**Reproductive suppression**

Reproductive suppression may be defined broadly as inhibition of reproductive physiology and/or reproductive behavior in an otherwise fertile individual in response to specific environmental or physiological conditions. By this definition, reproductive suppression involves disruption of normal reproductive processes by inhibitory influences, rather than simply the absence of stimulatory influences. Reproductive suppression has been documented in a broad range of taxa and occurs in both sexes. It may be triggered by a variety of factors from the internal and external environments, and may involve inhibition at a number of different stages of the reproductive process. Reproductive suppression can occur in response to variation in either physiological or environmental factors that are otherwise associated with, or predictive of, poor reproductive outcomes. Physiologically, the most important of these variables is energy balance. Reproduction in many (e.g. mammals) but not all (e.g. reptiles) taxa is suppressed when animals enter negative energy balance as a consequence of such factors as low food availability, high workload or activity levels, and low ambient temperature, or combinations of these factors. The metabolic signal(s) detected by the body and transduced into reproductive suppression are unknown. A critical role of body fat, once thought to be the key signal, has largely been discounted, and more recent attention has focused on potential roles of other metabolic fuels and metabolic hormones. In addition to energy balance, reproduction may be suppressed by such physiological states as lactation and illness. The external environmental factors that influence reproductive outcomes can generally be categorized as dietary, physical or social in origin. In some cases, these same factors are used as proximate cues to trigger suppression (or activation) of reproduction. In other cases, animals respond more directly to factors that are not inherently crucial for reproduction but are predictive of critical changes in climatic or dietary conditions. For example, many species become reproductively quiescent on a seasonal basis, thereby avoiding breeding during periods of low food or water availability or adverse climatic conditions. The environmental cues that may be used to synchronize reproductive activity with seasonal changes in the environment are quite diverse, however, including such variables of direct reproductive significance as rainfall (e.g. zebra finch, Taeniopygia guttata castanotis), ambient temperature (e.g. green anole lizard, Anolis carolinensis) and food availability (e.g. Columbian ground squirrel, Spermophilus columbianus), as well as such predictive variables as photoperiod (e.g. sheep, Ovis aries) and availability of non-nutritive plant compounds (e.g. montane vole, Microtus montanus). Reproductive suppression is less common and, usually, less pronounced in males than in females, presumably reflecting the lower costs of reproduction and/or higher maximum potential reproductive success in males. Suppression in males may involve either a delay in the initial onset of reproductive function or a subsequent inhibition of reproductive activity in mature, potentially fertile adults. Male orangutans (Pongo pygmaeus), for example, may undergo a prolonged adolescent period, characterized by reduced levels of androgens and gonadotropic hormones, arrested development of secondary sexual characteristics and low attractiveness to females, if living in proximity to an adult male. In other species, fully mature, socially subordinate males may undergo inhibition of sexual behaviour (e.g. dwarf mongoose, Helogale parvula), impairment of spermatogenesis (e.g. naked molerat, Heterocephalus glaber) and/or suppression of androgen secretion (e.g. Alpine marmot, Marmota marmota).

Females have considerably more complex reproductive physiology than males and, not surprisingly, exhibit a greater variety of mechanisms by which reproduction can be suppressed. As in males, organismic or environmental factors may inhibit or delay maturation in young females or may reversibly impair reproductive function in otherwise fertile adults. Interactions with or cues from dominant females, for example, can delay puberty (e.g. Mongolian gerbil, Meriones unguiculatus), suppress ovulation (e.g. pine vole, Microtus pinetorum), inhibit sexual behaviour (e.g. rhesus macaque, Macaca mulatta), delay conception (e.g. yellow baboon, Papio cynocephalus), block implantation (e.g. white-footed mouse, Peromyscus leucopus), induce spontaneous abortion or prenatal litter reduction (e.g. golden hamster, Mesocricetus auratus) or impair maternal care (e.g. ring-tailed lemur, Lemur catta) in subordinate females.

The environmental and organismic factors that determine poor reproductive outcomes may be considered stressors, and reproductive suppression is frequently assumed to be mediated by a stress response. Although reproduction can certainly be impaired by aspects of the stress response (e.g. elevated circulating concentrations of glucocorticoids or endogenous opioids), it is becoming increasingly clear that reproductive suppression frequently occurs in the absence of generalized stress and may instead be mediated by more specialized neuroendocrine mechanisms. The final common pathway for many of these mechanisms may be disrupted hypothalamic secretion of gonadotropin-releasing hormone, leading to inhibited release of gonadotropins from the pituitary gland and, consequently, to impaired endocrine, gametogenic and/or ovulatory function in the gonads.

Reproductive suppression may have profound implications for captive breeding and conservation programs. As a consequence of the reproductive system’s sensitivity to environmental factors, a particular species may show contrasting reproductive patterns in captivity and in the field, or even in different captive or natural environments, and may fail to breed under non-natural conditions. Clearly, the success of breeding and conservation programs may be critically dependent upon an understanding of the organismic, environmental and social influences on reproduction.