

Pseudoparadoxical Impulsivity in Restrictive Anorexia Nervosa: A Consequence of the Logic of Scarcity

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Abstract: Objective: *To explain an apparently paradoxical pattern wherein sufferers of restrictive anorexia nervosa exhibit both rigorous self-restraint and episodic impulsivity.* **Method:** *The experimental, historical, and clinical literatures were examined for evidence of psychological and behavioral changes accompanying severe dietary constriction; such changes were noted and compared with those reported to occur in anorexics.* **Results:** *Increased impulsivity in association with dietary constriction is described in diverse literatures. A number of lines of evidence suggest that the serotonergic system mediates this change.* **Discussion:** *Many forms of impulsivity can be understood as having once constituted fitness-enhancing responses to resource scarcity. It is suggested that an evolved psychological mechanism calibrates the individual's sensitivity to risk in light of future prospects. Self-injurious behaviors are explicable as misfirings of such a mechanism. Similarly, excessive exercising by anorexics may reflect the misdirection of reward systems that normally encourage adaptive increases in ranging behavior under conditions of scarcity.* © 2002 by Wiley Periodicals, Inc. *Int J Eat Disord* 31: 376–388, 2002.

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INTRODUCTION

The Apparent Paradox of Impulsive Behavior Among Restrictive Anorexics

Restrictive Anorexics Are Highly Self-Controlled

Restrictive anorexia nervosa has been characterized as a disease of excessive control, with sufferers focusing exacting self-discipline on the restriction of food intake and the reduction of body weight (Casper, 1998; cf. Banks, 1996). Consistent with a tendency toward over-control, anorexics typically score significantly higher than controls on perfectionism (Lovece, 1997) and harm avoidance (Brewerton, Hand, & Bishop, 1993; Kleifield, Sunday, Hurt, & Halmi, 1994), and lower on sensation seeking (Rossier, Bolognini, Plancherel, & Halfon, 2000). Following rehabilitative weight gain, anorexics exhibit supranormal ser-

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otonergic activity (Kaye, Gendall, & Strober, 1998). Serotonergic functioning is strongly associated with impulse control (reviewed in Hollander & Rosen, 2000), suggesting that anorexics possess an underlying personality structure characterized by extreme inhibition of impulses and other episodic motivational factors (Kaye et al., 1998). Overall, anorexics display behaviors and personality traits similar to those of religious ascetics, individuals for whom the control of bodily impulses is a defining feature of identity (Banks, 1992; Barrett & Fine, 1990; Huline-Dickens, 2000; Rampling, 1985; Tait, 1993).

Restrictive Anorexics Exhibit Impulsivity

Remarkably, given their highly self-controlled nature, restricting anorexics can also be impulsive. Comparisons across eating-disordered subjects indicate that, although a wide variety of impulsive behaviors are more common among individuals suffering bulimia nervosa than among those suffering anorexia nervosa, nonetheless, pathological impulsivity is not negligible among restricting anorexics (Nagata, Kawarada, Kiriike, & Iketani, 2000). Herzog, Keller, Sacks, and Yeh (1992) report that 10% of surveyed sufferers have a history of suicide attempts; Vandereycken and van Houdenhove (1996) report that 35.3% have a history of stealing; Fava, Rappe, West, and Herzog (1995) report that 28% have experienced (and later regretted) uncontrollable anger attacks; Thompson, Wonderlich, Crosby, and Mitchell (1999) report that 49% have engaged in violence, 3.6% have engaged in robbery with a weapon, and a substantial number abused drugs; and Yaryura-Tobias, Neziroglu, and Kaplan (1995) describe a number of cases of self-mutilation. Similarly, Askenazy et al. (1998) found high rates of impulsive behavior (nonpremeditated suicide attempt, self-harm, kleptomania, and alcohol use) among a mixed sample of anorexics with and without bulimic features; neither the Barratt Impulsivity Scale nor the Impulsivity Rating Scale differentiated among the two groups, with both groups scoring significantly higher than controls. Strober, Freeman, and Morrell (1999) found that nearly 30% of restricting anorexics eventually develop impulsive binge eating.

It appears paradoxical that highly self-controlled restricting anorexics sometimes display a wide variety of impulsive behaviors. One possible resolution of this paradox lies in the recognition that impulsivity may stem from multiple sources. Specifically, rather than reflecting longstanding personality traits, anorexics' impulsive behavior may sometimes be a consequence of dietary constriction.

METHODS

Evidence that Impulsivity Is a Consequence of Severe Dietary Constriction

To evaluate the possibility that impulsivity observed among restricting anorexics results from their dietary constriction rather than from the underlying factors responsible for their anorexia, the literature was examined for information on psychological and behavioral changes accompanying dietary constriction in non-anorexic individuals. Sources were located through searches of the Medline, PsychInfo, Biosis, and Melvyl databases, and via a snowball strategy using the bibliographies obtained thereby.

Evidence from Normal Subjects

A variety of sources document a marked rise in impulsivity in normal individuals in conjunction with starvation. The Minnesota Semi-Starvation Experiment (Kays et al.,

1950) is an invaluable source of data on the psychological concomitants of severe dietary restriction. Thirty-six physically and mentally healthy young men voluntarily subsisted on a nutritionally balanced but calorically restricted diet for 6 months, losing 25% of their body weight. Psychological evaluations before, during, and after the experiment led investigators to propose that semi-starvation is accompanied by a distinct form of neurosis, with the severity positively correlated with degree of starvation, and with recovery occurring in proportion to weight regained.

As in two smaller semi-starvation experiments (Benedict, Miles, Roth, & Smith, 1919; Fichter, Pirke, & Holsboer, 1986), the Minnesota subjects evinced hyperirritability, with some individuals experiencing barely containable violent impulses. For example, Keys et al. report that one subject “expressed the fear that he was going ‘crazy.’ . . . He felt that he was losing his inhibitions . . . On many occasions . . . he had impelling desires to smash or break things,” (Keys et al., 1950, p. 903). Another subject reported “Someone across the table—I can’t remember who—will never know how close he came to having a tray smash down on his head. He’d done nothing,” (Keys et al., 1950, p. 895).

