

## The Social Competition Hypothesis of Depression

JOHN PRICE, LEON SLOMAN, RUSSELL GARDNER, Jr, PAUL GILBERT and PETER ROHDE

Depressive personality and depressive illness are examined from an evolutionary adaptationist standpoint. It is postulated that the depressive state evolved in relation to social competition, as an unconscious, involuntary losing strategy, enabling the individual to accept defeat in ritual agonistic encounters and to accommodate to what would otherwise be unacceptably low social rank.

There is some agreement that depressive states represent 'a psycho-biological response pattern' which is part of the inherited behavioural repertoire of the human organism (Lewis, 1934; Hill, 1968; Beck, 1987; Nesse, 1990; Gilbert, 1992; Powles, 1992). This means that depression performed some function over the course of our evolution and that those of our ancestors who had the capacity to become depressed survived at the expense of those who did not. However, it is easier to agree that there was a function than to agree on what that function was. To ignore the problem would be to limit our understanding of the biology of depression and possibly forego pointers to research into aetiology, classification and treatment.

Performance is limited in depression. There is impairment of perception, of execution and of the central processes which mediate between perception and execution, experienced as difficulty in making decisions (Radford *et al*, 1986). Even in mild depressions there is some impairment, particularly for tasks requiring initiative.

Impairment of performance is not incompatible with a biological function. Performance is impaired in sleep and hibernation; viewed out of the context of circadian and circannual change we might be sceptical of their adaptive value.

It is in relation to social competition that depression can be seen to exercise a function (Price, 1967; Sloman, 1976; Gardner, 1982; Sloman *et al*, 1989; Gilbert, 1992). The result of competition is that winners and losers behave differently, and it may be that mood change is the mechanism that mediates this variation in behaviour.

Identification of depression as a component of a behavioural system which we share with other animals anchors our subject firmly to the basic disciplines of comparative ethology (the study of behaviour as it occurs in nature) and behavioural ecology (the analysis of behaviour in terms of function), thus supplementing the pioneering work of John Bowlby on attachment behaviour (Goldberg, 1991).

Recent work in behavioural ecology has been concerned with situations in which an animal utilises only one from a set of two or more alternative behavioural strategies (Krebs & Davies, 1987). Depression may be identified as a losing or de-escalating strategy and elevation of mood as a winning or escalating strategy.

Since adopting a losing strategy often implies foregoing resources which may contribute to reproduction, depression might also fall into the category of altruistic behaviour, which has been of interest in recent evolutionary theory (Hamilton, 1963; Krebs, 1987).

Finally, the mathematical analysis of animal contest behaviour requires a variable to express the animal's knowledge of its own fighting capacity. This animal self-concept has been termed 'resource-holding potential' (RHP) and may be the evolutionary primordium of human self-esteem (Parker, 1974; Wenegrat, 1984; Archer, 1988). RHP determines whether an animal escalates a confrontation and attacks, or de-escalates and adopts the 'involuntary subordinate strategy', which we think may be the primordium of depressive states. Thus we are able to use the tools of behavioural ecology in the analysis of the mutual interaction of self-esteem and mood change, which permeates much of psychiatric practice.

### Statement of the hypothesis

The social competition hypothesis of depression is that human beings share with their more primitive ancestors a mechanism for yielding in competitive situations. This 'involuntary subordinate strategy' has three main functions: (a) an executive function which prevents the individual from attempting to make a 'come-back' by inhibiting aggressive behaviour to rivals and superiors (but not to dependents) and by creating a subjective sense of incapacity; (b) a communicative function which signals 'no threat' to rivals and 'out of action' to any kin or supporters who might wish to push the individual back into the

arena to fight on their behalf; and (c) a facilitative function which puts the individual into a 'giving up' state of mind which encourages acceptance of the outcome of competition and promotes behaviour which expresses voluntary yielding. This leads to reconciliation and the termination of whatever conflict triggered the 'involuntary subordinate strategy'. But if voluntary yielding is blocked for any reason, the involuntary subordinate strategy may become intense and prolonged and may be recognised as depressive illness.

