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Research Focus

Deception and the origin of honest signals

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Deceptive signals are a challenge to explain because on average, signals should be reliable. When being deceived is costly to the receiver, a coevolutionary struggle between senders and receivers can ensue. Recent work by Macías Garcia and Ramirez raises the intriguing possibility that through such a coevolutionary process, cheats can become honest.

A signalling paradox

The evolution of signals poses a paradox. Senders are expected to try to manipulate receivers for their own interests because the interests of senders and receivers will often conflict [1]. Yet, to elicit the desired response, signals must, on average, be reliable or honest [2]. Determining what maintains signal honesty and prevents 'cheats' has been a central problem in animal communication research for almost three decades. In the coevolutionary struggle between senders and receivers, 'cheating' or deception can, and does, occur. For instance, males can use deceptive 'sensory traps' to entice females to mate. These 'traps' are male signals that mimic stimuli to which females respond in a different context from courtship or mating [3], such as prey or other feeding stimuli. Such signals are inherently deceptive because females do not distinguish between the original stimulus (model) and the male signal (mimic).

Although the evidence that some signals originated as sensory traps is convincing (reviewed in [3]), explaining the evolutionary consequences of deception remains a challenge because these depend on the costs and benefits of deception to both senders and receivers. For instance, in systems where male signals mimic feeding stimuli [3–5], females are likely to suffer fitness costs from being deceived owing to reduced foraging efficiency, suboptimal mating or a combination of the two. Females are therefore expected to learn to distinguish the model from the mimic. In return, males might evolve more elaborate signals to continue to elicit a response from females. Recent research by Macías Garcia and Ramirez [6] suggests one intriguing outcome of such a coevolutionary process of male signal elaboration and female resistance. If only high-quality males can produce a sufficiently stimulating signal and females eventually base mating decisions on this trait, a signal that originated as a sensory trap could evolve into an honest signal of male quality.

Tasty and sexy

Males of several species of central Mexican fish belonging to the sub-family Goodeinae have conspicuous terminal yellow bands (TYBs) on their tails (Figure 1). As the tail undulates, the TYB resembles a yellow worm or larva, which form part of the diet of these fish. To establish whether TYBs evolved as a sensory trap that mimicked prey to attract females, Macías Garcia and Ramirez [6] conducted three experiments on six species that were chosen based on their phylogenetic position and presence or degree of TYB elaboration (Box 1).

The first experiment tested one important requirement of the sensory trap hypothesis: that female response to TYBs evolutionarily pre-dates the expression of the trait in males. The authors found that females of all species, including those basal in the phylogeny in which males lack a TYB, showed a strong preference for males with more conspicuous TYBs. In a second set of experiments (Box 1), Macías Garcia and Ramirez showed that TYBs also elicit foraging behaviours in males and females of all species, especially those lacking a conspicuous TYB. How strong are these feeding responses? The third experiment showed that in the most basal species lacking a TYB, fish preferentially approached and attacked a conspicuous TYB when presented with a choice of a conspicuous model TYB and a damsel fly larva (Box 1). Taken together, these experiments indicate that male TYBs evolved as a sensory trap, exploiting female feeding responses to lure potential mates.

From deception to honesty

For a deceptive signal to evolve into an honest signal, two requirements must be met. First, responses to the model and mimic must become uncoupled: females must stop being deceived. Second, females must base mating

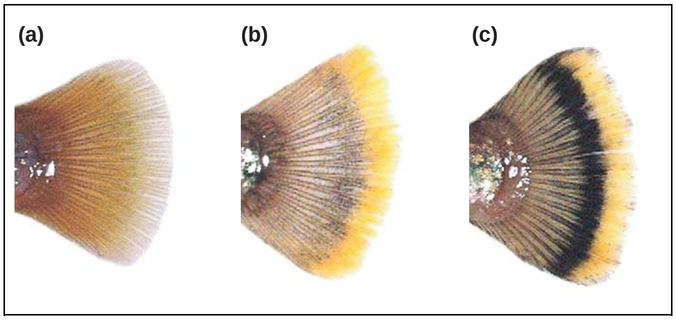

Figure 1. Variation in male terminal yellow band (TYBs) conspicuousness. *Xenotoca eiseni* **(a)** has no TYB, *Chapalichthys pardalis* **(b)** has a moderately conspicuous TYB, and *Ameca spendens* **(c)** has a highly conspicuous TYB, emphasized by the contrast with a sub-terminal black band. Reproduced with permission from Elvia Ramirez and Andrés Ocampo.

