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## Deception: the correct path to enlightenment?

Determining whether an animal is being deceived by a signal is very difficult. In their recent *TREE* Perspective on behavioural deception, Semple and McComb<sup>1</sup> advocate a definition of deception that includes '...as the result of the behaviour of the signaller, the receiver registers a certain situation that is not in reality occurring.' To make this more operationally useful, they suggest a cost-benefit criterion: 'if the receiver pays no cost, or indeed derives benefit from the interaction, the application of the label "deception" is inappropriate.' Addressing the controversy over whether female pied flycatchers (*Ficedula hypoleuca*) are deceived about the status of already-mated males, they argue that deception requires that (1) secondary females pay a cost, and (2) they are unable to distinguish between mated and unmated males. Each of these requirements is problematic.

I'll address the 'unable to distinguish' requirement first. The problem with this is that it perpetuates the false dichotomy that signals are either distinguishable or not, honest or deceptive, beneficial or costly. This false dichotomy misses

all the important lessons from signal detection theory (SDT)<sup>2,3</sup>. SDT is a branch of bayesian decision theory that addresses situations where there is a loose correlation between appearance and quality. I applied SDT to the controversy over deception in pied flycatchers to establish the following points: (1) signals can have variable levels of partial discriminability, and (2) receivers can vary their discrimination by trading off the probabilities of different kinds of errors<sup>4,5</sup>. If female pied flycatchers seem to be only partially deceived, maybe it is because they are selective enough to reject some of the more obviously mated males but unwilling to pay the costs necessary to reject all of the less obviously mated males. They are using appearances to improve the odds but do not remove all the risk. It is not that they are unable to distinguish male status, but rather they are unwilling to pay the additional costs necessary to distinguish perfectly. This is a trade-off constraint, not an either-or dichotomy.

Now consider the 'pay a cost' requirement. Once we look at signal discrimination as gambling, the meaning of 'cost' becomes ambiguous. A wise gambler might read all the signals correctly, choose the best bet, correctly expect a positive payoff (on average) and yet lose the gamble. A female pied flycatcher might: (1) attend to all the available signals, (2) adjust her selectivity to optimize the trade-offs between search costs and

discrimination errors (misses and false alarms), and (3) lose the gamble (get an already mated male). Should we infer that these gamblers were deceived by the signals they used because they lost and paid a cost? First consider this: if they had done absolutely nothing differently but won, would we even ask if they were deceived? It would be a legitimate question. For all we know, many primary female pied flycatchers were deceived about the odds and just 'lucked out'. There might be no difference between some primary and secondary female pied flycatchers except luck.

I think we would make better progress on deception in animals if we could agree on its meaning in terms of the concepts of imperfect and incomplete information<sup>6</sup>. In behavioral mimicry, the receiver does not have perfect information about each model and mimic. However, it may have complete information about the model-mimic complex. If a signal allows a receiver to adjust correctly the odds, expected payoffs, and so on, it is not deceived by the signal or the complex as a whole.

This illustrates serious shortcomings in the original definition advocated by Semple and McComb. The 'registered situation' and 'reality' are both ill-defined. Both may refer to individual plays of the game or to the rules of the game itself. Suppose I travel to the island of liars and truth-tellers in search of enlightenment. I know

that half the inhabitants are liars and half are truth-tellers. I also know that one third of the liars wear a red hat and two thirds of the truth-tellers wear a red hat. When I come to a fork in the road there is a man in a red hat. I ask him which path leads to enlightenment. He says it is the path to the left. I take it and fail to find enlightenment. Was I deceived? How can you tell whether I have 'register[ed] a certain situation that is not in reality occurring'? This not the correct path to enlightenment.

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Semple and McComb<sup>1</sup> proposed that behavioral deception occurs only when senders benefit and receivers pay a cost as a result of their interaction. Except for stating that their definition of deception is functional, they did not explain why these fitness effects on senders and receivers are necessary conditions for deception.

