may further be contingent on the market—the behavior and attractiveness of neighboring males that are simultaneously courting the female (e.g., Plath et al., 2008; Oh and Badyaev, 2010). For example, males may shift from courting high to low value females if there is a superior competitor present on the lek, similar to sellers avoiding potential buyers

who are already in negotiations with a superior seller (Moorthy, 1988; Jackson, 2007). Outside options are critical for this shift; less competitive males may preferentially court low-quality females since negotiations are more likely to succeed with a female who has poor outside options; but this is only predicted when encounters with females are neither so common to make competition unlikely (i.e., the male has many outside options), nor so rare that males should court any female they come across (Venner et al., 2010).

## 2.3 Building trust with a negotiating partner

Economic models of negotiation and other games have shown very different outcomes depending on the relationship between the players before the game begins—relationships built on trust and reputation (e.g., Tenbrunsel et al., 1999; Bazerman et al., 2000; Hammerstein and Hagen, 2005; McNamara et al., 2009a). In the early stages of a negotiation with an unknown partner, building a relationship is critical to a favorable outcome and occurs during the pre-negotiation phase (Druckman, 1967; 1968). Empirical studies on humans across cultures have shown that negotiating partners do this through personal introductions before negotiation begins (Zartman, 1989; Senger, 2002). In animal courtship between unfamiliar partners, building trust before or during the early stages of negotiation may be similarly important, especially in species where males walk a fine line between attracting females to mate and scaring them away (Borgia, 1995; Berglund et al., 1996). For example, female satin bowerbirds prefer more intense and aggressive displays from males, but males who display too intensely early in courtship scare the females away; the most successful males begin courtship at low intensity and increase only when females show signals of comfort (Patricelli et al., 2002).

In addition to considering the comfort of the target female, males may also need to take into account other females who may be eavesdropping on the courtship negotiation. This may be particularly important on leks, where open arenas provide a great deal of public information. In addition to allowing females to observe the mating decisions of other females (Gibson and Höglund, 1992), eavesdropping may allow females to assess whether a male will make a safe negotiation partner. Therefore when there are multiple females on the lek, males may attempt fewer aggressive behaviors, such as forced-copulation attempts, if observing these behaviors will deter other females from approaching the aggressive male.

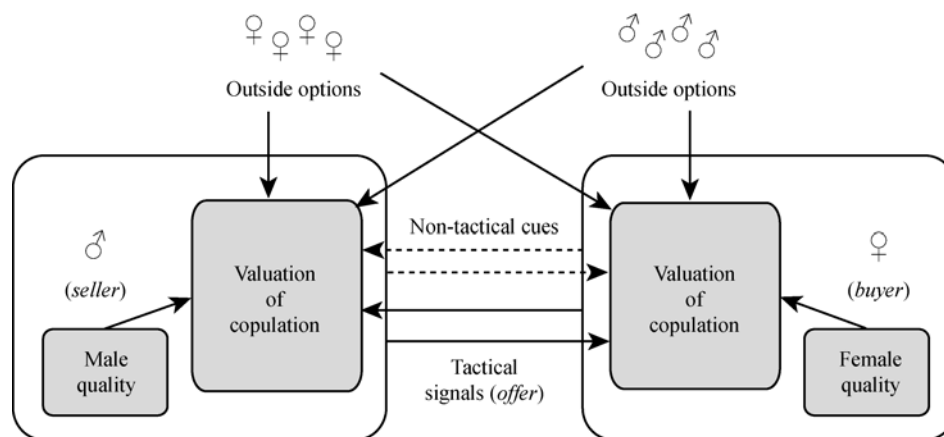
Economic transactions are not limited to isolated ne-

