Motivation and Melancholy: A Darwinian Perspective

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Introduction and Overview

Depression, the plague of our time, is fundamentally a disorder of motivation. To prevent and treat it effectively, we need to understand why motivation systems are the way they are, in addition to explaining how they work. Such an understanding must be grounded in an understanding of how natural selection shaped the mechanisms that regulate motivation. To continue to try to study depression without this basic knowledge is like trying to understand renal failure without knowing what the kidneys are for. The study of disease was stymied until the basic science of physiology revealed what organs are for in connection with how their mechanisms work. As we develop parallel knowledge in psychology, our efforts will become steadily more solid and cumulatively productive.

Before reviewing the pitfalls that have slowed progress for this enterprise, and possible ways around them, consider the terrible irony of the world we have constructed for ourselves. We have followed our desires to create societies that meet most of our needs superbly. Even middle class people now live better than kings of just a century ago. The most obvious luxury is fresh tasty food—we can have as much of whatever we want, whenever we want it. For most of us in developed societies, hunger is a problem only when we are dieting, which is increasingly often. Of nearly equal value are adequate shelter, heating and cooling, sanitation systems, medicine that can prevent and treat many diseases, dramatic expansions of longevity, far less exposure to the pain of bereavement, and, in just the past decade, the ability to communicate with anyone anywhere and access to any entertainment imaginable. This list could be expanded for pages. The point is that our motivation systems have led us to create a society that satisfies most of our wants, but leaves a vast number of people feeling hopeless, helpless and as if life is not even worth living. Some of these people have suffered reverses in life, but others have a superfluity of the resources that people have sought for centuries. We have largely achieved the goals that our motivations point us towards, but dissatisfaction is rampant and depression is epidemic. This is a cruel irony, one that should motivate deep efforts to understand its origins.

How prevalent is depression? According to the most recent epidemiological studies, the lifetime rates of disorders severe enough to require treatment according to the Diagnostic and Statistical Manual

of the American Psychiatric Association range from about 2% in Taiwan to about 5% in the USA and over 15% in France and Lebanon (Blazer, Kessler, McGonagle, & Swartz, 1994; Kessler et al., 1994; Weissman, Bland, & Canino, 1996). These figures are suspect, however. First, the criteria, while operationally sound, are fundamentally arbitrary with regards to choosing a level of severity that qualifies for a diagnosis. There is, for example, no natural break point in the distribution of number of depression symptoms that would suggest a basis for distinguishing demoralization from depression (Kendler & Gardner, 1998). Furthermore, diagnoses based on recollection are biased by strong tendencies to forget, or at least not report, prior well-documented episodes, and subsyndromal depressions are often serious. The 5-year prevalence of depression found in longitudinal studies of young urban women is 50% (Judd, Akiskal, & Paulus, 1997).

Public health data confirm the vast impact of depression. According to a WHO study, for women of reproductive age in developed societies, depression accounts for fully 19% of all disability lost years, three times higher than the next highest cause (schizophrenia at 7 %), and four times higher than the first physical disease on the list, osteoarthritis (Murray, Lopez, Harvard School of Public Health., World Health Organization, & World Bank, 1996). There is controversy about whether the prevalence of depression is increasing, (Cross-National Collaborative Group, 1992) or if we are just recognizing it more as other diseases are being controlled (Murphy, Laird, Monson, Sobol, & Leighton, 2000). Despite their limits, the data make it clear that depression is a massive problem. A look around at our neighbors, our friends, our family members and ourselves, confirms the pervasiveness and devastating effects of depression.

Shoals

Before proceeding to the main analysis of depression and motivation in an evolutionary context, it is worth pausing to review several common sources of confusion on which most attempts founder. The first is the illusion that aversive states are abnormal. This is so pervasive, not just in psychiatry but throughout medicine, that it deserves to be called the "Clinician's Illusion." Pain, nausea, fever and cough, just like anxiety and low mood, are aversive states associated with useful defenses. The illusion

that these defenses are pathological arises for simple psychological reasons. First, they are reliably associated with pathological or at least disadvantageous situations. When you have a fever, something is definitely wrong. But the fever is not the problem, it is part of the body's attempt at a solution (Kluger, 1979). Like other latent traits, it is aroused only in response to cues that indicate a specific kind of danger. The second reason defenses seem to be defects is because they are painful. It is very hard for us to see how suffering can be useful. We imagine that eliminating the possibility of pain would be wonderful, but, in fact, individuals who lack the capacity for pain are almost all dead by their mid-thirties (Sternbach, 1963). Nonetheless, we can use drugs to block pain with apparent impunity. Likewise, we routinely block fever, nausea, cough, diarrhea and anxiety with few apparent ill effects.