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Box 1. The experimental procedure

Study system

Macías Garcia and Ramirez used six species of fish belonging to the sub-family Goodeinae in their experimental set up [6]:

- *Characodon audax* (no TYB basal in the phylogeny)
- 'Xenotoca' eiseni (no TYB)
- *Xenoophorus captivus* (inconspicuous TYB)
- *Xenotoca variata* (moderately conspicuous TYB)
- *Chapalichthys pardalis* (highly conspicuous TYB)
- *Ameca splendens* (very highly conspicuous TYB)

Experiment 1. Female sexual responsiveness

Females of all species were presented with two conspecifics that differed in TYB conspicuousness. Mate preference was measured as frequency and duration of visits, a common measure of mate choice that is associated with mating probability in goodeid fish. In species with conspicuous TYBs (*X. variata*, *C. pardalis* and *A. splendens*), natural variation in male TYB conspicuousness was assessed. In addition, for all six species, preference for a normal conspecific and conspecific with a painted, more conspicuous TYB was assessed. Females consistently preferred males with more conspicuous TYBs in both natural and artificial TYB trials.

Experiment 2. Feeding responsiveness

Males and females of all species were presented with a male of a species with an equally or more conspicuous TYB (*X. variata* or *A. splendens* depending on the focal species) and a female *X. variata* without a conspicuous TYB. Only the tails of the stimulus fish were visible. Feeding responses were measured as duration and frequency of visits and frequency of bites. Both sexes of species without a conspicuous TYB bit conspicuous TYBs and all species visited conspicuous TYBs more often and for longer.

Experiment 3. Strength of feeding response

Male and female *C. audax* were presented with a male *X. variata* TYB and a damsel fly larva of similar length. Strength of feeding response was assessed as above. Overall, *C. audax* showed stronger feeding responses to the TYB than to the larva.

Experiment 4. Cost of conspicuous TYBs

Tail damage on *A. splendens* kept in outdoor ponds was quantified for males and females with similar-sized tail bands (females have inconspicuous TYBs). Male fins were also experimentally clipped and fin regeneration and weight loss assessed weekly over a two-month period. Males suffered significantly more damage to their tails, especially to the TYB, than did females. Males that had their fins experimentally clipped lost weight in proportion to the amount of tail tissue regenerated.

decisions on the trait because it is an indicator of male quality. What distinguishes Macías Garcia and Ramirez's study is the experimental demonstration that female responses to the model (prey items) and the mimic (male TYBs) have become uncoupled in species with conspicuous TYBs. Crucial to showing this was the comparison of feeding responses in species with increasingly elaborate TYBs (experiment 2). The strength of the feeding response (of both sexes) varied from frequent bites in species lacking TYBs to only some interest in species with conspicuous TYBs, indicating uncoupled responses in the latter. Importantly, by uncoupling responses to prey and TYBs, foraging efficiency is retained because fish continue to respond to a common prey item rather than increasing resistance to the male signal (mimic) as well as to the prey (model).

Although TYBs no longer elicit strong foraging behaviour in species with conspicuous TYBs, they do elicit a strong preference response (experiment 1). This suggests that females of these species have switched from perceiving TYBs as potential prey to perceiving them as an indicator of male sexual attractiveness. In a final experiment (Box 1), Macías Garcia and Ramirez tested whether TYBs are costly, and therefore honest, signals of male quality. The results confirmed that TYBs are costly because conspicuousness is positively associated with tail damage inflicted by conspecifics and tail regeneration is at the expense of body mass. If sexual and feeding responses to TYBs become entirely uncoupled, however, TYB costliness will be associated more with production costs (e.g. carotenoid limitation) and increased predation risk than with tail damage from conspecifics. To demonstrate conclusively that TYBs are honest signals of male quality, it must be shown that TYBs carry production or maintenance costs that are independent of conspecific tail damage and that male TYB conspicuousness is associated with female reproductive success. Macías Garcia and Ramirez's results do constitute convincing evidence, however, that a male signal currently used as a criterion for female mate choice has its evolutionary origins as a deceptive sensory trap.