gotiation events; successful interactions may lead to longer-term buyer-seller relationships. Negotiating parties may benefit from extended exchanges in a number of ways, including increased information sharing, trust, preferred treatment, joint pay-offs or other synergistic arrangements (Spekman, 1988; Dabholkar et al., 1994; Ganesan, 1994). In addition to relationships built during early stages of courtship, there may long-term relationships between males and females and between competing males that affect how negotiation proceeds, particularly in long-lived lekking species where females may revisit males over several consecutive breeding seasons (Uy et al., 2000). In such cases, the costs of being overly eager or aggressive during courtship may increase if males have to consider their long-term reputation with courted and eavesdropping females. Relationships among males on a lek may also be important. For example, social connectedness in young males can predict social ascension and breeding success in lekking manakins, possibly as a result of creating and maintaining relationships (McDonald, 2007; Ryder et al., 2008). Improved monitoring techniques in addition to long-running data sets of lekking species may help researchers learn more about causes and consequences of relationships on the lek.

## 2.4 Courtship haggling

After buyers and sellers choose their partners and approach them, the next phase of the negotiation is bargaining over the price. Sellers in a market face a number of decisions during this haggling process: where to set

the initial asking price, how much to change that price to make a deal, and how long to persist before moving on to the next potential buyer (Muthoo, 1999; Camerer, 2003). These decisions involve trading off an investment of time and advertising costs in the current negotiation against possible future negotiations. During courtship, males and females haggle over copulation, and therefore access to each other's gametes. A lekking male is in a position similar to a seller, making an offer (display effort: including display intensity, persistence and/or quality) in hopes of convincing the buyer (the female) to choose his wares over those of other contenders (Real, 1991). The female may accept his offer or remain "coy" to gather more information (Fig. 2). Time and energy spent in one courtship negotiation is unavailable for other courtships, so males may benefit from tactically adjusting their courtship behaviors. For example, males may display at a low level at first and increase only if the female is unimpressed. But if the female remains unmoved, when should he cut his losses and walk away? How does this vary with male condition, and the probability of future courtship opportunities? The idea of tactical adjustments in courtship effort has been around since the early days of behavioral ecology (Parker, 1974), however there are still surprisingly few models of courtship dynamics (Real, 1991; Payne and Pagel, 1996; Payne, 1998; McNamara et al., 2009b) and many of the existing models cannot readily be applied to signaling on a lek. Bargaining theory may offer a useful framework on which to build such models.



**Fig. 2** A conceptual model of courtship haggling on the lek

Both the male and female have private information unknown to the other (gray regions); this information includes their quality, and their valuation of their current negotiating partner. These valuations are influenced by their own respective qualities, as well as their outside options of other opposite-sex individuals on the lek. In aggregations such as leks, these outside options may be public information. Males and females negotiate (i.e. make offers and counter-offers) by means of tactical signals, including sexual displays by the male or signals of interest or coyness by the female. Valuations by either party may also be influenced by non-tactical cues, such as age or body size.

In economic bargaining models, a number of factors determine which party comes closer to their optimal outcome, including the cost of haggling to each party, the risk of unpredictable factors causing a breakdown of bargaining, asymmetry of information about valuation of the resource, and the outside options available to both parties (Muthoo, 1999); we will discuss only the latter two factors here, though all may be important in courtship negotiations on a lek.

Incomplete information about valuation of the resource and resource quality can lead to less efficient and predictable bargaining, since players must juggle the often-conflicting goals of maximizing their outcome and conveying information (Rubenstein, 1982; Muthoo, 1999; Binmore, 2010). Males on a lek may have incomplete information if there is variation in the level of display females require from males before consent to copulation. This may occur due to variation in female preference among or within females (Jennions and Petrie, 1997), or if females are using a comparative assessment tactic and males do not know where they fall among the  $n$  other males sampled (Real, 1990; Luttbeg, 1996). Economic models of one-sided asymmetry can favor sellers who adjust their prices, beginning high and lowering until the offer is accepted by the buyer (Rapoport et al., 1995). Therefore, considering only the male's tactics on the lek, we may predict that males will begin courtship at a low rate (i.e., sell their goods at a high price) and increase their rate only if females demand more. Indeed, such gradual increases of display intensity during courtship have been found in fiddler crabs (How et al., 2008) and many other species (e.g., Gibson, 1996; Patricelli et al., 2002) and are predicted by some dyadic models of signaling interactions (Payne and Pagel, 1996; Payne and Pagel, 1997; Payne, 1998). However, asymmetries are unlikely to be one-sided, since females also have incomplete information about males. As discussed above, there may be reason for males to place different value on females of different age or condition (Dugatkin and Godin, 1993; Schroeder et al., 1999; Venner et al., 2010), so we cannot assume that males will have the same valuations of the resource the female has to offer. But more importantly, females have incomplete information about male quality, and she gains more complete information based on his offers during bargaining, which changes her valuation of the male. Therefore, models are needed which account for both male and female strategies, and which address the signaling function of male display.