If these defenses are so useful, and their regulation has been shaped by natural selection, how can we block them so readily with so few complications? There are several specific reasons. First, the body has redundant defense mechanisms. If fever is artificially decreased, the immune system still goes about its business. Second, and of great importance for our current topic, mechanisms that regulate defenses are shaped according to the "smoke detector principle" (Nesse & Williams, 1994, pp. 213-214; Nesse, in press). If the cost of a defense is low (say 300 calories for vomiting), and the cost of not expressing the defense is very high (say, a 5% chance of death), then natural selection will shape a defense regulation mechanism that expresses the defense whenever the cost of the defense is less than the cost of the harm times the probability that the danger is actually present. Because the rustle behind the rock may be a bird, not a lion, and because the few molecules of salmonella toxin detected in the stomach may or may not be accompanied by others, the system must carry out the equivalent of a signal detection analysis to yield an optimal response. The result is a system that normally expresses many false alarms for every case where the danger is actually present. This makes it appear that the defense is unnecessary. In many cases, however, especially when there is no back up defense, blocking the defense causes serious complications. When shigella bacteria infect the intestines, for instance, taking medications that block diarrhea greatly increases the frequency of prolonged illness and complications (DuPont & Hornick, 1973).

The second shoal, closely related to the Clinician's Illusion, is the tendency to define depression as a pathological state, thus obviating the possibility that it may have utility or connections with useful

responses. In fact, the boundaries between normality and pathology can be defined scientifically only after we understand the tendency to treat all depression as the same illness just because it has the same phenomenology. Even aside from different etiologies that bring about clinical depression, there might be subtypes of depression or low mood, shaped by natural selection to help cope with different kinds of situations.

A third shoal is the tendency to confound the question of why individuals differ in their vulnerability to depression, with the question of why we all have a capacity for low mood and depression (Nesse, 2000a). These questions are substantially different. They are confounded largely because of the widespread tendency to try to explain depression as a disease unconnected with any normal system that regulates motivation and affect. We could conceivably learn why some people are so much more vulnerable to depression than others without ever understanding why we all have a capacity for low mood. However, once we know what low mood is for and how it is regulated, this will likely be of great value in studying why people differ in susceptibility to depression.

The final shoal is an overly simple approach to the task of analyzing the functions of emotions. The temptation is to attempt to provide an explanation of the evolution of each special state in terms of a specific function that give selective advantages. In this vein, communication and motivation are often cited. The functional significance of different aspects of emotions—especially cognition, physiology, behavior, subjective experience and facial expression—is given priority by different authors. From an evolutionary point of view, however, all of these characteristics are components of emotions. Each emotion is an integrated system that has been shaped by natural selection to adjust organisms in ways that increase their ability to cope with the adaptive challenges that typically arise in a particular kind of situation (Nesse, 1990). Certain situations have recurred so often the course of evolutionary history that organisms with such special modes of operation will have a selective advantage. For instance, individuals who experience symptoms of a panic when faced with a predator will be more likely to survive than individuals whose state remains unperturbed (Cannon, 1929). The wish to escape is readily understandable; the sweating prepares for flight and makes the body slippery, and the increased breathing and heart rate speed flight (Marks & Nesse, 1994). These aspects of panic are not useful in every

situation, but only in situations of severe danger.

In short, is generally a mistake to try to explain different emotions in terms of different functions. Instead, each emotional state is shaped to cope with the various challenges characteristic of a certain kind of situation. In order to understand low mood, we must understand in what situation it might be useful, and how. Like sweating, shivering, pain and nausea, emotions are latent traits that cannot even be detected until they are aroused by cues that engage the regulation mechanism. In order to understand the possible utility of low mood, this means that we must look not directly for its function or functions, but instead, first, as the kinds of situations in which characteristics are likely to be useful. Based on the assumption that the regulation mechanism expresses low mood mainly when it is useful, we can use those clues, and the characteristics of depression and low mood, to infer the situations in which they might be useful.