Hyperirritability is redundantly reported in accounts of starvation due to disaster or war (reviewed by Keys et al., 1950, pp. 784–818). A number of the Minnesota subjects also engaged in impulsive shopping sprees, frequently buying unneeded items that they could not afford. Despite strong dedication to the experiment, four subjects engaged in compulsive binge eating. Binge eating is reported in a large number of historical accounts of starvation (Hagan, Whitworth, & Moss, 1999). One Minnesota subject suffered kleptomania; among liberated survivors of the Belsen Nazi concentration camp, impulsive food theft persisted even after it was clear that food was no longer in short supply (Niremberski, 1946). The same Minnesota subject experienced suicidal ideation and required hospitalization. Another subject engaged in repeated acts of self-mutilation, eventually chopping off three of his fingers (Keys et al., 1950, pp. 892–897). Accidental injuries increased dramatically in the course of the Dutch famine during World War II (reviewed in Keys et al., 1950, p. 898), and high rates of both accidental and intentional self-injury also occurred among starving Allied prisoners of war in Japanese POW camps (Curtin, 1946).

Evidence from Obese Subjects

Additional data concerning the effects of severe dietary restriction come from reports of psychological changes accompanying crash dieting and voluntary (‘therapeutic’) starvation in obese subjects.¹ Robinson and Winnik (1973) report that, during severe dietary restriction, obese patients with no history of psychiatric disorders manifested a variety of impulsive behaviors, including exhibitionism and suicidality; Kollar and Atkinson (1966) and Glucksman and Hirsch (1968) likewise report suicidality. Uncontrollable binge eating is common during therapeutic starvation (Glucksman & Hirsch, 1968; Glucksman, Hirsch, McCully, Barron, & Knittle, 1968; Kollar & Atkinson, 1966; Swanson & Dinello, 1970). While this may not be surprising given the subjects’ initial problems with food, less expected are the marked changes in emotion: Many investigators report dramatic increases in anger and aggression, in some cases constituting a stunning

¹The therapeutic aspect of these procedures is highly questionable. In those cases where patients were monitored after release, nearly all individuals regained most or all of the weight lost during the procedure. Animal models indicate that binge eating persists long after starvation has been reversed (Hagan & Moss, 1997), and studies of human survivors of catastrophic starvation reveal the same pattern (Favaro, Rodella, & Santonastaso, 2000; Hagan et al., 1999). The continuation of binge eating after the alleviation of resource scarcity may reflect the workings of an adaptive mechanism designed to gauge the local environment—if famine has occurred once during an individual’s lifetime, the likelihood may be increased that it will occur again, and hence the persistence of intake-maximizing behaviors may be adaptive.

character reversal compared with features observed early during treatment; symptoms are generally mitigated by refeeding (Crumpton, Wine, & Drenick, 1966; Glucksman & Hirsch, 1968; Glucksman et al., 1968; Rowland, 1968; also Kollar & Atkinson, 1966). For example, Swanson and Dinello report that their patients were initially compliant, pleasant, and optimistic, yet became impulsively angry to the point of physical abuse during therapeutic starvation. The authors note "One man asked for help . . . because he was so angry when in traffic that he feared he would kill any aggravator by smashing his car into them," (Swanson & Dinello, 1970, p. 124). Lest these responses be dismissed as simple frustration in response to the noxious experience of starvation, it is important to recognize that Swanson and Dinello's patients did not experience hunger after the first 48 hours of fasting (Swanson & Dinello, 1970, p. 122). Indeed, subjects "denied physical hunger but finally explained they must eat or go 'crazy,'" (p. 125) [Keys et al. also report that in total (but not semi-) starvation, "the sensation of hunger disappears in a matter of days," (Keys et al., 1950, p. 829)].²

The Rationale for Including Observations of Obese Subjects

Although obesity distinguishes the above subjects from average individuals, this does not exclude obese subjects as sources of relevant information. As will be discussed at length, the relationship between dietary constriction and impulsivity is explicable in terms of the workings of an evolved mechanism that adjusts risk sensitivity in light of current status and future prospects. From an evolutionary perspective, obese subjects provide an acceptable source of data because obesity is an evolutionarily novel condition. Ancestral populations were unlikely to have regularly encountered superabundant food that did not require significant energetic expenditure to obtain. Accordingly, natural selection is unlikely to have crafted mechanisms that are calibrated to the possibility of extremely large fat reserves. Rather, evolved mechanisms can be expected to be sensitive to sudden alterations in caloric intake as indices of ensuing changes in resource availability. Evidence in support of this proposal comes from the analogous case of amenorrhea accompanying weight loss. It is unlikely that adiposity per se contributes to the regulation of ovulation (Bronson & Manning, 1991). Instead, it appears that changes in leptin levels play a critical role (Thong, McLean, & Graham, 2000), and leptin declines in response to caloric restriction (Kolaczynski et al., 1996). The strong parallels between the transient psychopathology and character changes that accompany crash dieting/therapeutic starvation and the effects observed in actual starvation are thus explicable as the product of a psychological mechanism that responds to drastic dietary constriction independent of initial body weight.

Evidence from Nonhuman Animals

Swanson and Dinello's starving patients, interviewed and examined regularly, were aware of, and able to describe, marked changes in themselves. For example, one subject "admitted to concern over some impulsive ideas which he was entertaining . . . he sensed a feeling of recklessness in himself," (Swanson & Dinello, 1970, p. 125). Self-reflective and able to communicate our experiences using language, humans can report on motivational changes accompanying severe dietary constriction. However, despite the absence of such

²These reports suggest that, even holding symbolic factors aside, eating is motivated via multiple subjective pathways. While hunger may serve as a motivator that maintains intake on a daily basis, less clearly defined subjective factors, including an obsessive preoccupation with food, may motivate intake under conditions of prolonged scarcity (cf. Curtin, 1946; Keys et al., 1950; Niremberski, 1946).

abilities, nonhuman animal models demonstrate many behavioral homologues of the patterns described above. For example, aggression increases in response to food deprivation in mollusks (Zack, 1974), hermit crabs (Hazlett, 1966), sunfish (Poulsen, 1976), blue-footed boobys (Nunez-de la Mora, Drummond, & Wingfield, 1996), pigeons (Fachinelli, Ison, & Rodriguez Echandia, 1996), mice (Rohles & Wilson, 1974), and rats (Lore, Gottdiener, & Delahunty, 1986), among others (but see also Loy, 1970; Crowell-Davis, Barry, Ballam, & Laflamme, 1995). Pigeons are more impulsive in their foraging behavior under greater dietary restriction (Snyderman, 1983), while salmon take more predation risks following food deprivation (Damsgard & Dill, 1998). Finally, food deprivation produces recurrent binge eating in rats (Hagan & Moss, 1997).

