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A switch to the hedonic mode

Most readers of ASCAP must by now be familiar with the concept of the "two modes", the brainchild of our first ASCAP president, Michael Chance. Every now and then one comes across a description of the two modes, and sometimes of switching from one mode to the other, using other language; and then I am impressed how the two mode concept is invariably a better descriptor than the language used by other theorists.

A short "filler" in the British Medical Journal described what I think is a switch from the agonic to the hedonic mode. Tony Fox from Rancho la Costa in California put up a humming bird feeder in his new house. He wrote (1):

> "...within five minutes of feeder installation, the first humming bird arrived. Within two hours, five of them were competing for this new food source hanging under the eaves of our house.
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> "Usually, humming birds are extremely territorial. A dominant male will vigorously defend, for hours on end, an artificial feeder, or even a single fuscia plant. To my surprise, the dominant hummingbird at this new house had an entirely different strategy from the one who was king of the feeder at the old place. This new chap sat on top of the feeder, thus being dubbed Snoopy by our young German guests, and drove off any competitor who attempted to feed three inches below. The boss at the old house perched and chirped in a nearby tree, and attacked his competitors at high speed, developed by diving from his sentinel position.
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> "And then it happened. Just after sunset, the belligerent Snoopy permitted no fewer than five other hummingbirds to share the four feeding apertures. In a moment, the ingrained, reproducible behaviour of a unique hummingbird had changed into exactly the opposite."

This switch from intimidation to sharing is the sort of thing we mean by a switch from the agonic to the hedonic mode, and the fact that it occurs in nature, and can be recognised as a category of behavioural change, is, I think, further justification for the "two mode" concept.

The vignette also describes two types of within-species variation in behaviour: the old despot and the new despot had different perching strategies; and, secondly, only the new despot manifested the agonic/hedonic switch.

The reason for the switch, and possibly for the variation in switching, is given by the author:

> "Hummingbirds need a lot of food in the evening. They then roost and drop their body temperature. This bedtime calorie load and reduced metabolic rate enables them to survive the night."

Comment

It looks as though the dominant hummingbird was in a trade-off situation between personal fitness and inclusive fitness. Although he wanted all the nectar for himself, when the time came near to roosting, he maybe could not finish it all himself, and he could afford to share it with his competitors, who may have been close relatives, in order to help them too to survive the night. He could assume that when he awoke from sleep the next morning, the fuscia/feeder would have replenished the supply of food, and then he could feed greedily and selfishly alone.

In red grouse the dominant territory owners defend their territories for the first two hours of the day, driving off male rivals, females and juveniles; after that they allow subordinates to feed freely on their patches (2). This is also a switch from the agonic to the hedonic mode, and perhaps evolved for the same reason as the hummingbird switch. Individual variation in this behaviour has not been reported in red grouse (but should be looked for).

Some animals like the wolf spend the breeding season in the agonic mode and then revert to the hedonic mode when not breeding. One lemur, once a year, switches to the hedonic mode at full moon (3).

When behavioural variation occurs within a species, we look for the operation of negative frequency dependent selection. If a behaviour becomes more successful as it gets rarer, variation will be maintained; but if the opposite occurs, variation will be selected out, and then we tend to see variation between closely related species. It seems likely that the agonic/hedonic switch would show positive frequency dependent selection, because a single despot showing mercy to subordinates would be crowded out and would be likely to fare badly. Our deduction from this is that the hummingbird despots in the old

and the new houses were from different species. What about it, hummingbird aficionados?

The two modes revisited

In the agonic mode, the individual is oriented towards agonistic behaviour (fighting, fleeing or submitting). In the hedonic mode, the individual is oriented towards a task, such as feeding or nest-building, or, in relation to conspecifics, towards co-operating, sharing or mating. In most animals, social competition is synonymous with the agonic mode, while the hedonic mode is characterised by co-operation, or at least mutual tolerance.

In our own species, however, and to some extent in chimpanzees, competition also takes place in the hedonic mode - we have called this prestige competition - and it is characterised by being attractive to fellow group members who act as a sort of panel of judges or evaluators, allocating differential prestige to all group members. This results in a status hierarchy of prestige which may be different from the dominance hierarchy based on intimidation, in both humans and chimpanzees.

Since humans can compete in the hedonic mode, we need to spend less time in the agonic mode. In fact, we do not need the agonic mode at all, but it is with us in the way that other obsolete characters are. Animals who are unable to compete in the hedonic mode need the agonic mode to sort out their differences of opinion about territory and rank, as is the case with the red grouse; but the quicker they can get it over with it, the better. Other species, such as the hummingbird, not only use the agonic mode to create asymmetry between dominants and subordinates, but also use it to maintain differential payoffs between dominants and subordinates - possibly because nectar is scarcer for the hummingbird than heather for the grouse. And so the red grouse can enjoy over twelve hours of hedonic mode per day, compared with half an hour or so for the hummingbird.

Just as groups can be in one or other mode, so dyadic relationships (such as marriage) can switch backwards and forwards between the two modes. Switching to the agonic mode is called "having a row". Switching back to the hedonic mode is called reconciliation. The Iranians even have names for the two states: the agonic mode in a relationship is called "qahr", the hedonic mode "ashti"; everyone knows which relationships are in qahr and which in ashti, and there are appropriate roles, such as mediator, for friends to adopt.

One important difference between a group and a dyad is that in a private relationship there can be no prestige competition (because there are no spectators/evaluators/judges). Therefore the main work of competition (allocation of rank and territory) has to be decided by other means, either by fighting or by negotiation. Because negotiation is so difficult (and recent in evolutionary terms), disputes are often settled by fighting. Which is why "marital disharmony" is so common.

The whole question of society's attitude to marital disharmony and dominance problems is fascinating. Pope caught the enigma well:

> She who ne'er answers till a husband cools,
> Or, if she rules him, never shows she rules;
> Charms by accepting, by submitting sways,
> Yet has her humour most, when she obeys.
>
> POPE (Epistles to several persons. Epistle 2: To a Lady)

There are adages such as "only a fool interferes between husband and wife". Of course, society lays down general guidelines about who should be dominant, and until recently it was the husband. This clear instruction must have saved a lot of fighting, at the cost of undesired subordination on the part of wives. But there were anomalous examples, such as Bishop Proudie and his wife portrayed by Trollope, and other cases in which the wife gained power by ingenious means. But the failsafe was fighting, and this is the ultimate cause of the paradoxical situation that agonistic behaviour which evolved as a male characteristic, or at least as intrasexual behaviour related to sexual selection, is now seen predominantly between the sexes, in situations in which sexual selection is not occurring. As they say in Mexico, "Marriage is the only war where one sleeps with the enemy."

1. Fox T: A salutary lesson: patients sometimes behave like our Snoopy. British Medical Journal, 1999;318:1131.

2. Wynne-Edwards VC: Social selection in Lagopus scoticus. In DC Glass (Ed.): Genetics (Biology and Behavior Series), New York: Rockefeller University Press, 1968, pp. 143-164.

3. Jolly A: Evolution of Primate Behaviour. New York: Macmillan, 1985.