Evolutionary possibilities

Traditionally, evolutionary biologists interested in animal signals have focused on the question of signal honesty and prevention of cheating [2]. As a corollary, several theoretical studies have examined the conditions under which cheating can arise, spread and become evolutionarily stable [1,7]. The study by Macías Garcia and Ramirez adds another dimension: can cheats become honest? These questions can only be answered by understanding costs and benefits to both senders and receivers (Figure 2).

In large part, the evolutionary response of receivers to deceptive signals will depend on whether the receiver suffers a fitness reduction as a consequence of being deceived (Figure 2). In all cases of deceptive signalling, the signaller gains a fitness benefit [8]. Whether the receiver must pay a fitness cost for the signal to qualify as deception has been the subject of much debate [8–10]. Some authors have argued that deceptive signals, such as sensory traps, might reduce the costs of mate searching and therefore be retained because they are, on average, cost-free or even beneficial to females [3,11]. In most cases, however, being deceived is likely to be costly [8]. In the case of male signals mimicking prey or feeding stimuli, reduction in foraging efficiency might represent an important and underappreciated cost of being deceived.

If the receiver pays a significant cost, there will be selection for the receiver to resist dishonest signals (Figure 2). The ensuing coevolutionary process of signal elaboration and receiver resistance to the signal might not necessarily result in the evolution of an honest signalling system (Figure 2). In the context of mating signals, another possibility is that females become resistant to the signal and base their reproductive decisions on completely different male traits [5,12]. Nevertheless, the study by Macías Garcia and Ramirez reminds us that processes governing the origin and current evolutionary maintenance or stability of a signal can differ (see [13]).