Experimental and theoretical studies of bargaining

have shown that outcomes are very different in dyadic haggling versus haggling at a market or bazaar, where the buyer and seller both have low-cost access to outside options (Bester, 1993; De Fraja and Muthoo, 2000; Cant and Johnstone, 2009). Applying the logic of outside options to the lek leads to interesting predictions about how display behavior will change with the number of males and females present. For example, males may have lower bargaining power when courting a solitary female on the lek, since she has many outside options and he has none, forcing the male to persist in courtships with extremely coy or less desirable females. Conversely, males have more bargaining power when there are multiple females available, favoring males who cut their losses with overly-coy females and direct their courtship effort to more attentive ones. This same factor may favor tactical deployment of coy behaviors by females (see also McNamara et al., 2009b). Parker (1974) arrived at similar predictions using modified optimal foraging patch models of male courtship persistence, considering females to be equivalent to a static resource patch. This model predicts that persistence should increase with increased valuation of the resource (receptive vs. unreceptive females) and a decrease in encounter rate (a measure of outside options). It remains to be seen whether these patterns/predictions will hold in a more realistic bargaining model that includes species-specific details, such as the cost of display for males of differing quality, the way in which energetic tradeoffs play out at different time scales (e.g., within days and among days), and non-independent mate choice (males may place higher value on copulations when there are multiple females present, if copulation inspires mate-choice copying; Gibson and Höglund, 1992).

In addition to increasing the accessibility of outside options, markets also allow buyers to compare the offers of multiple sellers simultaneously (thereby gaining more information about the quality of their outside options), and for sellers to adjust their offers according to competitor behavior (thereby increasing their attractiveness relative to the buyer's outside options; Noë and Hammerstein, 1994; 1995). The amount of power gained through having outside options will depend in part on the information available to both players about the offers being made by other bargainers, and the mechanism by which the partners are paired (Binmore, 2007). Therefore, females gain bargaining power along with their ability to assess multiple males' offers simultaneously; this power may force males to begin with



higher offers to retain bargaining partners and tempt females away from other males across the lek. However, it is unlikely that females can assess all males on the lek simultaneously, since the efficacy of courtship likely decreases with distance (Gibson, 1996), allowing males to retain some bargaining power during courtship. Males may also gain bargaining power through increased information about the quality and coyness of other females on the lek. These models once again highlight the need to learn more about the flow of information across the lek, the cognitive processes by which females compare multiple males (Bateson and Healy, 2005), and how this information affects female movements among males. With this information, we may improve our ability to predict how males should optimally adjust their offers according to the quantity, quality and behavior of other males and females on the market.

## 2.5 Conclusion

Courtship is often viewed as a black box, in which males and females assort themselves according to the strength of her preference and the quality of his trait, but where the process producing this pattern is obscure or irrelevant. By looking inside the black box to view courtship as a process, involving multiple stages with different tactics, we can better understand how selection acts on male signals (Real, 1990; Payne, 1998; Luttbeg, 2004). More importantly, we will reveal a host of other traits that are not typically considered sexual traits—behavioral tactics and social skills in both sexes that are critical to competition over mates. Male courtship tactics have been described in a wide diversity of invertebrate and vertebrate taxa (discussed above), but because we lack a framework in which to view these behaviors, they are often descriptive studies in individual species, rather than empirical tests of optimal courtship models. Economic models of negotiation offer a conceptual framework that emphasize courtship as a process in which the male and female bargain to reach a deal, influenced by the haggling of other players in the market. We believe that theoretical development in this area has enormous promise for increasing our understanding of the evolution of complex, dynamic sexual signals and social intelligence. Using a combination of detailed observation and field experimentation, lekking species offer an excellent model to study courtship tactics and assets in a natural mating market.