Depression Phenomenology

Intense recent scrutiny now provides a fairly clear picture of depression phenomenology (Akiskal, 1994; Akiskal & McKinney, 1973; Beck, 1967; Kendler, 1998; Kessler, Zhao, Blazer, & Swartz, 1997; McGuire, Troisi, & Raleigh, 1997; Whybrow, Akiskal, & McKinney, 1984). While most people are familiar with at least the basic picture, a brief review will facilitate further exposition. At the core of depression is decreased motivation, characterized by decreased interest in ordinary activities, decreased pleasure, inhibited initiative and a tendency to withdraw from other people. The appetites for food and sex are usually decreased, and they bring little pleasure. Cognitively, undue pessimism about the future is closely associated with hopelessness. Behavior is characterized by slowed movements or by agitation. Physical symptoms of constipation, aches, pains and fatigue are common. Sleep is disrupted, with early morning awakening typical. Subjectively, depressed people typically feel inadequate, guilty and self-critical. Often they feel that life is not worth living, sometimes they have thoughts of killing themselves, and some commit suicide. Overall, people with depression feel hopeless, helpless, guilty, worthless, and disinclined to do much of anything. It is as if the gain on the motivation system has been turned down so low that pleasure is absent, initiative stalls, and behavior ceases.

In the past generation, powerful new treatments, especially new medications, have been found to relieve depression (Shaffer, 1986). Prozac sales now top ten billion dollars per year, and yet these sales account for only about half of the antidepressant market. There also have been advances in cognitive behavioral and interpersonal therapies which, for mild depression, are equally effective (Keller et al., 2000). These new treatments have spawned new attempts to convince people that depression is not a personal failing but a medical disorder that can be treated (O'Hara, Gorman, & Wright, 1996). Despite these efforts, only about a third of people with depression in the USA have received treatment, and only a tiny percent of those with current depression are taking medication (Druss, Hoff, & Rosenheck, 2000).

The effort to find the causes of depression has become massive. The vast bulk of this effort has, understandably, gone into trying to find differences between people that explain why some become depressed and others do not. Several epidemiological studies have laid bare the extent of the problem. Major depression affects over 10% of the population in a lifetime, women being affected at twice the rate of men (Kessler et al., 1994). The onset is most often in early adulthood, but for many, symptoms continue intermittently throughout life. With each episode, the risk of having another episode increases (Kupfer et al., 1992), so that many psychiatrists now recommend continuing drug treatment indefinitely for people who have had three or more bouts of depression (Greden & Tandon, 1995). The onset of the first episode is precipitated by a severe life event in about 80% of cases, but only about a third of people who experience a severe life event will develop psychiatric symptoms (Brown, Bifulco, Harris, & Bridge, 1986). Life events are intimately related to life goals that Oatley and Bolton (1985, p. 294) define a severe life event as "one that removes from a person the possibility of enacting a role…that fulfills an important goal." Who develops depression is somewhat predictable based on vulnerability factors including prior negative affect, lack of social support, stress sensitivity, and genetic factors (Kupfer & Frank, 1997). Genetic factors account for most of the individual differences in vulnerability to manic depressive illness, some of the differences in vulnerability to early onset major depression, but little of the variance in vulnerability to mild depression (Lyons et al., 1998). A massive search is on for genetic factors that influence the risk of depression, with surprisingly few solid results so far. For reasons outlined below, I anticipate that specific genes that contribute to manic depression will be identified, but

that finding genes that cause more common kinds of depression will prove much more difficult.

An enormous investment has also been made to find the brain mechanisms that regulate mood and cause depression, often based on the assumption that depression is an abnormal state caused by specific kinds of brain pathology (Andreasen, 1984). Somewhat surprisingly, there still is no physiological or biochemical test that can reliably differentiate depressed people from others (McGuire & Troisi, 1998). Some findings, however, offer useful leads. In particular, the stress system, especially the hypothalamic-pituitary-adrenal axis, turns out to be in overdrive in many people with severe depression (Carroll et al., 1981). Furthermore, the cues that usually down-regulate the system, especially increased levels of cortisol, are relatively ineffective, as if the stress system has become autonomous (Young & Vasquez, 1996). Interestingly, exposure to extreme events that cause posttraumatic stress disorder seems to down-regulate levels of cortisol (Hoffman, Watson, Wilson, & Montgomery, 1989). For a time it appeared that the low levels of serotonin found in spinal fluid of people who had committed suicide were clues to the pathogenesis of depression, but now it appears that these levels are more characteristic of people who are impulsive and potentially violent (Virkkunen et al., 1994).

There is no doubt that states of depression are results of brain changes, nor is there doubt that the etiology of some cases originates in brain abnormalities, whether from genetic differences, developmental experiences or exposure to toxins or trauma. It is increasingly clear, however, that many of these brain changes are induced by social experiences. Whether these changes are pathological, like those associated with epileptic seizures, or whether they are aspects of a normal defensive system, like those associated with fever or pain, is a question yet to be answered (Nesse, 2000a).