Serotonin, Impulse Control, and Dietary Constriction

As noted earlier, serotonergic functioning is central to the regulation of impulsive behavior. Irritability and impulsive aggression have been extensively shown to be associated with reduced serotonergic activity (reviewed in Hollander & Rosen, 2000; Davidson, Putnam, & Larson, 2000), and a similar association obtains in regard to impulsive buying (Black, 1996), binge eating (McElroy et al., 2000), kleptomania (reviewed in Hollander & Rosen, 2000), self-mutilation (New et al., 1997), exhibitionism (Abouesh & Clayton, 1999; Zohar, Kaplan, & Benjamin, 1994), and suicidality (Oquendo & Mann, 2000). In short, all of the impulsive behaviors exhibited under conditions of severe dietary constriction are linked to diminished serotonergic activity.

Serotonin, which plays a key role in the control of feeding behavior and the experience of satiety (Simansky, 1995), is endogenously produced from dietary precursors, the most important of which is tryptophan (reviewed in Fernstrom, 1994). There is considerable evidence that a drastically restricted diet is accompanied by reductions in serotonergic functioning. Examination of rats sacrificed following a restricted feeding regimen that produced a 15–20% reduction in body weight revealed lowered concentrations of serotonin, and reduced rates of serotonin synthesis, in the hypothalamus (Haleem & Haider, 1996; see also Fernstrom & Wurtman, 1971). Young rats maintained on 50% of their normal diet exhibit marked reductions of frontal cortex binding sites for serotonin transporters (Huether, Zhou, Schmidt, & Wiltfang, 1997); Zhou et al. report that equivalent dietary constriction causes approximately a 30% reduction in the density of cortical serotonin transporters (Zhou, Huether, Wiltfang, Hajak, & R  ther, 1996). Paralleling these animal models, underweight anorexics exhibit deficits in a variety of direct and indirect measures of serotonergic functioning (plasma tryptophan, urinary 5-HIAA, platelet serotonin binding, and basal cerebrospinal fluid 5-HIAA), deficits that are eliminated by weight restoration (Kaye, Gwirtsman, George, & Ebert, 1991; Leibowitz, 1990). Hence, it appears likely that the various impulsive behaviors that occur during starvation are different manifestations of a single behavioral mechanism that is intimately linked to food intake.³

³Kaplan, Klein, and Manuck (1997) review an extensive body of work linking cholesterol, serotonergic functioning, and impulsivity, and present a similar adaptive argument regarding the association between the availability of dietary animal fat and risk-taking behavior. Although some of the cholesterol evidence is compelling, results are mixed, and recent studies have failed to find a correlation with impulsive violence (Steinert, Woelfle, & Gebhardt, 1999). Moreover, the specificity of the authors' argument with regard to the importance of hunting in human evolution places an unnecessary constraint on what appears to be a motivational system of widespread utility across species, thus making it difficult for Kaplan et al. to account for similar effects in noncarnivorous animals (cf. Kaplan et al., 1997, p. 36). Finally, recent findings indicate that, despite high levels of impulsivity and low levels of serotonergic activity, malnourished anorexics nevertheless exhibit normal or even elevated levels of cholesterol (Feillet et al., 2001).

AN EVOLUTIONARY EXPLANATION OF THE LINK BETWEEN DIETARY CONSTRICTION AND IMPULSIVITY

The Logic of Scarcity

Although the behavior of starving volunteers, prisoners, victims, patients, and anorexics may at first appear bizarre and nonsensical, an evolutionary approach sheds light on this constellation. The body's response to starvation can be characterized as a reallocation of available resources away from longterm goals in favor of shortterm objectives. For example, the amenorrhea that accompanies severe dietary constriction can be understood as a strategic postponement of reproductive expenditures in favor of maintenance: Female mammalian reproduction is a prolonged and energetically costly enterprise, one that can be ill-afforded if available reserves are insufficient. Natural selection has therefore favored mechanisms that delay reproduction under conditions of scarcity so as to maximize the likelihood that the individual will survive to see the day when resource abundance permits a resumption of cycling (Panter-Brick, Lotstein, & Ellison, 1993). Immune functioning can be similarly conceptualized as a longterm investment: In immune responses, resources are expended warding off pathogens today so that survival and reproduction will be enhanced tomorrow. However, immune functioning is a luxury that cannot be afforded if it is questionable whether available resources suffice to sustain the body—there is no point fighting off next month's cold if, in doing so, one starves today. Accordingly, the multiplex reduction in immune functioning that accompanies starvation (Hulsewé, van Acker, von Meyenfeldt, & Soeters, 1999) can be seen in part as a strategic reallocation of dwindling supplies away from longterm investments in favor of immediate survival.

The same logic that informs bodily responses to starvation also pertains to behavioral responses. The environment presents organisms with a wide range of opportunities for action. Those opportunities vary both with regard to (a) the potential benefits or costs involved (i.e., risk), and (b) the likelihood that those benefits or costs will be realized (i.e., uncertainty). Under conditions of resource abundance, the optimal strategy consists of minimizing the possibility that actions will prove costly: Because it is not worth gambling with an otherwise relatively secure future, opportunities to reap large immediate rewards should be forgone if there is a significant likelihood that high costs will be incurred (Daly & Wilson, 1988). However, under conditions of resource scarcity, the converse strategy is optimal, namely maximizing the possibility that actions will prove rewarding: Because there is no point trying to protect a future that will not be realized if death by starvation intervenes beforehand, opportunities to reap large immediate rewards should be pursued even if there is a significant likelihood that high costs will be incurred. In short, individuals who are starving have little to lose, and much to gain, by pursuing the promise of immediate resource acquisition regardless of potential cost. Phrased in behavioral terms, *under conditions of severe scarcity, impulsivity is the optimal orientation to the world* (cf. Kirk & Logue, 1997).

