

# The evolution of courtship rituals in monogamous species

Carl-Adam Wachtmeister and Magnus Enquist

Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden

In this paper we propose an alternative explanation for the evolution of courtship rituals in monogamous species. We demonstrate, using computer simulations, how male courtship might develop as males exploit response biases in females to manipulate the female into starting reproduction before she has been able to assess the male's intentions. In our coevolutionary simulations, a recurrent, artificial neural network is used to model the female recognition mechanism, while the displaying male is represented by a sequence of signals. Our particular model situation is just one example of how a reproductive conflict could result in the evolution of ritualized displays in monogamous species. Since reproductive conflicts occur even after pair formation, the explanation we propose may also apply to rituals that occur after pair formation. *Key words:* artificial neural networks, courtship, ritualization, coyness, manipulation, mate choice, monogamy, reproductive conflict, receiver bias, sexual selection. [*Behav Ecol* 11:405–410 (2000)]

A variety of signals and behaviors are used in interactions with the opposite sex. In monogamous species these rituals may occur over an extended period of time. Many of these interactions are identified as courtship and are today often regarded as means of assessing partner quality (Andersson, 1994; Trivers, 1972). For instance, partner quality may be revealed because high-quality males can afford to use more elaborate displays or because a direct relationship exists between quality and performance (see, e.g., Andersson, 1994). Older ethological explanations of courtship rituals have stressed the importance of stimulation and cooperation, rather than choice of partner. For instance, Huxley (1914: 516) proposed that these ritualized displays serve "to keep the two birds of a pair together, and to keep them constant to each other" (see also Armstrong, 1963). A similar idea is that courtship rituals provide necessary stimulation and that they coordinate the reproductive physiology of the male and the female (Bastock, 1967; Lehrman, 1959, 1964). The elaboration of displays was considered to reduce ambiguity (Cullen, 1966).

In this paper we describe a new hypothesis for the evolution of rituals within a monogamous pair. Here the courtship display is not informative to the female apart from indicating the presence of a male of her own species. Our hypothesis accords with classical ethology (theories of ritualization; see, e.g., Eibl-Eibesfeldt, 1975) insofar as the emphasis is on stimulation, but it rests on reproductive conflict and manipulation rather than on cooperation. In monogamous species there are a variety of such reproductive conflicts, many concerning parental duties. To illustrate how this can lead to evolution of elaborated display and manipulations, we developed a model. Consider a female that has to find a partner in an environment of both faithful and philandering males. These males differ in the amount of parental care that they provide. Males are eager to court any female and start reproduction as soon as they meet a female. Females, on the other hand, might benefit by staying coy and evaluating the intention of a potential partner before actual reproduction, even if this is associated with some costs (Wachtmeister and Enquist, 1999). Our suggestion is that

complex rituals may evolve as a male attempts to manipulate the female's decision process to start reproduction earlier than is optimal for her.

For manipulation to be possible, biases must exist in receiver's behavior so that it is possible for a sender to elaborate on existing stimuli and thereby elicit responses more favorable to the sender. There is ample evidence that receivers are biased in this way; the classical evidence is from studies of supernormal stimuli in ethology (e.g., Tinbergen, 1951) and peak shift in learning psychology (e.g., Mackintosh, 1974). More systematic studies have recently been introduced studying biases in related species and taking phylogeny into consideration (Basolo, 1990; Ryan et al., 1990). The latter studies have shown that the same bias may exist in related species, although it has only been exploited in some of them. That receiver biases can drive evolution has been suggested many times (Dawkins and Krebs, 1978; Enquist and Arak, 1993; Holland and Rice, 1998; Krakauer and Johnstone, 1995; Krebs and Dawkins, 1984; Leimar et al., 1986; O'Donald, 1977; Ryan, 1998; Staddon, 1975).

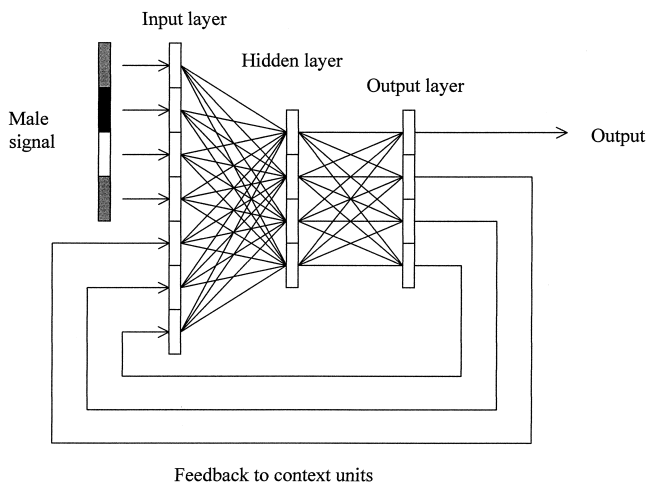
It is difficult to account for the possibility of manipulation with traditional modeling techniques such as game theory because the reaction to novel stimuli is problematic. The reason for this is that such reactions are not shaped by selection with any precision. Instead, reactions to novel stimuli are determined largely by the mechanism that has been established to deal with familiar stimuli. Thus, to study manipulation we need knowledge about how real biological recognition systems operate, and we need suitable models of such systems.