Social competition can be described at a number of different levels and the hypothesis relating depression to social competition can be expressed in terms of each level, as follows.

### Sexual selection

Darwin (1871) pointed out that alongside natural selection, a social process operates in animal species to determine which individuals in each generation reproduce (Ryan, 1985; Harvey & Bradbury, 1991). He called this phenomenon sexual selection and subdivided it into *inter-sexual* selection (in which one sex chooses another for mating), and *intra-sexual* selection in which each sex competes with members of the same sex for access to the other sex (Sloman & Sloman, 1988). The implication of this hypothesis is that in each generation one or more social processes divide the population into those who are successful and those who are either unsuccessful or unable to maintain the success that they have achieved. Clearly, the successful and unsuccessful must show a major difference in behaviour; for instance, the unsuccessful must suffer a relative inhibition of reproductive behaviour. Recognisable states of inhibition include:

- (a) death; rare in vertebrates, common in invertebrates, e.g. spiders (Huntingford & Turner, 1987)
- (b) physiological suppression of sexual development, as occurs, for example, in the naked mole rat and in some New World monkeys (Abbott *et al.*, 1989)
- (c) inhibition of sex change, so that the subordinate individual is maintained in the opposite sex by the signals of the dominant individual, as occurs in some fish (Keenleyside, 1979)
- (d) some psychiatric syndromes, including the phenomena we recognise clinically as depression; this depression could occur as a lifelong phenomenon, in the form of depressive personality, in the case of those who are never successful, or as an episode of depressive 'illness' in those who achieve success and then lose it.

### Social hierarchy

The social roles of successful and unsuccessful animals are represented in two different but related ways. In some species the two contrasting roles are 'territory owner' and 'non-territory owner'. In other species they are high ranking and low ranking within a social hierarchy.

We suggest that depression is a component of the behavioural strategy evolved for the role of non-territory owner and low ranker.

We would expect to find depression manifesting in the form of both illness and personality, reflecting the fact that some individuals achieve ownership and/or high rank and then lose it, whereas others have never achieved these objectives in the first place.

A social hierarchy performs two different functions. First, it regulates the transfer of power and of breeding opportunities from one generation to the next. Second, it stratifies each generation in terms of power and breeding opportunities, and it is this second function which mediates sexual selection.

The simplest hierarchy is the asymmetrical, two-person relationship. There are many ways of negotiating the one-down position in such a relationship (Price, 1988, 1992a) and these may be associated with perceptual and cognitive distortion in the one-down member. There may be adulation in which the status of the one-up member is magnified, and there is depression in which the status of the one-down member is diminished. Both ensure a stable complementarity of the relationship and avoid the disruptive 'arms race' of symmetrical schismogenesis (Bateson, 1972). Unlike adulation, the depressive mechanism allows for a switch in one-upness, when chronic depression in the formerly one-down member may be replaced by an acute depression in the formerly one-up member (Price, 1991). The association of depression with loss of social rank in animals has been discussed for birds (Price & Sloman, 1987), monkeys (Price, 1989) and lizards (Price, 1992b).

### Ritual agonistic behaviour

Ritual agonistic behaviour is the social interaction which produces these role asymmetries in the majority of vertebrate species. An encounter between competitors is followed by ritualised fighting. The ritualisation reduces the physical risk to both parties. The losing behaviour is as ritualised as the fighting. Depression can be seen as a ritual form of losing behaviour producing temporary psychological incapacity which signals submission to the winner but preserves the loser without physical damage. It performs the function which death performs in unritualised fighting, and which the referee performs in culturally ritualised competition.

### Resource-holding potential (RHP)

Agonistic behaviour can be described in terms of a self-concept called resource-holding potential (RHP) (Parker, 1974, 1984). RHP is an estimate of fighting capacity by both the individual and others. Size, strength, skill, previous success, weapons and allies all indicate increased fighting capacity. The output from a high self-perception of RHP is threat or attack.