All organisms are subject to the same logic of scarcity, and hence, it is understandable that increases in impulsivity are observed in response to dietary constriction in a wide variety of species. Moreover, we can expect natural selection to have fine-tuned these changes so that they are congruent with the particular costs and benefits relevant to each organism. Cross-species comparison reveals a positive relationship between metabolic rate and impulsivity in response to food reinforcers (Tobin & Logue, 1994), while within-species differences in metabolic rate predict aggressivity following food deprivation in

mice (Rohles & Wilson, 1974) and predator avoidance in fish (Krause, Loader, McDermott, & Ruxton, 1998). These relationships are to be expected given that the higher an animal's metabolic rate, the lower its tolerance for fluctuations in energy availability in a given time period, and hence, the more strongly future prospects should be discounted in favor of immediate opportunities under conditions of scarcity.

The Adaptive Value of Impulsive Behaviors

The utility of some impulsive behaviors exhibited by humans facing dietary constriction is clear. Binge eating is a highly effective means of maximizing intake from an available resource before circumstances, or competitors, preclude further access—this is precisely why opportunistic social carnivores such as canines ‘wolf’ down their food (Thorne, 1995). Anger, the emotion prototypically elicited by transgression, motivates punitive assaults that serve to both curtail ongoing transgressions and deter future ones (Fessler, forthcoming). Increases in both sensitivity to transgression and willingness to respond aggressively thus decrease the likelihood that resources will be appropriated by competitors. The scarcer those resources become, the more it pays to get angry, and hence hyperirritability and impulsive aggressivity have considerable utility during famine conditions. The converse of defending against transgression is engaging in transgression. When resources are scarce, natural selection favors individuals who seize opportunities for resource acquisition even if they do not have rightful possession. Starving individuals who steal are more likely to survive and reproduce than starving individuals who do not, and thus impulsive thievery would have been highly adaptive under ancestral conditions. Finally, the presence of impulsive thieves increases the utility of hair-trigger disproportionate responses to transgression, thereby further favoring aggressivity.

Critics might object that the above account is not consistent with the behavior of restrictive anorexics because, with the exception of binge eating, much of their impulsive behavior seems not to result in food consumption. However, in considering these behaviors it is important to differentiate the *form* of the action from the *content*. Normal individuals facing severe dietary constriction develop an obsessive preoccupation with obtaining and consuming food, and this shapes impulsive behavior such as theft (Keys et al., 1950). In contrast, much of the ideation of restrictive anorexics revolves around preoccupations with body weight, a conscious concern that is apparently able to guide manifestations of impulsivity such that behavior often does not result in eating. By way of comparison, the Minnesota subjects' dedication to the goals of the experiment was generally sufficient to keep them from impulsively buying food; instead, they found themselves buying cooking implements, cook books, and miscellaneous items (Keys et al., 1950). Hence, conscious goals can sometimes rechannel impulsive behaviors in ways that subvert the evolved mechanism responsible for increased impulsivity.

Self-Injurious Behaviors as Misfirings of Evolved Mechanisms

In contrast to binge eating, enhanced aggressivity, and kleptomania, self-mutilation and suicidality are maladaptive under nearly all circumstances, and this would have been as true in our ancestral past as it is today. To understand how natural selection

could have increased the likelihood of self-mutilation and suicide under conditions of dietary constriction, it is important to recognize that selection often produces imperfect mechanisms. Organisms are generally well served by a sensitivity to, and avoidance of, bodily harm. However, under conditions of scarcity, the optimal fitness maximizing strategy entails a reduction in sensitivity to costs, including the risk of bodily harm. Although the fear of pain normally constitutes a significant deterrent to a wide variety of behaviors, this factor adaptively loses its motivational salience during severe dietary constriction. Combined with the fatigue that accompanies prolonged caloric deficit, this change accounts for the high accident rates reported for starving populations. However, accidental injury as a consequence of a reduction in the salience of harm is not the same as active self-mutilation. Rather, it appears that this maladaptive behavior occurs because, under special circumstances, a feature of the normal response to trauma can become a reward for injury.

The subjective experience of pain is not an inevitable mechanical consequence of the disruption of tissue. Rather, pain is actively produced by specialized components of the nervous system (Treede, 1995), presumably because of its utility in promoting (a) escape from injurious stimuli, (b) learning from injurious events, and (c) subsequent avoidance of harm. However, for each of these goals, it is likely that the prolongation of a given pain event over time produces diminishing returns (cf. Jacob, 1981). For example, if a child sticks his finger in a flame, withdrawal, learning, and subsequent avoidance are likely driven by the initial moments of experience—beyond a certain point, additional benefits are probably not commensurate with the costs of continuing to dedicate attention and other resources to the pain. Perhaps as a consequence of this economic logic, prolonged injury may be accompanied by the release of opiate-like beta-endorphins, a mechanism that modulates activity in many areas of the CNS (Porro et al., 1999), and apparently serves to curtail the experience of pain.

One consequence of a generalized reduction in the motivational salience of bodily harm is the removal of impediments to intentional self-harm. Once such barriers are absent, the potential exists for a perversion of the function of beta-endorphins—rather than serving to counterbalance pain, these substances may become positive reinforcers for injury. Anorexic self-mutilation can thus be seen as a maladaptive misfiring of both (a) the normally adaptive decrease in the salience of harm under conditions of scarcity and (b) the normally adaptive counterbalancing effects of endogenous antinociceptive substances. While self-reflection and symbolic mediation may influence cognitions surrounding such behavior (cf. Strong, 1998), these are likely secondary, rather than primary causes; by way of comparison, in a pharmacologically mediated animal model of self-mutilation, the target behavior increased in response to food deprivation (Katsuragi, Ushijima, & Furukawa, 1984).

