



Nosy neighbours

By snooping on one another's social lives, animals can work out how to behave when they meet in the future. John Whitfield listens in on the natural world's eavesdroppers.

Nosiness isn't nice. But in the past few years, behavioural biologists have shown the trait in a more positive and intriguing light. Animals from fish to songbirds, they have found, can achieve success by keeping watch on their neighbours' social lives. Such eavesdropping may also be woven into the fabric of human societies — and might even help to explain why people often behave charitably.

Prying animals reap significant rewards. They know when to pick a fight and when to back down; who to mate with, and who to cuckold. Not surprisingly, perhaps, researchers have also found that animals behave differently depending on who is watching or listening. Animal communication, experts are coming to realize, has evolved to fit into a social network, rather than being a collection of signals intended simply to impress a particular mate or rival¹.

Eavesdropping shows “how incredibly subtle animal strategies are”, says evolutionary biologist Lee Dugatkin of the University of Louisville in Kentucky. This subtlety explains why it went unnoticed until recently — it's tricky to design experiments to tease out the effects on one animal of watching other animals interact. Peter McGregor, a behavioural ecologist at the University of Copenhagen in Denmark, suggests that researchers may also have neglected such experiments because they underestimated animals' cunning. “For most people, fish don't rate when it comes to cognitive abilities,” he observes.

Yet McGregor's team has shown that Siamese fighting fish (*Betta splendens*), pictured above, possess considerable social nous. Males of this famously aggressive species defend their territories with displays of fin-waving and gill-raising. But if this doesn't settle matters, things turn physical — sometimes fatally so.

Like human boxers, Siamese fighting fish study their opponents' previous bouts. Males pay more attention to their neighbours when they fight than at other times, McGregor and his colleagues found. And after viewing such contests, males approach the winners more warily than they do the losers, relying more on visual displays and less on biting².

Verbal abuse

Some researchers have questioned whether such experiments prove that bystanders scrutinize the interaction between opponents — they might be responding to the animals' inherent toughness or weediness. McGregor's team tackled this issue in great tits (*Parus major*) by using recordings of the birds' songs. To a male great tit, victory is a question of timing. A male threatens a rival by singing over his song, and shows deference by singing only in the gaps between the other's choruses. This allowed the researchers to use the same songs, regardless of any intrinsic property they might have, to denote attack or defence, belligerence or tact.

Setting up two loudspeakers outside a male's territory, the researchers played out

duets of differing structures and outcomes. They then moved either the winning or losing speaker into the bird's territory, and noted his reaction. Males sang less to losers³, perhaps because they regard them as less of a threat, or perhaps because they are more ready to escalate contests with losers to visual displays or violence. A winner got the same cautious treatment as a stranger.

Playback experiments with nightingales (*Luscinia megarhynchos*) yield similar results — except that males intensify their singing towards winners, rather than giving losers the silent treatment^{4,5}. Again, it is hard to know whether the differences reflect a more, or less, aggressive response. “The interpretation can go into hand-waving,” McGregor admits. But in each case, it is clear that eavesdropping influences the animals' subsequent behaviour.

Watching a fight also changes physiology. Cichlid fish (*Oreochromis mossambicus*) that



Nosiness alters physiology, says Lee Dugatkin.

see a contest experience a rush of testosterone, perhaps priming them to fight⁶. Dugatkin believes that the next challenge is to integrate behavioural and physiological data on eavesdropping. “There are very few studies looking at the physiology and behaviour of one system,” he says. “I think that synthesis is going to happen soon.”

Males are not the only



Daniel Mennill found that female black-capped chickadees will cheat on mates that lose fights.

ones noting the results of their neighbours' squabbles — females use the same information to help them to choose their mates. Again using song playback, McGregor's team escalated contests with some male great tits, while backing down against those on neighbouring territories. Subsequently, the mates of defeated males were more likely to visit the adjacent territory⁷. Seemingly disenchanted with their partner — but impressed by what they heard coming from next door — the females were presumably seeking what behav-

oural ecologists call 'extra-pair copulations'.

Experiments on a closely related species lend support to this idea. Daniel Mennill of Queen's University in Kingston, Ontario, and his colleagues picked playback fights with male black-capped chickadees (*Poecile atricapillus*), and then analysed the DNA of the chicks born to their mates. The researchers found that the female partners of defeated males were about five times more likely to lay eggs fertilized by other males, compared with females who never heard their partner get beaten⁸.

