More about voles

Further reply to A. Randrup & G. Sorenson

ASCAP (somewhere)

I am impressed by the great variation in hierarchical behaviour both within and between species, such that in some hierarchies to be subordinate gives rise to no problems, whereas in others the subordinate role seems to be one of continuous terror and humiliation. In your own work with bank voles (1), you found that an enriched environment greatly reduced the "putting down" of subordinates by high ranking voles; but even in the enriched environment there was one tyrant who persecuted the subordinate for no apparent reason, and in the pernicious environment some hierarchies were peaceful. In many species the unprovoked bullying of subordinates is enough to induce a state of learned helplessness - no electrified grid is necessary in these species. In some species there are physiological effects in subordinates which seem an important part of their adaptation; inhibition of sex change in certain fish, adoption of juvenile colouring in lizards, inhibition of ovulation in mice and some New World monkeys; we do not know the mechanisms of these changes, nor whether they are related to the central nervous mechanisms responsible for psychogenic death. Nor do we know whether hypertension and other causes of psychogenic death are entirely mediated by the increased secretion of corticosteroids and/or catecholamines which are recognised accompaniments of subordinate status. Research on subordination has a long way to go; at present it seems to be mainly motivated by cadiologists, gastroenterologists, nephrologists and more recently immunologists; only in Denmark is it realised that psychological problems may intervene between aversive social experiences and serious physical disease.

I would agree with you that subordination is not pathogenic in itself: only in certain circumstances. These circumstances would seem to be:

1. If the environment is unfavourable so that agonistic interactions are increased.
2. If the higher ranking individual is a bully or lacks the social skill to accept submission.
3. If the individual lacks the social skill to submit adequately (or does not wish to submit) or lacks other skills for coping with subordination such as the stereotypies in your voles.

It might clarify things if we reserved the term submission for voluntary acceptance of subordination, in contrast to its involuntary depressive counterpart, which could be called depressive yielding. The title of my essay was confusing, suggesting that depression masquerading as physical illness was a metaphor of submission, whereas, being totallly involuntary, it should not have come into the category of submission at all. The title should have been "Metaphors of yielding." If you submit voluntarily, you do not need to undergo depressive yielding.

Report from the Institute of Zoology in London

After writing the above, I attended a meeting of the Association for the Study of Animal Behaviour at the London Zoo. The subject was "Neural and Endocrine Mechanisms in the Control of Behaviour." Three of the talks were relevant to the above discussion and I would like to share with you my somewhat patchy memory of them.

Norbert Sachser from Bayreuth in Germany described his work on captive colonies of guinea pigs. Two dozen mixed sexed animals kept in a 12 metre square enclosure develop a stable social structure in which there is social asymmetry among the males but not among the females. About three males become territorial males, relating to half a dozen females; each territorial male has two or three satellite males, who each relate to two or three only of the territorial male's females. Other males occupy the space between the territories and do not relate to any females. There is little fighting and the territorial males do not try to mate with each other's females, even if they stray onto their territories. There is no difference in adrenal cortical or medullary function or in testosterone levels between the three categories of males.

If two strange males are caged together with a strange female, the outcome depends on the social history of the males. If they have been brought up with other males, there is a day or two of intense fighting and then one submits and becomes a satellite male, and the fighting stops. If the two males have been brought up with females only, the fighting goes on and the loser dies, not of wounds but of metabolic disorder; it seems that the losing male has never learned to submit. Without this learning experience, the guinea pigs are like those of von Holst's losing tree shrews who hid away and died; with learning, the guinea pigs did much better as the adrenomedullary function of the losers returned to normal, unlike that of the other category of losing shrews who became uneasy subordinates. It seems that some animals like the wolf and the rhesus monkey have an innate capacity for submission, others like the guinea pig have the capacity to learn submission, others like the tree shrew and the male patas monkey lack the capacity to learn submission. This no doubt reflects social structure during evolution. The wolf always lived in groups, the tree shrew always lived in territorial pairs, the guinea pig had a more flexible social structure. John Crook once said: "Ecology determines social structure which determines personality."

