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Progress In Neuro-Psychopharmacology & Biological Psychiatry

Progress in Neuro-Psychopharmacology & Biological Psychiatry 30 (2006)  $815-826\,$ 

www.elsevier.com/locate/pnpbp

#### Review article

# Darwinian models of depression: A review of evolutionary accounts of mood and mood disorders

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Available online 27 April 2006

#### Abstract

Over the last ten years, there has been increased interest in the evolutionary origins of depressive phenomena. The current article provides a review of the major schools of thought that have emerged in this area. First, we consider important Darwinian explanations of depressed mood, including an integrative social risk hypothesis recently proposed by the authors. According to the social risk hypothesis, depression represents an adaptive response to the perceived threat of exclusion from important social relationships that, over the course of evolution, have been critical to maintaining an individual's fitness prospects. We argue, moreover, that in the ancestral environment, depression minimized the likelihood of exclusion by inducing: (i) cognitive hypersensitivity to indicators of social risk/threat; (ii) signaling behaviours that reduce social threat and elicit social support; and (iii) a generalized reduction in an individual's propensity to engage in risky, appetitive behaviours. Neurobiological support for this argument is also provided. Finally, we review three models that endeavour to explain the relationship between the adaptations that underlie depressed mood and clinically significant, depressed states, followed by a consideration of the merits of each.

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Keywords: Darwinian medicine; Depression; Evolutionary psychology; Mood; Social risk

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#### 1. Introduction

In the past, theoretical and empirical approaches to depression have been dominated by investigations targeting the symptomatology and treatment of severe, clinically-significant depressed states, and questions of etiology have been largely reserved for precipitants of immediate relevance to the depressed individual. While such proximate causes are undoubtedly of central importance to an understanding of depressive phenomena, more recently an expanding body of literature has focused on evolutionary, or functional, explanations. Arguably, Darwinian explanations of depression (e.g., Allen and Badcock, 2003; Bowlby, 1980; Gilbert, 1992; Nesse, 2000; Price et al., 1994; Watson and Andrews, 2002) are of practical and theoretical importance for three reasons. First, an understanding of the role of depressive phenomena in an evolutionary context provides insight into why people experience depression. If depressed states evolved in response to certain adaptive problems in our evolutionary history, they may be said to perform a particular adaptive function. By isolating that function, one stands to introduce a new tier of explanation — an understanding of depression rooted in the lives of our ancestors. Notably, such an approach is also likely to yield direct, practical implications with regards to treatment (Price et al., 1994; Watson and Andrews, 2002). Second, an evolutionary account of depression challenges the more traditional view that depressed states are intrinsically associated with dysfunction (Gilbert, 1998). If it can be shown that it played an adaptive role in our past, it follows that in some situations, depression provided reproductive benefits for the individual or their kin. Third, and finally, a Darwinian framework provides a powerful heuristic for generating testable hypotheses concerning psychological phenomena (Cosmides and Tooby, 1994), and facilitating broadly integrative explanations of them (Buss, 1995).

The idea that depression has evolved in response to specific adaptive problems is by no means a theoretical novelty. The argument enjoys a six-decade history (McGuire and Troisi, 1998), and has drawn contributions from a broad range of theorists (e.g., Allen and Badcock, 2003; Bowlby, 1980; Gilbert, 1992; Nesse, 2000; Price et al., 1994; Watson and Andrews, 2002). Generally, explanatory frameworks that have emerged from this expanding body of literature can be meaningfully grouped into two broad categories: explanations of normative, depressed mood, and explanations that explicitly target more severe, clinically significant depressed states. We shall now consider each of these prevailing schools of thought in turn.

### 2. Darwinian models of depressed mood

Although the concept of adaptation should not be reflexively applied to biological and behavioural features without sound logical reasons, we propose that mood states are appropriate targets for an evolutionary analysis. First, they are ubiquitous human capacities indicating a considerable degree of specialization (Cosmides and Tooby, 1994). Second, they are activated by specific contexts, suggesting that their input is specialized (Oatley, 1992). Finally, mood states are characterized by com-

plex but coordinated sets of output in the form of physiology, overt behaviour, and conscious experience.

While there has been some very useful work on the distinct adaptive functions of other negative mood states like anxiety (Öhman et al., 1985), the adaptive significance of depressed mood has proven more elusive. For example, there is considerable evidence that the essential psychological "theme" of anxiety is threat, whereas the "theme" for depression is loss (Clark and Beck, 1989) or defeat (Price, 1972; Gilbert, 1992). Despite such distinctions, the argument that anxiety is an adaptive response to threat (facilitating early detection and responses) is more widely accepted than any evolutionary claim regarding depression. Indeed, it is not even clear what kind of loss is most relevant to depression (McGuire et al., 1997).

Nesse (1998) has argued that circumstances involving the loss (or the threat thereof) of a reproductive resource are likely to shape negative mood states, while circumstances involving the gain (or potential gain) of such resources are likely to shape positive ones. Thus, an evolutionary understanding of depression should depend on: i) identifying recurrent situations in the ancestral environment typically associated with biologically significant loss or gain; ii) describing the selection pressures in such situations (i.e., the particular social-reproductive goals that they would have threatened); and iii) isolating the features of depressed mood that would have enabled the organism to cope with these pressures (Nesse, 1990). While this approach has engendered a range of propositions, three prevailing schools of thought characterize the literature: the conservation of resources, social competition, and attachment theories of depression.

#### 2.1. Theories of resource/energy conservation

Conservation of resource theories assert that the inhibition of appetitive functions associated with depression (i.e., low levels of energy, pleasure, and appetitive motivation) is likely to be adaptive by allowing an individual to conserve resources and later redirect them towards more productive endeavors. According to such views, depressed mood is instigated by a low rate of positive reward or insufficient control over rewards or punishments. Seligman's (1975) learned helplessness theory, for example, was founded on studies of animals exhibiting helpless behaviour when subjected to uncontrollable aversive events. Nesse's (2000) resource allocation model concentrates more on low rates of rewarding outcomes. Here, depressed mood represents an adaptive response to the propitiousness of situations by adjusting resource allocation (e.g., energy and investment) to inhibit investments in poor pay-off activities. In a similar vein, incentive disengagement theory (Klinger, 1975, 1993) proposes that depressed states disengage an organism from unobtainable incentives or goals, whilst Leahy's (1997) "sunk costs" model suggests that depression occurs when people persevere too long with behaviours resulting in low or diminishing rewards. Consistent with such models, Champion and Power (1995) have argued that depression-prone people tend to over-invest in a limited number of goals and, when such goals fail, there is a collapse in an individual's incentive and motivational systems.

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