Although self-mutilation is often placed on a continuum with suicidality, with both behaviors seen as manifestations of a generalized self-destructiveness (Stanley, Winchel, Molcho, & Simeon, 1992), it is likely that, while related, self-mutilation and suicidality constitute distinct phenomena. Suicide, a behavior that is probably unique to humans, may stem from our unmatched ability to conceptualize future possibilities, to 'run scenarios in our heads.' Suicidal ideation often includes thoughts about how unpleasant life is currently, and how death would both bring an end to suffering and achieve a variety of other personal goals, such as inflicting harm on others (Menninger, 1933). While healthy individuals may occasionally entertain such thoughts, these imagined rewards are normally countered by the fear of injury and death. However, truly suicidal individuals appear to be indifferent to such prospects—they see only the benefits of suicide, and are

blind to the costs.⁴ Severe dietary constriction may thus produce both self-mutilation and suicidality because both behaviors are accidental misfirings of a normally adaptive reduction in the motivational salience of the prospect of bodily harm—while self-mutilators get a kick from the endorphin system that modulates pain, suicidal individuals seek the imagined benefits of an end to life.

The Relationship Between Severe Dietary Constriction and Locomotory Behavior

Although it is more easily categorized as compulsive rather than impulsive, an additional noteworthy feature of the behavior of some restricting anorexics is a pattern of excessive exercising (Davis et al., 1997). In many animals, dietary constriction elicits increased locomotion (Routtenberg & Kuznesof, 1967). Animal models demonstrate that starving individuals who are allowed to exercise have higher levels of serotonergic activity than those who are not (Broocks, Schweiger, & Pirke, 1991). Conversely, serotonin agonists reduce exaggerated locomotory behavior (Wilckens, Schweiger, & Pirke, 1992). It thus appears that serotonin is part of a reward system that encourages enhanced movement in response to dietary constriction. Although increasing energy expenditures in the face of resource scarcity might at first seem maladaptive, it is important to note that vital resources are often unevenly distributed across the landscape. Accordingly, mechanisms that greatly increase ranging behavior in response to dietary constriction are adaptive in that they enhance the likelihood that the organism will encounter resource patches or regions of greater resource abundance. It appears that, in the case of restricting anorexics, this usually adaptive constellation misfires: Casper (1998) describes a pattern seen in some underweight anorexics of paradoxical liveliness and hyperactivity accompanied by euphoria. Casper suggests that, while other factors may contribute to the initial pathogenesis of anorexia nervosa, the euphoric state induced by exercise during starvation may ironically reward undernourishment and promote over-exercising, thus contributing to the perpetuation of anorexic behavior.⁵

Inter-Individual and Inter-Group Differences in Impulsivity Under Dietary Constriction

The studies discussed in the first section of this article report frequencies of various impulsive behaviors among restrictive anorexics ranging from 10% to nearly 50%. This raises two questions: (1) What factors are responsible for inter-individual differences in the form of impulsivity manifested under dietary constriction?; (2) What is the absolute frequency of impulsivity among restricting anorexics? With regard to the first question, it is likely that the specific impulsive behaviors exhibited by a given individual are a complex product of idiosyncratic and contextual factors. For example, while aggressivity likely increases in all individuals facing dietary constriction, it is probably most overtly manifest in persons who, for reasons of temperament, personality, or values, are predisposed toward hostile behavior (cf. Keys et al. 1950). Similarly, individuals who frequently encounter frustration or transgression are more likely to behave aggressively

⁴The assertion that suicidality is in part the product of a generalized reduction in the salience of risk is supported by the positive correlation between suicidal ideation and carrying a weapon, fighting, boating or swimming after drinking, riding with a driver who had been drinking, driving after drinking, and rarely or never using seat belts (Barrios et al. 2000).

⁵Keys et al. report that “[f]eeling ‘high’ was sometimes attributed by the men to a ‘quicken[ing]’ effect of starvation . . . These feelings of well-being and exhilaration lasted from a few hours to several days,” (Keys et al., 1950, p. 836).

under conditions of dietary constriction than are individuals who rarely encounter such insults.

With regard to the second question, at present several obstacles preclude estimating the total proportion of restricting anorexics exhibiting some form of impulsivity. First, no study performed to date encompasses all forms of impulsivity, a necessary condition given the possibility of incomplete overlap among categories of individuals (i.e., some subjects who manifest behavior x do not manifest behavior y , and vice versa). Second, an evolutionary perspective suggests that impulsivity should increase as a function of both the severity and the duration of dietary constriction, yet these factors were not systematically evaluated in a number of the studies conducted thus far.

Published accounts of nonanorexics facing dietary constriction typically involve small sample sizes and widely varying circumstances, making it difficult to establish baseline frequencies of impulsivity under dietary constriction. Nevertheless, there are a priori reasons for believing that such rates will be higher than those observed in restricting anorexics. Given that they exhibit supranormal serotonergic indices following rehabilitative weight gain, it is likely that restricting anorexics are constitutionally buffered against the serotonergic consequences of dietary constriction, suggesting that impulsive behaviors will occur at lower frequencies among this group than would occur among nonanorexics under analogous conditions.

CONCLUSION

The apparent paradox of impulsive behavior among restricting anorexics, individuals who normally exhibit inordinate self-control, is resolved once it is recognized that, via serotonergic mediation, severe dietary constriction enhances impulsivity. While the etiology of restrictive anorexia nervosa is still debated, many of the behaviors and subjective experiences seen in this condition are explicable as the product of adaptations that normally serve to increase survivorship during periods of drastic food scarcity; additional facets of the syndrome can be understood as misfirings of the same adaptations. This explanation is imminently testable: If anorexic impulsivity is a consequence of dietary constriction, then, as occurs in both normal and obese individuals, the frequency and severity of many impulsive behaviors should increase as a function of weight loss and decrease as a function of refeeding. Finally, a Darwinian approach to eating disorders may illuminate a wide variety of seemingly strange and nonsensical phenomena, potentially providing insight that is of value to clinicians, patients, and family members in coping with these conditions.