In sum, efforts to identify the factors that make people different in their susceptibility to depression have not been balanced by efforts to understand the normal functions and regulation of the mood system. As a result, we lack answers to many fundamental questions about mood. Why do we even have a capacity for depression? How is depression related to ordinary low mood? What environmental cues regulate mood and what brain mechanisms mediate this regulation? Are there situations in which low mood is useful, or is it always pathological? Without answers to these questions, our efforts find the causes of depression are like efforts to find the causes of cancer without understanding

the mechanisms that regulate cell division. Depression is, first and foremost, a disorder of motivation. Before we can fully understand depression, we must understand the systems that normally regulate motivation. We especially need to know if there are situations in which low mood is useful.

Darwinian medicine

Darwinian medicine addresses these different kinds of question about the origins of disease (Williams & Nesse, 1991; Nesse & Williams, 1994; Nesse & Williams, 1998). Instead of trying to understand why people are different, it tries to understand why we all have vulnerabilities to certain diseases. In other words, it asks why natural selection has not made the body better designed. It turns out that there are only a few possible answers to this question. The first possibility, that natural selection simply is too random, and not strong enough to make the body better, does explain some susceptibility to disease, but far less than most people think. Far more powerful is the second possibility—much disease results from differences between environment in which we live and the environment in which we evolved. Natural selection simply has not had time to adapt the body to the change in circumstances. This accounts for a high proportion of modern diseases, including most of the complications of atherosclerosis, many cancers, automobile accidents, and substance abuse with all its complications. A third explanation is based on the trade-offs that characterize the design of all biological traits. The bones in your forearm would break less easily if they were thicker, but you would no longer be able to execute the exquisite rotation at the wrist that make possible dexterity and accurate throwing. Trade-offs exist also at the level of the gene. Of the tiny proportion of mutations that are selected for because they give a fitness benefit, most will have some disadvantages as well as advantages, thus giving rise to disease. Two further explanations are based on misunderstandings about what natural selection shapes. Organisms are not shaped for maximum health, but for maximum reproduction. If there is the trade-offs between them, as there often is, reproduction will dominate. This is why males have higher mortality rates than females in many species. Natural selection, furthermore, does not shape benefits for groups, or even individuals, but only for genes. An "outlaw" gene can become the increasingly frequent with successive generations, even if it severely impairs individual reproductive success. Such genes are uncommon because successful

reproduction usually requires a healthy phenotype. An individual who does not do what is good for the group may pass on more genes to the next generation than an individual who contributes more to the good of the group. Another major cause of vulnerability to disease arises from competition between organisms. We remain vulnerable to infection because pathogens evolve faster than we do. Likewise, predators have evolved to keep pace with defense mechanisms in their prey, otherwise they go extinct. And then there is competition within a species for resources, status and mates, a cause of substantial disease in many species, and especially in modern humans.

Finally, and of special relevance to understanding depression, there are bodily defenses and their exigencies. These are not exactly vulnerabilities to disease, but, as noted above, they are often confused with disease. Pain, fever, cough, nausea, vomiting, diarrhea, fatigue and anxiety are not diseases, they are defenses against diseases, dangers and bodily damage. Each is aroused by cues associated with a certain kind of danger, and each adjusts the body to a state in which it can better protect against those dangers.

The illusion that defenses are defects is pervasive. This is quite understandable on several counts, the first of which is their consistent association with aversive subjective experience. The exemplar, pain, it is nothing more or less than a pure aversive experience of a particularly excruciating kind. Other defenses, however, such as cough, vomiting, and anxiety are also, however, associated with profoundly negative feelings. The illusion that defenses are diseases arises not only from the associated subjective suffering, but also because the situations in which they are aroused are almost all disadvantageous. Finally, the "Clinician's Illusion" makes these defenses appear as if they are unnecessary. Much of everyday medicine consists of using drugs to block pain, fever, nausea, vomiting etc., and the results are only rarely untoward. If defenses are so useful, then how can it be that blocking them has so few untoward effects? The smoke-detector principle, described above, provides a partial explanation. The expression of a defense, such as vomiting, is relatively inexpensive, compared to the potential life-threatening cost of not expressing a defense if a serious danger is actually present. Thus, the optimum regulation for such defenses expresses them when there is even a small chance that the dangers present. Another factor is the redundancy of defense mechanisms, so that blocking one does not necessarily cause serious impairment. If you take medication to block fever, several other aspects of your immune system

will help clear influenza virus from your body.