In this study we used an artificial neural network to model the female's behavioral mechanism (see Enquist and Arak, 1998; Ghirlanda and Enquist, 1998, for information about artificial neural networks as models of stimulus control). The displaying male is represented by a sequence of visual signals. In one set of simulations the male can use different signals in the sequence, and in another set he is limited to repeating a single signal. Neural network models have been used earlier to study the evolution of signals (e.g., Enquist and Arak, 1993, 1998) and have revealed some basic evolutionary relationships between conflicts of interests, ornamentation, and manipulation. The current study is technically different from our earlier simulations in that the network now has internal feedback loops and thereby can react to a sequence of stimuli.

Address correspondence to C.-A. Wachtmeister. E-mail: carladam@zool.su.se.

Received 8 February 1999; revised 26 October 1999; accepted 10 November 1999.

© 2000 International Society for Behavioral Ecology



**Figure 1**

A recurrent artificial neural network represents the female recognition mechanism. The displaying male is represented by a sequence of signals. For each time step,  $s$ , that a male spends with a female, he stimulates her with a new signal.

### Simulation model

In this section we introduce the female and male player and continue with an explanation of the game. We finish with a description of the evolutionary algorithm.

An artificial neural network models the female recognition mechanism. This network has three layers and is partially recurrent (Hutchinson, 1994). The input layer consists of seven cells, the hidden layer of four cells, and the output layer of four cells (Figure 1). Three feedback loops from three cells in the output layer provide input to a corresponding number of cells in the input layer. These input layer cells receiving feedback are referred to as context unit cells. These context cells provide the network with a memory of the past and recurrent networks of this architecture can thus be used to recognize signal sequences (Hertz et al., 1991).

The different displays used by a courting male are represented by a sequence of signals (one signal for each time step). Each signal in the sequence consists of four components. Each component activates a single input layer cell in the network with a value between 0 and 1 (Figure 1). Two types of sequences are considered. In one set of simulations we allow the male to use different signals, referred to as a variable sequence. In the other set males can only repeat a single signal, referred to as a uniform sequence. A male uses the same signal sequence independent of whether he is faithful or philandering.

The network receives input from a sequence of signals. Four of the input cells are activated by the signal. The three others are each activated by one of the three output layer cells involved in the feedback system. Each cell in the middle layer receives input from each cell in the first layer, and each output cell receives input from each middle layer cell. Any middle or output layer cell,  $j$ , produces an output,  $s$ , according to the sigmoid function

$$s_j = \begin{cases} 1 - 1/2(1 + a_j) & a_j \geq 0 \\ 1/2(1 - a_j) & a_j < 0, \end{cases}$$

where  $a_j$  is the cell's activation level. This activation level is the sum of all outputs from the previous layer factored by their connection weights.

In all, the probability of response depends on the properties of the signal, the state of the network, and on an addi-

tional motivational factor. This motivational factor varies according to a normal distribution with mean 0 and a standard deviation of 0.01. If the sum of the network's output and the internal factor is greater than a threshold of 0.5, the receiver reacts. The varying internal factor means that a particular stimulus and network state produce slightly different responses at different occasions. For more information about how artificial neural networks can be used for modeling receivers, see, for example, Enquist and Arak (1993, 1998).

A single female regularly meets potential mates that are either faithful or philandering. The faithful male remains with the female after reproduction. The philandering male stays with the female until she either starts to reproduce or she exposes and rejects him. A female that rejects a philandering male will search for a new mate.

Let  $x$  be the duration of female coyness; that is, the time that a female spends with a particular male before she starts reproducing. The time that has passed from the start of the season is denoted  $t$ . Both  $x$  and  $t$  are measured in discrete time units. After the male and female pair, the male stimulates the female, using his particular courtship sequence. A female can only reproduce once in a season, and her reproductive success declines exponentially (rate  $r$ ) with time of onset of reproduction in the season. Female reproductive success also depends on whether she reproduces with a faithful or a philandering male. If the male is a philanderer, female reproductive success is devalued with a factor  $\delta$ .