REFERENCES

- Abouesh, A., & Clayton, A. (1999). Compulsive voyeurism and exhibitionism: A clinical response to paroxetine. *Archives of Sexual Behavior, 28*, 23–30.
- Askenazy, F., Candito, M., Caci, H., Myquel, M., Chambon, P., Darcourt, G., & Puech, A.J. (1998). Whole blood serotonin content, tryptophan concentrations, and impulsivity in anorexia nervosa. *Biological Psychiatry, 43*, 188–195.
- Banks, C.G. (1992). "Culture" in culture-bound syndromes: The case of anorexia nervosa. *Social Science & Medicine, 34*, 867–884.
- Banks, C.G. (1996). "There is no fat in heaven": Religious asceticism and the meaning of anorexia nervosa. *Ethos, 24*, 107–135.
- Barrett, D., & Fine, H.J. (1990). The Gnostic Syndrome: Anorexia nervosa. *Psychoanalytic Psychotherapy, 4*, 263–270.

- Barrios, L.C., Everett, S.A., Simon, T.R., & Brener, N.D. (2000). Suicide ideation among US college students: Associations with other injury risk behaviors. *Journal of American College Health*, 48, 229–233.
- Benedict, F.G., Miles, W.R., Roth, P., & Smith, H.M. (1919). Human vitality and efficiency under prolonged restricted diet. Washington, DC: Carnegie Institution of Washington.
- Black, D.W. (1996). Compulsive buying: A review. *Journal of Clinical Psychiatry*, 57(Suppl 8), 50–55.
- Brewerton, T.D., Hand, L.D., & Bishop, E.R. (1993). The Tridimensional Personality Questionnaire in eating disorder patients. *International Journal of Eating Disorders*, 14, 213–218.
- Bronson, F.H., & Manning, J.M. (1991). The energetic regulation of ovulation: A realistic role for body fat. *Biology of Reproduction*, 44, 945–950.
- Broocks, A., Schweiger, U., & Pirke, K.M. (1991). The influence of semistarvation-induced hyperactivity on hypothalamic serotonin metabolism. *Physiology and Behavior*, 50, 385–388.
- Casper, R.C. (1998). Behavioral activation and lack of concern, core symptoms of anorexia nervosa? *International Journal of Eating Disorders*, 24, 381–393.
- Crowell-Davis, S.L., Barry, K., Ballam, J.M., & Laflamme, D.P. (1995). The effect of caloric restriction on the behavior of pen-housed dogs: Transition from unrestricted to restricted diet. *Applied Animal Behaviour Science*, 43, 27–41.
- Crumpton, E., Wine, D.B., & Drenick, E.J. (1966). Starvation: Stress or satisfaction? *Journal of the American Medical Association*, 196, 394–396.
- Curtin, A.P. (1946). Imprisonment under the Japanese. *British Medical Journal*, 2(4476), 585–586.
- Daly, M., & Wilson, M. (1988). *Homicide*. New York: A. de Gruyter.
- Damsgard, B., & Dill, L.M. (1998). Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch*. *Behavioral Ecology*, 9, 26–32.
- Davidson, R.J., Putnam, K.M., & Larson, C.L. (2000). Dysfunction in the neural circuitry of emotion regulation—a possible prelude to violence. *Science*, 289(5479), 591–594.
- Davis, C., Katzman, D.K., Kaptein, S., Kirsh, C., Brewer, H., Kalmbach, K., Olmsted, M.P., Woodside, D.B., & Kaplan, A.S. (1997). The prevalence of high-level exercise in the eating disorders: Etiological implications. *Comprehensive Psychiatry*, 38, 321–326.
- Fachinelli, C., Ison, M., & Rodriguez Echandia, E.L. (1996). Effect of subchronic and chronic exposure to 5-hydroxytryptophan (5-HTP) on the aggressive behavior induced by food competition in undernourished dominant and submissive pigeons (*Columba livia*). *Behavioural Brain Research*, 75, 113–118.
- Fava, M., Rappe, S.M., West, J., & Herzog, D.B. (1995). Anger attacks in eating disorders. *Psychiatry Research*, 56, 205–212.
- Favaro, A., Rodella, F.C., & Santonastaso, P. (2000). Binge eating and eating attitudes among Nazi concentration camp survivors. *Psychological Medicine*, 30, 463–466.
- Feillet, F., Feillet-Coudray, C., Bard, J.M., Parra, H.J., Favre, E., Kabuth, B., Fruchart, J.C., Vidailhet, M. (2000). Plasma Cholesterol and Endogenous Cholesterol synthesis during refeeding in anorexia nervosa. *Clinica Chimica Acta*, 294, 45–56.
- Fessler, Daniel, M.T., (forthcoming). The male flash of anger: Violent response to transgression as an example of the intersection of evolved psychology and culture. To appear in *Missing the Revolution: Darwinism for Social Scientists*. J. Barkow, ed. New York: Oxford University Press.
- Fruchart, J.C., & Vidailhet, M. (2000). Plasma cholesterol and endogenous cholesterol synthesis during refeeding in anorexia nervosa. *Clinica Chimica Acta*, 294, 45–56.
- Fernstrom, J.D. (1994). Dietary amino acids and brain function. *Journal of the American Dietetic Association*, 94, 71–77.
- Fernstrom, J.D., & Wurtman, R.J. (1971). Brain serotonin content: increase following ingestion of carbohydrate diet. *Science*, 174, 1023–1025.
- Fichter, M.M., Pirke, K.-M., & Holsboer, F. (1986). Weight loss causes neuroendocrine disturbances: Experimental study in healthy starving subjects. *Psychiatry Research*, 17, 61–72.
- Glucksman, M.L., & Hirsch, J. (1968). The response of obese patients to weight reduction: A clinical evaluation of behavior. *Psychosomatic Medicine*, 30, 1–11.
- Glucksman, M.L., Hirsch, J., McCully, R.S., Barron, B.A., & Knittle, J.L. (1968). The response of obese patients to weight reduction: II. A quantitative evaluation of behavior. *Psychosomatic Medicine*, 30, 359–373.
- Hagan, M.M., & Moss, D.E. (1997). Persistence of binge-eating patterns after a history of restriction with intermittent bouts of refeeding on palatable food in rats: Implications for bulimia nervosa. *International Journal of Eating Disorders*, 22, 411–420.
- Hagan, M.M., Whitworth, R.H., & Moss, D.E. (1999). Semistarvation-associated eating behaviors among college binge eaters: A preliminary description and assessment scale. *Behavioral Medicine*, 25, 125–132.
- Haleem, D.J., & Haider, S. (1996). Food restriction decreases serotonin and its synthesis rate in the hypothalamus. *Neuroreport*, 7, 1153–1156.
- Hazlett, B.A. (1966). Factors affecting the aggressive behavior of the hermit crab *Calcinus Tibicen*. *Zeitschrift fuer Tierpsychologie*, 23, 655–671.
- Herzog, D.B., Keller, M.B., Sacks, N.R., & Yeh, C.J. (1992). Psychiatric comorbidity in treatment-seeking anorexics and bulimics. *Journal of the American Academy of Child & Adolescent Psychiatry*, 31, 810–818.
- Hollander, E., & Rosen, J. (2000). Impulsivity. *Journal of Psychopharmacology*, 14(2,Suppl1), S39–S44.