Covert struggle

With such high stakes, it is likely that eavesdroppers have shaped the evolution of animal communication. Some behaviours seem adapted to avoid prying ears. In many songbirds, says Mennill, the longest, most evenly matched song duels are the quietest. Where both males are struggling to dominate, he suggests, "they might not want to broadcast what's going on".

The effect of an audience on animals' social interactions is harder to study than eavesdropping, and this work is at an early stage. Again working with fighting fish, McGregor's team has found that males display to each other differently when a female is watching⁹. They reduce their aggression, and switch to conspicuous displays incorporating some of the elements used in courting, such as tail waving. And in July, Michael Kidd of the University of New Hampshire in Durham told the Animal Behavior Society's annual meeting at Indiana University in Bloomington that defeated male fighting fish prefer to court females that didn't witness their humiliation. "They have a fairly strong preference for females that didn't see them lose," says Kidd.

Eavesdropping is thought to help animals to avoid fights they cannot win. But paradoxically, eavesdroppers might make contests more aggressive, according to evolutionary biologist Rufus Johnstone of the University of Cambridge, UK. He used game theory to analyse the costs and benefits of winning and

losing fights, and of backing down quickly versus a prolonged tussle. Eavesdroppers, he found, increase the value of victory: an animal that wins its current contest will get the deterrent benefit of a tough-guy reputation, and so is more likely to escalate a fight¹⁰. "Eavesdropping can evolve to reduce the risk of fighting, but once it becomes established it promotes aggression," says Johnstone.

Replace acts of violence with ones of charity, and Johnstone's model becomes similar to those used to explain apparently selfless kindness. We often help people we are unlikely to meet again. One reason might be that good deeds get their perpetrator a glowing reputation that helps them in the future. Theoretical models suggest that altruism can survive in populations where individuals trust those they have seen cooperate with others, but give nothing to those they have seen behave selfishly¹¹.

Research by Manfred Milinski, a behavioural ecologist at the Max Planck Institute for Limnology in Plön, Germany, and his colleagues supports this idea. In one experiment, volunteers were given money and told they could donate some of it to the other participants over a series of rounds. This benefited the recipients more than the donors, because the experimenters supplemented each donation. Even though participants could not donate to someone who had given to them, they were more generous towards those who they had seen give to others¹². In another game, Milinski found that people were more likely to contribute to a public fund if their enhanced reputation could be used to attract private donations from other players¹³.

The behavioural science of eavesdropping might soon be tested in the human social marketplace. Milinski's research has attracted the attention of managers trying to control demands on Germany's health service. He suggests that doctors could publish lists of how many treatments they have prescribed and how much each has cost. Even without naming names, Milinski argues, people might be so concerned about gaining a bad reputation that they will be shamed out of seeking needless medical attention. "If peoples' reputation is at stake they are much more cooperative," he says. ■

John Whitfield works in Nature's news syndication team.

1. McGregor, P. K. & Peake, T. M. *Acta Ethol.* **2**, 71–81 (2000).
2. Oliveira, R. F., McGregor, P. K. & Latruffe, C. *Proc. R. Soc. Lond. B* **265**, 1045–1049 (1998).
3. Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. *Proc. R. Soc. Lond. B* **268**, 1183–1187 (2001).
4. Naguib, M. & Todt, D. *Anim. Behav.* **54**, 1535–1543 (1997).
5. Naguib, M., Fichtel, C. & Todt, D. *Proc. R. Soc. Lond. B* **266**, 537–542 (1999).
6. Oliveira, R. F., Lopes, M., Carneiro, L. A. & Canário, A. V. M. *Nature* **409**, 475 (2001).
7. Otter, K. *et al. Proc. R. Soc. Lond. B* **266**, 1305–1309 (1999).
8. Mennill, D. J., Ratcliffe, L. M. & Boag, P. T. *Science* **296**, 873 (2002).
9. Doutrelant, C., McGregor, P. K. & Oliveira, R. F. *Behav. Ecol.* **12**, 283–286 (2001).
10. Johnstone, R. A. *Proc. Natl Acad. Sci. USA* **98**, 9177–9180 (2001).
11. Nowak, M. A. & Sigmund, K. *Nature* **393**, 573–577 (1998).
12. Wedekind, C. & Milinski, M. *Science* **288**, 850–852 (2000).
13. Milinski, M., Semmann, D. & Krambeck, H.-J. *Nature* **415**, 424–426 (2002).



Good guys win: Manfred Milinski has shown that we help those with a charitable reputation.