A female may be unpaired, paired, or reproducing. An unpaired female finds a male with probability  $(P_c + P_d)$  during a time unit, where  $P_c$  and  $P_d$  are the probabilities of meeting a faithful or philandering male, respectively. An unpaired female always pairs with an encountered male. If the male is a philanderer, she will detect this with a probability  $q$  each time step. How is it possible for a female to detect a philanderer? First, a philanderer might expose himself by not being able to spend as much time with the female as a faithful male (e.g., Stenmark et al., 1988). Second, the primary female of an already mated male that philanders might intervene or be detected (Breihagen and Slagsvold, 1988). Once the female has detected a philanderer, she rejects the male and starts searching for a new one. The longer the female is paired with a male, the more certain she is of his intentions. The probability of being paired to a faithful male increases with the time the female spends with the male without rejecting him. Details depend on the possibility to expose philanders (i.e., the detection rate,  $q$ ) as well as on the proportion of philanders in the male population,  $P_d/(P_c + P_d)$ . Every time step that a female is unpaired, she is stimulated by a uniform sequence in which each component is set to 0. This stimulus indicates that no conspecific male is present.

In all coevolutionary simulations, both the network population and the signaler population is fixed at 1,000,000 individuals each, and the parameters are set to  $q = 0.2$ ,  $r = 0.03$ ,  $\delta = 0.15$ ,  $(P_c + P_d) = 0.6$ , and  $P_d/(P_c + P_d) = 0.8$ . In each population there can be a maximum of 20 types of individuals. All simulations start out with a male and a female population, each consisting of a single type referred to as the starting male type and the starting female type, respectively. Independent of whether the simulation allows males to use a variable or a uniform sequence, the starting male type is a uniform signal sequence with all signal components set at 0.5. The starting female type is a network that responds optimally to this uniform male type. This starting female type was produced by letting the network evolve in a simulation where the starting male signal was kept unchanged until the optimal response was reached. During the simulation each type in the population contributes to the next generation in proportion to their

frequency and their fitness (see below). Each simulation consists of 60,000 generations.

In each generation, provided that there are fewer than 20 types, a maximum of 2 individuals in the population is mutated. Each mutated individual becomes a new type initially represented by a single individual.

When a male with a variable sequence mutates, there is a probability of 0.1 that each signal in the sequence is modified. A signal chosen for modification can either be exchanged for another signal in the sequence (probability 0.99) or be slightly altered (probability 0.01). In the latter case each signal component is changed with a probability of 0.25 by adding a normally distributed increment ( $\mu = 0$ ,  $\sigma = 0.1$ ) given that the component remains between 0 and 1. In males with a uniform sequence, the signal was mutated by letting each component change with a probability of 0.25 by adding a normally distributed increment ( $\mu = 0$ ,  $\sigma = 0.1$ ), given that the component remains between 0 and 1. Females are mutated by modifying each connection weight with probability of 0.045 by adding a normally distributed increment ( $\mu = 0$ ,  $\sigma = 0.05$ ).

To compute the average coy response of a female of a particular type  $i$ , we first calculate the distribution of coy responses,  $v_{ij}$ , toward a given male type  $j$ . We then sum over all male types weighting with their frequencies,  $m_j$ , in the male population.

$$\bar{x}_i = \sum_j \sum_x m_j v_{ij}(x) x.$$

The fitness of a female type depends on whether the male is faithful or philandering and when reproduction starts in the season and is calculated as

$$u_i = \sum_t h_i(t) [c_i(t) + \delta d_i(t)] e^{-rt},$$

where  $h$  is the distribution of start times. Given that reproduction starts at time  $t$ , the probability that the male is faithful or not is  $c(t)$  and  $d(t)$ , respectively. When reproducing with a philandering male, female reproductive success is devalued by a factor  $\delta$  ( $0 < \delta < 1$ ). Reproducing without any male renders no fitness to the female. The value of reproducing declines exponentially with time in season at rate  $r$  (see above).

For males we used a fitness function that declines with duration of coyness. Using the distributions of coy responses from above and the distribution of female types  $f_j$ , we define male fitness as

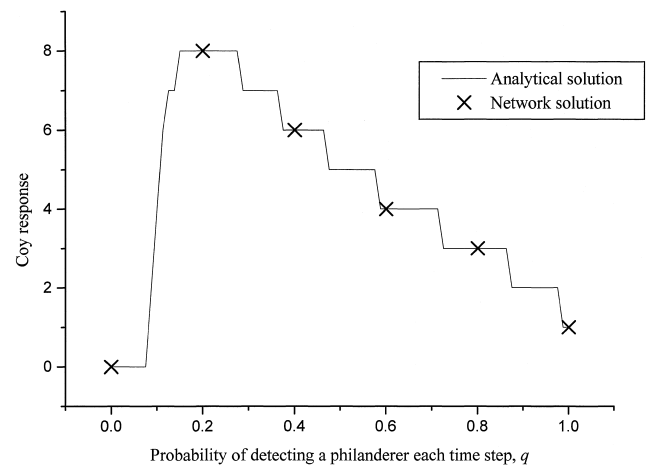
$$u_j = \sum_i \sum_x f_i v_{ij}(x) e^{-rx}.$$

This expression of fitness is somewhat simplified but serves the purpose of favoring in evolution male types that can persuade females to start reproducing earlier.