- Huether, G., Zhou, D., Schmidt, S., & Wiltfang, J. (1997). Long-term food restriction down-regulates the density of serotonin transporters in the rat frontal cortex. *Biological Psychiatry*, 41, 1174–1180.
- Huline-Dickens, S. (2000). Anorexia nervosa: Some connections with the religious attitude. *British Journal of Medical Psychology*, 73, 67–76.
- Hulsewé, K.W., van Acker, B.A., von Meyenfeldt, M.F., & Soeters, P.B. (1999). Nutritional depletion and dietary manipulation: Effects on the immune response. *World Journal of Surgery*, 23, 536–544.
- Jacob, J. (1981). Endogenous morphines and pain. *Agents and Actions*, 11, 634–636.
- Kaplan, J.R., Klein, K.P., & Manuck, S.B. (1997). Cholesterol meets Darwin: Public health and evolutionary implications of the cholesterol-serotonin hypothesis. *Evolutionary Anthropology*, 6, 28–37.
- Katsuragi, T., Ushijima, I., & Furukawa, T. (1984). The clonidine-induced self-injurious behavior of mice involves purinergic mechanisms. *Pharmacology, Biochemistry & Behavior*, 20, 943–946.
- Kaye, W.H., Gendall, K., & Strober, M. (1998). Serotonin neuronal function and selective serotonin reuptake inhibitor treatment in anorexia and bulimia nervosa. *Biological Psychiatry*, 44, 825–838.
- Kaye, W.H., Gwirtsman, H.E., George, D.T., & Ebert, M.H. (1991). Altered serotonin activity in anorexia nervosa after long-term weight restoration. Does elevated cerebrospinal fluid 5-hydroxyindoleacetic acid level correlate with rigid and obsessive behavior? *Archives of General Psychiatry*, 48, 556–562.
- Keys, A., & University of Minnesota Laboratory of Physiological Hygiene (1950). *The biology of human starvation* (Vol. 2). Minneapolis: University of Minnesota Press.
- Kirk, J.M., & Logue, A.W. (1997). Effects of deprivation level on humans' self control for food reinforcers. *Appetite*, 28, 215–226.
- Kleinfeld, E.I., Sunday, S., Hurt, S., & Halmi, K.A. (1994). The Tridimensional Personality Questionnaire: An exploration of personality traits in eating disorders. *Journal of Psychiatric Research*, 28, 413–423.
- Kolaczynski, J.W., Considine, R.V., Ohannesian, J., Marco, C., Opentanova, I., Nyce, M.R., Myint, M., & Caro, J.F. (1996). Responses of leptin to short-term fasting and refeeding in humans: a link with ketogenesis but not ketones themselves. *Diabetes*, 45, 1511–1515.
- Kollar, E.J., & Atkinson, R.M. (1966). Responses of extremely obese patients to starvation. *Psychosomatic Medicine*, 28, 227–246.
- Krause, J., Loader, S.P., McDermott, J., & Ruxton, G.D. (1998). Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. *Proceedings of the Royal Society of London Series B Biological Sciences*, 265, 2373–2379.
- Leibowitz, S.F. (1990). The role of serotonin in eating disorders. *Drugs*, 39 Suppl 3, 33–48.
- Lore, R., Gottdiener, C., & Delahunty, M.J. (1986). Lean and mean rats: Some effects of acute changes in the food supply upon territorial aggression. *Aggressive Behavior*, 12, 409–415.
- Lovece, I. (1997). *Characterological issues in anorexia nervosa*. Unpublished doctoral dissertation, New School For Social Research, New York.
- Loy, J. (1970). Behavioral responses of free-ranging rhesus monkeys to food shortage. *American Journal of Physical Anthropology*, 33, 263–272.
- McElroy, S.L., Casuto, L.S., Nelson, E.B., Lake, K.A., Soutullo, C.A., Keck, P.E., Jr., & Hudson, J.I. (2000). Placebo-controlled trial of sertraline in the treatment of binge eating disorder. *American Journal of Psychiatry*, 157, 1004–1006.
- Menninger, K.A. (1933). Psychoanalytic aspects of suicide. *International Journal of Psycho-Analysis*, 14, 376–390.
- Nagata, T., Kawarada, Y., Kiriike, N., & Iketani, T. (2000). Multi-impulsivity of Japanese patients with eating disorders: primary and secondary impulsivity. *Psychiatry Research*, 94, 239–250.
- New, A.S., Trestman, R.L., Mitropoulou, V., Benishay, D.S., Coccaro, E., Silverman, J., & Siever, L.J. (1997). Serotonergic function and self-injurious behavior in personality disorder patients. *Psychiatry Research*, 69, 17–26.
- Niremberski, M. (1946). Psychological investigation of a group of internees at Belsen Camp. *Journal of Mental Science*, 92, 60–74.
- Nunez-de-la Mora, A., Drummond, H., & Wingfield, J.C. (1996). Hormonal correlates of dominance and starvation-induced aggression in chicks of the blue-footed booby. *Ethology*, 102, 748–761.
- Oquendo, M.A., & Mann, J.J. (2000). The biology of impulsivity and suicidality. *Psychiatric Clinics of North America*, 23, 11–25.
- Panter-Brick, C., Lotstein, D.S., & Ellison, P.T. (1993). Seasonality of reproductive function and weight loss in rural Nepali women. *Human Reproduction*, 8, 684–690.
- Porro, C.A., Cavazzuti, M., Baraldi, P., Giuliani, D., Panerai, A.E., & Corazza, R. (1999). CNS pattern of metabolic activity during tonic pain: evidence for modulation by beta-endorphin. *European Journal of Neuroscience*, 11, 874–888.
- Poulsen, H.R. (1976). *Predation, aggression, and activity levels in food deprived sunfish (Lepomis Macrochirus and L. Gibbosus): Motivational Interactions*. Unpublished doctoral dissertation, University of Colorado.
- Rampling, D. (1985). Ascetic ideals and anorexia nervosa. *Journal of Psychiatric Research*, 19, 89–94.
- Robinson, S., & Winnik, H.Z. (1973). Severe psychotic disturbances following crash diet weight loss. *Archives of General Psychiatry*, 29, 559–562.
- Rohles, F.H., & Wilson, L.M. (1974). Hunger as a catalyst in aggression. *Behaviour*, 48, 123–130.

