Dear Russ and Mark, One of the advantages of being in Goa is that there is time to read (it being too hot to do anything else!) and I have just finished:

Sapolsky, Robert M. (2001) A Primate's Memoir: Love, Death and Baboons in East Africa. London: Jonathan Cape.

And thoroughly recommend it. The style is very racy but the content is fascinating. He describes a wild troop of olive baboons that he studied for several years, measuring their blood steroids, and finding them correlated with low rank, fighting and lack of affiliation. I wrote to him some years ago and asked him whether he had been able to confirm Michael McGuire's findings on blood serotonin, but he replied that he was not able to take enough blood for serotonin estimations, which I think was a mistake on his part as the serotonin finding is much more interesting than the corticosteroid one, which was more or less predictable. Anyway, his description of the hierarchy of this baboon troop is riveting, and he makes clear how the loss of rank on the part of an alpha can be a very variable thing, from the total collapse of Saul, who had been alpha for three years, to the much less serious reactions of the "group of six" who deposed him, and among whom the alpha position changed frequently over the next couple of years. Schjelderup-Ebbe made the same point about deposed alpha birds – it was the ones who had been alpha for a long time that had the worst depressive reactions. Sapolsky describes the different ways that subordinate baboons cope with low rank – surprisingly varied. He uses the term "moping" to describe the mental state after loss of rank, and I think this is the zoologist's term for depression in animals – Wynne-Edwards used it for the Scottish red grouse who lost their territories or failed to get them. Quite apart from the baboons, his descriptions of his adventures in Africa are well worth reading.

Added later: reflections after reading Robert Sapolsky's book:

1. What courage it must have taken to do all the things he described.
2. How well he writes – his style is racy but he gets away with it.
3. How corrupt Kenyan society is, from the very top to the very bottom.
4. How important the hierarchy is to the baboon troop.
5. How varied are the strategies adopted by the males – I suspect this is due to interbreeding between subspecies which have different social structures (olives, geladas, hamadryas).
6. How catastrophic the loss of the alpha position may be (but not always).
7. He observed one instance in which total submission was not enough to turn away the wrath of the victor – the defeated baboon presented his behind in the usual way, and the winner then slashed it with his canines. This was one instance in many years of observation – the winner had a reputation as a vicious character!
8. How devastating is the effect of bovine tuberculosis on the baboon body.
9. What a shame it was he did not measure serotonin.
10. His observations support our theory about the relation between mood and hierarchy.

I have also been reading:

Maynard Smith, J. & Harper, D.G.C. (1988) The evolution of aggression: can selection generate variability? Philosophical Transactions of the Royal Society of London, Series B, 319, 557-570.

They discuss various game theory models of pairwise contests, being concerned with a concept they call aggressiveness, and whether it can be honestly signalled, especially by physical characteristics such as plumage, and they conclude that it can be signalled, provided dishonest signallers are punished.

Seeing their term for the payoff for the "hawk versus hawk" contest in the hawk-dove game, which is $(V - C)/2$, where V is the value of what is being fought about, it occurs to me that C (the cost of losing) represents the incapacity of the ISS – because if the action is ritualised, all the disadvantage of losing is ritual (psychological). So, by extension, depression can be represented by a symbol in a game theory equation! The original meaning of the term C is of course physical damage or death, but once the process has been ritualised, virtually the whole of C is psychological.

Two hawks fighting is what Sapolsky is describing in his accounts of the battles for the alpha position. Game theory is clearly important in determining not only who wins, but also the size of the cost in the loser. This is in contrast to the depressions suffered by the low-ranking monkeys who are bullied by the seniors. In these cases, game theory does not apply. There is no "game" – only exploitation and bullying (or nurturance and caring a la Birtchnell)). Instead, we are talking in terms of homeostasis of the R-gap. It is an entirely different model. The function of the depression is the same, to inhibit retaliation, but the circumstances that give rise to it are quite different. In the case of R-gap, the fear of retaliation is balanced against the motivation not to incapacitate the subordinate too much, since the subordinate is likely to be a wife or employee, and to carry out work on which the higher-ranking one depends, so he wants the R-gap to be large enough to prevent retaliation, but not large enough to prevent working. So the depressive communication of incapacity is more important in the R-gap case, whereas the communication of submission is more important in the game theory case. Does this make sense? It motivates me to work more on our classification paper. It seems to me that the evidence from ethology and that from behavioural ecology are saying the same thing; namely, that there are two types of depression which occur in different circumstances and whose rules are determined by different models.

In addition to V, RHP and ownership there is another variable, which determines the outcome of fights, which is more difficult to grasp. They call it "aggressiveness" in this paper, and define it as the amount of cost an animal is willing to accept before he submits. Of course, it can only be determined after the event. They discuss whether it can be signalled, and if so, whether the signals are likely to be honest. It can be a continuous variable (aggressiveness) or a categorical variable, and in the latter case it is the difference between hawk and dove. The variation can be between people (a genetic polymorphism) or within people (play hawk or dove with probability p). I think aggressiveness is a poor term for it, for it does not describe things like willingness to get into fights or tendency to bully subordinates, but rather the quality shown by Sapolsky's Saul, who hardly ever fought, but if he did do so, he won it or nearly died in the attempt. I think this elusive quality is more like courage than what we mean by aggressiveness.

If hawk is genetic, people should play it in every fight, so that they would get a reputation for courage, and also self-confidence themselves, so that RHP would be increased. In fact, you would get a gradual transformation of aggressiveness into RHP. But if it is a probability thing, this would not happen, as no one could predict the hawkishness of any individual on any one occasion. Perhaps the

uncertainty about how much of aggressiveness has been transferred to RHP is what makes this subject rather difficult to think about.

Turning to Cost and the proximal causes of Cost, these are of course catathetic signals. Perhaps we could try a different term, and one that is more easily quantified, and talk about punishment units (PUs). Then Cost could be defined as the number of PUs the animal would accept before de-escalating. In the hawk/hawk game, the PUs do not have any effect until suddenly escalation is turned into de-escalation, so there must be some mechanism totting up PUs quietly in the background, and then when it gets to the limit (C) tripping the switch mechanism into de-escalation. Of course, in the fight, there is symmetry until the last moment, so that all the PUs are reciprocated, and it is the last PU which is not reciprocated (but is answered with submission) that signals the end of the fight. In the case of the R-gap animal, it is also getting PUs, but they are not reciprocated PUs, so we could call these unreciprocated punishment units UPUs, in contrast to reciprocated punishment units (RPUs). What we don't know is whether UPUs are totted up like RPUs until they get to a limit and then trigger a further de-escalation, or whether each UPU just makes the animal more depressed. Then again, we have been talking about the reptilian brain response, but what are these RPUs doing at the limbic level? In the case of UPUs, it seems reasonable to suggest that they give rise to depressed emotion. In the case of RPUs, perhaps they lead to anger until the limit is reached, and then switch to depressed emotion.

Anyway, after all these ramblings, our predictions about the two types of depression remain the same, with possibly a third one added:

1. In the game theory depression, there should be a change in personality or behavioural style, as described by family or friends, whereas in the R-gap case, the patient should remain "much the same only more so".
2. In the game theory case, there should be delusionally depressive thinking about the past, especially previous rank, but in the R-gap depression this would not occur (there might be guilt about previous ideas of resentment and rebellion).
3. In the game theory case, the communication should be one of submission and "no threat", whereas in the R-gap case the message is one of inability to perform tasks (e.g., tiredness, physical incapacity).

Enough for now. I hope you all had a good time in Chicago, and that the van Gogh and Gaugin came up to scratch.
Hedonically, John.