## RESULTS

Before starting any simulations, we checked whether a female (i.e., the network) is able to evolve an optimal coy response to a courting male when the male is not allowed to change the signal sequence. As shown in Figure 2, the female always evolves the optimal response, as compared with results from an analytical model (Wachtmeister and Enquist, 1999). In both simulation types, new, more stimulating male displays repeatedly emerged, causing females to start reproducing earlier than optimal. In response, the female continuously evolved a reduced sensitivity to the new successful displays.

During all five simulations with a variable male sequence (Figure 3), females typically stayed coy between five and six time steps, although optimal response is eight time steps (Figure 4a). The average coyness is 5.6 (excluding the first turbulent 5000 generations). Studying the results in closer detail,



**Figure 2**

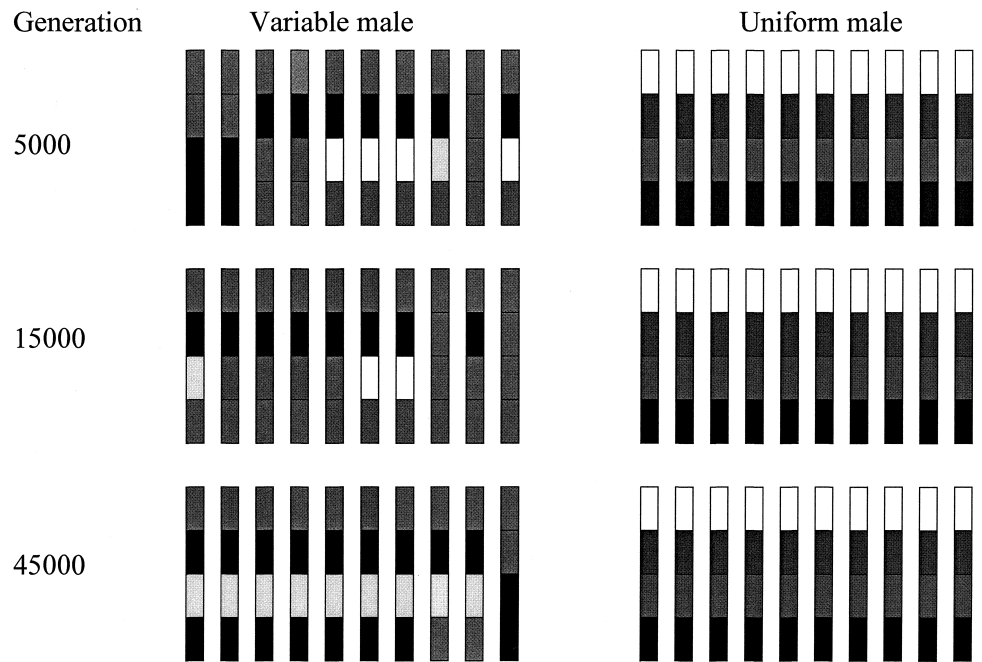
Against the same nonevolving male (starting male type, see text), we evolved female (network) coy responses for a number of different probabilities of detecting a philanderer,  $q$ . The results agree with the analytical solutions from a dynamical optimization model (Wachtmeister and Enquist, 1999). For instance, the coy response of the neural network is 8.0 when  $q = 0.2$ . Other parameter values are  $P_c = 0.12$ ,  $P_d = 0.48$ ,  $\delta = 0.15$ , and  $r = 0.03$ .

we notice that shorter or longer intervals of no or small changes of stability appear between the more turbulent periods (Figure 4b). This indicates that it takes the evolutionary processes some time to come up with better solutions both in males and females. We also see in Figure 4b that sometimes females exist that are coyer than the optimal duration of coyness (i.e., super coy females). These females have replaced less fit sub-coy females. Excluding the first 5000 generations, the average rate of change in males is 2.1 and in females 1.9. Rate of change is measured as the rate of replacement of the most common type in a 5000-generation interval.