These principles apply to depression. The question is whether depression is more like epilepsy (a pathological condition with no utility) or chronic pain (a dysregulation of a useful response) or like fever (a useful response). Much has been written on this question, often with great confidence. Some writers express great certainty that depression is not only always maladaptive, but that it is unrelated to any useful state. At the other extreme, some attribute adaptive functions even to the characteristics of severe depression. These opinions have important consequences. A doctor who believes that depression is purely pathological is likely to attend in only a cursory way to a person's life circumstances and psychodynamics. Such a doctor may well recommend medication treatment with little thought to the possibility that the state of low mood could have utility. Conversely, a metal health clinician who believes that depression is an adaptation may put extraordinary and expensive efforts into trying to understand its ecological origins and utility. It is increasingly clear that clinical anecdotes and rhetorical arguments will not resolve this issue. The suffering and disability associated with depression do not offer definitive evidence of its pathological nature, any more than would be the case for pain. Conversely, the utility of depression is not a necessary consequence of its close association with certain life circumstances. The only solution is to try to figure out whether depression is a dysregulation of some adaptive state, and if so, what that state is, in what situations it gives an advantage, and how. The best candidate for such a state is "low mood," for now left vaguely defined as a state of low motivation and self criticism that is less severe than depression, but otherwise similar.

What Motivation Must Do

Behavior regulation mechanisms have, necessarily, been shaped by natural selection to maximize fitness. To accomplish this, they must get and use information to make three crucial decisions: 1) What rate of effort expenditure is optimal for the current task? 2) When should the organism stop the current activity? 3) What should the organism do next? If these three decisions are made correctly, fitness will follow.

This way of parsing the problem of motivation is predicated, of course, on the assumption that behavior is broken into blocks in which the organism is mainly pursuing one activity. While there are often simultaneous goals, such as getting food and avoiding predators, large scale activities can be coded reliably according to whether the animal is foraging, consuming, grooming, nursing young, resting, fighting, playing, monitoring for predators, or some other activity. Behavior is divided into bouts for the good reason that almost all activities have startup costs. Switching too quickly from one activity to another is inefficient, as everyone with a tendency to attention deficit disorder knows all too well. It is also possible, as we shall see, to stay too long in one activity.

The first challenge is to determine the optimal rate of effort expenditure for the current activity. That depends on the shape of the curve that describes the net gain as a function of the level of effort. Organisms have remarkable capacities to match their level of effort expenditure to that which gives the greatest payoff. When the function is shaped like a simple hill, this may be simple. Walking too slowly will incur substantial opportunity costs and increased risks of predation, while running too fast will use precious unnecessary calories, and may damage body tissues. For many activities the curve is "s" shaped. When a woodpecker makes holes in the bark, a low rate of effort may yield few insects, while a doubled level of effort may give four times the benefit. In such situations bursts of intense activity are optimal. For arms races, such as a predator pursuing prey, this reaches an extreme, with a maximum pay-off often occurring at the maximal possible level of effort. Even a 10 percent increase in the cheetah's speed is likely to give a much greater proportional increase in the likelihood that will catch its prey, so the system is pushed to a limit defined by other constraints. The optimum is wherever the benefits minus the costs are maximal, a point that may be not be on the overall peak. These concepts are well known in economics and bioenergetics. Their application here is just to note how organisms benefit from adjusting levels of effort to payoffs available at each level.

The second decision an animal must make, and the one of most importance to motivation and depression, is how long to persist in its current activity before doing something different. This has been modeled exquisitely using the optimal foraging theorem (Charnov, 1976). The theorem predicts what an animal needs to do to get the maximum rate of return when it is foraging in somewhat separated patches,

each of which gives a high rate of return at first followed by decline. The time it takes to get between patches is usually fixed, so the decision the organism must make is when to stop feeding on a given patch. The general, simple, and profound answer is that rate of energy intake is maximized by moving to a new patch as soon as the rate of return in the current patch declines below the overall rate of return across all patches, including travel time.

–Insert Figure 1 here—

The power of this theory has been confirmed in many laboratory and field studies. Sophisticated derivative theories incorporate variations in quality of patches or risk of predation while moving between patches (Stephens & Krebs, 1986). The significance of this paradigm for understanding mood is based on the decreased motivation that the animal demonstrates just prior to moving to a new patch. If motivation for effort in the current patch does not decline, an organism will persist too long, and will be at a selective disadvantage. One wonders exactly what is happening in the brains and minds of animals as they experience a declining rate of return in a given patch. Perhaps the inhibition of motivation is an active organized process. If so, then activating this system too intensely or too long would give a syndrome akin to depression, and it should be possible to turn off this system by disrupting it at multiple points in the mediating chain.