All the phenomena of ritual agonistic behaviour can be described in terms of signals of either absolute or relative RHP (Price, 1988). Ritual agonistic behaviour can then be conceptualised as an RHP management system which produces a rank order of individuals according to differences in RHP.

Self-esteem is the nearest we can get to RHP in human terms, and our hypothesis is that self-esteem evolved out of RHP. This would explain two aspects of self-esteem which would seem to be puzzling: its global nature and the great variation in self-esteem in the population (*Lancet*, 1988); both these features are essential to the function of RHP. Re-phrasing our hypothesis in terms of RHP, we can state that depression in its chronic form is a function of low RHP, and in its acute form a function of falling RHP. If we now substitute self-esteem for RHP, and also adopt the current ethological practice of regarding behavioural variation as alternative strategies, we can formulate depression as a low self-esteem strategy.

It may be asked how such a system can evolve, when all the advantage seems to be on the side of the high self-esteem strategy. In fact the advantages of the two strategies are likely to be equalised by negative frequency-dependent selection, as has been shown by Maynard Smith (1982), using what is known as evolutionary game theory. He calls the high self-esteem strategy a 'hawk' strategy, which is characterised by escalation of agonistic encounters, and the low self-esteem strategy a 'dove' strategy, which is characterised by de-escalation. He has demonstrated in his evolutionary model that, given certain conditions, a pure hawk strategy is not 'evolutionarily stable', in that it can be infiltrated by a mixed hawk/dove strategy. In this model it is assumed that in encounters between hawk and dove the hawk has the higher pay-off, in terms of survival and reproduction; but when hawk meets hawk, the pay-off is lower because of the risk of escalation to unritualised combat with consequent serious injury or death. Yielding ensures the loser survives.

The low self-esteem strategy can be seen as a form of altruistic behaviour which promotes the survival and reproduction of close relatives and so raises 'inclusive fitness' (Hamilton, 1963; Krebs, 1987).

In fact, an alternative term for the low self-esteem strategy might be 'kin-helper strategy', contrasting with the 'self-helper' high-esteem strategy.

### Human social competition

We have presented the yielding hypothesis in terms of ritual agonistic behaviour, suggesting that the mechanisms of depression evolved when ritual agonistic behaviour was the principal form of social competition underlying sexual selection, as it is in most vertebrate species today. However, ritual agonistic behaviour is not the main form of human social competition. As pointed out by Barkow (1989) and by Gilbert (1992), competition by attraction has largely replaced competition by intimidation, and is the main form of competition seen in primitive tribes by anthropologists. In order to achieve the prestige which guarantees reproductive success (usually the possession of more than one wife in the case of males, and marriage of children to high-ranking partners in the case of females), individuals have to make themselves attractive to others, either to their peers or to particular patrons, and it is the latter who make the decisions which determine the differential allocation of rank.

If it were not for the findings of ethology, it would be doubtful whether we would recognise ritual agonistic behaviour as occurring in human beings. Agonistic behaviour and social asymmetries have been ascribed to cultural factors, or to the carry-over into adult life of the parent-child asymmetry and the punishment which is a common component of child-rearing. Such was the view of Freud, who did not have the benefit of the ethological descriptions of agonistic behaviour and social asymmetry in such a wide variety of vertebrate species, including many reptiles who have no parent-offspring contact at all. Thus it was natural for him to conceptualise the neuroses associated with adult power struggles in terms of unresolved nursery conflicts, a view which was corrected by neo-Freudians such as Sullivan and Horney (Birnbach, 1962); but even the latter saw adult conflict in cultural terms, and did not conceive that mankind might share with animals a phylogenetically old mechanism for creating social asymmetry between previously equal adults.

### Accounting for the features of depression

Our hypothesis is concerned with 'ultimate' causes (the function of the 'involuntary subordinate strategy' during evolution) and is therefore to some extent independent of proximal causes. However, it is compatible with what is known about the social origins

of depression (Brown *et al.*, 1986; Powles, 1992; Kendler *et al.*, 1993), and it is only the constraint of space which prevents us from pursuing at length this interesting topic.