Limiting the males to use only a uniform sequence (Figure 3) results in a drastically reduced success at manipulating a female's reproductive decision. In five simulations of the coevolutionary process between females and males with uniform sequences, it is only at the start of the simulations that the males have some success (Figure 5a), when the females still are naive. In the subsequent intervals the females continually respond with near optimal coyness. The average coyness is 8.0 (excluding the first turbulent 5000 generations), clearly higher compared with the simulations in which males use a variable signal sequence (Mann-Whitney  $U$  test,  $U = 0$ ,  $p = .0040$ , exact one-tailed probability). The rate of change is also lower. A uniform male signaler is obviously limited in its ability to design a more stimulating sequence (compare Figure 5b and Figure 4b). Excluding the first 5000 generations, the average rate of change is 0.4 for both males and females.

## DISCUSSION

Here we have given one example of how a reproductive conflict might give rise to behavior rituals and attempts at manipulating the female. The display itself does not provide any information about the female apart from indicating the presence of a conspecific male. These results agree with other theoretical studies of coevolution between senders and receivers in conflict (Arak and Enquist, 1995; Enquist and Arak, 1998). An important result is that coevolution between senders and receivers never settles at equilibrium with respect to signal form and the receivers' reactions to the signal (Arak and Enquist, 1995). The effect of this coevolutionary race on



**Figure 3**

Examples of the first 10 signals in the signaling sequence of the most common male type at generation 5,000, 15,000 and 45,000 for two sets of coevolutionary simulations (i.e., with a uniform male and a variable male). The variable male is free to develop a signal sequence, where all components of all signals independently may vary between 0 and 1. The uniform male is limited to repeat a single signal in the sequences.

the senders has been investigated in a number of studies (Arak and Enquist, 1993, 1995; Enquist and Arak, 1993, 1994, 1998; Enquist and Johnstone, 1997; Hurd et al., 1995; Phelps and Ryan, 1998). It is shown how increasing conflict between senders and receivers results in more elaborate and costly displays (Arak and Enquist, 1995).

How the coevolution affects the receiver has received less attention (but see Johnstone, 1994; Phelps and Ryan, 1998). Dawkins and Krebs (1978, Krebs and Dawkins, 1984), in their pioneering work on sender–receiver coevolution, argued that receivers might be manipulated. Manipulation occurs when the receiver (in our model the female) makes a suboptimal decision due to the display of the sender (in our model the male). Models of behavioral mechanisms such as artificial neural networks provide us with a tool to study manipulation (e.g., Enquist and Arak, 1998; Ghirlanda and Enquist, 1998). Our results show how females can be manipulated by displaying males that exploit biases in recognition systems. Once manipulation becomes costly for the female, selection will favor reduced sensitivity to the current display. However, any change in the females' memory will create new biases (Enquist and Arak, 1998), and selection will favor males that can exploit these biases, leading to a never-ending race.

Our simulations gave us two types of results. When male signals were variable, females started reproduction earlier than was optimal. When male signals were uniform, the manipulation was transient. Our results suggest that manipulation will be more common when signals are free to vary. This is, of course, because this freedom permits a more exhaustive search of receiver biases by the evolving signal. Conversely, the evolution of manipulation also depends on how rapidly receivers can evolve resistance.

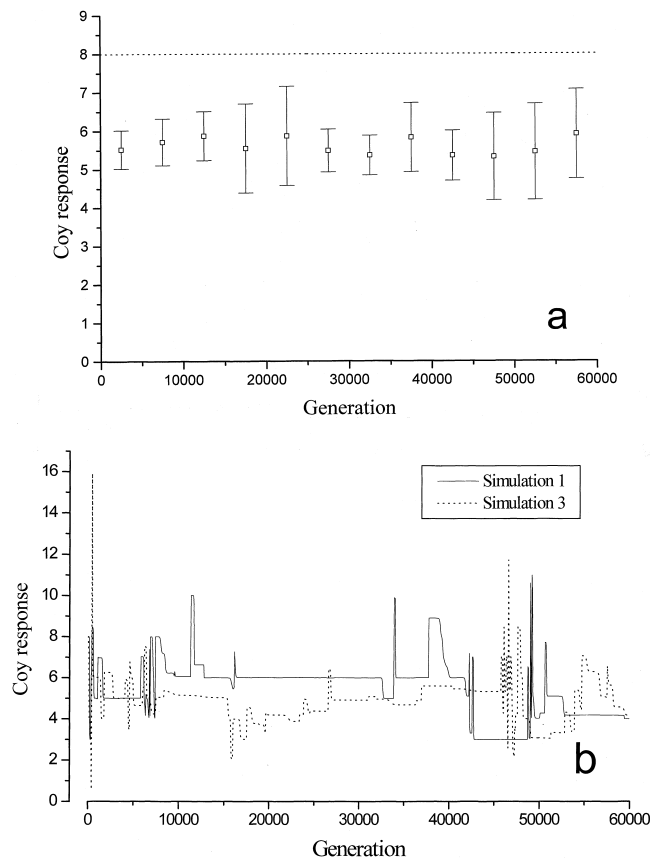
To what degree are females manipulated in nature? This is a difficult problem, and to our knowledge no information exists on manipulation in natural interactions between monogamous males and females. Our results show that both successful (variable) and unsuccessful (uniform) males develop conspicuous signals. A consequence of this is that by observing display alone, it is hard to infer whether females really are manipulated to any significant degree. However, the hypothesis we propose here for the evolution of behavioral rituals in