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## References

- Alexander RD, 1975. Natural selection and specialized chorusing behavior in acoustical insects. In: Pimental D ed. *Insects, Science and Society*. New York: Academic Press, 35–77.
- Alonso W, 1964. *Location and Land Use: Towards a General Theory of Land Rent*. Cambridge, MA: Harvard University Press.
- Bateson M, Healy SD, 2005. Comparative evaluation and its implications for mate choice. *Trends in Ecology & Evolution*. 20: 659.
- Bazerman MH, Curhan JR, Moore DA, Valley KL, 2000. Negotiation. *Annual Review of Psychology*. 51: 279–314.
- Beehler BM, Foster MS, 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. *The American Naturalist*. 131: 203–219.
- Berglund A, Bisazza A, Pilastro A, 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*. 58: 385–389.
- Bester H, 1993. Bargaining versus price competition in markets with quality uncertainty. *The American Economic Review*. 83: 278–288.
- Binmore KG, 1985. Bargaining and coalitions. In: Roth AE ed. *Game-Theoretic Models of Bargaining*. Cambridge: Cambridge Univ. Press, 269–304.
- Binmore KG, 2007. *Playing for Real: A Text on Game Theory*. Oxford: Oxford University Press.
- Binmore KG, 2010. Bargaining in biology? *Journal of Evolutionary Biology*. 23: 1351–1363.
- Borgia G, 1995. Threat reduction as a cause of differences in bower architecture, bower decoration and male display in two closely related bowerbirds *Chlamydera nuchalis* and *C. maculata*. *Emu*. 95: 1–12.
- Bradbury JW, Gibson RM, 1983. Leks and mate choice. In: Bateson PG ed. *Mate Choice*. Cambridge: Cambridge University Press.
- Bro-Jørgensen J, 2010. Dynamics of multiple signalling systems: Animal communication in a world in flux. *Trends In Ecology & Evolution*. 25: 292–300.
- Brown S, 1989. Retail location theory: The legacy of Harold Hotelling. *Journal of Retailing* 65: 451–471.
- Camerer CF, 2003. *Behavioral Game Theory: Experiments in Strategic Interaction*. Princeton, NJ: Princeton University Press.
- Cant MA, Johnstone RA, 2009. How threats influence the evolutionary resolution of within-group conflict. *The American Naturalist*. 173: 759–771.
- Christaller W, 1966. *The Central Places in Southern Germany*. Englewood Cliffs, NJ: Prentice Hall.