One finding in the guinea pig work deserves special mention. When two strange group-reared animals are matched in a fight, the first clue to the outcome of the fight is a huge increase in adrenocortical activity in the eventual loser; at the same time the winner-to-be and the female make mutual courtship gestures; both these changes occur before there is any differentiation in the agonistic behaviour of the two males. This suggests at least two possibilities. One is that the winner-to-be is emitting an olfactory agonistic signal. The other is that the corticosteroid response to the stress of fighting is part of a feed-back loop which triggers the decision to lose in the eventual loser; this would fit in with the ideas of Leshner (2) and his findings that adrenalectomised mice show delayed losing, and normal mice injected with ACTH or cortisone show exaggerated losing behaviour.

The other two relevant talks concerned the social suppression of ovulation. Dave Abbott, recently moved from the London Zoo to Wisconsin Primate Centre, described his work on the marmoset. In a group of marmosets there are separate male and female linear hierarchies, and only the alpha male and female mate. The subordinate females have low serum LH and undeveloped ovaries. The mechanism that blocks sexual development is a scent emitted by the alpha female, as anosmic subordinate females ovulate normally (unless they have been subordinate for a long time). Subordinate females with apparatus that administered intermittent subcutaneous doses of gonadotrophin releasing hormone also ovulated normally.

Chris Faulkes of the Institute of Zoology described his work on captive naked mole rats, in which the situation seems to be very similar to the marmoset, except that it has not been shown conclusively that the suppression is effected by a scent from the alpha female. The degree of suppression is prodigious: one "queen" may suppress a hundred subordinate females for as long as fifteen years; the junior subordinates dig tunnels and collect roots and tubers which they bring back to the queen in the nest chamber; the senior subordinates protect the colony from snakes and other predators. In the subordinate females the preoptic area of the hypothalamus is loaded with gonadotrophin releasing hormone (more so even than the alpha female) but it is not released.

I think the guinea pig, the marmoset and the mole rat are instructive examples of subordinate behaviour but I do not think they offer promising animal models of human depression. Human depression has a long time scale and a momentum of its own once it has started; in all the cases described above the subordinate animals return to normal as soon as they can get away from the dominant animals. Male guinea pigs whose sexual behaviour has been suppressed for many months start mating within minutes when put on their own with a female. And the female marmosets start ovulating straight away. The suppressed males have motile sperms - this is necessary because it takes six weeks to manufacture a sperm, whereas ovulation can occur quickly enough to allow fertilisation from a mating occurring immediately after release from suppression; in this way a suppressed couple which suddenly obtains a territory can achieve a fertile mating without delay. Unlike depression, these rodent forms of subordination are mediated by olfaction, and the subordination depends on the continued presence of the olfactory stimulus; this seems to be true of rodent subordination generally. In "depressed" dogs and vervet monkeys the behavioural change is not contingent on the continued presence of a dominant animal. Also, the strategy is different in the two cases: the subordinate rodent is waiting to get away, and alert for the opportunity to do so. The human undergoing depressive yielding is learning to adjust to an unfavourable social situation (lowered social status) and is not alert about anything. My guess is that vertebrates have only one mechanism for making a long-term behavioural response to an unfavourable situation; rodents have used this for responding to unfavourable weather; primates, and possibly other orders, have used it for responding to social adversity. But I am probably wrong, and even if the guess were correct, I think this work on rodent agonistic behaviour is of great importance for a science of social behaviour basic to the study of psychopathology, and we should add our psychiatric voice to the cardiologists and reproductive physiologists who are supporting it.

1. Sorenson, G. (1987) Stereotyped behaviour, hyperaggressiveness and "tyrannic" hierarchy induced in bank voles (Clethrionomys glareolus) by a restricted cage milieu. Progress in Neuro-psychopharmacology and Biological Psychiatry, 11, 9-21.

2. Leshner, A.I. (1983) The hormonal responses to competition and their behavioral significance. In Hormones and Aggressive Behavior Ed. by B.B.Svare. New York: Plenum Press.