monogamous species has the advantage of being valid in a wider context than theories building on mate choice (e.g., sexual selection). For instance, there are a lot of ornamented rituals performed between the two members of a monogamous pair that continue far beyond the act of pair formation (Armstrong, 1963, 1965; Huxley, 1923). These can be understood if we recognize that the conflict between the male and the female continue after the choice of a partner. These conflicts might concern investments in parental duties such as nest building, incubation, feeding of young, territory defense, and whether or not to have another clutch.

Our results depend partly on the artificial neural network we use as the model of the females' recognition mechanism. These models are, of course, crude in comparison with real nervous systems and do not closely imitate the structure and complexity of a biological neural network (Dawkins and Guilford, 1995). Despite this, these models can still capture the most basic properties of stimulus control. These simple networks are capable of generalization and develop response biases as a by-product of discrimination and have successfully repeated results from experimental psychology (Enquist and Arak, 1998; Ghirlanda and Enquist, 1998). Today, there are no good alternatives to artificial neural networks when modeling how stimulus controls response. Also, all other models of stimulus control are actually much simpler than network models. Furthermore, this is one of the first studies using networks that considers time as a parameter. For another such successful attempt, see Phelps and Ryan (1998).

Our simulations contain some deliberate simplifications. For instance, the probability of meeting a male, as well as the proportion of philanderers in the male population, remains constant throughout the season. This and the fact that reproductive success declines exponentially with time in season results in a constant female coy response (Wachtmeister and Enquist, 1999).

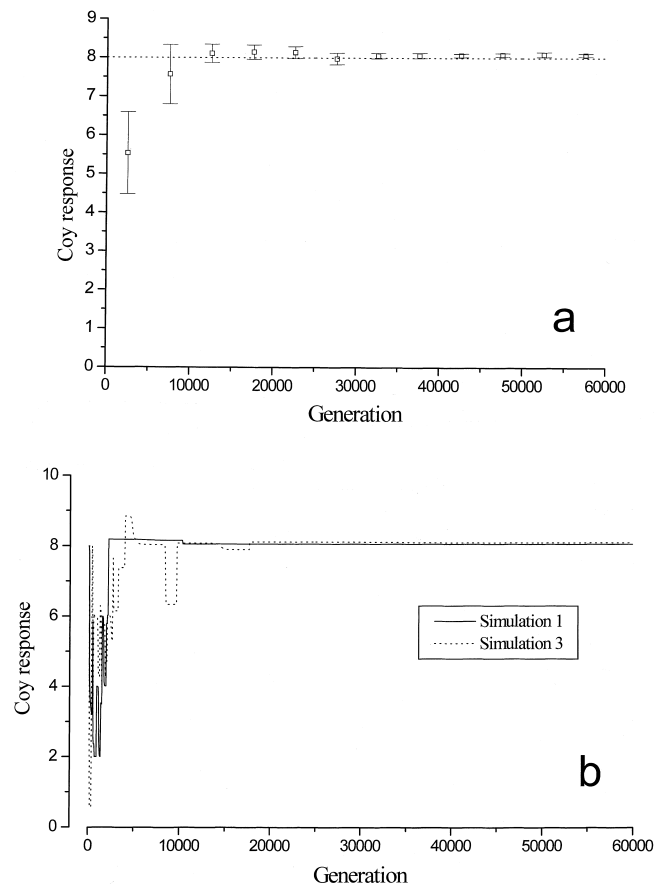
An interesting development of our model would be to let the time that the male stays in the presence of the female influence her reproductive decision. This would directly model the female assessment process. Philanders may be less attentive because they also are involved with other females. This would be one way to investigate the old pair-bond hypothesis



**Figure 4**  
Results from the coevolutionary simulations with a variable male. Variable males are able to successfully influence females' coy response. The graphs show the coy response of the most common female type. Optimal coy response is eight time steps, represented by the dotted line. Other parameter values are  $P_c = 0.12$ ,  $P_d = 0.48$ ,  $\delta = 0.15$ ,  $q = 0.2$ , and  $r = 0.03$ . (a) The average coy responses  $\pm$  SD of each 5000-generation interval from five coevolutionary simulations show that males are able to continually manipulate the females to reproduce already after between five and six time steps of coyness. (b) Results from simulations 1 and 3 show the coevolutionary process in detail. Periods of stability are mixed with periods of great turbulence. An interesting but occasional short-term effect of manipulation is that females might respond superoptimally.