- Clutton-Brock TH, Price OF, MacColl ADC, 1992. Mate retention, harassment, and the evolution of ungulate leks. *Behavioral Ecology* 3: 234–242.
- Dabholkar P, Johnston W, Cathey A, 1994. The dynamics of long-term business-to-business exchange relationships. *Journal of the Academy of Marketing Science*. 22: 130–145.
- De Fraja G, Muthoo A, 2000. Equilibrium partner switching in a bargaining model with asymmetric information. *International Economic Review* 41: 849–869.
- Droney DC, 1994. Tests of hypotheses for lek formation in a Hawaiian *Drosophila*. *Animal Behaviour*. 47: 351–361.
- Druckman D, 1967. Dogmatism prenegotiation experience and simulated group representation as determinants of dyadic behavior in a bargaining situation. *Journal of Personality and Social Psychology*. 6: 279–290.
- Druckman D, 1968. Prenegotiation experience and dyadic conflict resolution in a bargaining situation. *Journal of Experimental Social Psychology* 4: 367–383.
- Dugatkin LA, Godin J-GJ, 1993. Female mate copying in the guppy *Poecilia reticulata*: Age-dependent effects. *Behavioral Ecology* 4: 289–292.
- Dugatkin LA, Reeve HK, 1998. *Game Theory and Animal Behavior*. New York: Oxford University Press.
- Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223.
- Enquist M, Leimar O, 1983. Evolution of fighting behaviour: Decision rules and assessment of relative strength. *Journal of Theoretical Biology*. 102: 387–410.
- Evans JP, Kelley JL, Ramnarine IW, Pilastro A, 2002. Female behaviour mediates male courtship under predation risk in the guppy *Poecilia reticulata*. *Behavioral Ecology and Sociobiology* 52: 496–502.
- Ganesan S, 1994. Determinants of long-term orientation in buyer-seller relationships. *The Journal of Marketing* 58: 1–19.
- Getty T, 1998. Handicap signalling: When fecundity and viability do not add up. *Animal Behaviour* 56: 127–130.
- Gibson RM, 1996. Female choice in sage grouse: The roles of attraction and active comparison. *Behavioral Ecology and Sociobiology* 39: 55–59.
- Gibson RM, Höglund J, 1992. Copying and sexual selection. *Trends in Ecology and Evolution* 7: 229–232.
- Grafen A, 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144: 517–546.
- Griffith SC, Sheldon BC, 2001. Phenotypic plasticity in the expression of sexually selected traits: Neglected components of variation. *Animal Behaviour* 61: 987–993.
- Hammerstein P, Hagen EH, 2005. The second wave of evolutionary economics in biology. *Trends in Ecology & Evolution* 20: 604–609.
- Harsanyi J, Selten R, 1988. *A General Theory of Equilibrium Selection in Games*. Cambridge MA: MIT Press.
- Hernandez ML, Houston AI, McNamara JM, 1999. Male rank and optimal lek size. *Behavioral Ecology* 10: 73–79.
- Höglund J, Alatalo RV, 1995. *Leks*. Princeton: Princeton University Press.
- Höglund J, Montgomerie R, Widemo F, 1993. Costs and consequences of variation in the size of ruff leks. *Behavioral Ecology and Sociobiology* 32: 31–39.
- Hotelling H, 1929. Stability in competition. *The Economic Journal* 39: 41–57.
- How MJ, Hemmi JM, Zeil J, Peters R, 2008. Claw waving display changes with receiver distance in fiddler crabs *Uca perplexa*. *Animal Behaviour* 75: 1015–1022.
- Jackson WA, 2007. On the social structure of markets. *Cambridge Journal of Economics* 31: 235–253.
- Jennions MD, Petrie M, 1997. Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society* 72: 283–327.
- Johnstone RA, 2000. Models of reproductive skew: A review and synthesis. *Ethology* 106: 5–26.
- Kelso EC, Verrell PA, 2002. Do male veiled chameleons *Chamaeleo calyptratus* adjust their courtship displays in response to female reproductive status? *Ethology* 108: 495–512.
- Kokko H, Lindstrom J, 1996. Kin selection and the evolution of leks: Whose success do young males maximize? *Proceedings of the Royal Society of London Series B*. 263: 919–923.
- Kokko H, Lindstrom J, Alatalo RV, Rintamäki PT, 1998. Queuing for territory positions in the lekking black grouse *Tetrao tetrix*. *Behavioral Ecology* 9: 376–383.
- Lande R, 1981. Models of speciation by sexual selection of polygenic traits. *Proceedings of the National Academy of Sciences* 78: 3721–3725.
- Luttbeg B, 1996. A comparative Bayes tactic for mate assessment and choice. *Behavioral Ecology* 7: 451–460.
- Luttbeg B, 2004. Female mate assessment and choice behavior affect the frequency of alternative male mating tactics. *Behavioral Ecology* 15: 239–247.
- Martin CH, 2010. Unexploited females and unreliable signals of male quality in a malawi cichlid bower polymorphism. *Behavioral Ecology* 21: 1195–1202.
- Maynard Smith J, 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- McDonald DB, 2007. Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences USA* 104: 10910–10914.
- McElreath R, Boyd R, 2007. *Mathematical Models of Social Evolution: A Guide for the Perplexed*. Chicago University of Chicago Press.
- McNamara J, Stephens P, Dall S, Houston A, 2009a. Evolution of trust and trustworthiness: Social awareness favours personality differences. *Proceedings of the Royal Society B: Biological Sciences* 276: 605–613.
- McNamara JM, Fromhage L, Barta Z, Houston AI, 2009b. The optimal coyness game. *Proceedings of the Royal Society B*. 276: 953–960.
- McNamara JM, Gasson CE, Houston AI, 1999. *Incorporating*