Proponents of an evolutionary hypothesis of any psychiatric condition also have a duty to show that it is consistent with the known features of the condition and that these features can perform the postulated function. In fact, the social competition hypothesis is the only evolutionary hypothesis which accounts for the incapacity of depression; indeed, we see the incapacity as the main functional feature of depression, which is hypothesised to be a ritual (psychological) substitute for the physical damage which is suffered by the loser of an unritualised contest.

The social competition hypothesis also accounts for the cognitive distortions of depression. Beck (1967) described a triad of distortions in which there are negative views of the self, the world and the future. These distortions are compatible with a 'de-escalating' state of mind. The depressed self is not a strong 'favourite' for successful competition; the world of the depressive is not a favourable arena for competing; and the pessimism of the depressive is in stark contrast to that optimism which seems to be required for successful competition. The depressive is not only pessimistic about the future, but has a distorted view of the past in which former rank, ownership and success seem to the patient like a sham, and, therefore, not to be regained.

Apart from ownership and RHP, the only variable which is important in the mathematical analysis of agonistic behaviour is 'resource value', which expresses the value of whatever is being fought about (Parker, 1984). The lower the resource value to a contestant, the more likely he is to yield (flee or submit) rather than to attack. In depression there is a generalised reduction in the perceived value and significance of all goals and incentives, which is usually described as loss of interest. The depressive loss of interest favours de-escalation of conflict. If the resource under consideration is the general one of social rank and success, then reduction in resource value is synonymous with loss of pride and ambition.

We feel that our hypothesis accounts for most of the features of depressive states. In particular, it accounts for the incapacity suffered by depressed patients and for the distortions in their thinking, features which are not explained by theories which see the function of depression to be the conservation of resources (Beck, 1987; Powles, 1992), the management of investment in the environment (Nesse, 1990), the relinquishing of unrealisable goals (Klinger, 1975; Hamburg *et al.*, 1975) or the redressing of imbalance in reciprocal exchange (Glantz & Pearce, 1989).

Our hypothesis is consistent with subjective heterogeneity in depression. It does not matter whether yielders refrain from fighting back because they are too tired, or too frightened, or feel too physically ill, or think they will not win, or that they do not deserve to win, or that their allies will not come to their support.

Ethological observations of depressed patients show that active (spontaneous, person-oriented) submission such as flattery is reduced, but passive submission such as looking down is increased (T. Schelde, personal communication, 1993), which highlights the difference between the 'involuntary subordinate strategy' underlying depression and the voluntary subordinate behaviour which may preempt or replace it.

### Epidemiological features

Our hypothesis is consistent with the fact that depression is more common, more severe and more prolonged in later life, for the most important acts of yielding are required when one generation is giving way to the next. We have dealt elsewhere with the fact that depression tends to follow 'exit' events such as bereavement, whereas it might be expected that yielding would more often be required following the entry of new members to the group (Price, 1988). We argue that social rank is so dependent on the support of others that loss of significant others has become the main predictor of loss of rank. The dependence of rank on support from kin and other allies is a widespread characteristic of non-human primates (De Waal & Harcourt, 1992), suggesting that it may have applied to the simian and human common ancestor some 40 million years ago, allowing sufficient evolutionary time for close interconnections to develop between the brain mechanisms subserving agonistic and affiliative behaviour.

We have also (Price, 1988) dealt with the problem that depression is commoner in women than men, whereas agonistic behaviour is thought to be more common in males. Our argument is that agonistic behaviour is more conspicuous but not more common in males, and, in any case, there is evidence that when women have equal opportunities, the female excess of depression disappears (Wilhelm & Parker, 1989).

