Using behavioural ecology to understand depression

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The nature of the interaction between biology and environment may be at the heart of understanding depression and much use has been made of animal models. These suffer the drawback that the adaptive functions of behaviours which are considered as 'depression-equivalents' are unclear (McKinney, 1992).

Behavioural ecology may be defined as the study of the 'survival value' of behaviour (Krebs, 1993), and is a discipline which examines animal behaviour from an evolutionary perspective. This enables us to understand the different conditions under which a behaviour may serve an adaptive function. If this can be integrated with the physiological perspective which already links animal and human behaviour, then the evolutionary history of human behaviour can be more coherently elucidated and animal models of mental illness can be better validated. Developments in two areas of behavioural ecology may be pertinent to our understanding of depression; the response to predatory threat and life history strategy change.

RESPONSE TO PREDATORY THREAT

The 'fight or flight' response is well known as the usual response to predatory threat. However, this may not be the case in more chronic threat and it may be helpful to think of the 'three little pigs' who stayed safely at home as the wolf prowled outside. Lima & Dill (1989) predict that animals will survive better by reducing activity when under threat, whether foraging or searching for a mate. Some of the studies they describe in support of their model, include those showing reduced activity of mice on moonlit nights, increased predation of grouse at leks and reduced calling of frogs when bats were flown above. In the laboratory, further support comes from Blanchard *et al* (1998) who showed similar behaviour in rats exposed to cats that habituated only minimally despite frequent repetition.

LIFE HISTORY THEORY

An organism's life history strategy is its pattern of development and reproduction. Important parameters are life span, number of offspring and when and how often the organism reproduces. Life history theory looks at how variation in factors such as mortality rate or food supply may lead to particular life history strategies which have evolved to optimise reproductive output over time (Stearns, 1992). Modellers have tended to view life history strategies as constant phenotypic characteristics rather like size or colour. This has recently changed with the introduction of state-dependent life history theory (SDLHT) by McNamara & Houston (1996). Here, an animal will vary its life history strategy according to its condition or environment. The authors have also called this 'phenotypic plasticity'. An animal's likelihood of reproductive success depends upon factors such as energy reserves, foraging skills, health and food availability. The condition of environment and animal are referred to as the 'state'. Breeding in a poor state may result in failure and possibly the animal's death, as it is well established that breeding has costs (Stearns, 1992). It is therefore proposed that an animal breeds according to its assessment of state, such that below a critical state it will not breed. Evidence comes from moose, bison and elephant seals who are reported by McNamara & Houston (1996) to delay the age of first breeding when in poor condition.

SDLHT suggests that subordination may be one such adaptive mechanism. Competing with another animal may be the animal's way of assessing its state. If it loses, it has assessed its state as poor and so does not breed. Rutting deer are a possible example. SDLHT proposes that specific biological mechanisms have evolved which mediate assessment of state and altered life history strategy. Some animal models (McKittrick *et al*, 1995; Sapolsky *et al*, 1997) have shown that subordinates have an activated hypothalamic–pituitary–adrenal (HPA) axis and as this system is also activated by other stresses, it is a good candidate for such a mechanism. Activation may also have long-term neurotoxic effects (O'Brien, 1997) so that stresses at differing developmental stages could affect life-history strategy.

RELATIONSHIP WITH DEPRESSION

The experience of predatory threat or an assessment of one's environment or condition as poor, can lead to an activated HPA axis, decreased activity and reproductive effort (including socialisation). These changes are comparable to depression in humans. Here also, decreased activity levels, libido, appetite and socialisation are central features and HPA axis activation is also thought to play a central role (Checkly, 1996). Indeed, the comparison could be extended to consider decreased activity in relation to immediate threat as comparable to non-melancholic depression with a high anxiety component. Melancholic depression may be comparable to a changing life history strategy.

Therefore, the biological basis of depression, may have evolutionary roots in an adaptive response to threat. Its roots may also lie in the context of altering life history strategy. It has been suggested that subordination is homologous to depression (Jones *et al*, 1995). This may be so, but perhaps only because it serves the function of mediating an altered life history strategy.

This theory can be tested in a number of ways. It predicts that the neurochemical and neuroendocrine changes associated with subordination and depression will also be found in other situations predicted by SDLHT. A specific prediction is that adolescents with depression will have delayed puberty. Further support will come from examining the analogies between depression and behavioural responses to threat or SDLHT; these relate to assessments of self-worth, behavioural features such as aggression and sleep disturbance and precipitating life-events such as reproduction or social isolation.

In conclusion, with its focus on adaptive function, behavioural ecological models may offer advantages over traditional socio-biological approaches in understanding the animal homologues of depression. As such, they are worthy of consideration.

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