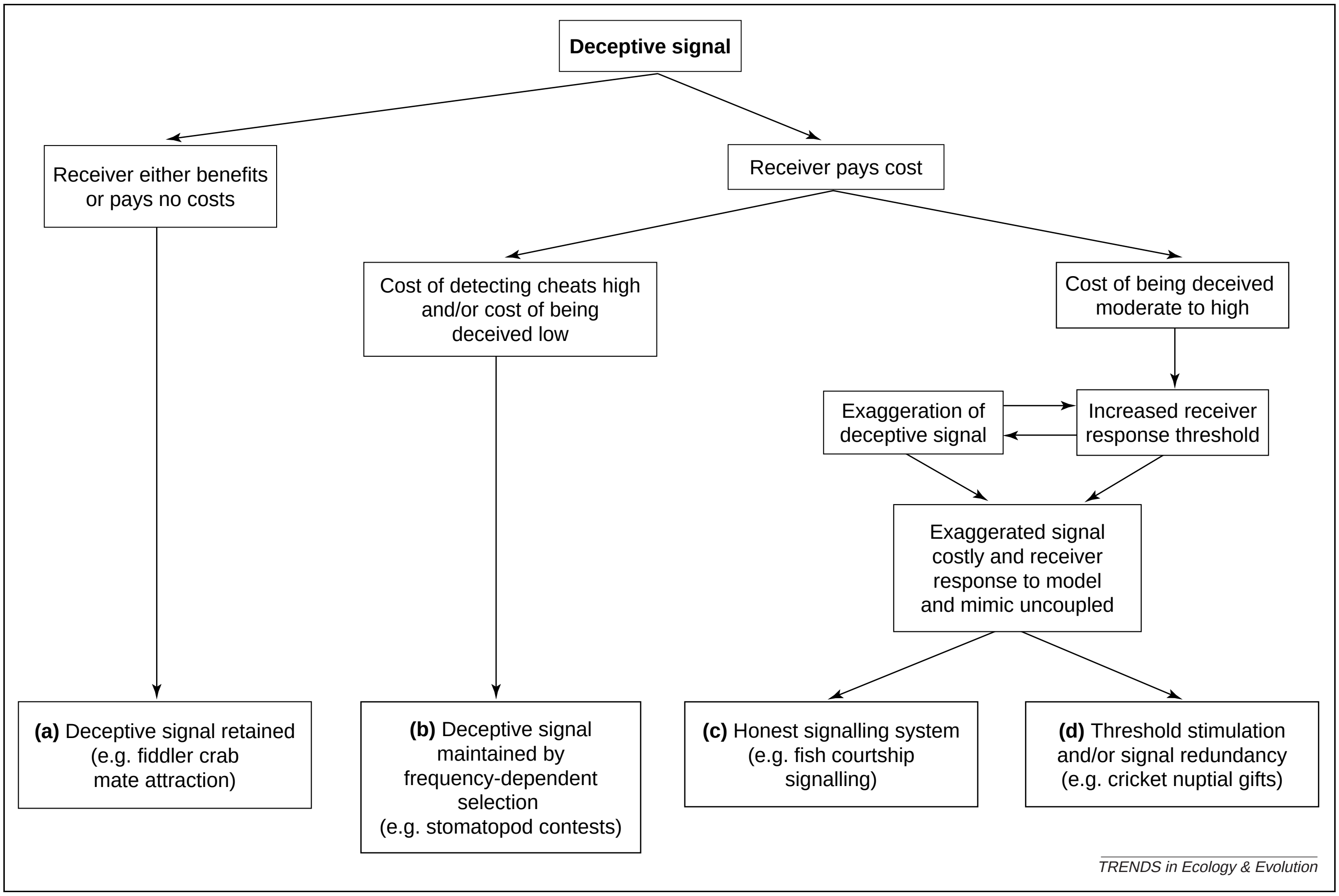

Figure 2. Evolutionary trajectories of deceptive signals. If the receiver pays no cost, or even benefits, selection will favour the retention of the deceptive signal [3,14]. If the receiver pays a cost, there will be selection for the receiver to resist dishonest signals and distinguish honest signallers from cheats. Once the cost of accurate detection and/or the benefit of responding to the original stimulus (model) outweighs, on average, the cost of being deceived, the deceptive signal might be maintained at low to moderate frequencies by frequency-dependent selection [7,15]. Alternatively, a coevolutionary process of signal elaboration and receiver resistance might ensue, leading either to the evolution of an honest signalling system [6], to signal redundancy, or to the signal being maintained as a minimum threshold requirement to attract females [5].

Both must be considered if we are to understand the remarkable diversity of animal signalling systems.

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References

1 Dawkins, M.S. and Guilford, T. (1991) The corruption of honest signalling. *Anim. Behav.* 41, 865–873
2 Maynard Smith, J. and Harper, D. (2003) *Animal Signals*, Oxford University Press
3 Christy, J.H. (1995) Mimicry, mate choice, and the sensory trap hypothesis. *Am. Nat.* 146, 171–181
4 Proctor, H.C. (1991) Courtship in the water mite *Neumania papillator*: males capitalise on female adaptations for predation. *Anim. Behav.* 42, 589–598
5 Sakaluk, S.K. (2000) Sensory exploitation as an evolutionary origin to nuptial food gifts in insects. *Proc. Biol. Sci.* 267, 339–343
6 Macías Garcia, C. and Ramirez, E. (2005) Evidence that sensory traps can evolve into honest signals. *Nature* 434, 501–505
7 Szamado, S. (2000) Cheating as a mixed strategy in a simple model of aggressive communication. *Anim. Behav.* 59, 221–230
8 Semple, S. and McComb, K. (1996) Behavioural deception. *Trends Ecol. Evol.* 11, 434–437
9 Christy, J.H. (1997) Deception: the correct path to enlightenment? *Trends Ecol. Evol.* 12, 160–160
10 Getty, T. (1997) Deception: the correct path to enlightenment? *Trends Ecol. Evol.* 12, 159–160
11 Dawkins, M.S. and Guilford, T. (1996) Sensory bias and the adaptiveness of female choice. *Am. Nat.* 148, 937–942
12 Candolin, U. (2003) The use of multiple cues in mate choice. *Biol. Rev. Camb. Philos. Soc.* 78, 575–595
13 LeBas, N.R. *et al*. (2003) Nonlinear and correlational sexual selection on 'honest' female ornamentation. *Proc. Biol. Sci.* 270, 2159–2165
14 Christy, J.H. *et al*. (2003) Attractiveness of sand hoods built by courting male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis. *Anim. Behav.* 66, 89–94
15 Steger, R. and Caldwell, R.L. (1983) Intraspecific deception by bluffing – a defense strategy of newly molted stomatopods (Arthropoda, Crustacea). *Science* 221, 558–560

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