### Implications for research

#### Animals

Our hypothesis suggests a wide choice of animal models for research into depression. Low rank and falling rank in animals have been used as models for

human physical disease, such as heart disease (Henry *et al*, 1986) and renal disease (von Holst, 1986) and it would be surprising if social stress intense enough to produce these physical pathologies did not also induce psychopathology. In his work on social stress in tree shrews, von Holst (1986) has observed two distinct forms of reaction to subjugation, one associated with increased adrenomedullary activity and one with adrenocortical activity, the latter showing extreme social withdrawal ending in death; these reactions in tree shrews bear a resemblance to the contrasting fight/flight and conservation/withdrawal clinical syndromes described by Powles (1992).

In equally promising work on guinea pigs, Sachser & Lick (1991) have shown that being brought up in a colony (as opposed to with a single female) abolishes the aggression which occurs when two strange males are put together in the presence of a female. This suggests that the experience of living with other males during adolescence may create the variation in resource-holding potential (RHP) which is required to avoid pairwise contests among adults. They also made the observation that the loser of a contest could be predicted from changes in the status of his adrenal and other hormones before there was any detectable change in his fighting behaviour; this supports Leshner's (1983) hypothesis that the switch from escalation to de-escalation involves a positive feedback loop which includes the adrenal cortex.

Some animals are promising for research because they show physical effects of rank change. Some reptiles and fish and at least one monkey change colour following rank change (Price, 1989); some fish change sex (Keenleyside, 1979). These might not only be possible markers for mood change, but they offer a path by which the mechanism responsible for the physical changes might lead to the central mechanism. Both low rank and depression are associated with increased activity of the hypothalamic-pituitary-adrenocortical axis, and there is an interesting association between rank and indolamine metabolism in both monkeys (McGuire, 1988) and fish (Winberg & Nilsson, 1993). A project currently under way in the Department of Psychiatry of the University of Tasmania is using low rank in a marsupial called the sugar glider as a model for depression (I. H. Jones & J. Mallick, personal communication, 1992).

### Human beings

Our hypothesis that depression evolved out of mechanisms mediating ranking behaviour throws a new light on the extensive work which has been carried out on the expression of hostility in

depression, and which has produced very conflicting results (Riley *et al*, 1989). Some workers have found that depressed patients express more anger than controls (Fava *et al*, 1993), and this might seem to conflict with our idea that depression functions to inhibit aggression.

In fact, our hypothesis states that only hostility to equal- and higher-ranking people is inhibited, whereas hostility expressed to lower-ranking people is often increased; and it is our clinical impression that hostility in depression is usually unexpressed or 'taken out on' the furniture, or expressed to subordinate spouses or children. No published study to date has considered whether the hostility is felt or expressed to a higher-ranking or a lower-ranking person. Yet from an ethological perspective, expressing hostility up a hierarchy is a very different matter from expressing it downwards. Our hypothesis predicts that, if depression occurs in one partner in a complementary relationship, hostility expressed by the patient to the other will be increased if it is the dominant partner who gets depressed, but will be reduced if it is the subordinate partner who gets depressed.

### Implications for treatment

#### Analysis of the patient's situation

The 'yielding' hypothesis helps the physician to explore the patient's situation, identify any conflictual relationships and assess the reasons for non-resolution of any agonistic interaction. There are five options:

(a) The conflict may be resolved by negotiation and compromise. Here we are talking in terms of reconciliation, which implies penitence, atonement, forgiveness and other forms of negotiation.

(b) The patient may be helped to win the conflict. This applies particularly to patients who are insufficiently self-assertive.

(c) The patient may be assisted to substitute voluntary yielding in the form of conscious submission for the involuntary and unconscious yielding of depression.

(d) The patient may be enabled to leave the arena. This may involve physical separation from the adversarial person and certainly involves mental detachment.

(e) Help may come from reducing the patient's assessment of the value of the resource being competed for. Aspirations may be excessive or too narrow, the patient having 'all his eggs in one basket'. These are concerns common to psychotherapy, philosophy and religion.