The criterion of sender benefits apparently follows from the authors' focus on deception affected by signals – that is, traits that evolve because receiver responses increase sender fitness. Communicative interactions can also be mediated by responses to cues – that is, traits (of senders) that evolve for reasons other than possible fitness benefits due to receiver responses<sup>2</sup>. Hence, cues can elicit responses that are either beneficial or costly to senders. Some of these responses may be based on misperceptions or categorical mistakes, receiver errors of the kind that lead to deception in signal-response contexts. Semple and McComb's definition of deception does not accommodate misleading cues. Since signals may often originate as cues<sup>3,4</sup>, the definition would be difficult to apply in studies of the historical origins of deception.

The reasons why the authors included receiver costs in their definition are less clear. Here I raise two issues. First, responses to deceptive behavior are also made in at least one other context – that which receivers mistakenly take to be true when they are deceived (Semple and McComb give examples). While a receiver may pay a cost as a consequence of its response to a deceptive behavior, the response should result in a net fitness gain considering its effects on the receiver's fitness in all the contexts in which the receiver makes the response. This net benefit

maintains the response in spite of its cost in the deceptive context<sup>5,6</sup>.

Second, the criterion of receiver costs would exclude the possibility of deception in mutually beneficial interactions, such as the symbiosis between anemone fish and their host anemones. Anemone fish, and at least some of their hosts, benefit from living together, and the relationship appears to be maintained by deceit<sup>7</sup>. During settlement (host recognition may not involve deception<sup>8</sup>) juvenile anemone fish smear themselves with their host's mucus, as do adult fish that return to their host after a time away. The mucus coat inhibits nematocyst discharge probably because the anemone mistakenly categorizes the fish as self<sup>9</sup>. Another example may be the simulation of ant brood pheromones by seeds of various epiphytic plants<sup>10,11</sup>. The receiver cost criterion is especially problematic in cases of intraspecific deception, such as male courtship signals that mimic stimuli to which females are selected to respond in some other context, and thereby catch females in a sensory trap<sup>12</sup>. As Semple and McComb point out, it is often extremely difficult to identify receiver costs in such interactions, perhaps because receivers actually benefit when they are deceived<sup>13</sup>.

A definition of behavioral deception that excludes reference to the fitness effects of the interaction on senders and receivers may be most useful. At minimum, we would not need another term for interactions orphaned from deception because receivers do not pay a cost when they mistakenly respond to a signal as that which it is not. A white lie would still be a lie.

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## Reply from S. Semple and K. McComb

Getty and Christy object to the functional definition of behavioural deception that we advocated in our original article<sup>1</sup>. Before dealing with specific examples raised, we want to make two main points in response to their arguments. First, as is clear from its application in our paper, our definition refers only to individual interactions, not to the whole signalling system. Second, the requirement that deceived animals pay a cost is critical for any definition of functional deception in non-human animals. Since mental states are not observable, the situation registered by a receiver must be inferred from the cost of its subsequent behaviour. Any definition of deception that does not accept this premise is inherently untenable.

With respect to the 'deception hypothesis' of mate selection in pied flycatchers<sup>2</sup>, we maintain the position stated in our original article: it would be possible to determine whether or not individual females are deceived by measuring the cost of their choice. The hypothesis that females are deceived cannot be accepted at present because studies measuring the relevant cost<sup>1</sup> have not been undertaken. The occurrence of deception would absolutely not be precluded by a receiver's possessing perfect knowledge of the odds of the game (as Getty argues in this case). This becomes obvious if we consider the example of male fireflies, which might correctly assess the risk of responding to female signals but still be deceived by predatory 'femme fatale' mimics<sup>3</sup>.

Christy's example of the anemone fish symbiosis highlights the importance of ascertaining whether receivers pay a cost. The behaviour of the fish in establishing the symbiosis should be regarded as a mechanism of settlement; there is no need to invoke an explanation involving deception. Furthermore, we strongly disagree that consideration of receiver cost is not useful in determining whether male courtship signals are deceptive. 'Sensory traps'<sup>4</sup> should only be considered deceptive if females pay a cost for responding. If no cost needs to be shown, we must regard female preference (as the result of pre-existing sensory bias) for long<sup>5</sup> or symmetrical<sup>6</sup> tails as deception by males! Clearly, consideration of receiver cost is vital in determining which signalling interactions should be regarded as deception.

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