- rules for responding into evolutionary games. *Nature* 401: 368–371.
- McNamara JM, Houston AI, 2009. Integrating function and mechanism. *Trends In Ecology & Evolution* 24: 670–675.
- McNaughton SJ, 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature* 334: 343–345.
- Moorthy KS, 1988. Product and price competition in a duopoly. *Marketing Science* 7: 141–168.
- Muthoo A, 1999. *Bargaining Theory with Applications*. Cambridge: Cambridge University Press.
- Muthoo A, 2000. A non-technical introduction to bargaining theory. *World Economics* 1: 145–166.
- Nash J, 1950. The bargaining problem. *Econometrica* 18: 155–162.
- Nash J, 1953. Two-person cooperative games. *Econometrica* 21: 128–140.
- Nelson RL, 1958. *The Selection of Retail Locations*. New York: F. W. Dodge.
- Noë R, Hammerstein P, 1994. Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology* 35: 1–11.
- Noë R, Hammerstein P, 1995. Biological markets. *Trends in Ecology & Evolution* 10: 336–339.
- Oh KP, Badyaev AV, 2010. Structure of social networks in a passerine bird: Consequences for sexual selection and the evolution of mating strategies. *The American Naturalist* 176: E80–E89.
- Parker GA, 1974. Courtship persistence and female-guarding as male time investment strategies. *Behaviour* 48: 157–183.
- Patricelli GL, Krakauer AH, 2010. Tactical allocation of effort among multiple signals in sage grouse: An experiment with a robotic female. *Behavioral Ecology* 21: 97–106.
- Patricelli GL, Uy JAC, Walsh G, Borgia G, 2002. Sexual selection: Male displays adjusted to female's response. *Nature* 415: 279–280.
- Payne RJH, 1998. Gradually escalating fights and displays: The cumulative assessment model. *Animal Behaviour* 56: 651–662.
- Payne RJH, Pagel M, 1996. When is false modesty a false economy? An optimality model of escalating signals. *Proceedings of the Royal Society B* 263: 1545–1550.
- Payne RJH, Pagel MD, 1997. Why do animals repeat displays? *Animal Behaviour* 54: 109–119.
- Plath M, Blum D, Schlupp I, Tiedemann R, 2008. Audience effect alters mating preferences in a livebearing fish, the Atlantic molly *Poecilia mexicana*. *Animal Behaviour* 75: 21–29.
- Rapoport A, Erev I, Zwick R, 1995. An experimental study of buyer-seller negotiation with one-sided incomplete information and time discounting. *Management Science* 41: 377–394.
- Real LA, 1990. Search theory and mate choice. I. Models of single-sex discrimination. *The American Naturalist* 136: 374–404.
- Real LA, 1991. Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *The American Naturalist* 138: 901–917.
- Reilly WJ, 1953. *The Law of Retail Gravitation*. New York: Pilsbury.
- Reynolds SM, Christman MC, Uy JAC, Patricelli GL, Braun MJ et al., 2009. Lekking satin bowerbird males aggregate with relatives to mitigate aggression. *Behavioral Ecology* 20: 410–415.
- Roth AE, 1985. *Game-Theoretic Models of Bargaining*. Cambridge: Cambridge Univ Press.
- Rubenstein A, 1982. Perfect equilibrium in a bargaining model. *Econometrica* 50: 97–110.
- Rubenstein A, Wolinsky A, 1985. Equilibrium in a market with sequential bargaining. *Econometrica* 53: 1133–1150.
- Ruiz M, Davis E, Martins EP, 2008. Courtship attention in sagebrush lizards varies with male identity and female reproductive state. *Behavioral Ecology* 19: 1326–1332.
- Ryan MJ, Tuttle MD, Taft LK, 1981. The costs and benefits of frog chorusing behavior. *Behavioral Ecology and Sociobiology* 8: 273–278.
- Ryder TB, McDonald DB, Blake JG, Parker PG, Loiselle BA, 2008. Social networks in the lek-mating wire-tailed manakin *Pipra filicauda*. *Proceedings of the Royal Society B* 275: 1367–1374.
- Schroeder MA, Young JR, Braun CE, 1999. Sage grouse: *Centrocercus urophasianus*. *Birds of North America* 425: 1–28.
- Selten R, 1978. The chain store paradox. *Theory and Decision* 9: 127–159.
- Senger JM, 2002. Tales of the bazaar: Interest-based negotiation across cultures. *Negotiation Journal* 18: 233–249.
- Shine R, Langkilde T, Mason RT, 2003. The opportunistic serpent: Male garter snakes adjust courtship tactics to mating opportunities. *Behaviour* 140: 1509–1526.
- Sockman KW, Sewall KB, Ball GF, Hahn TP, 2006. Economy of mate attraction in the cassin's finch. *Biology Letters* 1: 34–37.
- Spekman RE, 1988. Strategic supplier selection: Understanding long-term buyer relationships. *Business Horizons* 31: 75–81.
- Számadó S, 2011. The cost of honesty and the fallacy of the handicap principle. *Animal Behaviour* 81: 3–10.
- Tenbrunsel AE, Wade-Benzoni KA, Moag J, Bazerman MH, 1999. The negotiation matching process: Relationships and partner selection. *Organizational Behavior and Human Decision Processes* 80: 252–283.
- Trivers RL, 1972. Parental investment and sexual selection. In: Campbell B ed. *Sexual Selection and the Descent of Man*, 1871–1971. London: Heinemann, 136–179.
- Uy JAC, Endler JA, 2004. Modification of the visual background increases the conspicuousness of golden-collared manakin displays. *Behavioral Ecology* 15: 1003–1010.
- Uy JAC, Patricelli GL, Borgia G, 2000. Dynamic mate-searching tactic allows female satin bowerbirds *Ptilonorhynchus violaceus* to reduce searching. *Proceedings of the Royal Society of London B* 267: 251–256.
- van Rhijn JG, 1983. On the maintenance and origin of alternative