The third decision an organism must make is what to do next. This could be resting, foraging, building a shelter, mating display, social exchange or any of the other activities organisms exhibit. Behavioral ecologists have developed a small set of categories to cope with this complexity, dividing effort into somatic, reproductive, and social effort (Krebs & Davies, 1997). Because every investment in one kind of effort subtracts from capacity to pursue another, these categories are extremely useful in analyzing the trade-offs that animals must make. Further divisions are also useful. Somatic effort can be divided into effort spent getting material resources, (food or money) and effort spent defending the self and those resources. Reproductive effort can be divided into mating effort and parenting effort. Social effort can be divided into effort to create and maintain alliances, and effort to increase one's rank in a

group. A male elephant seal, for instance, stops feeding during mating months in order to defend his harem. This extremely costly strategy nonetheless increases reproductive success more than if he were to exert some effort in the pursuit of resources. Humans face trade-offs that are just a serious, if not always quite so stark. Someone who devotes hours each day to increasing physical attractiveness cannot devote as much time to advancing in a career. Someone who works 80 hours a week will have a difficult time finding a mate. In social psychology these phenomenon have been extensively studied as goal choice conflicts.

Goals

Much behavior, for animals as well as humans, is organized by plans and goals (Miller, Galanter, & Pribram, 1965). We humans are extreme in this tendency, however. We don't just ramble from patch to patch, we plan ahead to achieve large goals (Gollwitzer, 1996). Our needs vary and so our goals vary (Lewin, 1936). Goals influence behavior by activating current concerns (Klinger, 1977) and by inducing "mind-sets" (Gollwitzer, 1990). As many have noted, goals are organized in hierarchies. There are moment-to-moment goals and medium-term goals, and goals that are central to a person's life strategy and sense of personal identity.

We recognize the central role of goals so readily that it is worth pausing to ask why complex behavior should be organized in this way, instead of just by learning. How does organizing behavior according to goals give a selective advantage? One benefit comes from savings on the startup costs associated with initiation of any activity. Whether walking to a distant grove to collect fruit or preparing a meal, or eating, there are start-up costs; respectively, they include organizing a foraging group, building a fire, and secretion of digestive juices. A digger wasp whose nest is disrupted must repeat every action in the fixed action sequence, no matter at what point the disruption occurred. An organism whose behavior is organized by goals can avoid waste by jumping ahead to the point necessary to achieve the goal.

Another benefit of organizing behavior according to goals is that it allows an individual to pursue larger goals that can only be accomplished over several time bouts, or even across a period of months or years. In fact, the capacity to think of and become committed to large-scale goals is a distinctly human

trait that yields huge benefits and, as we will see, major problems. The pursuit of large-scale enterprises necessitates making significant investments prior to receiving any pay off. In many instances, there is no certainty that there will ever be any pay off. Thus, individuals often find themselves exerting substantial effort towards an large payoff whose attainment is increasingly uncertain. People in this situation must decide whether to give up or to continue pursuing the goal. Such decisions are difficult. Giving up consigns considerable effort to waste and requires seeking other strategies, and often scaling down ambitions. Persisting, however, saps crucial energy, time and resources that could be put to other uses. Making these decisions well is crucial to an organism's fitness. For organisms that pursue large-scale goals with uncertain payoffs, the decision is especially important and difficult. Furthermore, as already emphasized, efforts towards one major goal intrinsically conflict with those towards others. Mating effort and parenting effort, for instance, are generally mutually exclusive. By studying ideographic goals, it is possible to apply nomothetic methods in the study of emotions (Diener & Fujita, 1995).

Emotions and Goal Pursuit

Emotions are specialized states shaped by natural selection to adjust multiple aspects of the individual in ways that enhance the ability to cope with the challenges that arise in certain situations (Nesse, 1990). These situations, such as attack by a predator, opportunity to mate, loss of a child, or attack by a higher ranked individual, contain major fitness challenges and have recurred often enough in the course of evolutionary history to have shaped specialized states of response. If the situations that arise in the pursuit of goals are indeed crucial to fitness, we should expect that each of them has shaped a corresponding emotion. Indeed, this seems to be the case. Some of our most powerful emotions fit naturally into simple table based on whether the goal is positive or negative, whether it is in the future or the past. This basic quadripartite structure is by no means new. Aqinas, following Plato in the Protagoras, recognized four main emotions: hope, fear, happiness and sadness. As illustrated in Table 1, these fundamental distinctions can be enhanced by incorporating two additional characteristics of goals (positive vs. negative goals, physical vs. social goals) and two additional columns to reflect emotions during the pursuit of a goal, and the difference between emotions after attainment of a goal, and failure to

reach a goal. The result shows how several important emotions are aroused by the specific situations that arise in the course of pursuing a goal. The adaptive challenges characteristic of each of these situations have, I argue, shaped the corresponding emotions to adjust the organism in ways that increase fitness.

