behaviour – including brooding and **nursing** – **paternal behaviour** and other aspects of parental behaviour, as well as behaviours associated with maximizing reproductive opportunity such as **territoriality**. (DSM)

See also: Reproduction

Reproductive suppression

Reproductive suppression may be defined broadly as inhibition of reproductive physiology and/or **reproductive behaviour** 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.

Reproduction can be highly risky and energetically demanding, especially for females. Moreover, the likelihood that any particular **breeding** attempt will succeed – that is, that it will produce surviving offspring – may depend upon prevailing conditions in the physical, biotic and social environment, as well as upon the potential breeder's physical and physiological condition. Thus, to the extent that current reproductive attempts decrease prospects for survival or future reproduction, individuals of many species may increase their lifetime reproductive success by timing their reproductive attempts to occur during favourable conditions and, correspondingly, curtailing their reproductive activity at other times. Natural **selection** may therefore be expected to favour those individuals that undergo reproductive suppression under inauspicious conditions.

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*).

In many species, reproductive physiology and/or reproductive behaviour may be partly or completely suppressed by cues from the social environment. Social suppression of reproduction often involves agonistic or dominance-related interactions between same-sex adults. Among cooperatively breeding naked mole-rats (*Heterocephalus glaber*) and common marmoset monkeys (*Callithrix jacchus*), for example, behaviourally subordinate females typically exhibit low reproductive hormone levels and atrophied reproductive tracts, fail to ovulate and engage in little or no sexual behaviour while living with a dominant female, but commence normal reproductive function shortly after separation from the dominant female. In other species, **pheromone**s may trigger reproductive suppression independently of direct behavioural interactions. For example, ovulatory or lactating rats (*Rattus norvegicus*), as well as female house mice (*Mus musculus*) living in large groups or dense populations, release chemosignals that extend or suppress oestrous cycles and reduce fertility in other females.

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 orang-utans (*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 mole-rat, *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 **stressor**s, 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 **opioid**s), 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 **gonadotropin**s from the **pituitary gland** and, consequently, to impaired endocrine, gametogenic and/or ovulatory function in the **gonad**s.

Reproductive suppression may have profound implications for **captive breeding** and **conservation** programmes. 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 programmes may be critically dependent upon an understanding of the organismic, environmental and social influences on reproduction. (WS)

Further reading

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Reptile

Traditionally, reptiles are the class of vertebrates that include squamates (lizards, snakes and amphisbaenids), turtles, crocodilians and the two species of the tuatara (found only on a few islands in New Zealand). Current taxonomic practice argues that if all these animals are in a single class, Reptilia, then so are their descendants – dinosaurs and birds. Others argue that the traditional Reptilia is not a monophyletic group, and thus should be broken up with, perhaps, only lizards and snakes as 'true' reptiles. Staying with traditional views, reptiles are ectothermic amniotes comprising roughly 3000 snakes, 4500 lizards, 160 amphisbaenians, 300 turtles and 23 crocodilians.

Reproductively, reptiles have traits found in both birds (oviparity) and mammals (viviparity). Post-hatching/-natal parental care, long thought absent in reptiles, is now known to be both complex and lengthy in all crocodilians studied, absent in virtually all turtles and the tuatara and highly variable in lizards and snakes. In fact, in some lizards, cohorts of offspring live with their parents and younger siblings for some years. Many crocodilians not only guard their nests for many months, but aid in the hatching of their babies when they hear them vocalize in the nest and transport them, very gently, to water. Probably the largest group, lizards, presents the most extreme diversity in terms of size, diet, reproductive mode, age at maturity, diversity of sensory mechanisms, parental care, sociality, social organization and habitat use. All this diversity makes any generalizations on biology, behaviour or husbandry impossible. Thus, it is necessary to consult references that provide such basic information, and some starting points are cited below.

Recognizing this diversity is also important because reptiles are increasingly featured in conservation plans, maintained and bred in **captivity** and even reintroduced to former native habitat. Conversely, many reptiles have been introduced into environments where they can be serious pests and do biological harm. The brown tree snake (*Boiga irregularis*), introduced from New Guinea into Guam, is perhaps the most egregious example, but in Florida alone the following are just a few of the introduced species that may need control: green iguanas (*Iguana iguana*), Nile monitors (*Varanus niloticus*), brown anoles (*Anolis sagrei*) and Burmese pythons (*Python molurus*). In Japan and Europe, North American emydid turtles such as red-eared sliders (*Trachemys scripta elegans*) are disrupting native species. Studies of natural history of these animals in native habitats, as well as in captivity, are needed if effective controls can be instituted. Unlike some invasive large mammals, the secretive nature and high reproductive potential of introduced reptiles makes control through hunting and trapping impractical and inefficient.

On the other hand, some species, especially edible reptiles, are being ranched and becoming domesticated. Alligator, iguana and turtle farms are prominent in several countries. In addition, many species of lizards and snakes are being bred for the **pet** trade, with aberrant colour morphs being developed. Such captive breeding is altering the behaviour and morphology of reptiles through both deliberate and unconscious **selection** (**domestication**), as well as through phenotypic plasticity.

The literature on captive reptile maintenance, **breeding** and rearing has greatly expanded since the late 1980s. There are extensive works on veterinary care and volumes on captive care of almost all major taxa. The most commonly maintained species have been the subjects of many reports, many developed and written by amateurs or professional breeders. Academic and **zoo** biologists have also contributed much. European and American herpetoculture magazines abound. These often contain useful hints as well as leads for suppliers of equipment, diets, food supplements, innovative caging and other supplies.

A misconception about reptiles, still widespread, is that their behaviour is relatively unaffected by their rearing conditions and environment. In other words, unlike birds and mammals, reptiles are often viewed as more 'hard-wired', learning little if at all, and are psychologically not affected by the nature of their environment. Thus, reptiles not on exhibit in zoos and laboratories are frequently reared in relatively sterile and non-stimulating environments. What is increasingly