### Sharing with the patient

It may or may not be desirable to share the yielding hypothesis with the patient; for instance, the therapist might say: "Your depression is serving an important function in your marriage, it is enabling you to submit to your husband's demands without rebellion, and is therefore saving your relationship from probable rupture". This is a form of 'positive connotation' of the symptom, a technique widely used in family therapy; and it is also a re-framing from the patient's previous formulations which may have been in terms of hormones or physical illness. It is also something of a challenge, suggesting to her that she need not submit to her husband's demands, puts in her mind the idea that there may be alternative ways of dealing with those of her husband's demands which she finds unacceptable.

To patients of a more scientific frame of mind, it may help simply to explain what is going on, since lack of meaning adds yet another morbid dimension to the experience of depression. We sometimes use the analogy of hibernation, explaining that while hibernation is nature's way of helping certain animals to survive unfavourable weather conditions, depression is nature's way of helping certain humans to survive unfavourable social conditions. This is often acceptable to depressed patients, who may themselves feel like curling up into a ball in a hole in the ground and staying there for a long time. And the seasonal recovery from hibernation helps the patient to believe in the likelihood of remission.

On the other hand, often the situation can be resolved without the patient being aware of conflict. Haley (1963), for instance, advocates the resolution of agonistic situations in marriage by means of non-agonistic interpretations, such as parent-child interaction, and we would endorse this view.

### Relation to other psychotherapies

Our evolutionary perspective supports those therapies aimed at resolving interpersonal conflict (Karasu, 1990; Stravynski & Greenberg, 1992) and the various schools of family therapy which are sensitive to deviations of hierarchy such as cross-generational coalitions (Haley, 1963).

Cognitive behaviour therapy appears to us to be a means for raising RHP and other components of self-esteem and of rendering the basis for these self-appraisals realistic. Both these aims are supported by our approach. We think our main contribution is the conceptualisation of depression as a fail-safe strategy to which there are alternatives at higher levels of mental organisation. Whereas

psychoanalysis aims to render unconscious thoughts conscious, therapy based on evolutionary principles aims to replace unconscious behavioural strategies with conscious ones.

### Acknowledgement

This paper is dedicated to Dr M. R. A. Chance whose insight into the relation between agonistic behaviour and psychopathology stimulated the train of thought summarised above.

### References

- ABBOTT, D. H., BARRETT, J., FAULKES, C. G., *et al* (1989) Social contraception in naked mole-rats and marmoset monkeys. *Journal of Zoology, London*, **219**, 703-710.
- ARCHER, J. (1988) *The Behavioural Biology of Aggression*. Cambridge: Cambridge University Press.
- BARKOW, J. H. (1989) *Darwin, Sex and Status: Biological Approaches to Mind and Culture*. Toronto: University of Toronto Press.
- BATESON, G. (1972) *Steps to an Ecology of Mind*. New York: Ballantine Books.
- BECK, A. T. (1967) *Depression: Clinical, Experimental and Theoretical Aspects*. New York: Hoeber.
- (1987) Cognitive models of depression. *Journal of Cognitive Psychotherapy*, **1**, 5-37.
- BIRNBACH, M. (1962) *Non-Freudian Social Philosophy*. Stanford: Stanford University Press.
- BROWN, G. W., ANDREWS, B., HARRIS, T., *et al* (1986) Social support, self-esteem and depression. *Psychological Medicine*, **16**, 813-831.
- DARWIN, C. (1871) *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- DE WAAL, F. B. M. & HARCOURT, A. H. (1992) Coalitions and alliances: a history of ethological research. In *Coalitions and Alliances in Humans and Other Animals* (eds A. H. Harcourt & F. B. M. De Waal), pp. 1-19. Oxford: Oxford University Press.
- FAVA, M., ROSENBAUM, J. F., PAVA, J. A., *et al* (1993) Anger attacks in unipolar depression. Part 1: clinical correlates and response to fluoxetine treatment. *American Journal of Psychiatry*, **150**, 1158-1163.
- GARDNER, R. J., Jr. (1982) Mechanisms in major depressive disorder: an evolutionary model. *Archives of General Psychiatry*, **39**, 1436-1441.
- GILBERT, P. (1992) *Depression: The Evolution of Powerlessness*. Hove: Erlbaum. New York: Guilford.
- GLANTZ, K. & PEARCE, J. K. (1989) *Exiles from Eden: Psychotherapy from an Evolutionary Perspective*. London: W. W. Norton.
- GOLDBERG, S. (1991) Recent developments in attachment theory and research. *Canadian Journal of Psychiatry*, **36**, 393-400.
- HALEY, J. (1963) Marriage therapy. *Archives of General Psychiatry*, **8**, 213-234.
- HAMBURG, D. A., HAMBURG, B. A. & BARCHAS, J. D. (1975) Anger and depression in the perspective of behavioral biology. In *Emotions: their parameters and measurement* (ed. L. Levi), pp. 235-278. New York: Raven Press.
- HAMILTON, W. D. (1963) The evolution of altruistic behaviour. *The American Naturalist*, **97**, 354-356.
- HARVEY, P. H. & BRADBURY, J. W. (1991) Sexual Selection. In *Behavioural Ecology: An Evolutionary Approach* (eds J. R. Krebs & N. B. Davies), pp. 203-233. Oxford: Blackwell.
- HENRY, J. P., STEPHENS, P. M. & ELY, D. L. (1986) Psychosocial hypertension and the defence and defeat reactions. *Journal of Hypertension*, **4**, 687-697.