- Rossier, V., Bolognini, M., Plancherel, B., & Halfon, O. (2000). Sensation seeking: A personality trait characteristic of adolescent girls and young women with eating disorders? *European Eating Disorders Review*, 8, 245–252.
- Routtenberg, A., & Kuznesof, A.W. (1967). Self-starvation of rats living in activity wheels on a restricted feeding schedule. *Journal of Comparative and Physiological Psychology*, 64, 414–421.
- Rowland, C.V., Jr. (1968). Psychotherapy of six hyperobese adults during total starvation. *Archives of General Psychiatry*, 18, 541–548.
- Simansky, K.J. (1995). Serotonergic control of the organization of feeding and satiety. *Behavioural Brain Research*, 73, 37–42.
- Snyderman, M. (1983). Optimal prey selection: The effects of food deprivation. *Behaviour Analysis Letters*, 3, 359–369.
- Stanley, B., Winchel, R., Molcho, A., & Simeon, D. (1992). Suicide and the self-harm continuum: Phenomenological and biochemical evidence. *International Review of Psychiatry*, 4, 149–155.
- Steinert, T., Woelfle, M., & Gebhardt, R.P. (1999). No correlation of serum cholesterol levels with measures of violence in patients with schizophrenia and non-psychotic disorders. *European Psychiatry*, 14, 346–348.
- Strober, M., Freeman, R., & Morrell, W. (1999). Atypical anorexia nervosa: Separation from typical cases in course and outcome in a long-term prospective study. *International Journal of Eating Disorders*, 25, 135–142.
- Strong, M. (1998). *A bright red scream: Self-mutilation and the language of pain*. New York: Viking.
- Swanson, D.W., & Dinello, F.A. (1970). Severe obesity as a habituation syndrome: Evidence during a starvation study. *Archives of General Psychiatry*, 22, 120–127.
- Tait, G. (1993). "Anorexia nervosa": Asceticism, differentiation, government. *Australian & New Zealand Journal of Sociology*, 29, 194–208.
- Thompson, K.M., Wonderlich, S.A., Crosby, R.D., & Mitchell, J.E. (1999). The neglected link between eating disturbances and aggressive behavior in girls. *Journal of the American Academy of Child & Adolescent Psychiatry*, 38, 1277–1284.
- Thong, F.S., McLean, C., & Graham, T.E. (2000). Plasma leptin in female athletes: Relationship with body fat, reproductive, nutritional, and endocrine factors. *Journal of Applied Physiology*, 88, 2037–2044.
- Thorne, C. (1995). Feeding behaviour of domestic dogs and the role of experience. In J. Serpell (Ed.), *The domestic dog: Its evolution, behaviour and interactions with people* (pp. 103–114). New York: Cambridge University Press.
- Tobin, H., & Logue, A.W. (1994). Self-control across species (*Columba livia*, *Homo sapiens*, and *Rattus norvegicus*). *Journal of Comparative Psychology*, 108, 126–133.
- Treede, R.D. (1995). Peripheral acute pain mechanisms. *Annals of Medicine*, 27, 213–216.
- Vandereycken, W., & Van Houdenhove, V. (1996). Stealing behavior in eating disorders: Characteristics and associated psychopathology. *Comprehensive Psychiatry*, 37, 316–321.
- Wilckens, T., Schweiger, U., & Pirke, K.M. (1992). Activation of 5-HT_{1C}-receptors suppresses excessive wheel running induced by semi-starvation in the rat. *Psychopharmacology*, 109, 77–84.
- Yaryura-Tobias, J.A., Neziroglu, F.A., & Kaplan, S. (1995). Self-mutilation, anorexia, and dysmenorrhea in obsessive compulsive disorder. *International Journal of Eating Disorders*, 17, 33–38.
- Zack, S. (1974). The effects of food deprivation on agonistic behavior in an opisthobranch mollusc, *Hermisenda crassicornis*. *Behavioral Biology*, 12, 223–232.
- Zhou, D., Huether, G., Wiltfang, J., Hajak, G., & Ruther, E. (1996). Serotonin transporters in the rat frontal cortex: Lack of circadian rhythmicity but down-regulation by food restriction. *Journal of Neurochemistry*, 67, 656–661.
- Zohar, J., Kaplan, Z., & Benjamin, J. (1994). Compulsive exhibitionism successfully treated with fluvoxamine: A controlled case study. *Journal of Clinical Psychiatry*, 55, 86–88.