- strategies in the ruff *Philomachus pugnax*. *Ibis* 125: 482–498.
- Vehrencamp SL, 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* 31: 667–682.
- Venner S, Bernstein C, Dray S, Bel-Venner MC, 2010. Make love not war: When should less competitive males choose low-quality but defensible females? *The American Naturalist* 175: 650–661.
- Widemo F, Owens IPF, 1995. Lek size, male mating skew and the evolution of lekking. *Nature* 373: 148–151.
- Wiley RH, 1991. Lekking in birds and mammals: Behavioral and evolutionary issues. *Advances in the Study of Behavior* 20: 201–291.
- Wolf JB, Brodie III ED, Moore AJ, 1999. Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. *The American Naturalist* 153: 254–266.
- Wong BBM, Candolin U, Lindström K, 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *The American Naturalist* 170: 184–189.
- Wong BBM, Svensson P, 2009. Strategic male signalling effort in a desert-dwelling fish. *Behavioral Ecology and Sociobiology* 63: 543–549.
- Young KA, Genner MJ, Joyce DA, Haesler MP, 2009. Hotshots, hot spots, and female preference: Exploring lek formation models with a bower-building cichlid fish. *Behavioral Ecology* 20: 609–615.
- Zartman IW, 1989. Prenegotiation- phases and functions. *International Journal* 44: 237–253.