- HILL, D. (1968) Depression: disease, reaction or posture? *American Journal of Psychiatry*, **125**, 445-456.
- HOLST, D. VON (1986) Vegetative and somatic components of tree shrews' behavior. *Journal of the Autonomic Nervous System*, (suppl.), pp. 657-670.
- HUNTINGFORD, F. & TURNER, A. (1987) *Animal Conflict*. London: Chapman & Hall.
- KARASU, T. B. (1990) Toward a clinical model of psychotherapy for depression. I: Systematic comparison of three psychotherapies. *American Journal of Psychiatry*, **147**, 133-147.
- KEENLEYSIDE, M. H. A. (1979) *Diversity and Adaptation in Fish Behaviour*. Berlin: Springer.
- KENDLER, K. S., KESSLER, R. C., NEALE, M. C., *et al* (1993) The prediction of major depression in women: toward an integrated etiologic model. *American Journal of Psychiatry*, **150**, 1139-1148.
- KLINGER, E. (1975) Consequences of commitment to and disengagement from incentives. *Psychological Review*, **82**, 1-25.
- KREBS, D. (1987) The challenge of altruism in biology and psychology. In *Sociobiology and Psychology* (eds C. Crawford, M. Smith & D. Krebs), pp. 81-118. Hillsdale: Erlbaum.
- KREBS, J. R. & DAVIES, N. B. (1987) *An Introduction to Behavioural Ecology*, 2nd edn. Oxford: Blackwell.
- LANCET (1988) Editorial: self-esteem. *Lancet*, *ii*, 943-944.
- LESHNER, A. I. (1983) The hormonal responses to competition and their behavioral significance. In *Hormones and Aggressive Behavior* (ed. B. B. Svare), pp. 393-404. New York: Plenum.
- LEWIS, A. J. (1934) Melancholia: a clinical survey of depressive states. *Journal of Mental Science*, **80**, 277-378.
- MCGUIRE, M. T. (1988) On the possibility of ethological explanations of psychiatric disorders. *Acta Psychiatrica Scandinavica*, **77**, suppl. 341, pp. 7-22.
- MAYNARD SMITH, J. (1982) *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- NESSE, R. M. (1990) Evolutionary explanations of emotions. *Human Nature*, **1**, 261-289.
- PARKER, G. A. (1974) Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, **47**, 223-243.
- (1984) Evolutionarily stable strategies. In *Behavioural Ecology: An Evolutionary Approach*, 2nd edn (eds J. R. Krebs & N. B. Davies), pp. 30-61. Oxford: Blackwell.
- POWLES, W. E. (1992) *Human Development and Homeostasis: The Science of Psychiatry*. Madison CT: International Universities Press.
- PRICE, J. S. (1967) Hypothesis: the dominance hierarchy and the evolution of mental illness. *Lancet*, *ii*, 243-246.
- (1988) Alternative channels for negotiating asymmetry in social relationships. In *Social Fabrics of the Mind* (ed. M. R. A. Chance), pp. 157-195. Hove: Erlbaum.
- (1989) The effect of social stress on the behaviour and physiology of monkeys. In *Contemporary Themes in Psychiatry* (eds K. Davison & A. Kerr), pp. 459-466. London: Gaskell Press.