(Armstrong, 1963, 1965; Huxley, 1923). A further possibility is to limit the number of males and to evolve their tendency to philander.

To summarize, we argue that courtship rituals evolve as a sender exploits biases in the receiver to influence the outcome of sender–receiver conflicts. According to our model, courtship is mainly manipulation and not an exchange of detailed information. It is important to notice that manipulation always is possible, although the degree of manipulation observed at any given time depends on how we choose to set the parameters. We may distinguish between two types of model parameters. The first type ( $q$ ,  $P_d$ ,  $P_c$ ,  $r$ , and  $\delta$ ) determines what is best for the female to do, thereby influencing the degree of conflict between males and females. When it pays the female to be more coy, the conflict increases as males always benefit from reproducing immediately. With growing conflict, the incentive for manipulation increases, which tends to result in more manipulation. The second type of parameters regulates the mutation processes, such as the number of new mutants per generation and the nature of these muta-



**Figure 5**  
Results from the coevolutionary simulations with a uniform male. The limited male is not very successful at influencing the female's coy response. The graphs show the most common female type's coy response. Optimal coy response is eight time steps, represented by the dotted line. Other parameter values are  $P_c = 0.12$ ,  $P_d = 0.48$ ,  $\delta = 0.15$ ,  $q = 0.2$ , and  $r = 0.03$ . (a) The average coy responses  $\pm$  SD of each 5000-generation interval from five coevolutionary simulations show that males, except for the first interval, are unable to in an important way manipulate the female. (b) Results from simulations 1 and 3 show the coevolutionary process in detail. Only occasionally does a male type appear that has some success at manipulating females. This success is short lived. Note that the relatively uncommon, but continuous changes in coyness after 20,000 generations are small and cannot be detected in the figure.

tions. Of key importance is the relative ability of males and females to adapt to each other. If mutation parameters are chosen so that favorable mutations appear at a faster rate in males than in females, we observe more manipulation than if favorable mutations appear faster in females. Note, however, as long as there is a conflict, new manipulative male signals will regularly evolve (Arak and Enquist, 1995). What varies is how quickly females counteradapt to these innovations. It is, of course, a weakness of our model that little is known about the relative evolutionary plasticity of senders and receivers in reality. Empirical observations of receivers range from those that seem completely fooled (e.g., foster parents that raise cuckoo chicks) to those that respond appropriately to subtle differences. In our simulation mutation parameters were chosen so that males and females evolved at similar rates.

A problem with testing our results is that some of our predictions coincide with those of models considering courtship as quality advertisement (Andersson, 1994; Zahavi, 1975, 1977). Both models predict a development of exaggerated sig-

nals in males and a preference for these signals in females. However, "good genes" models require that signals are costly and that only males of high quality can afford to develop the most extreme and the most preferred signals (Grafen, 1990; see also Krakauer and Johnstone, 1995). Our model, on the other hand, makes these predictions whether signals are costly or not and whether there is an important difference in quality or not (Enquist and Arak, 1998). In conclusion, our model offers an alternative explanation to male courtship sequences in monogamous species in which reproductive conflicts and the females' recognition mechanisms are key factors.

We thank Stefano Ghirlanda, Risa Rosenberg, Innes Cuthill, and two anonymous referees for suggestions and comments. This research was supported by grants from the Swedish Natural Science Research Council, from Marianne och Marcus Wallenbergs Stiftelse, from Riddarhuset, and from Wachtmeisterska släktföreningen.