	Domain	Before	During	After Success	After Failure
OPPORTUNITY(Positive Goal, Promotion)	*Physical*	Desire	Progress Flow	Pleasure	Disappointment
	Social	Hope	ObstacleFrustration Unreachable Low mood UncertainConfusion	Happiness	Disappointment
THREAT (Negative Goal, Prevention)	*Physical*	Fear	Positive Expectation Hope Negative Expectation Despair	Relief	Pain
	Social	Anxiety		Relief	Sadness

Table 1: Situations that Arise in Goal Pursuit, and Corresponding Emotions

An enormous body of work documents the relationship between goal pursuit and affect (Gollwitzer & Moskowitz, 1996). Except for a hiatus during the heyday of behaviorism, goals and their effects and associated affects have been a central concern in social psychology. Behavioral strategies are influenced by the content of goals, their conflicts with other goals, and how they are framed. Several closely related varieties of goals have been defined, including current concerns (Klinger, 1975), personal strivings (Emmons & King, 1988), personal projects (Little, Lecci, & Watkinson, 1992), life tasks (Cantor, 1994) For a summary, see Emmons (1999). With few exceptions (Buss, 1995; Klinger, 1998), however, this enterprise has proceeded independently from developments in evolutionary biology and behavioral ecology.

On the core topic of interest here, there is considerable consensus that low mood is reliably aroused by persisting in the pursuit of an unreachable goal (Brickman, 1987; Carver & Scheier, 1990; Emmons, 1996; Klinger, 1975; Pyszczynski & Greenberg, 1987). The down regulation of motivation in this situation is exactly what is called for to avoid expending energy unnecessarily. In most circumstances, it leads to disengagement and turning effort elsewhere. When organism is committed to a goal, however, and persists in unrewarded effort for which the likelihood of reward is increasingly slim, ordinary low mood often seems to escalate into depression (Janoff-Bulman & Brickman, 1982). Therefore, the question of why some individuals tend to persist excessively in the pursuit of unreachable goals is of crucial significance.

Clinical experience suggests that certain kinds of people seem predisposed to get trapped in this situation. Some are unwilling to give up large ambitions. Everyone knows of someone who has spent years trying to break into the national music scene or to get into an elite training program. Other people are fearful, and cannot give up their current unsatisfactory situation because they fear change. Some are emotionally attached and stay attached even when abused. Many people are sensitive to social expectations and their own inner sense of duty. Perhaps the most common, and most devastating situation, however, is when a goal that is central to a person's identity and purpose in life increasingly appears unreachable. It may be a marriage, hopes for a beloved child who is doing poorly, career ambitions, or an idiosyncratic personal goal. In any of these cases, people who cannot give up a major life goal are likely to become depressed. As Oatley puts it, "Depression…is a crisis in a plan that leaves the person without alternative plans for fulfilling a goal that has been lost." (Oatley, 1992, p. 299) Although this position is widely accepted, not much formal data to support it has yet been collected in community samples. Preliminary results from our detailed study of life goal pursuit and mood in a community sample of 100 adults suggest that depression is indeed more prevalent in those individuals who are trapped by commitments to goals they can neither reach nor give up, and a high proportion of those who are so trapped are depressed. While the question of causation cannot be answered by such cross-sectional studies, they can help to identify the relative contributions of various difficult life situations to causing depression, and they may be able to link life events research even more tightly to the

psychology of goal pursuit.

Emotions are gradually shaped into partially overlapping subtypes to deal with different varieties of a situation. This is clear in anxiety disorders where subtypes correspond to different dangers (Marks & Nesse, 1994). The various phobias—fear of heights, public speaking, blood, small animals, etc.—each correspond to a different kind of danger. In sadness and depression, the situation is much less clear, but it there are hints that losses of different kinds of resources arouse different kinds of emotions. The most devastating loss is, of course, death of a loved one; the corresponding emotion is grief. Potential loss of a mate to a competitor arouses jealousy, and persistence in trying to get a mate's love is a common source of depression. Loss of physical resources arouses sadness which in some instances may help to prevent further losses. When the loss of such resources makes a previous strategy nonviable, then effort put into the old strategy will be wasted and low mood and depression can arise.