- (1991) Homeostasis or change: a systems theory approach to depression. *Journal of Medical Psychology*, **64**, 331-344.
- (1992a) The agonistic and hedonic modes: definition, usage, and the promotion of mental health. *World Futures*, **34**, 234-269.
- (1992b) Accentuate the positive, eliminate the negative: the role of boosting and putting-down signals in mental health. In *Promotion of Mental Health, Vol. 1, 1991* (ed. D. Trent), pp. 89-101. Aldershot: Avebury.
- & SLOMAN, L. (1987) Depression as yielding behavior: an animal model based on Schjelderup-Ebbe's pecking order. *Ethology and Sociobiology*, **8** (suppl.), 85-98.
- RADFORD, M. H. B., MANN, L. & KALUCY, R. S. (1986) Psychiatric disturbance and decision-making. *Australian and New Zealand Journal of Psychiatry*, **20**, 210-217.
- RILEY, W. T., TREIBER, F. A. & WOODS, M. G. (1989) Anger and hostility in depression. *Journal of Nervous and Mental Disease*, **177**, 668-674.
- RYAN, M. J. (1985) *The Tungara Frog: a Study in Sexual Selection and Communication*. Chicago: University of Chicago Press.
- SACHSER, N. & LICK, C. (1991) Social experience, behavior and stress in guinea pigs. *Physiology and Behavior*, **50**, 83-90.
- SLOMAN, L. (1976) The role of neurosis in phylogenetic adaptation with particular reference to early man. *American Journal of Psychiatry*, **133**, 543-547.
- SLOMAN, S. & SLOMAN, L. (1988) Mate selection in the service of human evolution. *Journal of Social and Biological Structures*, **11**, 457-468.
- SLOMAN, L., GARDNER, R. & PRICE, J. S. (1989) Biology of family systems and mood disorders. *Family Process*, **28**, 387-398.
- STRAVYNSKI, A. & GREENBERG, D. (1992) The psychological management of depression. *Acta Psychiatrica Scandinavica*, **85**, 407-414.
- WENEGRAT, B. (1984) *Sociobiology and Mental Disorder*. California: Addison-Wesley.
- WILHELM, K. & PARKER, G. (1989) Is sex necessarily a risk factor to depression? *Psychological Medicine*, **19**, 401-403.
- WINBERG, S. & NILSSON, G. E. (1993) Time course of changes in brain serotonergic activity and brain tryptophan levels in dominant and subordinate juvenile arctic char. *Journal of Experimental Biology*, **179**, 181-195.

\*John Price, DM, MRCP, FRCPsych, *Odintune Place, Plumpton, E. Sussex, BN7 3AN*; Leon Sloman, FRCP(C), *Associate Professor, Clarke Institute of Psychiatry, Toronto, Canada*; Russell Gardner, Jr, MD, *Professor of Psychiatry, University of Texas Medical Branch, Galveston, Texas, USA*; Paul Gilbert, PhD, FBPSS, *Professor of Clinical Psychology, Derby University*; Peter Rohde, MB, BCh, FRCP(E), FRCPsych, *53 Harley Street, London W1N 1DD*

\*Correspondence: *Department of Psychiatry, Wellington School of Medicine, Wellington, New Zealand*

(First received May 1993, final revision September 1993, accepted September 1993)