## REFERENCES

- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Arak A, Enquist M, 1993. Hidden preferences and the evolution of signals. *Phil Trans R Soc Lond B* 340:207–213.
- Arak A, Enquist M, 1995. Conflict receiver bias and the evolution of signal form. *Phil Trans R Soc Lond B* 349:337–344.
- Armstrong EA, 1963. A study of bird song. London: Oxford University Press.
- Armstrong EA, 1965. Bird display and behaviour. New York: Dover.
- Basolo A, 1990. Female preference predates the evolution of the sword in swordtail fish. *Science* 250:808–810.
- Bastock M, 1967. Courtship: an ethological study. Chicago: Aldine.
- Breichagen T, Slagsvold T, 1988. Male polyterritoriality and female-female aggression in pied flycatcher, *Ficedula hypoleuca*. *Anim Behav* 36:604–606.
- Cullen JM, 1966. Reduction of ambiguity through ritualization. *Phil Trans R Soc Lond B* 251:363–374.
- Dawkins MS, Guilford T, 1995. An exaggerated preference for simple neural network models of signal evolution? *Proc R Soc Lond B* 261:357–360.
- Dawkins R, Krebs JR, 1978. Animal signals: information or manipulation? In: Behavioural ecology. An evolutionary approach (Krebs JR, Davies NB, eds). Oxford: Blackwell; 282–309.
- Eibl-Eibesfeldt I, 1975. Ethology. New York: Holt, Rinehart & Winston.
- Enquist M, Arak A, 1993. Selection of exaggerated male traits by female aesthetic senses. *Nature* 361:446–448.
- Enquist M, Arak A, 1994. Symmetry, beauty and evolution. *Nature* 372:169–172.
- Enquist M, Arak A, 1998. Neural representation and the evolution of signal form. In: Cognitive ecology. The evolutionary ecology of information processing and decision making (Dukas R, ed). Chicago: University of Chicago Press; 21–87.
- Enquist M, Johnstone R, 1997. Generalization and the evolution of symmetry preferences. *Proc R Soc Lond B* 264:1345–1348.
- Ghirlanda S, Enquist M, 1998. Artificial neural networks as models of stimulus control. *Anim Behav* 56:1383–1389.
- Grafen A, 1990. Biological signals as handicaps. *J Theor Biol* 144:517–546.
- Hertz J, Krogh A, Palmer RG, 1991. Introduction to the theory of neural computation. Redwood City, California: Addison-Wesley.
- Holland B, Rice W, 1998. Perspective chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* 52:1–7.
- Hurd PL, Wachtmeister C-A, Enquist M, 1995. Darwin's principle of antithesis revisited: a role for perceptual biases in the evolution of intraspecific signals. *Proc R Soc Lond B* 259:201–205.
- Hutchinson A, 1994. Algorithmic learning. Oxford: Clarendon Press.
- Huxley JS, 1914. The courtship-habits of the great crested grebe (*Podiceps cristatus*); with an addition to the theory of sexual selection. *Proc Zool Soc Lond* 35:491–562.
- Huxley JS, 1923. Courtship activities in the Red Throated Diver (*Colymbus stellatus* Pontopp.); together with a discussion of the evolution of courtship in birds. *J Linn Soc (Zool)* 35:253–292.
- Johnstone R, 1994. Female preferences for symmetrical males as a by-product of selection for mate recognition. *Nature* 372:172–175.
- Kraukauer DC, Johnstone R, 1995. The evolution of exploitation and honesty in animal communication: A model using artificial neural networks. *Proc R Soc Lond B* 348:355–361.
- Krebs JR, Dawkins R, 1984. Animal signals: Mind-reading and manipulation. In: Behavioural ecology. An evolutionary approach (Krebs JR, Davies NB, eds). Sunderland, Massachusetts: Sinauer Associates; 380–420.
- Lehrman DS, 1959. Hormonal responses to external stimuli in birds. *Ibis* 101:478–497.
- Lehrman DS, 1964. The reproductive behaviour of ring doves. *Sci Am* 211:48–54.
- Leimar O, Enquist M, Sillén-Tullberg B, 1986. The evolutionary stability of aposematic coloration and prey unprofitability: a theoretical model. *Am Nat* 128:469–490.
- Mackintosh NJ, 1974. The psychology of animal learning. London: Academic Press.
- O'Donald P, 1977. Theoretical aspects of sexual selection. *Theor Popul Biol* 12:298–334.
- Phelps M, Ryan MJ, 1998. Neural networks predict response biases of female túngara frogs. *Proc R Soc Lond B* 265:279–285.
- Ryan MJ, Fox JH, Wilczynski W, Rand AS, 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66–67.
- Ryan MJ, 1998. Sexual selection, receiver bias, and the evolution of sex differences. *Science* 281:1999–2003.
- Staddon JER, 1975. A note on the evolutionary significance of "supernormal" stimuli. *Am Nat* 109:541–545.
- Stenmark G, Slagsvold T, Lifjeld JT, 1988. Polygyny in pied flycatcher, *Ficedula hypoleuca*: a test of the deception hypothesis. *Anim Behav* 36:1646–1657.
- Tinbergen N, 1951. The study of instinct. Oxford: Clarendon Press.
- Trivers RL, 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man, 1871–1971 (Campbell B, ed). London: Heinemann; 136–179.
- Wachtmeister CA, Enquist M, 1999. The evolution of female coyness—trading time for information. *Ethology* 105:983–992.
- Zahavi A, 1975. Mate selection—a selection for a handicap. *J Theor Biol* 53:205–214.
- Zahavi A, 1977. The cost of honesty (further remarks on the handicap principle). *J Theor Biol* 67:603–605.