Losses of status and social power are of particular import, as has been emphasized by a group of researchers (Price, Sloman, Gardner, Gilbert, & Rohde, 1994; Price & Sloman, 1987; Sloman & Gilbert, 2000) who study "involuntary yielding." They note the utility of submissive behaviors in many animal species where failure to submit results in recurrent attacks by dominants. Humans are preoccupied by their social position, and try to defend it, often when that is not possible. This is a classic example of the larger category of being unable to give up striving for an unreachable goal. The loss of status has special significance, however, because inhibition of drives and lowered self-esteem may be especially useful in this circumstance—characteristics that are hard to explain otherwise (Hartung, 1988). It will be interesting and important to determine if low self-esteem and inhibited ambition are more common in depression precipitated by loss of status as compared to loss of other resources.

Attachment, Commitment, and Goals

The most potent precipitant of depression is loss of a deep intimate relationship. The tendency of evolutionary psychology to interpret relationships in terms of instrumental exchange makes it hard to understand why people would persist in unsatisfying relationships, but they do. Two kinds of fitness benefits, those from kin selection and those from reciprocal exchange, have been burdened with

explaining all sociality (Cosmides & Tooby, 1992). They have been analyzed nearly to death using game theory models. The grand conclusion is that they are indeed powerful and accurate explanations, but they have difficulty explaining "anomalies" in human behavior (Bowles & Gintis, 1999). Examples include the tendency of people to cooperate excessively in one-shot prisoner's dilemma games, and the tendency of people playing "take it or leave it" games to be excessively fair as the proposer, and excessively punitive as the decider. In real relationships, of course, people do all kinds of things that cannot be explained by kin selection or reciprocity. They take care of their spouses with Alzheimer's disease, they leave spouses who have vast wealth and power, and they invest huge efforts in caring for children with disabilities. Much such behavior can be explained by the human capacity for subjective commitment (Frank, 1988; Hirshleifer, 1987; Schelling, 1978). Individuals gain a huge ability to influence others if then can convince others that they will, in a specified future situation, act in ways that will not then be in their best interests. Some such communications are promises to help, others are threats of spiteful harm. Such strategies are deeply paradoxical, but very effective. People who have the capacity to make these subjective commitments have a major selective advantage. There is every reason to believe that natural selection has shaped a capacity for both profound subjectivity, and also persistence in maintaining commitments in the face of major evidence that the commitment will not yield a net benefit (Nesse, 2000b; Nesse, in preparation). Social groups give rise to emergent forces of natural selection, as those who break their commitments learn. They become non-players in the social network.

This brief digression to the large topic of commitment is essential because emotional commitment is so often responsible for inability to disengage from unreachable goals. Unrequited love is all around us. Apparently irrational commitment to career goals is the root of much depression. Even prolonged or severe bereavement can be interpreted as persisting in an unavailable relationship. Natural selection seems to have shaped systems that nearly ensure inability to give up some goals, despite the depression that so often arises in this situation.

Conclusion

Low mood and depression are phenomena of motivation. To understand them we need to understand how motivation regulation systems have been shaped by natural selection. Positive mood can certainly be useful (Fredrickson, 1998), but only in certain situations. In other situations, where effort will be dangerous or unproductive, decreasing the level of motivation will be useful. In situations where no possible action will pay off, global decrease in motivation is adaptive. Mood varies as a function of the propitiousness of the situation. Whether high or low mood is useful depends entirely on the situation.

These principles have been studied in animals, although much of the relevant work has been conducted in a behavioral framework that neglects the natural environment and the influence of behaviors on reproductive success. Extinction can be reexamined as a mechanism designed to maximize net caloric intake in the natural environment. The brain mechanisms aroused by extinction should be the same as those involved in motivating an animal to move to a new patch, or to cease foraging altogether. Drugs that influence these mechanisms should alter mood, offering a potentially novel way to recognize new antidepressant medications.

For all the power of an evolutionary approach to make links with animal behavior, however, it also reveals profound differences in how our human behavior is organized. We pursue large-scale goals, often several conflicting ones all at once. We break off our behavior in pursuit of one goal in order to pursue another, allocating our effort in patterns that, by the end of life, tend to maximize fitness (at least in the natural environment). However, we pursue goals in very complex and indirect ways, often by making commitments that obligate us to give up the pursuit of important goals in certain circumstances. In short, we humans are complicated, our emotions are crucial to their relationships, and social structures have profound effects that often swamp other factors that influence our behavior. An evolutionary approach to human behavior does not mean treating people as more crude or more rational than they really are. It can, instead, provide a nomothetic framework that can help us to understand how emotions arise from the exigencies that inevitably arise in the pursuit of individual idiosyncratic goals. Such understanding will be essential to finding the origins of depression in our evolved motivation systems, and this knowledge will be, in turn, crucial to making prevention and treatment more effective.

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Figure 1

Optimal Foraging: The tangent to the utility curve is the optimal feeding time. Each of the other lines gives a lower utility per unit time.